

## Review of Conservation Challenges and Possible Solutions for Grassland Birds of the North American Great Plains



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### ABSTRACT

North America's grassland birds remain in crisis despite decades of conservation efforts. This review provides an overview of factors contributing to these declines, as well as strategies and resources available to a diversity of stakeholders to help conserve grassland bird communities with an emphasis on the Great Plains—a grassland region of global ecological significance and a habitat stronghold for grassland birds. Grassland bird declines are driven by historical and continuing threats across the full annual cycle including grassland habitat loss, agriculture intensification, woody encroachment, and disruption of fire and grazing regimes. More recently, energy development activities, the use of neonicotinoid pesticides, and anthropogenic climate change have emerged as additional threats. While threats to grassland birds are numerous and often synergistic, possibilities for conservation are also diverse and multifaceted. Land set-aside programs, incentives and voluntary practices for producers, improved environmental management by energy and utility companies, and policy and regulation can all contribute to the conservation of these unique species. We suggest that future grassland bird research should focus on poorly studied aspects of the annual cycle, such as overwinter survival and habitat use, and the migratory period, which remains completely unexplored for many species. Filling these knowledge gaps may facilitate more sophisticated population modeling that can identify limiting factors and more effectively guide investment in conservation.

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## Introduction

Since the first long-term trend analyses of North American Breeding Bird Survey (BBS) data were completed more than 2 decades ago, grassland birds have been recognized as among the most steeply and persistently declining avian groups in North America (Knopf 1994; Herkert 1995; Peterjohn and Sauer 1999). Despite this recognition and numerous calls to conserve these species in the interim (Vickery et al. 1999; Brennan and Kuvlesky 2005; McCracken 2006; Askins et al. 2007), recent analyses have shown not only the continuation of declines but also staggering losses in abundances among formerly common species (Rosenberg et al. 2019). From 1970 to 2017, 74% of grassland bird species have declined (BBS trends; Appendix A), resulting in an estimated reduction in collective abundance of > 700 million birds (Rosenberg et al. 2019).

Historically, these declines were driven by massive losses of grassland habitat during European settlement of the Great Plains and subsequent disruption of natural fire and grazing regimes (Knopf 1994; Samson et al. 2004; Augustine et al. 2021). Today, temperate grasslands are among the most threatened and least protected (e.g., areas under legal protection from development and conversion) ecosystems on Earth (Hoekstra et al. 2005; Henwood 2010; Scholtz and Twidwell 2022). In the Great Plains, approximately 50% of the original grassland extents of Canada and the United States have been lost (Augustine et al. 2021; Scholtz and Twidwell 2022). Although losses have slowed since colonial times, it is estimated that 8 000 km<sup>2</sup> of grassland (including native, non-native, and planted grasslands) is still converted to row-crop agriculture annually in the Great Plains (WWF 2021). Loss of grassland habitat has also occurred in the wintering geographies of many grassland bird species. The Chihuahuan Desert, which provides the primary wintering grounds for 85% of grassland-obligate birds breeding in the Great Plains, has suffered cumulative grassland losses of 39% relative to historic extents (Comer et al. 2018). Similarly, South America's Pampas grassland, a region that provides winter habitat for species such as Bobolink (*Dolichonyx oryzivorus*), Dickcissel (*Spiza americana*), and Swainson's Hawk (*Buteo swainsoni*), has experienced extreme grassland conversion with an estimated 10–30% of the original extent remaining (Medan et al. 2011; Scholtz and Twidwell 2022). The southeastern United States also contains a diversity of drygrass prairie, coastal grasslands, and pine and live-oak savannas that have suffered conversion rates of > 80% (Noss 2013), and much of this remaining habitat is unsuitable for grassland birds because of chronic fire suppression. These southern grasslands are important wintering grounds for species such as Henslow's Sparrow (*Centronyx henslowii*) and Eastern Meadowlark (*Sturnella magna*) (Askins et al. 2007).

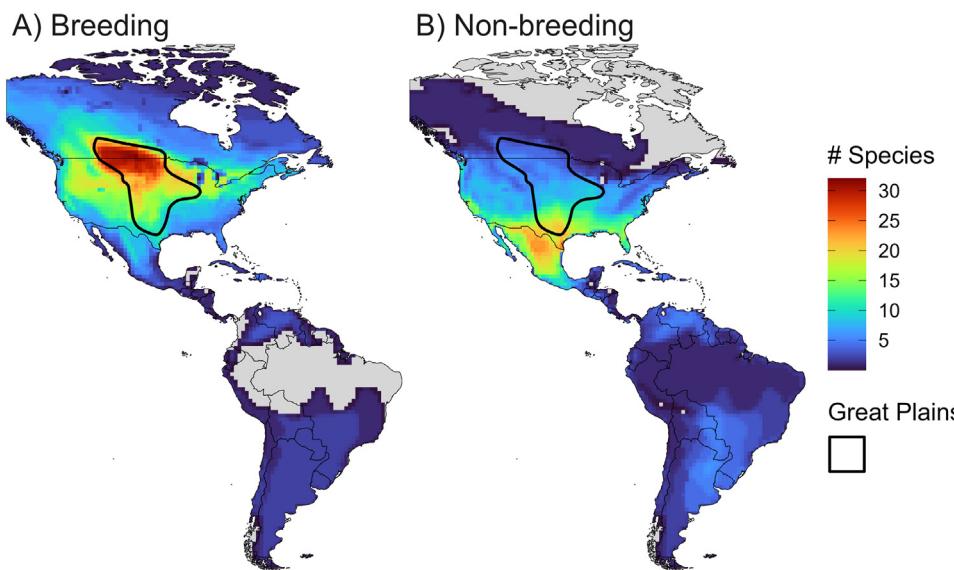
While the loss of grassland habitat remains the primary driver of grassland bird decline (Murphy 2003; Hill et al. 2014; Stanton et al. 2018), grassland birds in the Anthropocene face a litany of additional threats across the full annual cycle. These include habitat degradation from energy development and infrastructure (Daniel and Koper 2019; Shaffer et al. 2019; Ott et al. 2021), agricultural intensification and pesticide use across working landscapes (Stanton et al. 2018; Moreau et al. 2022; Douglas et al. 2023), shrub encroachment on both breeding and wintering grounds (Van Auken 2009; Scholtz et al. 2018; Andersen and Steidl 2019), continued management challenges concerning fire and grazing (Fuhlendorf et al. 2012; Duquette et al. 2022; Raynor et al. 2022), and the growing threat of climate change (Wilsey et al. 2019; Maresh Nelson et al. 2023), a stressor that is likely to exacerbate existing threats.

Here, we review these threats to grassland birds, some proposed management and conservation solutions, and key knowledge gaps to be addressed. While grassland birds occur in a wide variety of grasslands and surrogate habitats across North America

(Askins et al. 2007), we focus our review specifically on grassland-obligate (species that depend exclusively on grassland habitat) and facultative species (those that are found in multiple habitats but make extensive use of grasslands) that breed in the Great Plains of North America. We largely follow Vickery et al. (1999) in these designations (see Appendices A-B for full species list and statuses), but we restrict our list to gamebirds, songbirds, shorebirds, and raptor species with breeding occurrences that overlap the Great Plains (shown as we define it in Fig. 1). This region contains the largest tracts of intact grasslands remaining in North America and represents a grassland area of global significance (Henwood 2010; Scholtz and Twidwell 2022). Consequently, the Great Plains provide habitat for numerous grassland bird species (see Fig. 1; Askins et al. 2007) and offer great opportunity for conservation action to benefit this guild. We do not include waterfowl in our review because this taxon has been recently addressed elsewhere (e.g., Anderson et al. 2018) and is no longer in decline (Rosenberg et al. 2019).

Although the grassland bird crisis has been thoroughly reviewed in the past (Brennan and Kuvlesky 2005; Askins et al. 2007), it has been approximately 15 yr since these efforts were published. The objective of this review is to provide an update on the status of grassland birds and also to place greater focus on aspects of this crisis that have previously been less emphasized. First, we seek to address more recent threats to grassland birds, such as energy development, neonicotinoid pesticides, and climate change. Second, > 85% of grassland bird species that breed in the Great Plains are migratory, and thus here we also discuss issues affecting grassland birds on their wintering grounds and highlight the importance of the full annual cycle. Third, most (~80%) remaining grasslands in the United States are now privately managed (NABCI 2013); similar statistics do not appear to be available for grasslands in Canada and Mexico, but 70–90% of all land in the prairie provinces is also privately owned (Table 1). The Great Plains of today consists of a patchwork of privately owned rangelands, Indigenous National Lands, and publicly owned rangelands that are collectively used or leased for livestock grazing (see Table 1). Therefore, in addition to federal, state/provincial and Indigenous agencies, ranching and farming communities are uniquely positioned to contribute toward the conservation of North America's grassland birds. Thus, a final objective of this review is to discuss what conservation and management measures might be taken by various stakeholders.

To that end, we provide some context, information, and resources useful to those interested in the conservation and management of grassland birds. However, we caution that while the information contained within this review is intended to broadly characterize the current state of our knowledge of grassland birds, effective conservation strategies must often be specific. Grassland bird responses to habitat and management may be highly individualistic, both among species and within species in different regions (e.g., Johnson and Igli 2001; Fuhlendorf et al. 2006; Shew and Nielsen 2021). Thus, we view this document as a starting point for the management of grassland birds and not a prescription for every case, as the latter will depend on the stakeholder involved and their specific objectives. For example, a policy advisor may read this review and conclude that a national incentive to preserve grassland habitat is a key conservation action. By contrast, a landowner seeking to maintain habitat for a given species may gain an understanding of grassland bird declines and management issues but be left with little specific guidance for his or her property. In this case, the next step for the landowner might be to read further on the management of the target species or reach out to a local agency or nonprofit for technical assistance (a topic discussed within). Ultimately, we hope that this document will be of use to researchers, managers, Indigenous Nations, and farmers and ranch-



**Figure 1.** Seasonal maps displaying approximate richness of grassland-obligate bird species of the Great Plains during **A**, breeding and **B**, nonbreeding seasons. Species ranges are provided by Birdlife International and NatureServe (2012). Full methods describing map generation are provided in Appendix C. Gray indicates no occurrence of focal species.

**Table 1**

Land ownership percentages stratified by state/province for the Great Plains (US data: USDA Natural Resources Conservation Service 2016; Canadian data unpublished). Note that Canadian percentages represent portions of the provinces within the Prairie Potholes Bird Conservation Region only.

State	Federal	NGO easements	Easement	State/county/city	Tribal	Private
Colorado	6.81%	0.23%	2.12%	7.11%	0.00%	83.60%
Illinois	0.88%	0.02%	0.49%	0.95%	0.02%	97.62%
Indiana	2.36%	0.07%	0.65%	0.98%	0.00%	96.08%
Iowa	0.06%	0.71%	0.79%	1.51%	0.00%	96.74%
Kansas	1.50%	0.01%	0.17%	0.42%	2.90%	97.60%
Minnesota	1.08%	0.23%	2.52%	1.94%	0.02%	94.19%
Missouri	1.84%	0.04%	0.95%	1.43%	0.02%	95.70%
Montana	24.30%	0.14%	0.27%	6.43%	8.00%	60.46%
Nebraska	8.50%	0.03%	0.81%	1.98%	4.46%	83.75%
New Mexico	2.00%	0.25%	0.34%	0.40%	0.82%	96.10%
North Dakota	2.50%	0.28%	0.17%	17.64%	0.00%	79.37%
Oklahoma	1.84%	0.17%	0.18%	8.87%	4.80%	83.97%
South Dakota	9.70%	0.10%	0.65%	2.24%	20.27%	66.99%
Texas	1.55%	0.02%	0.10%	0.70%	0.00%	97.60%
Wisconsin	1.82%	0.00%	0.99%	2.75%	0.00%	94.40%
Wyoming	17.44%	0.00%	0.67%	7.90%	0.00%	73.95%
Average across United States Great Plains	5.26%	0.00%	0.74%	3.95%	4.59%	87.38%
Alberta	2.24%		0.75%	15.68%	2.03%	79.76%
Saskatchewan	0.91%		1.30%	12.72%	1.89%	83.45%
Manitoba	0.63%		NA	8.49%	0.74%	90.65%
Average across Canadian Great Plains	2.16%		1.03%	12.30%	1.55%	84.62%

ers (hereafter referred to as producers) who wish to contribute to the conservation of grassland bird communities across working landscapes in the Great Plains of North America.

