

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Remaining large grasslands may not be sufficient to prevent grassland bird declines

Kimberly A. With^{a,*}, Anthony W. King^b, William E. Jensen^c

^aDivision of Biology, Kansas State University, Manhattan, KS 66506, USA

^bEnvironmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA

^cDepartment of Biological Sciences, Emporia State University, Emporia, KS 66801, USA

ARTICLE INFO

Article history:

Received 30 May 2008

Received in revised form

9 September 2008

Accepted 19 September 2008

Keywords:

Migratory songbirds

Grazing effects

Prescribed burning

Habitat degradation

Land management

Population viability

Rangeland

ABSTRACT

Grassland birds are in steep decline throughout many regions of the world. In North America, even some common species have declined by >50% over the last few decades. Declines in grassland bird populations have generally been attributed to widespread agricultural conversion of grasslands; more than 80% of North American grasslands have been converted to agriculture and other land uses, for example. Remaining large grasslands should thus be especially important to the conservation of grassland birds. The Flint Hills of Kansas and Oklahoma (USA) preserves the largest intact tallgrass prairie (~2 million ha) left in the world. The Flint Hills supports a major cattle industry, however, and therefore experiences widespread grazing and frequent burning. We assessed the regional population status of three grassland birds that are considered the core of the avian community in this region (Dickcissel, *Spiza americana*; Grasshopper Sparrow, *Ammodramus savannarum*; Eastern Meadowlark, *Sturnella magna*). Our approach is founded on a demographic analysis that additionally explores how to model variability in empirically derived estimates of reproductive success across a large heterogeneous landscape, which ultimately requires the translation of demographic data from local (plot) to regional scales. We found that none of these species is demographically viable at a regional scale under realistic assumptions, with estimated population declines of 3–29%/year and a likelihood of regional viability of 0–45% over the two years of study. Current land-management practices may thus be exacerbating grassland bird declines by degrading habitat in even large grassland remnants. Habitat area is thus no guarantee of population viability in landscapes managed predominantly for agricultural or livestock production.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Grasslands are among the most endangered ecosystems in the world (White et al., 2000), primarily as a result of widespread conversion to agriculture, which represents one of the more significant global changes wrought by humans (Vitousek et al., 1997). For example, <4% of the tallgrass prairie of the North American Great Plains remains (Samson and

Knopf, 1994), most of which (~80%) is found in the Flint Hills of Kansas and Oklahoma. Given the magnitude of grassland converted to other land uses, it is not surprising that grassland bird populations in North America have declined sharply throughout their range, more so than any other bird group (Knopf, 1994; Peterjohn and Sauer, 1999). In 2007, the National Audubon Society released a report documenting significant declines in more than 20 still-common bird species (those

* Corresponding author: Tel.: +1 785 532 5040.

E-mail address: kwith@ksu.edu (K.A. With).

0006-3207/\$ - see front matter © 2008 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2008.09.025

with populations >500,000 and a range >10⁶ km²) that had declined by >50% in the past 40 years (Butcher and Niven, 2007). Eight of these 20 species are associated with grasslands (40%), with six grassland birds in the top ten. Although much of the conversion of native grasslands in the Midwestern United States to agriculture was completed by the 1940s (Waisanen and Bliss, 2002), grassland bird populations have continued to decline. Despite the slowing rates of agricultural conversion in recent decades, modern agricultural practices that involve increased mechanization and more intensive management practices, such as intensive grazing, frequent prescribed burns, and increased frequency of haying, may be altering the suitability of remaining, now largely agricultural grasslands to support grassland birds. Agricultural intensification, such as the conversion of pasture to arable land, has also been implicated in the decline of farmland birds throughout Europe (Fuller et al., 1995; Donald et al., 2001), and thus represents a global trend that is not unique to North America.

Given that extinction risk – and population viability more generally – is expected to be inversely correlated with habitat area, remaining large grasslands should be especially important for the conservation of grassland birds (Herkert et al., 2003). The Flint Hills represents the largest intact tallgrass prairie landscape (~2 million ha) remaining in the world. It escaped widespread agricultural conversion because its shallow rocky soils were simply not suitable for cultivation. The region supports a major cattle industry, however, with an inventory of 1 million cattle and annual sales of over \$500 million (USDA, 2002). Thus, far from being pristine prairie, this grassland is intensively managed for cattle production, which involves widespread grazing pressure and frequent pre-

scribed burning across much of the region (Fig. 1). Although fire and grazing have always been part of the natural disturbance regime of this system, current management practices seek to maximize livestock production by promoting uniform forage and grazing across the landscape, which produces a much more homogeneous pattern of disturbance than the shifting disturbance mosaic that characterized the historical landscape (Fuhlendorf and Engle, 2001, 2004).