## Threats to Grassland Birds

### Overview

Over the past 2 decades, our understanding of factors contributing to the decline of North America's grassland birds has increased substantially. Conversion of grasslands to cropland remains the most salient example of habitat loss in the Great Plains (WWF 2021), and agriculture has been identified as the greatest threat to grassland birds globally (Douglas et al. 2023). Following agriculture, energy development is the next largest contributor to grassland habitat loss throughout parts of the Great Plains (Shaffer et al. 2019; Ott et al. 2021), and woody encroachment is a further source of loss (e.g., Scholtz et al. 2018; Andersen and

Steidl 2019). In addition to direct habitat loss, changes to spatial configuration of habitat associated with altered land use have created a highly fragmented grassland landscape (Augustine et al. 2021). An important consequence that has emerged from studies of this fragmentation is the sensitivity of many grassland birds to small patches and high edge-densities on the landscape, which appear to negatively affect both occupancy and demographics of many species (e.g., Helzer and Jelinski 1999; Herkert et al. 2003; Ribic et al. 2009; Lockhart and Koper 2018; Herse et al. 2020).

Beyond habitat loss and fragmentation, there are many other sources of habitat degradation affecting grassland birds. Perhaps foremost among these have been the ancillary effects of continental-scale agricultural intensification over the past 50 yr (Stanton et al. 2018). The widespread application of pesticides and neonicotinoid compounds appears to be an important driver of grassland bird declines (Stanton et al. 2018; Li et al. 2020). Another management challenge facing grassland birds is one that has continued since European settlement: widespread fire suppression

and the removal of native grazers resulting in the homogenization of grasslands (Samson et al. 2004; Fuhlendorf et al. 2012; Duquette et al. 2022). Although there has been a great deal of research on the application of fire and grazing to benefit grassland birds (e.g. Fuhlendorf et al. 2006; Derner et al. 2009; Lipsey and Naugle 2017), it has remained difficult to generalize best practices. Moreover, fire and grazing practices on both public and private land are often inexorably linked to producer livelihoods. Thus, the need to promote solutions that both benefit grassland birds and allow producers to remain economically viable cannot be overstated (Drum et al. 2015; Keyser et al. 2022). Finally, 42% of North American grassland bird species are considered highly vulnerable to climate change (Wilsey et al. 2019). A more extreme climate will have demographic consequences for grassland birds (e.g., Conrey et al. 2016; Pérez-Ordoñez et al. 2022; Maresh Nelson et al. 2023), and climate change is also likely to interact with existing stressors, thus complicating management and exacerbating habitat limitation (e.g., McCauley et al. 2017; Zuckerberg et al. 2018; Yurkonis et al. 2019).

#### Cropland expansion

Loss of grassland habitat to cropland conversion is likely the greatest threat to grassland birds of the Great Plains on both breeding and wintering grounds. In the United States and Canada, grassland losses began in the 1860s and 1870s, respectively, when governments of both countries actively encouraged settlement and agricultural conversion of grassland (Samson et al. 2004). The habitat consequences of this era have been dramatic; some grassland biomes such as the highly arable northern and central tallgrass prairies have suffered continentwide reductions of > 90% (Comer et al. 2018). While shortgrass and mixed-grass prairie biomes have fared better because of less productive conditions for row-crop agriculture, these systems have still experienced massive cumulative losses (Comer et al. 2018). Today, approximately 41% of the US Great Plains is cropland (Augustine et al. 2021). Contemporary agricultural expansion in the region is a continuing source of grassland habitat loss (Lark 2020; WWF 2021), and three primary factors appear to drive this process.

First, the rise of biofuel demand over the past 2 decades has triggered an increase in the value of specific crops, such as corn and soybean, creating economic incentive for grassland conversion (Wright and Wimberly 2013; Littlejohns et al. 2018). The United States alone produces nearly half the world's ethanol while Canada is among the world's top six producers (Wiens et al. 2011). From 2008 to 2012, 77% of all cropland conversion in the United States occurred on grasslands—amounting to roughly 23 067 km<sup>2</sup> in grassland habitat loss during this period—and corn and soybean together accounted for nearly half of this expansion (Lark et al. 2015). A second contributor to continued grassland conversion in the US Great Plains has been a decline in enrollment of lands in the Conservation Reserve Program (CRP), the United States' largest land set-aside program and one that has benefited many grassland birds (Veech 2006; Herkert 2009; Niemuth et al. 2017; Pavlacky et al. 2022). Nationally, and in the Great Plains, enrollment in CRP has declined over the past decade (Wright and Wimberly 2013; Stubbs 2014; Morefield et al. 2016). The primary drivers of declining CRP enrollment and expiration have been both low government incentives for CRP relative to commodity prices, enrollment caps at the federal level, and challenges to understanding program options locally (Stubbs 2014; Caldas et al. 2016; Wimberly et al. 2017; Barnes et al. 2020). A third factor influencing grassland conversion in the United States is crop insurance and farm policy (Lark et al. 2019). A review by the General Accountability Office (GAO 2007) found that farm program payments (such as crop insurance payments) provide significant incentives for producers to

convert grassland to cropland because they increase the profitability of farming while lowering risk. Additionally, such farm payments work at cross purposes with programs under the conservation side of the farm bill. For example, between 1982 and 1997, 1.69 million acres of cropland in South Dakota were enrolled in CRP, and during the same period 1.82 million acres of grassland in South Dakota were converted to cropland (GAO 2007). In the Canadian Great Plains, where no analog to CRP is currently in effect, agricultural conversion risk is driven more strongly by land suitability and neighborhood effects from surrounding land uses (H. Wang et al. 2016).

In Mexico's Chihuahuan Desert, cropland conversion is fueled by the subsidized expansion of the electric grid that facilitates the pumping of groundwater for crop production (Scott and Shah 2004), a process that began in the mid-1900s. From 2006 to 2011, cropland expansion in one of the largest Grassland Priority Conservation Areas (GPCAs) in Mexico, the Valles Centrales region of Chihuahua, progressed at a rate of 6.1% annually, converting almost 700 km<sup>2</sup> of grassland and shrubland to cropland in just 5 yr (Pool et al. 2014). At this rate, valley-bottom grasslands have been projected to be almost completely converted by 2025. Such expansions have also been documented in other GPCAs. In Janos (northwestern Chihuahua), for example, intensive-agriculture land cover nearly doubled in 15 yr (1993–2008; Ceballos et al. 2010). Grassland protection in the Chihuahuan Desert is challenging due to patterns of land ownership and management. Many grasslands in the Chihuahuan Desert are communally owned and managed through a type of property known as “ejidos”—lands used for agricultural production including both livestock and crops (Hruska 2020). The vast majority of none-jido grasslands in Mexico are privately owned beef-producing ranches. There are also rare cases of federally protected grasslands in Mexico, but this land is often developed regardless of federal mandates. For example, the Janos Biosphere Reserve in Chihuahua, Mexico is the only large area of grassland under federal protection in Mexico, but the clearing of grassland and shrubland for new crop development has continued since its designation as a protected area (Ceballos et al. 2010). Similarly, many state-protected grassland areas in Mexico have also seen continued conversion after designation (Zaragoza-Quintana et al. 2012), often driven by planting of potato crops (Ruvalcaba-Ortega et al. 2017).

Grassland areas in the southeastern portion of South America, including the Pampas region of Argentina, experience much of the same pressures from cropland conversion as grasslands in North America. However, in South America, conversion and disturbance associated with European settlement began as early as the 15th century (Azpiroz et al. 2012). The Pampas region has undergone significant change since this time, and today only 30% of this grassland region remains in native cover and only 1% is protected (Henwood 2010). Cropland conversion in this region has continued in the modern era (Azpiroz et al. 2012), and relatively recent decreases in grassland land cover have been correlated with increases in cropland for soybean, sunflower, wheat, and corn (Baldi and Paruelo 2008).

#### Anthropogenic development

Following cropland expansion, energy development is the second largest driver of grassland bird habitat loss and affects habitat availability through both direct and functional mechanisms (Shaffer et al. 2019). In the Great Plains, this loss is primarily driven by conventional oil and natural gas sectors and, more recently, increasing wind and solar development (Ott et al. 2021). Energy development—and the infrastructure associated with these activities—is currently the largest driver of land use change in the United States, and by 2040, it is estimated that an additional 800

**Table 2**

Selected studies documenting direct and indirect negative effects of infrastructure from oil and gas, wind energy, solar energy, roads, and transmission lines on grassland bird taxa of the Great Plains.

Effect	Type	Infrastructure	Taxa	References
Habitat destruction	Direct	All	All	1, 2, 3, 4
Nest destruction	Direct	Oil and gas, wind, roads, transmission lines	Songbirds, gamebirds, shorebirds	5, 6
Collision and electrocution mortality	Direct	Wind, solar, roads, transmission lines	All	5, 7, 8, 9, 10, 11, 12, 13
Contamination mortality	Direct	Oil and gas	All	14
Solar flux mortality	Direct	Solar	Songbirds, raptors	15
Avian avoidance	Indirect	Oil and gas, wind, roads, transmission lines	Songbirds, gamebirds, shorebirds	16, 17, 18, 19, 20, 21, 22, 23
Decreased nesting success	Indirect	Oil and gas, wind, roads	Songbirds, shorebirds, raptors	16, 24, 25, 26, 27, 28, 29
Increased brood parasitism	Indirect	Oil and gas, roads	Songbirds	30
Reduced productivity	Indirect	Oil and gas, roads	Songbirds	16, 29, 31, 32
Anthropogenic noise	Indirect	Oil and gas, wind	Songbirds	32, 33, 34, 35
Stress physiology	Indirect	Oil and gas	Songbirds	36
Vegetation alteration	Indirect	All	All	2, 3, 29, 31, 37

From Copeland et al. 2011,<sup>1</sup> Ott et al. 2021,<sup>2</sup> Riley et al. 2012,<sup>3</sup> Trainor et al. 2016,<sup>4</sup> Calvert et al. 2013,<sup>5</sup> Van Wilenburg et al. 2013,<sup>6</sup> Bishop and Brogan 2013,<sup>7</sup> Conkling et al. 2022,<sup>8</sup> Kemper et al. 2013,<sup>9</sup> Loss et al. 2014,<sup>10</sup> Loss et al. 2013,<sup>11</sup> Martin et al. 2022,<sup>12</sup> Rioux et al. 2013,<sup>13</sup> Trail 2006,<sup>14</sup> Kagan et al. 2014,<sup>15</sup> Daniel and Koper 2019,<sup>16</sup> Leddy et al. 1999,<sup>17</sup> Londe et al. 2019,<sup>18</sup> Nenninger and Koper 2018,<sup>19</sup> Pruitt et al. 2009,<sup>20</sup> Shaffer and Buhl 2016,<sup>21</sup> Sliwinski and Koper 2012,<sup>22</sup> Thompson et al. 2015,<sup>23</sup> Bernath-Plaisted and Koper 2016,<sup>24</sup> Kolar and Bechard 2016,<sup>25</sup> Ludlow and Davis 2018,<sup>26</sup> Mahoney and Chalfoun 2016,<sup>27</sup> Miller et al. 1998,<sup>28</sup> Yoo and Koper 2017,<sup>29</sup> Bernath-Plaisted et al. 2017,<sup>30</sup> Ludlow et al. 2015,<sup>31</sup> Ng et al. 2019,<sup>32</sup> Antz and Koper 2018,<sup>33</sup> Rosa and Koper 2022,<sup>34</sup> Whalen et al. 2018,<sup>35</sup> Des Brisay et al. 2022,<sup>36</sup> Rodger and Koper 2017.<sup>37</sup>

000 km<sup>2</sup> of land will be affected (Trainor et al. 2016). In the United States and Canada, land use change associated with energy development has disproportionately affected rangelands (Allred et al. 2015), and an estimated 20% of grassland habitat in western North America may currently be affected by energy leases (Copeland et al. 2011). The Chihuahuan Desert has also been subject to a high level of energy development activities on both sides of the border, and in the US portion of this region, an estimated 27% of habitat has been impacted (McClung et al. 2019). In South America, the expansion of wind energy into grassland regions has also contributed to grassland bird habitat loss and degradation (Azpiroz et al. 2012).

Energy development can affect grassland birds and their habitats, both directly and indirectly, in numerous ways (Bayne and Dale 2011; Riley et al. 2012; Smith and Dwyer 2016; Ott et al. 2021; Table 2). Although individual energy leases are typically only several hectares in area (Van Wilenburg et al. 2013; Ott et al. 2021), the high density of leases across the Great Plains has resulted in a significant cumulative habitat loss. In the United States nationally, 82 000 km<sup>2</sup> of habitat was directly impacted by energy infrastructure in just 4 yr (Trainor et al. 2016). In Canada's mixed-grass prairie region, an estimated 435 km<sup>2</sup> of habitat is disturbed each breeding season by oil and gas activities alone (Van Wilenburg et al. 2013). This development results in the estimated annual destruction of > 5 881 grassland songbird nests at lease sites in Canada (Van Wilenburg et al. 2013). Substantial additional nest mortality also occurs as a result of road and transmission line maintenance (Calvert et al. 2013). Similarly, for avian species broadly, collision with traffic, transmission lines, wind turbines, and other structures is also a large annual source of mortality (Cartron et al. 2005; Bishop and Brogan 2013; Calvert et al. 2013; Loss et al. 2013, 2014; Martin et al. 2022). Some grassland birds, such as Horned Lark (*Eremophila alpestris*), may be especially vulnerable to vehicle collisions due to their ground-dwelling behavior and attraction to roadside foraging opportunities (Sutter et al. 2000; Ingelfinger and Anderson 2004). Electrocution from power transmission lines is another mortality source among raptor species (Kemper et al. 2013; Dwyer et al. 2020). Finally, waste water and other toxic byproducts of oil and gas production are further sources of adult mortality for grassland birds (Riley et al. 2012; Calvert et al. 2013). For instance, oil pits in the United States alone may kill up to a million birds annually, 63% of which are ground foragers (Trail 2006).

Though more difficult to quantify than direct mortality and habitat loss, the indirect effects of energy development on grassland birds likely occur over larger spatial extents. The sprawl of roads, transmission lines, and pipelines associated with relatively compact lease sites affect a disproportionate habitat area through fragmentation, edge effects, and other forms of degradation (Trainor et al. 2016; Daniel and Koper 2019; Ott et al. 2021; Davis et al. 2023). For example, it is estimated that for every oil well, 100 ha of road is constructed (Riley et al. 2012), and some of the ecological effects of these roads may extend up to 1 km (Benítez-López et al. 2010). Roads cut through otherwise intact grassland landscapes and can act as corridors for invasive vegetation (Forman and Alexander 1998; Gelbard and Belnap 2003), alter predator communities (Frey and Conover 2006; Glass and Eichholz 2022), and create movement barriers for grassland bird species (Londe et al. 2022). Numerous studies of grassland birds have documented not only avoidance of roads (Sutter et al. 2000; Sliwinski and Koper 2012; Wellicome et al. 2014; Thompson et al. 2015) but also depressed reproductive success and increased parasitism by brown-headed cowbirds (*Molothrus ater*) with proximity to roads (Miller et al. 1998; Bernath-Plaisted et al. 2017; Daniel and Koper 2019).

Similarly, structures such as oil and gas wells, compressor stations, and wind turbines can also act as anthropogenic edge in grassland landscapes influencing the abundance and reproductive success of species. Although species responses are typically individualistic (Davis et al. 2023), a pattern of apparent avoidance of energy infrastructure by some grassland obligates has emerged, and the presence of development may alter the structure of grassland bird communities (Maguire and Papeş 2021). Specifically, there is evidence that abundances of grassland-obligate songbirds such as Baird's Sparrow (*Centronyx bairdii*), Sprague's Pipit (*Anthus spragueii*), and Savannah Sparrow (*Passerculus sandwichensis*) decline with presence of oil (Thompson et al. 2015; Nenninger and Koper 2018; Daniel and Koper 2019) and gas (Rodgers and Koper 2017; Davis et al. 2023) infrastructure and disturbance. There is also evidence that grassland shorebird and raptor species may avoid or nest at lower densities near oil and gas structures (Wiggins et al. 2017; Ludlow and Davis 2018). The effects of wind turbines on avian abundance are less clear with one study finding avoidance by many grassland species (Shaffer and Buhl 2016) and another reporting avoidance of turbines by female prairie

grouse (Lloyd et al. 2022), but most others finding little evidence of displacement (Niemuth et al. 2013; Stevens et al. 2013; Hale et al. 2014). More studies on the indirect effects of wind and solar energy on grassland birds are needed, as both infrastructure types will likely become increasingly prevalent in grassland areas throughout North America (Ott et al. 2021).

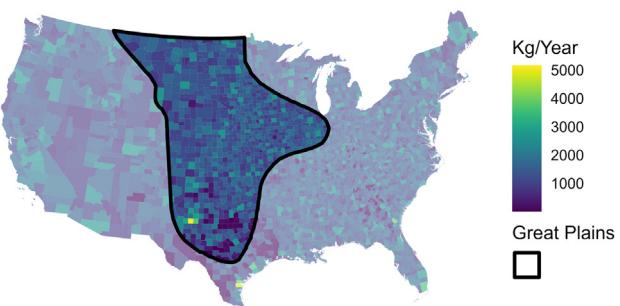
In contrast to avoidance behaviors or reduced abundances, certain species may display attraction to infrastructure of various types. This has been documented in species such as Vesper Sparrow (*Pooecetes gramineus*) (Shaffer and Buhl 2016; Rodgers and Koper 2017), Horned Lark, and Chestnut-collared Longspur (*Calcarius ornatus*) (Davis et al. 2023). This may occur because species find certain features associated with structures attractive, such as perches or additional bare ground. These species may be at risk for ecological traps (Bernath-Plaisted and Koper 2016; Ludlow and Davis 2018; Des Brisay et al. 2022). Other species may display no abundance or habitat use response to energy development (e.g., Ludlow et al. 2015; Daniel and Koper 2019), but these species may nonetheless suffer demographic consequences. Energy infrastructure can reduce the reproductive success of grassland birds by altering predator communities and/or disrupting the behavior of nesting birds. For example, studies on the effects of oil and gas infrastructure on nesting birds have found decreased nesting success, increased parasitism, elevated stress levels, and reduced parental care (Bernath-Plaisted and Koper 2016; Bernath-Plaisted et al. 2017; Ng et al. 2019; Des Brisay et al. 2022), though others have found few strong effects (Ludlow et al. 2015; Yoo and Koper 2017). Similarly, documented effects of turbines on nesting success have been mixed with some studies reporting negative responses and others finding no effect (Hatchett et al. 2013; McNew et al. 2014; Mahoney and Chalfoun 2016). Importantly, prairie grouse species may be particularly impacted by wind energy, as lek (groups of displaying, breeding birds) persistence can be reduced near wind turbines (Winder et al. 2015), and females may avoid nesting near tall structures (Lloyd et al. 2022).

In addition to their physical impact on the landscape, anthropogenic structures and activities may also negatively impact grassland birds through noise that extends beyond areas of physical disturbance (Barber et al. 2011; Klingbeil et al. 2020; Senzaki et al. 2020). Traffic noise, construction activities, and machinery noise from oil and wind energy structures have all been shown to negatively impact grassland birds (McClure et al. 2013; Sutter et al. 2016; Whalen et al. 2018; Des Brisay et al. 2022; Rosa and Koper 2022). One important mechanism by which anthropogenic noise affects grassland birds is through acoustic masking (the overlap of background noise with an acoustic signal), as loud environments may disrupt communication, interfere with vigilance and interpretation of audial cues, and heighten the energetic costs of vocalization (Antze and Koper 2018; Whalen et al. 2018). The extent to which these effects are generalizable across species is not currently known, but physical impacts of structures appear to be more common than those that can be isolated to noise alone (Bernath-Plaisted and Koper 2016; Nenninger and Koper 2018; Raynor et al. 2019).

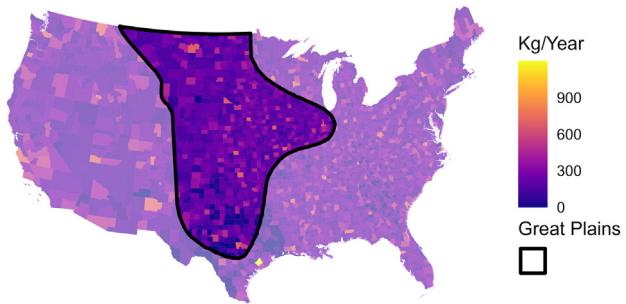
#### Agricultural intensification

The term *agricultural intensification* refers to a global shift toward large, monocultural, mechanized farming operations that rely heavily on chemical inputs (Wilson et al. 2005; Stanton et al. 2018). In arid regions of the western Great Plains, groundwater pumping associated with agriculture has also affected habitat (Dilts et al. 2012; Pool et al. 2014). Following initial habitat losses during European settlement, many grassland bird species shifted to a reliance on planted and agricultural grasslands and farmland-adjacent habitats throughout the western hemisphere

A) All pesticides



B) Neonicotinoid compounds



**Figure 2.** Estimated use of **A**, all pesticides and **B**, neonicotinoid compounds only by county for the coterminous United States, 2013–2017. Counties in the Great Plains are highlighted for emphasis. Pesticide data were sourced from the US Geological Survey Pesticide National Synthesis Project.

(Herkert 1995; Askins et al. 2007; Azpiroz and Blake 2009). However, subsequent changes in agricultural practices have greatly reduced the quality of these surrogate habitats. Declines of North American grassland birds are highly correlated with major changes in farming practices that occurred during the 1960s–1980s (Stanton et al. 2018), and these declines appear to be steeper among grassland bird populations in areas of high agricultural development (Murphy 2003; Hill et al. 2014). Similar patterns have been observed in the decline of European grassland birds (Fuller et al. 1995; Newton 2004; Rigal et al. 2023). While these declines are likely driven strongly by the habitat loss associated with this agricultural development (Hill et al. 2014), agricultural intensification encompasses several specific practices that are known to be harmful to grassland birds including the use of lethal pesticides and mechanical mowing activities.