Because of mounting concern over how land-management practices may be altering habitat quality for grassland birds in this region (Robbins et al., 2002; Fuhlendorf et al., 2006; Rahmig et al., in press), we sought to develop a region-wide assessment of the population viability of three species, the Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus savannarum*) and Eastern Meadowlark (*Sturnella magna*). These three species are considered to represent the core of the tallgrass prairie bird assemblage in this region (Zimmerman, 1993). Eastern Meadowlarks and Grasshopper Sparrows have declined globally by 72% and 65%, respectively, over the past 40 years (Butcher and Niven, 2007). The Dickcissel, although currently exhibiting “stable” population trends (i.e., its rate of decline is not statistically significant; Butcher and Niven, 2007), has experienced significant declines in the past and is therefore still considered a species of conservation concern (National Audubon Society, 2004).

The development of a regional assessment of population viability presents a number of challenges that we sought to overcome in developing this particular modeling approach. Although founded on demographic analysis, our approach explicitly models the heterogeneity or variation that occurs in reproductive success both within and among managed

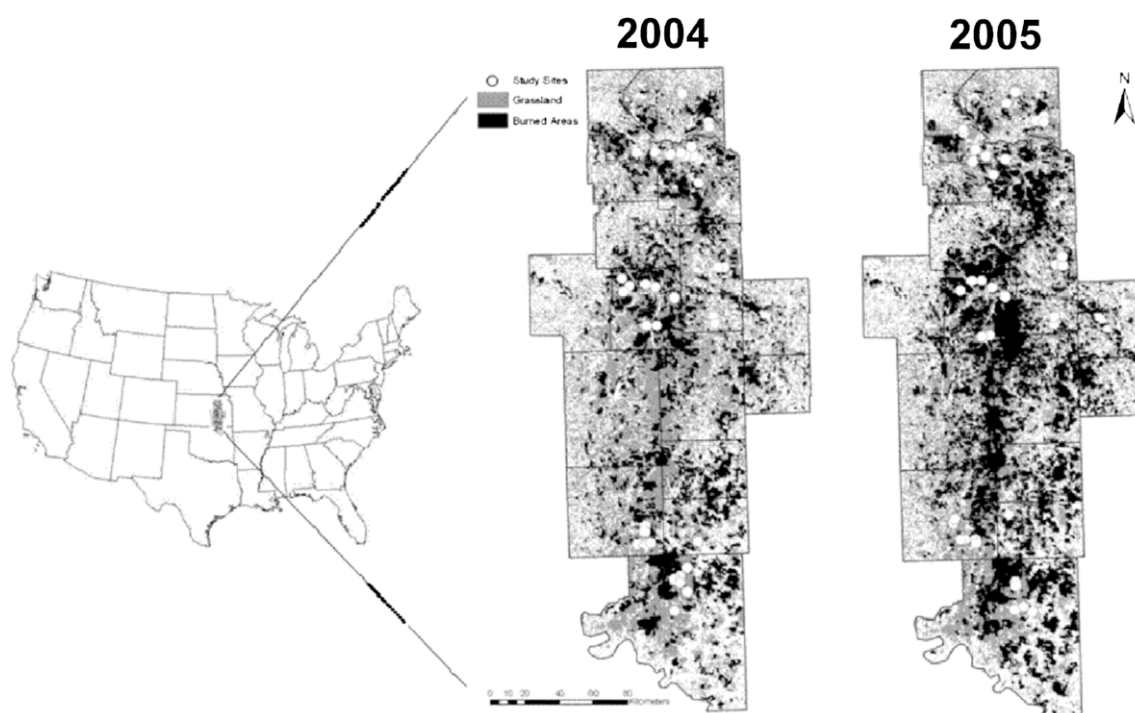


Fig. 1 – Extent of tallgrass prairie and burned grassland in the Flint Hills, the largest remaining tallgrass landscape in North America, based on analysis of remotely sensed imagery (MODIS; R. Mohler and D. Goodin, unpublished data).