Pesticides are used widely in cropland systems, and often in direct proximity to grassland bird habitats (Etterson et al. 2017; Stanton et al. 2018; Mitra et al. 2021; Fig. 2A). Increasingly, evidence suggests that a diversity of such pesticides may be detrimental to grassland birds through multiple pathways such as adult mortality, sublethal effects on physiology, altered parental care, reduced fecundity, and impaired migratory ability (Eng et al. 2017; Etterson et al. 2017; Mitra et al. 2021; Moreau et al. 2022). A recent review of the effects of pesticides on grassland birds found that the overwhelming majority of studies on the subject have reported negative effects (Stanton et al. 2018). Of particular concern is a class of pesticides known as neonicotinoids, which were first introduced in the 1990s and are now the most widely used insecticide globally (Wood and Goulson 2017; Frank and Tooker 2020). Neonicotinoids are remarkable for both their water solubility (which allows them to systematically disperse through plant tissues) and high potency—a lethal combination for grassland birds. The consumption of just several seeds treated with neonicotinoids is sometimes sufficient to kill even medium-size songbirds (Stanton et al. 2018).

Risk of exposure to traditional pesticides is primarily determined by proximity to agricultural lands and variation in compounds applied to different crop types (Mineau and Whiteside 2006). However, exposure to neonicotinoids is more difficult to predict, both spatially and temporally, as these systematic compounds may travel widely through water contamination, can potentially contaminate multiple trophic levels, and have a long half-life in the environment (Frank and Tooker 2020; Pietrzak et al. 2020; Roy and Chen 2023). Further, neonicotinoid use is highly prevalent in most major cereal crops grown in North America (Douglas and Tooker 2015; Main et al. 2015). In the United States, it is used widely throughout the Great Plains (see Fig. 2B). It is not currently known to what extent grassland bird species may differ in their risk of exposure to neonicotinoids based on geography and life-history traits. A recent study conducted across multiple ecosystems and species groups in Texas found that 36% of wild birds sampled in nonagricultural areas showed evidence of neonicotinoid exposure and further that exposure was not well explained by foraging guild—suggesting that exposure is widespread (Anderson et al. 2023). There is evidence that exposure to neonicotinoids in prairie grouse and quail species is common (Sabin and Mora 2022; Roy and Chen 2023), but it remains unknown to what extent many other grassland bird species may consume contaminated seeds and plant material, water, and insects. However, increased neonicotinoid use in the United States is associated with recent declines in avian biodiversity, particularly for grassland and insectivorous species (Li et al. 2020).

Pesticides are also widely applied to croplands throughout the nonbreeding ranges of many grassland birds (Bartuszevige et al. 2002; Ruvalcaba-Ortega et al. 2017). For example, pesticide use on wintering grounds has been implicated as a source of mortality for grassland shorebird and songbird species, such as Long-billed Curlew (*Numenius americanus*) and Bobolink (Renfrew and Saavedra 2007; Olalla-Kerstupp et al. 2020). An exploratory study conducted in a heterogeneous agricultural landscape in Mexico's El Tokio GCPA (a grassland and shrubland habitat area) found physiological evidence of pesticide exposure in a diversity of grassland bird species (Ruvalcaba-Ortega et al. 2017).

Like pesticide use, mowing and haying activities on agricultural grasslands have intensified dramatically over the past century and are a large source of nest loss and avian mortality (Askins et al. 2007; Tews et al. 2013). When the timing of mowing activities overlaps the breeding season, the effects on grassland bird nesting success can be catastrophic (Bollinger et al. 1990; Perlut et al. 2006). Mowing not only destroys nests and clutches, but the timing of these activities in mid to late summer often coincides with high fledgling abundances resulting in large juvenile mortality from machinery collision (Tews et al. 2013). Certain species that now more commonly breed in hayfields than native prairie in parts of their ranges (either because of habitat limitation or preference), such as Bobolink and Savannah Sparrow, are especially at risk for loss of productivity from mowing and haying (Bollinger et al. 1990; Perlut et al. 2006). Annual incidental take in Canada alone is estimated between 321 000 and 483 000 young that would otherwise have fledged for the two species, respectively (Tews et al. 2013).

#### Woody encroachment

Woody encroachment, also referred to as *shrub invasion* or *afforestation*, has been occurring in North American grasslands throughout the past century and affects many regions of the Great Plains in Canada, the United States, and Mexico's Chihuahuan Desert (Van Auken 2009; Symstad and Leis 2017; Dettlaff et al. 2021; Morford et al. 2022; Weber-Grullon et al. 2022). Increases in the density of shrub and woody plant species—such as juniper (*Juniperus* sp.), mesquite (*Prosopis* sp.), and Aspen (*Populus*

sp.)—in grassland biomes are driven by the interaction of several mechanisms. These include fire suppression, grazing issues, climate change, and human behavior (Van Auken 2009; Berg et al. 2015; Caracciolo et al. 2016; Symstad and Leis 2017; Naugle et al. 2020). In the northern and central regions of the Great Plains, shrub invasion has largely been driven by a combination of shelter belt planting (e.g., trees and shrubs planted to block wind and provide livestock shelter) and widespread disruption of fire and grazing disturbances that once prevented woody species establishment (Brennan and Kuvlesky 2005; Twidwell et al. 2013; Fuhlendorf et al. 2017). Additionally, high levels of fragmentation in the Great Plains may also facilitate woody encroachment by limiting landscape processes such as large fires (Scholtz et al. 2018). In arid desert grasslands, such as the Chihuahuan Desert, overgrazing is a more common problem because the underlying primary productivity of these grassland communities is lower. Consequently, heavy grazing of grasses and forbs in areas at risk for shrub encroachment may facilitate the expansion of woody plants, which resist grazing once established and thus gain a competitive advantage (Caracciolo et al. 2016). This process begins a positive feedback loop by which woody plants continue to dominate through mechanisms including reduced fire frequency due to loss of grass fuels, increased erosion preventing grass seed from establishing, and allelopathy of some shrub species excluding herbaceous vegetation (Caracciolo et al. 2016; Li et al. 2022). There is also evidence that elimination of prairie dogs (*Cynomys* sp.), which deplete the seeds of some woody plants, may also have contributed to encroachment in this region (Weltzin et al. 1997). Lastly, climate change may also influence rates of shrub encroachment in all regions, as rising CO<sub>2</sub> concentrations allow woody plants to gain biomass more quickly, and changes to precipitation patterns also affect shrub dynamics (Van Auken 2009; Caracciolo et al. 2016; Weber-Grullon et al. 2022).

Woody encroachment is a problem for grassland birds in several ways contributing to habitat fragmentation (Fuhlendorf et al. 2017; Scholtz et al. 2018; Augustine et al. 2021), functional habitat loss via avian avoidance of shrubs, and habitat degradation through shrub-associated predators (e.g., Grant et al. 2004; Klug et al. 2010). Many species of grassland birds avoid habitats with high densities of woody vegetation, and some will not use habitats above certain density thresholds (Coppedge et al. 2001; Ribic and Sample 2001; Graves et al. 2010). In particular, grassland obligates appear to respond more negatively to woody cover than facultative species (Andersen and Steidl 2019). Nesting success for many species of grassland birds also declines with the presence of woody vegetation (With 1994; Graves et al. 2010; Davis et al. 2019), though responses are mixed (Andersen and Steidl 2022). Possible explanations for negative demographic responses to woody plants on the breeding grounds include the association of snake and ground squirrel predators with shrubs (With 1994; Klug et al. 2010; Thompson and Ribic 2012), and increased cowbird parasitism (Shaffer et al. 2003; Patten et al. 2006). Avoidance of shrubs and decreased overwinter survival with high shrub cover has also been reported for some grassland bird species in the southern United States and northern Mexico, likely because shrubs may serve as perches for avian predators in this region (Igl and Ballard 1999; Macías-Duarte et al. 2017).

#### Fire and grazing

The role of fire and grazing in maintaining healthy and diverse grassland habitats in North America is a complex topic and one that is worthy of its own review. Therefore, we do not attempt exhaustive coverage of this topic but rather seek to broadly outline the importance of these processes and the challenges involved in managing fire and grazing activities to benefit grassland birds.

Historically, the distribution of grassland across North America has been driven by two fundamental conditions: 1) low and irregular precipitation and 2) frequent disturbance by fire and herbivore grazing (Samson et al. 2004; Gibson 2009; Augustine et al. 2021). In addition to maintaining habitat free of woody species, fire and grazing also redistribute nutrients, remove dead plant material, and create structural heterogeneity (Fuhlendorf et al. 2009; Gibson 2009). Before European settlement, grazing by bison and other mammalian herbivores, frequent wildfires triggered by lightning, and fires intentionally set by Indigenous peoples were the major sources of disturbance in North American grasslands (Gibson 2009; Roos et al. 2018; Samson et al. 2004). Indigenous peoples in North America practiced various forms of nomadic pastoralism and regularly applied fire in sophisticated ways to maintain habitat suitable for hunting, promote desirable plant species, and control pests (Kimmerer and Lake 2001). These practices helped to maintain grasslands and also promoted habitat heterogeneity. However, the arrival of European colonizers led to both the elimination of free-ranging herbivores and widespread fire suppression—a disruption that continues today in many areas—creating a unique challenge for the management of grassland birds (Brennan and Kuvlesky 2005).

Classically, grassland birds are positioned along a continuum of habitat preference from short and sparse to denser and taller vegetation (Fig. 3). For example, Mountain Plover (*Charadrius montanus*), Thick-billed Longspur, Lark Bunting (*Calamospiza melanocorys*), and Chestnut-collared Longspur may all inhabit the same shortgrass prairie biome, but each requires different vegetation structure within this ecosystem. Mountain Plover and Thick-billed Longspur occupy extremely short and sparse habitats created by heavy grazing while Lark Bunting and Chestnut-collared Longspur prefer more intermediate vegetation heights and areas subject to moderate grazing intensity (Derner et al. 2009). A similar pattern is observed in mixed-grass prairie where grazing intensity and vegetation structure strongly drive avian community composition (Lipsey and Naugle 2017; Pulliam et al. 2020). Like grazing, prescribed fire is also an important tool that structures grassland bird habitats and communities, and it is of particular importance in mesic tallgrass systems where frequent burns are required to prevent woody encroachment (Ratajczak et al. 2016). Some species, such as Upland Sandpiper (*Bartramia longicauda*) prefer shorter vegetation structure relative to most tallgrass species and appear to benefit from burn frequencies of 1–2 yr, while others, such as Eastern Meadowlark and Henslow's Sparrow, require high litter depths and thus habitat managed with longer fire returns (Fuhlendorf et al. 2006, 2009; Coppedge et al. 2008; Powell 2008). There is also a temporal dynamic to the influence of fire on grassland birds, and species abundances often decline initially following a burn but ultimately reach their peaks several years later (Fuhlendorf et al. 2006; Powell 2008). Therefore, even species that prefer taller vegetation structure may not always benefit from sustained fire suppression.

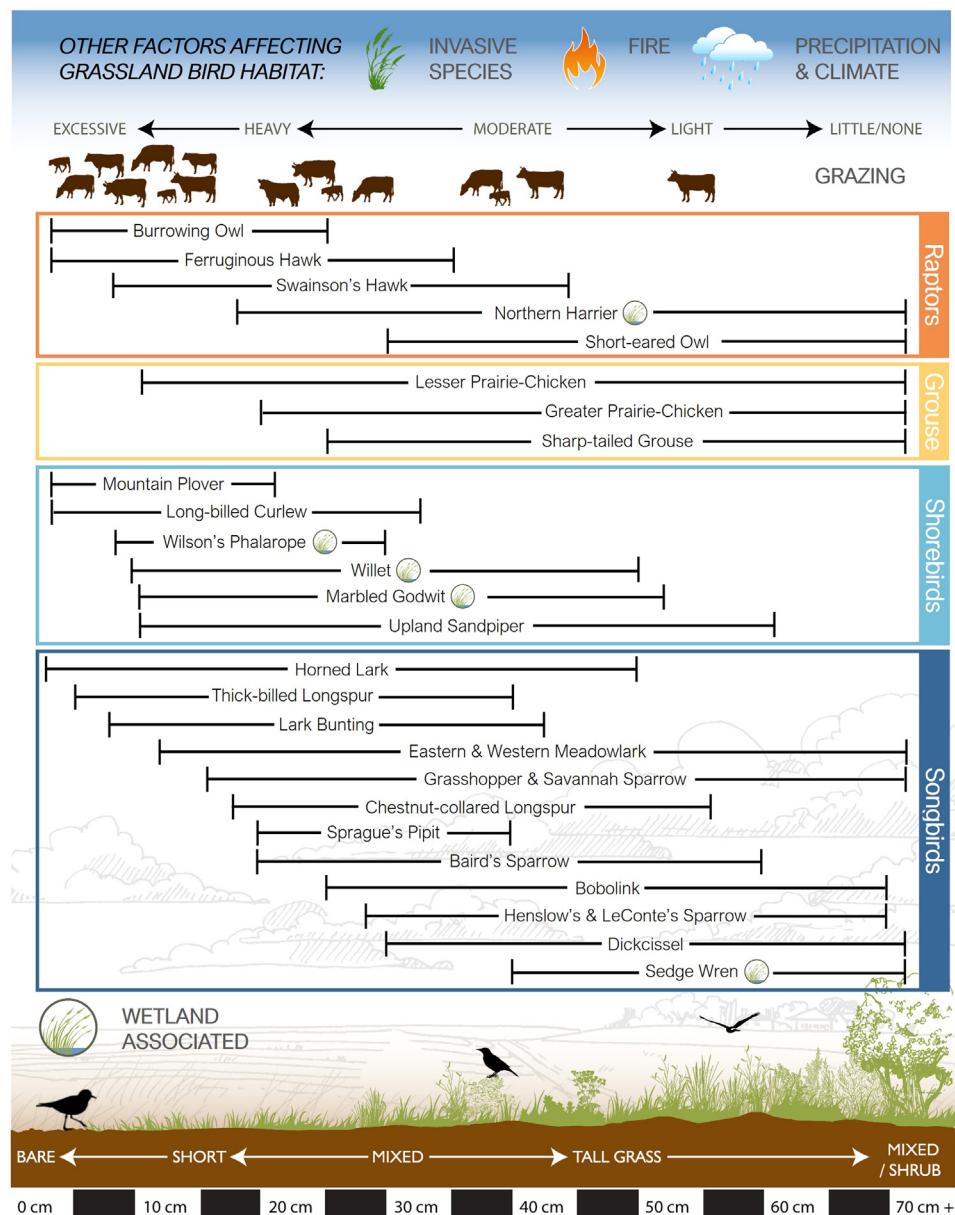
While it is evident that fire and grazing regimes that create and maintain grassland heterogeneity are critical to the conservation of grassland birds (e.g., Fuhlendorf et al. 2006; Derner et al. 2009; Duchardt et al. 2016; Lipsey and Naugle 2017; Davis et al. 2021), it has been difficult to widely achieve this goal for several reasons. Although natural fire and grazing regimes have been replaced by the grazing of domestic cattle and the application of prescribed fire, these practices are not perfect substitutes. For example, bison and cattle behave and graze differently (Kohl et al. 2013), and current rangeland practices often promote grazing strategies that create uniform conditions (Holocheck et al. 2010; Fuhlendorf et al. 2012). From a producer standpoint, it is easy to understand the logic of such an approach, as this paradigm allows the optimization of forage while also protecting rangelands from overgrazing

(Fuhlendorf et al. 2012). Unfortunately, these practices do not promote grassland biodiversity and may not provide habitat for grassland birds with preferences on extreme ends of the vegetation structure spectrum (Fuhlendorf et al. 2006, 2009, 2012; Somershoe 2018). Likewise, the application of prescribed fire, while serving the purposes of preventing woody encroachment and clearing dead vegetation, does not mimic the patchiness and spatial complexity of wildfire. Instead, prescribed fires are typically complete burns that tend to homogenize conditions within burn units. Further, in some regions, the frequency of prescribed fire application is simply not sufficient to mimic natural fire regimes (Ratajczak et al. 2016). Prescribed fire often faces social and cultural obstacles as well, as many communities have concerns about burns near homes and properties. Finally, traditional management practices often implement fire and grazing independently limiting the interaction of these processes (Fuhlendorf and Engle 2004; Allred et al. 2011), as well as their interaction with sources of inherent heterogeneity such as soil type, topographic complexity, and wetland occurrence (Duquette et al. 2022). Collectively, these practices have reduced the range and spatial complexity of heterogeneity in grassland habitats.

In addition to homogenizing grassland structure, modern practices in rangeland management, such as spring deferment (delayed grazing), periodic rest, moderate utilization, and infrequent fire, may inadvertently create conditions that favor the encroachment of exotic species (Printz and Hendrickson 2015; Kobiela et al. 2017). The invasion of non-native plant species is another source of grassland degradation in the Great Plains, and some of the most widespread invasive grasses in the region include Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), and crested wheatgrass (*Agropyron cristatum*)—all species that may outcompete native species and reduce grassland diversity over time (Vaness and Wilson 2007; DeKeyser et al. 2013; Grant et al. 2020). Although some grassland birds will readily use habitats dominated by these species (e.g., Davis and Duncan 1999; Lloyd and Martin 2005; Jaster et al. 2014), others may avoid non-native cover (Davis and Duncan 1999; Pulliam et al. 2020). There is also evidence that non-native vegetation cover is correlated with reduced nesting success and postfledging survival in grassland birds (Lloyd and Martin 2005; Fisher and Davis 2011; S. K. Davis et al. 2016; Maresh Nelson et al. 2018; Bernath-Plaisted et al. 2021). The mechanism by which non-native plants degrade breeding habitat for grassland birds is not yet clear, although reduced arthropod food availability and changes to predator behavior or density have been proposed (e.g., Lloyd and Martin 2005; Maresh Nelson et al. 2018).

#### Climate change

According to the IPCC's Sixth Assessment Report, global surface temperatures will exceed 2°C by the mid-20th century, and by 2100, average temperature increases in excess of 3–4°C are extremely likely (Pörtner et al. 2022). At the same time, the frequency and severity of extreme cold events may also increase throughout much of North America (Cohen et al. 2021). In the Great Plains, these temperature changes will be accompanied by shifts in precipitation patterns, with drying projected to occur in the southern Great Plains and the Chihuahuan Desert, and wetter conditions throughout central and northern regions expected (Patricola and Cook 2013; Pörtner et al. 2022). However, even in regions projected to experience wetter conditions on average, additional rainfall is likely to manifest in the form of extreme precipitation events rather than sustained increases (Pörtner et al. 2022). Further, increases in the severity and frequency of severe drought are also projected throughout the Great Plains region (Cook et al. 2022). Grassland regions may be poorly buffered from these changes as a consequence of their low-elevation occurrence and



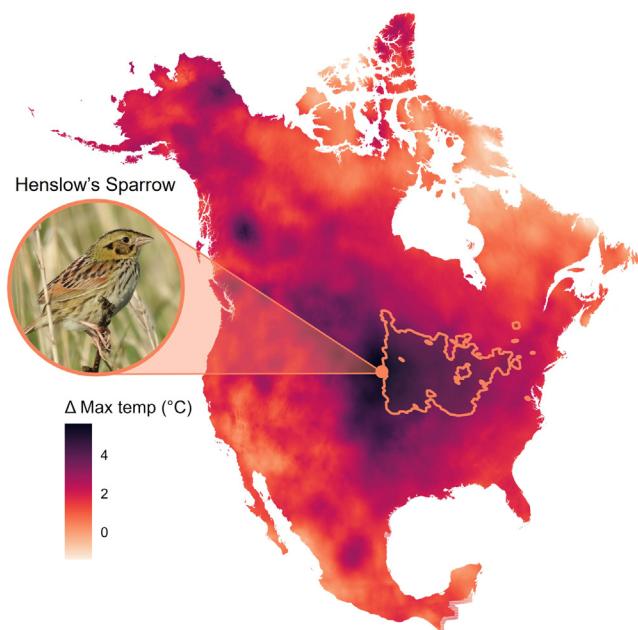
**Figure 3.** Vegetation structure preferences for selected obligate and facultative grassland birds of Great Plains. Habitat preference brackets are general guidelines only and approximated from species accounts created by the US Geological Survey (Effects of Management Practices on Grassland Birds series) and Cornell Lab of Ornithology Birds of the World, as well as expert opinion. Many other factors influence the quality of habitat for grassland birds including fire and grazing regimes, invasives species, climate conditions, and others. This figure is inspired by Knopf (1996) and Derner et al. (2009).

open structure—relative to forested and montane systems (Loarie et al. 2009; Dobrowski et al. 2013; Murali et al. 2023). For grassland birds, these factors may result in greater exposure to increasingly hostile climate conditions (Fig. 4) and thus greater vulnerability (Jarzyna et al. 2016; Wilsey et al. 2019).

Climate conditions can affect numerous aspects of grassland bird ecology, though not all effects are negative (see McCauley et al. 2017 and Maresh Nelson et al. 2023 for a complete review of potential mechanisms). For example, while high mean and minimum temperatures often have positive or neutral effects on grassland bird demographics, and responses to precipitation are mixed, the influences of elevated maximum temperatures and drought are strongly negative (Maresh Nelson et al. 2023). Climate context is also an important mediator of these responses, and the effects of maximum temperature may be more detrimental in warmer regions just as heavy precipitation is more problematic in historically dryer regions (Maresh Nelson et al. 2023). Heat and drought ex-

tremes during the breeding season may depress reproductive success through mechanisms such as heat stress mortality and egg unviability, thermoregulatory behavioral trade-offs, reduced food availability, changes to vegetation structure, and truncated breeding seasons (e.g., Conrey et al. 2016; George et al. 1992; Cady et al. 2019; Verheijen et al. 2022). By contrast, warmer average temperatures during the breeding season may benefit grassland bird reproduction through earlier breeding phenology, increased food availability and foraging efficiency, and reduced exposure to early-season cold snaps (Skagen and Yackel Adams 2012; Renfrew et al. 2013; Zuckerberg et al. 2018). Similarly, warmer temperatures could also benefit overwinter survival in some regions through enhanced foraging opportunities and reduced thermoregulatory demands (Macías-Duarte et al. 2017; Pérez-Ordoñez et al. 2022).

The effects of precipitation on grassland bird demographics are also complex, and the timing and intensity of precipitation events



**Figure 4.** Projected changes in maximum temperatures across North America for 2041–2070, relative to current climate normals. Projections are overlaid with the breeding range of a specialized grassland songbird, the Henslow's Sparrow (*Centronyx henslowii*), to illustrate the future exposure of this species to heat extremes under climate change. Climate data are sourced from AdaptWest (T. Wang et al. 2016) and species data from ebird Status and Trends (Fink et al. 2022).

are important. While greater average precipitation may facilitate more productive grasslands, and subsequently greater food availability (McCauley et al. 2017; Zuckerberg et al. 2018), increased heavy rainfall or hail events may cause mortality and nest destruction, disrupt foraging activity, and cause physiological stress (Fisher et al. 2015; Carver et al. 2017; Freeman et al. 2023). In short-grass prairie songbirds, storm events were linked to declines in daily nest survival while lighter rain events had the opposite effect (Conrey et al. 2016). However, the long-term effects of precipitation can be more difficult to determine, and the demographic influence of such effects is often lagged. For example, heavy precipitation in the previous year may benefit nesting success the following year (Zuckerberg et al. 2018). Similarly, grassland bird abundances on the wintering grounds of the Chihuahuan Desert are strongly associated with summer precipitation (Macías-Duarte et al. 2009, 2018), and increasing aridity associated with severe drought may threaten these winter habitats. The influence of rainfall may differ between wintering and breeding geographies and can also influence patterns of dispersal and emigration in grassland birds (Silber et al. 2023).

The complexity and diversity of climate-driven effects on grassland birds make the ultimate consequences of climate change difficult to predict. However, there is consensus among species distribution projections that many grassland birds will face large contractions in both breeding and nonbreeding ranges under various carbon emissions scenarios. Currently, range-limited species are likely to be most affected, as regional changes to climate may affect the entirety of seasonal distributions for some species (McCauley et al. 2017; Wilsey et al. 2019). By 2080, Baird's Sparrow, Sprague's Pipit, and Thick-billed Longspur could each lose up to 100% of current summer ranges and > 22% of winter ranges, and Chestnut-collared Longspur is predicted to lose 75% of its current breeding range (Distler et al. 2015; Langham et al. 2015; Schuetz et al. 2015). Currently, only 9% of projected habitat strongholds for grassland birds under climate change are legally protected (Grand et al. 2019).

Some of the most severe effects of climate change on grassland birds may result from synergies with existing stressors. Grassland habitat loss and degradation driven by agriculture are likely the most prominent threats to grassland birds today (Stanton et al. 2018; Shaffer et al. 2019; Douglas et al. 2023), and changes to growing conditions and crop yields could spur massive shifts in the spatial distribution of North America agriculture (King et al. 2018; Olimb and Robinson 2019). For example, by 2055, it is estimated that wheat acreage in parts of the Dakotas could increase by up to 54% (Arora et al. 2020). Greater demand for biofuels (Wright and Wimberly 2013; Lark et al. 2015), as well as increased use of wind and solar energy (Ott et al. 2021) with a transition away from fossil fuels, could also drive additional grassland habitat loss. Further, the cessation of cattle on rangelands throughout North America may incentivize landowners to convert to more profitable land uses as drought, heat extremes, and uncertainty make ranching economically unviable (McCollum et al. 2017; Briske et al. 2021). Climate change may also exacerbate issues associated with fragmentation of remaining habitats as fragmented landscapes tend to be associated with greater climate vulnerability and avian population decline (Northrup et al. 2019; Zhao et al. 2019). Indeed, the Great Plains has been identified as a region in which the interaction of climate change and habitat fragmentation is projected to have severe consequences for biodiversity (Segan et al. 2016). For grassland birds, fragmentation may limit the adaptive movements of species in response to changing climate conditions (Bateman et al. 2015), increase the probability of local extinction for populations under climate stress by reducing connectivity (e.g., Augustine et al. 2021), and possibly reduce the capacity of grasslands to buffer negative demographic effects from climate (Zuckerberg et al. 2018).

Finally, changing climate conditions may worsen management challenges over both breeding and wintering geographies. For example, overwinter survival of Henslow's Sparrows in the southeastern United States is much higher in frequently burned pine savanna (Thatcher et al. 2006), but warmer temperatures and increasing drought severity projected for this region will make prescribed fire more difficult, and more dangerous, to implement (Mitchell et al. 2014). Difficulty implementing prescribed fire may also threaten habitat quality for many species in tallgrass prairie regions, where fire is an important tool in preventing shrub encroachment (Ratajczak et al. 2016). Similarly, variability in precipitation can strongly influence the productivity of rangelands; thus, climate change may necessitate carefully designed and intensively managed grazing strategies to avoid overgrazing in low-productivity years (Lipsey and Naugle 2017; Davis et al. 2021; Raynor et al. 2022). In agricultural areas, shifts in the timing of mowing and haying activities associated with a changing climate could also increase conflicts with breeding grassland birds (McGowan et al. 2021).

## Conservation and Management Solutions

### Overview

Despite the conservation challenges facing grassland birds of the Great Plains, there are mitigation strategies that can be employed by a diversity of stakeholders (Drum et al. 2015). At a national level, government-sponsored land set-aside programs have proven their efficacy in reducing grassland habitat loss and even slowing or reversing regional grassland bird declines (e.g., Herkert 2007; Pavlacky et al. 2021, 2022). Pesticide use associated with agricultural intensification is another challenge that could be addressed at the national level through policy. Given mounting evidence against detrimental compounds such as neonicotinoids—which have already been banned in Europe—regulation in this area is badly needed (Stanton et al. 2018; Brain and Anderson 2019; Li

**Table 3**

Selected cost-sharing and landowner programs for wildlife friendly practices, improvements, and habitat restoration in North American grasslands.

Program	Agency	Country	State/Province	Services and improvements	Web link
Environmental Quality Incentives Program (EQIP)	USDA NRCS	USA	National	Funding for soil health and erosion, water quality and conservation, habitat restoration, woody plant removal, and free technical assistance	<a href="https://www.nrcs.usda.gov/programs-initiatives/eqip-environmental-quality-incentives">https://www.nrcs.usda.gov/programs-initiatives/eqip-environmental-quality-incentives</a>
Conservation Stewardship Program (CSP)	USDA NRCS	USA	National	Funding to expand existing conservation practices on properties	<a href="https://www.nrcs.usda.gov/programs-initiatives/csp-conservation-stewardship-program">https://www.nrcs.usda.gov/programs-initiatives/csp-conservation-stewardship-program</a>
Working Lands for Wildlife (WLFW)	USDA NRCS	USA	CO, KS, MT, NE, NM, ND, OK, SD, TX, WY	Funding and technical assistance for woody encroachment and invasive species control, and easements and grazing infrastructure for expiring CRP land	<a href="https://www.nrcs.usda.gov/programs-initiatives/working-lands-for-wildlife">https://www.nrcs.usda.gov/programs-initiatives/working-lands-for-wildlife</a>
The Meadowlark Initiative	North Dakota Game, and many others	USA	ND	Funding and technical assistance for infrastructure cost-share, invasive species control, prescribed burn, grazing mentorship, and habitat restoration. Available to producers and homeowners	<a href="https://gf.nd.gov/meadowlark-initiative">https://gf.nd.gov/meadowlark-initiative</a>
Sustainable Ranching Initiative	World Wildlife Fund	USA	MT, NE, SD, WY	Easements, incentive programs, and cost-shares	<a href="https://www.worldwildlife.org/projects/sustainable-ranching-initiative">https://www.worldwildlife.org/projects/sustainable-ranching-initiative</a>
Alternative Land Uses Services (ALUS)	Weston Family Initiative	CA	National	Funding for water quality and wetland improvements, wildlife habitat and native cover, pollinator habitat and buffer strips	<a href="https://alus.ca/communities/">https://alus.ca/communities/</a>
Various programs	Ducks Unlimited Canada	CA	National	Easements, payment for protections, funding for conversion of crop to forage, buffer strip and pollinator habitat, and wetland restoration	<a href="https://ag.ducks.ca/programs/">https://ag.ducks.ca/programs/</a>
Various programs	Canadian Agricultural Partnership (CAP)	CA	National but implementation varies by province	Cost-sharing for perennial cover, infrastructure, livestock management in riparian areas, and various sustainability practices	<a href="https://agriculture.canada.ca/en/department/initiatives/canadian-agricultural-partnership">https://agriculture.canada.ca/en/department/initiatives/canadian-agricultural-partnership</a>

et al. 2020). Similarly, regulations to minimize the impact of energy development on grassland habitat could greatly benefit grassland birds and, in many cases, at a minor cost to energy companies.

State and provincial agencies and nongovernmental organizations (NGOs) can also play many roles in grassland bird conservation. Wildlife agencies and large NGOs often supplement federal conservation programs through land acquisition and conservation easements, and these efforts are invaluable. Outreach to private landowners and producers, as well as programs that incentivize sustainable practices and fund habitat improvements on private lands, are also critically important (Ciuzio et al. 2013; Morgan et al. 2019). Given the amount of human disturbance affecting grassland landscapes and the linkages between production and grassland bird habitat, conservation interventions on working landscapes will likely play an important role in grassland bird conservation (e.g., Cheng and Ma 2023). Many agencies and NGOs employ private lands wildlife biologists who can provide expertise and outreach to producers and assist them in accessing various programs available throughout the United States and Canada (Table 3). Such programs often provide incentive payments and cost shares for habitat restorations, perennial cover, improvements to water and soil quality, and wildlife-friendly infrastructure such as fence markers (to reduce collision) and stock tank ladders (to prevent birds from drowning). Greater inclusivity to make such programs available to Indigenous landowners and incorporation of Indigenous leadership and traditional ecological knowledge could help to expand the reach of these efforts to Indigenous lands. Unfortunately, funded land set-aside and improvement options are limited on wintering grounds in Mexico and South America, and until such mechanisms are available, grassroots approaches to conservation such as landowner outreach and land acquisition by local NGOs may be the only option to conserve disappearing nonbreeding habitat. Importantly, successful conservation efforts in these regions may also hinge on greater inclusion and support for scientists and conserva-

tionists from these countries and a deeper understanding of local issues and culture (Ruelas Inzunza et al. 2023; Soares et al. 2023).

Finally, at the individual level, interested producers can also contribute to grassland bird conservation independently. The voluntary adoption of regenerative agricultural practices at the farm level can have a positive impact by reducing grassland bird exposure to harmful pesticides and increasing farm-level biodiversity (Green et al. 2005). Such practices may include maintaining habitat patches and seminatural areas throughout agricultural landscapes, increasing plant diversity and integrating cropping with livestock to reduce the need for pesticide and fertilizer use, and maintaining greater permanent cover (LaCanne and Lundgren 2018). Producers can maintain grassland habitat within agriculture-dominated landscapes by introducing prairie strips between plantings; these grassland habitats increase both avian and insect biodiversity while simultaneously preventing erosion and increasing pollination rates (Schulte et al. 2016, 2017). Although small habitat strips may not directly benefit many grassland birds, there is evidence some generalist and facultative grassland species will use these habitats (Schulte et al. 2016). Further, these vegetated areas may help to reduce the leaching of pesticides and fertilizers into surrounding habitat. Deferring mowing and haying activities until after the breeding season is another voluntary farm-level practice that can help prevent the destruction of nests and reduce fledgling mortality (Tews et al. 2013). Producers can also implement practices on rangelands that promote biodiversity and heterogeneity. These may include increased use of native forage, alternative grazing regimes such as patch-burn and adaptive multipaddock systems, and more frequent application of fire (Fuhlendorf et al. 2012; Keyser et al. 2019; Raynor et al. 2022).

#### Conservation of grassland habitat

Given the numerous detrimental effects of habitat loss and fragmentation discussed herein, conserving and expanding large tracts

of grassland habitat are vital to the conservation of North American grassland birds. While what is considered sufficiently large may be debated—and likely varies by species, habitat quality, and region—such debate may not be fruitful given the scale of grassland losses and urgency of grassland bird declines. It is more practical to state that we must conserve (e.g., prevent wholesale conversion and development) as much grassland as possible, and when feasible, land acquisitions and easements should be strategic with respect to patch size, connectivity, landscape context, and future changes to land use and climate (Ribic et al. 2009; Lipsey et al. 2015; Herse et al. 2017; Grand et al. 2019; Augustine et al. 2021). Although it is generally preferable to conserve larger patches over smaller ones, it is important to note that small habitat patches are not worthless. In regions where large undisturbed grassland tracts are lacking, small grasslands can still provide useable habitat for some species (Weidman and Litvaitis 2011; McLaughlin et al. 2014). While many grassland birds are area sensitive (e.g., Ribic et al. 2009), it is important to realize that minimum area requirements are relatively small for some species with many requiring areas  $< 50$  ha and some as little as 5 ha (Herkert 1994; Davis 2004). Small habitat patches also have the potential to act as stepping-stones to facilitate habitat connectivity (Wintle et al. 2019), and their value as stopover habitat during migration remains unknown. Thus, small restoration efforts by private landowners or local NGO chapters, urban grasslands and preserves, and prairie strips in agricultural lands should all be promoted.

Larger-scale conservation of North American grasslands will, however, require significant financial investment, and compelling economic incentives may be necessary to achieve producer buy-in (Hanley et al. 2012). In the United States, CRP is currently among the most powerful existing mechanisms by which this might be achieved. CRP provides financial incentives to producers choosing to seed grass or forb cover on previously tilled cropland, removing that land from crop production and resulting in the return of grass cover to these parcels. Nearly 4 million km<sup>2</sup> of land were cumulatively enrolled in CRP from 1985 to 2018, and in 2023, approximately 20 000 km<sup>2</sup> will enter the program (USDA 2020). An additional 12 000 km<sup>2</sup> were also enrolled in Grassland CRP, a program reauthorized in the 2018 Farm Bill to target grassland properties specifically (USDA 2020). CRP has proven to be an effective mechanism for grassland bird conservation in the United States, and CRP land is consistently positively associated with grassland bird population trends (Veech 2006; Herkert 2009; Pavlacky et al. 2021). Importantly, however, some of the most steeply declining grassland obligates, such as Sprague's Pipit and Baird's Sparrow, do not appear to benefit greatly from CRP (Johnson and Schwartz 1993; Pavlacky et al. 2022). This is likely because of these species' stronger preferences for native prairie habitats (Pulliam et al. 2020). For these species such as these, a payment for ecosystem services (PES) model might be a more effective apparatus for conservation (Farley and Costanza 2010; Bengtsson et al. 2019). Ultimately, CRP remains a blunt instrument and could benefit from continued improvements and more targeted application.

Originally, CRP was designed primarily to combat erosion in farmlands and reduce surplus commodity products. Over time, the program has evolved to be more conservation focused. Although still not a requirement, planting native species is now incentivized by a point system during the application process, and this system similarly allows properties in conservation priority areas to be funded more easily (USDA 2020). Historically, grazing was not allowed on CRP properties, but these restrictions have been eased to allow grazing during drought emergencies and for limited non-emergency periods that may vary by state (USDA 2020); several studies have shown that introducing grazing to CRP lands can improve heterogeneity and increase grassland bird diversity (Kraus et al. 2022; Wilson et al. 2022). Even so, the program still lacks rig-

orous requirements for diversity and heterogeneity of plantings or postplanting management prescriptions to ensure that habitat remains optimal. For example, most seed mixes still include non-natives and lack short-structured grasses to promote habitat for shortgrass specialists (e.g., Horned Lark and Thick-billed Longspur). Thus, CRP could be improved by allowing greater flexibility to accommodate the needs of a broader range of species and adjustment of practices for regional variation in climate and productivity. Federal funding caps and an inability to track fluctuations in crop commodity prices also hamper the program (Lark 2020). Both issues could be solved at the policy level but would require additional funding through the Farm Bill. Finally, the expansion of US Department of Agriculture Farm Bill programs to Indigenous lands would also benefit the conservation of grassland birds and simultaneously advance environmental justice. As of November 2022, the USDA reached an agreement with the Cheyenne River, Oglala, and Rosebud Sioux tribes in the Great Plains regions to make their lands eligible for the Conservation Reserve Enhancement Program (CREP), marking a step in the right direction in this regard (USDA 2022).

Unlike the United States, Canada currently lacks an omnibus federal land set-aside mechanism. In the early 1990s, Agriculture Canada's Permanent Cover Program (PCP) was implemented, which led to the conversion of  $> 4\ 450$  km<sup>2</sup> of cropland to perennial vegetative cover (McMaster and Davis 2001). In this program, landowners committed to maintaining these lands as hay fields or pastures for 10- or 21-yr periods. PCP lands had high grassland bird species richness, and many sensitive species, such as Grasshopper Sparrow (*Ammodramus savannarum*), Baird's Sparrow, and Chestnut-collared Longspur, were observed more frequently than in adjacent cropland areas (McMaster and Davis 2001). Unfortunately, after only 2 yr, the PCP was discontinued and the program has not been replaced. While the reinstatement of such a national program in Canada would be ideal, there are currently many other programs that incentivize herbaceous cover available to landowners in the country today. These are implemented through a combination of NGOs, provincial agencies, and federal-provincial partnerships. For example, the Canadian Agricultural Partnership (CAP) provides a combination of federal and provincial funds to implement various programs at the provincial level (Agriculture Canada 2016). In Saskatchewan, these funds were used to create the Farm Stewardship Program (FSP), which provides 50% cost sharing for tame permanent cover and 90% for native permanent cover (Canadian Agricultural Partnership 2018). Other prairie provinces, such as Manitoba and Alberta, provide similar programs with this funding source. Bird Studies Canada has compiled a guide to incentive and easement programs available to landowners in Canada (available at <https://www.birdscanada.org/bird-science/grassland-birds-at-risk>).

Although many of the programs and services discussed earlier are critical to the conservation of grassland bird breeding grounds in the Great Plains, programs in the United States and Canada can currently do little to address severe habitat loss from conversion to cropland on wintering grounds (e.g., Pool et al. 2014). If successful, legislation such as the North American Grassland Conservation Act (S.4639) could help to address this issue by providing dedicated funding for trinational grassland conservation. Currently, the Mexican government does not have a nationally funded means for incentivizing private land conservation, and irrigated agriculture continues to be more profitable than ranching. However, there is one program available to private landowners in Mexico knowns as Areas Voluntarily Destined for Conservation (<https://advc.conanp.gob.mx/>), which provides technical assistance for sustainable land uses while limiting more intensive resource exploitation on properties. Mexico has also recently taken steps to promote biodiversity as an aspect of sustainable development in the country (Petersen and

Huntley 2005; Redford et al. 2015), and public policy has begun to focus on designing subsidy programs in agriculture (like the USDA Farm Bill) to achieve sustainable production while also preserving and enhancing biodiversity. While this is a key step, new policies must also address rangeland health and the needs of biodiversity targets such as grassland birds. Further, Mexico has had difficulty enforcing current environmental practices and land use regulations (Pool et al. 2014), an issue that is beyond the control of conservationists. Consequently, several NGOs have begun initiatives to directly conserve rangelands in Mexico's Chihuahuan Desert. For example, Bird Conservancy of the Rockies has worked with private landowners to create a Sustainable Grazing Network to conserve wintering habitat for grassland birds and combat shrub encroachment. Similarly, American Bird Conservancy has partnered with Mexican NGO Pronatura Noreste to promote sustainable practices in the region. Another Mexican NGO, Especies, Sociedad, y Hábitat (Species, Society, and Habitat), has primarily worked with ejidos to conserve habitat through agreements, community ordering (*ordenamientos comunitarios*), restoration and soil quality improvements, and by promoting agroecological practices. Critically, these efforts focus on not only protecting grassland bird habitat but also improving rangeland health to benefit local producers.

#### *Management of remaining grasslands*

While restoration and acquisition of new grasslands to create and maintain habitat for grassland birds are paramount, the management of current grassland habitat to facilitate heterogeneity and rangeland health is also important. One approach that is often promoted to improve habitat for grassland birds is patch-burn grazing, a strategy by which livestock are allowed to graze freely in pastures containing both burned and unburned areas (e.g., Fuhlendorf et al. 2006). There is evidence that this strategy can be effective in tallgrass prairie and results in greater habitat heterogeneity and grassland bird diversity (Fuhlendorf et al. 2006; Coppedge et al. 2008; Duchardt et al. 2016). Patch-burn grazing can yield additional benefits to producers such as greater plant diversity and soil health and reduced expenses associated with supplemental feed, brush control, herbicides, and insecticides (Fuhlendorf et al. 2012; Scasta et al. 2016). However, its effects on nesting success have been mixed (Hovick et al. 2012; C. A. Davis et al. 2016; Verheijen et al. 2022). Further, there appears to be less support for patch-burn grazing in more western grassland bird communities (Augustine and Derner 2015; Skagen et al. 2018). One explanation for the discrepancy among ecoregions may be that in more arid grasslands where vegetation structure is already sparse, retaining taller habitat patches (especially during periods of drought) may be an important management goal for many species that is less compatible with a patch-burn approach (Skagen et al. 2018).

It has become increasingly evident that there is no silver bullet grazing strategy (Hovick et al. 2012; di Virgilio et al. 2019), and approaches that are appropriate both for producers and grassland birds vary by region, climate year, and local site features (Ahlering and Merkord 2016; Lipsey and Naugle 2017; Davis et al. 2020; Duquette et al. 2022). For example, season-long continuous grazing may be an effective strategy for creating heterogeneous grassland conditions in areas with topographic complexity and variation in soil productivity (Duquette et al. 2022). Rotational grazing schemes that provide pasture rest may help to build grass banks for drought mitigation while simultaneously creating habitat for species that prefer taller vegetation. By contrast, high-intensity, short-duration grazing is an option that can create suitable habitats for species with sparse vegetation requirements (Davis et al. 2020). Adaptive models such as AMP grazing can allow greater flexibility to address variations in site productivity and climate and also produce habitat heterogeneity among paddocks (Raynor et al. 2022).

Recent development in virtual fencing technologies has made such grazing schemes simpler and more cost-effective to implement (Horn and Isselstein 2022). Ultimately, managers and interested producers should familiarize themselves with the habitat requirements of their target species and select a grazing scheme from a range of options that can meet these requirements but is also suitable for their climate region, property features, and economic constraints (Duquette et al. 2022; Raynor et al. 2022). Many NGOs and agencies, such as Bird Conservancy of Rockies and Bird Studies Canada, produce manuals available on their websites (e.g., <https://www.birdconservancy.org/resource-center/publications/>; <https://www.birdscanada.org/bird-science/bird-friendliness-index>) that can help landowners understand the habitat needs of species in their region and make informed management decisions to benefit grassland birds. NGOs can also help to promote and incentivize grazing practices that benefit grassland birds through grassland-friendly marketing campaigns and certifications (Drum et al. 2015). This approach can both improve the economic outlook for producers and increase public awareness surrounding grassland issues. For example, The Audubon Society's Bird Friendly Beef certification (<https://www.audubon.org/conservation/ranching>) promotes and markets beef producers that meet criteria for maintaining grassland bird habitat on ranches.

In addition to grazing strategies, restoring historical fire regimes is important for improving and maintaining grassland bird habitat, particularly in eastern regions of the Great Plains (Ratajczak et al. 2016; Keyser et al. 2019). Historical fire regimes in prairie ecosystems of central North America were characterized by recurring fires at intervals ranging from 1 to 35 yr (Zhouhar 2021). Research has shown that frequent fire improves rangeland health in many ways, such as preventing woody encroachment, combating invasive species, and stimulating new growth (Fuhlendorf and Engle 2004; Gibson 2009; Fuhlendorf et al. 2012; Ratajczak et al. 2016). Therefore, returning grassland properties to fire intervals appropriate for regions and ecosystems is an important goal. However, although simple in concept, there are many implementation challenges. These include a lack of resources to conduct frequent burns, risks associated with conducting burns in semipopulated areas, and cultural discomfort with fire in some communities. Continued outreach and education efforts by agencies and NGOs regarding the importance of fire and its natural place in prairie ecosystems, as well as burn cooperatives that can provide labor, equipment, and expertise to safely conduct burns, can help to address these issues (Twidwell et al. 2013; Diaz et al. 2016). Finally, in areas where woody encroachment is severe, or fire is restricted for other reasons, mechanical shrub removal is another option to maintain grassland structure. This approach has been employed successfully to restore prairie grouse habitat in the Great Plains (Miller et al. 2017) and maintain grassland bird wintering habitat in the Chihuahuan Desert (Coffman et al. 2014).

#### *Mitigating anthropogenic development*

Given human society's current dependence on fossil fuels, and likely future dependence on renewable energy sources, broad solutions for energy development in the Great Plains are beyond the scope of this review. However, there are practical strategies that can be employed to reduce the impact of such development on grassland birds and their habitats. First, the locations of new leases and their extent and associated infrastructure may be mitigated in several ways. For example, wind and solar energy structures can often be placed in areas of existing development, such as wind leases in agricultural areas or solar panel installations in parking lots and on rooftops. Other sites such as landfills, mines, and areas of existing energy development could also be used (Ott et al. 2021). Targeting new development in these locations could

reduce the disturbance of natural habitats. For oil and gas, the use of space optimization and multibore well pads, which reduce the need for additional pads and associated roads, can greatly reduce habitat loss (Thompson et al. 2015). Additionally, timely reclamation of inactive energy sites with native plantings and research-backed restoration practices can reduce the amount of disturbance on the landscape and improve recovery speed (Walsh and Rose 2022). Many companies already have sustainability plans that can be modified and improved in consultation with agencies and experts.

There are also simple engineering solutions that can target harmful aspects of specific infrastructure types. For example, markers on both fences and transmission lines can reduce avian collision, particularly for larger species such as raptors and prairie grouse (Stevens et al. 2012; Sporer et al. 2013; Bernardino et al. 2018). This could be accomplished through retrofitting existing structures and regulation of new development (Dwyer and Mojica 2021).

New technologies such as the installation of line markers via Unpiloted Aircraft Systems (e.g., drones) continue to make solutions less expensive and more feasible (Lobermeier et al. 2016). Further, the use of ultraviolet light to illuminate transmission lines is also showing promise in reducing collisions (Baasch et al. 2022). In Nebraska, Sandhill Crane (*Antigone canadensis*) collisions were reduced by 98% when lines were illuminated with ultraviolet light (Dwyer et al. 2019). Similarly, improvements could be made to reduce avian collision mortality from wind turbines. One study found that simply painting rotor blades with high-contrast black markings lowered annual avian mortality by 70% (May et al. 2020), though further study and replication on the subject are needed.

In addition to mitigating the physical impacts of structures, engineering solutions can also reduce anthropogenic noise associated with structures. Noise control technologies and sound walls could be employed to reduce noise from loud structures such as compressor stations and oil wells (Francis et al. 2011; Rosa and Koper 2022). Given that noise associated with oil and gas production is also a human health concern (Hays et al. 2017), such measures could be seen as a win-win for grassland birds and communities in areas of high development activity. Short of policy and regulation forcing energy companies to comply with various mitigations, continued engagement from the public, stakeholders, and researchers may also be effective. Many energy companies recognize the importance of public perception in today's climate, as well as the costs and limitations that may be imposed on them by the federal listing of grassland species in the United States and Canada. Therefore, companies may exhibit a willingness to make wildlife-friendly improvements and adjust environmental management strategies, especially given that many such measures are relatively inexpensive.

#### *Regulating neonicotinoids*

There is no longer ambiguity regarding the harmfulness of pesticides to grassland birds and other wildlife (Stanton et al. 2018; Li et al. 2020; Mitra et al. 2021; Moreau et al. 2022). While the use of conventional pesticide compounds will likely continue into the near future, efforts to ban or regulate the use of neonicotinoids could have a better chance of success. Neonicotinoids are comparatively recent, far more potent than traditional pesticides, and their detrimental effects on bees and pollinators are already known to the public. Therefore, directed campaigns to regulate their use in the United States and Canada may be worthwhile, and should such efforts succeed, the benefits to grassland birds would likely be great. Both the Environmental Protection Agency (EPA) and Health Canada have precedents for regulating pesticide use and removing products from the market if they are demonstrated to be harmful

enough. In 2020, the EPA declined to remove neonicotinoids from US markets but did place some restrictions on their use in proximity to bees (US EPA 2022), and the US Fish and Wildlife Service has banned their use in federal wildlife refuges. Health Canada has taken stronger measures and canceled specific uses and application methods, placed limitations on the timing of applications to protect pollinators, and increased buffer zones (Health Canada 2021). While industry has and will likely continue to resist further restrictions (Boone et al. 2014; Ellis 2019), efforts by organizations and individuals to push for additional neonicotinoid regulation are essential.

#### *Climate change adaptation*

Climate change is a diffuse global threat that manifests locally in various ways. This makes it difficult to prescribe specific adaptation strategies. Ultimately, mitigating the threat of climate change itself will depend on societal and geopolitical decisions that influence future emissions (Pörtner et al. 2022)—something over which conservationists and grassland managers have little influence. In general terms, the best climate adaptation strategy to conserve grassland birds may simply be to ensure that species populations and their grassland habitats are as healthy and resilient as possible by addressing the various synergistic threats discussed throughout this document. However, there are two areas in which direct climate change adaptation for grassland birds may be possible.

First, given range shifts and losses projected for many grassland bird species (e.g., Langham et al. 2015), conservation planning to protect habitat in locations where grassland birds may be in the future is critical. Strategic investment in grassland areas that have been identified as habitat strongholds under a changing climate could help to ensure the survival of species (Grand et al. 2019). Similarly, protecting habitat patches that can serve as stepping stones to facilitate range shifts in response to climate change is also important (Hannah et al. 2014; Saura et al. 2014). Grassland birds often display a high capacity for adaptive regional movements in response to climate extremes (Bateman et al. 2015; Silber et al. 2023); thus, maintaining high connectivity between grasslands is a climate adaptation strategy that is consistent with current and future habitat needs of grassland birds (Augustine et al. 2021).

Second, microclimate variation may also offer an opportunity for adaptive management. Only recently have ecologists begun to consider the thermal environment as a spatially explicit aspect of habitat at fine scales (Elmore et al. 2017), and there is evidence from forest and montane systems that microclimates can act as microrefugia, buffering species from extirpation as the broader climate becomes unsuitable (Suggitt et al. 2018; Kim et al. 2022). While this mechanism has not yet been demonstrated in grasslands, a recent study found that grasslands may harbor significant microclimate variation (Bernath-Plaisted et al. 2023), and there is already evidence that microclimates can influence habitat use, survival, and nesting success in some grassland birds (Hovick et al. 2014; Grisham et al. 2016; Carroll et al. 2018). Thus, managing for heterogeneity and conserving grasslands with high topographic complexity may provide greater habitat buffering potential for grassland birds. The Nature Conservancy's Resilient Land Mapping Tool is one example of a product that may help identify such areas (Anderson et al. 2018b).

#### **Knowledge Gaps and Future Directions**

Perhaps the most conspicuous remaining knowledge gap for grassland birds of the Great Plains is a lack of research on habitat use and demographics during the nonbreeding phases of the annual cycle. Given continued declines in grassland birds (Rosenberg

et al. 2019), it is important to avoid overlooking important drivers of decline that may occur in times and places that are more difficult to study. Existing research on grassland birds has been heavily biased toward breeding season abundance/occupancy and nesting success (Muller et al. 2021). Only a handful of studies have been conducted on aspects of grassland bird wintering ecology including work on survival (Thatcher et al. 2006; Macías-Duarte et al. 2017; Pérez-Ordoñez et al. 2022), habitat use (Marx et al. 2008; Macías-Duarte et al. 2009; Macías-Duarte and Panjabi 2013; Muller et al. 2018; Alfaro et al. 2019; Strasser et al. 2019; Franco et al. 2022), and diet (Renfrew et al. 2017; Titulaer et al. 2017, 2018; Olalla-Kerstupp et al. 2020; Guerrero et al. 2022). Further, most existing studies on the topic have been conducted on mixed-grass prairie songbirds, leaving many species virtually unstudied during this period. Our knowledge of grassland bird movements and habitat requirements during migration is even poorer, and only recently has the topic been examined in detail for any species at all (Ellison et al. 2017; Hill and Renfrew 2019; Glass et al. 2023).

We suggest that understanding the full annual cycle ecology of grassland birds should be an important research priority to advance the conservation of these species. Knowledge of nonbreeding habitat use and geography is essential for both the conservation and management of wintering and migratory stopover habitats (Hill and Renfrew 2019; Muller et al. 2021) and conservation planning to address specific threats such as climate change and impacts of development on migration routes (Pocewicz et al. 2013; Grand et al. 2019). Understanding demographic rates and producing survival estimates during nombreeding periods is also critically important to inform management (Thatcher et al. 2006; Macías-Duarte et al. 2017) and produce better population models.

A lack of reliable survival estimates during winter and migration periods for most species makes it difficult to model true annual survival (e.g., Hostetler et al. 2015), thus limiting the ability to model population dynamics. While approaches that focus on managing for single demographic parameters can be useful (e.g., nesting success), determining which demographic rates and associated geographies across a species' life cycle have the largest impact on overall population growth rates may enable more targeted and effective management (Fletcher et al. 2006; Drum et al. 2015). Integrated population models (Schaub and Abadi 2011; Woodworth et al. 2017) are a powerful modeling framework that can be employed to identify the most limiting periods across the annual cycle and direct conservation dollars toward the most effective actions (Rushing et al. 2017). However, such approaches are data intensive and require data collection throughout various life stages and geographies (e.g., Rushing et al. 2016; Bernath-Plaisted et al. 2021). Therefore, to make more sophisticated modeling of grassland bird population dynamics possible, a greater focus on less-studied phases of the annual cycle is needed. While filling information gaps is important, deep knowledge of every aspect of a species' ecology is not necessarily required to protect it. Investment in conserving large swaths of habitat across both breeding and winter ranges is a direct strategy that can be implemented immediately to benefit grassland birds. However, targeted research efforts to fill key knowledge gaps may help to ensure that such conservation investments have the greatest impact possible.

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## Supplementary materials

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