grasslands within this system, by focusing on the observed data distributions rather than just the central tendency (i.e., the mean or average response to a particular management treatment) to parameterize the model. A region as large as the Flint Hills is expected to encompass considerable environmental variation, beyond that created by different grassland management practices and other land uses, and thus heterogeneity needs to be addressed in a meaningful way beyond just simply deriving single parameter estimates within different habitat types. The other significant challenge we faced is the translation of local, plot-based estimates of nest success into meaningful estimates of regional viability. Although most ecological or environmental data are collected locally (e.g., within sampling quadrats or plots), rarely – if ever – are the limits to extrapolation explored to determine how robust these measures are when scaling-up from local to landscape or regional scales to assess population viability or extinction risk. Given that these are fundamental issues in conservation that apply to all population assessments conducted at broad landscape or regional scales, our modeling approach and examination of the scaling error associated with translating data across scales may be useful in the context of other research beyond this regional assessment of grassland birds in the Flint Hills.

2. Methods

2.1. Study region and site selection

The Flint Hills region runs north–south across eastern Kansas and into Oklahoma within the central Great Plains region of the United States (38° N, 96° W). The Flint Hills encompasses over 50,000 km² of native tallgrass prairie, which is dominated by the perennial warm-season (C₄) grasses big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*). In 2004 and 2005, we surveyed grassland bird populations and nest success within 36, 10-ha plots distributed among sites representing the major grassland management practices of the Flint Hills (Table 1 and Fig. 1). Because of changes in property access or burning, only 24 plots were sampled in both years of study, which required sampling 12 different sites during the second year to complete the study design (i.e., 48 plots were sampled over the course of the study). Plots thus may have changed treatment between years with respect to burning (e.g., a hayfield that was burned one year may have been unburned in the second). Other than burning, sites were managed consistently between years (a hayfield one year was a hayfield the next), and as far as we know, had been managed as such in the year(s) immediately preceding the study, although site history was largely unknown and anecdotal, assessed through informal interviews with landowners. We had no say in how landowners managed their pastures and fields.

Given our objectives and modeling approach, we sought to capture the magnitude of heterogeneity or environmental variation present within the system, both within and among the various habitat types (i.e., different types of management treatments). For this reason, study sites were stratified

by management type (Table 1) and were also blocked by sub-region within the Flint Hills (northern, central and southern Flint Hills) to encompass environmental variation in precipitation, temperature, productivity and other ecological factors (e.g., predator densities or intensity of brood parasitism by Brown-headed Cowbirds, *Molothrus ater*; Jensen and Cully, 2005) that were expected or known to occur across the region. Sampling across the entire region was also necessary in order to properly extrapolate from our local-scale estimates of fecundity to the entire region. Although the goal of sampling is often to minimize environmental variation (e.g., to increase measurement precision, reduce sampling error, or increase power of statistical tests), the range or variation is ultimately more important to our objectives here than the mean response. As will be discussed, our demographic modeling approach does not rely upon a single parameter estimate (i.e., for fecundity), but instead simulates statistical distributions derived from the observed sampling distributions.

2.2. Grassland management in the Flint Hills

Land-use/land-management statistics for the Flint Hills are not readily available and thus had to be derived from various sources. The vast majority of grassland in the Flint Hills is under private landownership, which makes these statistics difficult to obtain. Grasslands such as tallgrass prairie must be managed through some combination of burning, grazing or mowing else they are rapidly invaded by woody species (e.g., eastern red cedar, *Juniperus virginiana*, in the Flint Hills; Briggs et al., 2002) and become unsuitable nesting habitat for grassland birds. Most (~91%) of the managed grassland in the Flint Hills is grazed rangeland (USDA, 2002; Table 1). The major grazing systems in this region involve either intensive early-stocking (1 head/0.8 ha for 90 days, mid-April through mid-July) or season-long stocking (1 head/1.6 ha for 180 days, mid-April through mid-October) (Smith and Owensby, 1978). To estimate grassland acreage managed under these different systems, we researched the Kansas Agricultural Statistics Service (KASS) “Bluestem Pasture Reports”, which give the percentage of tallgrass prairie (“bluestem”) pasture under partial summer (intensive early-stocked pastures), summer-long, and year-long grazing contracts (the latter two were considered “season-long” grazed for our purposes), and the percentage of ranchers reporting burning across 14 counties in the Kansas Flint Hills. We additionally obtained county-wide statistics on total acreage of grazed pasture, acreage under different grazing contracts, and average size of land-holdings from the KASS. From these we estimated the proportion of total pasture acreage burned, assuming that ranchers who reported burning burned their entire land-holdings. Prescribed burning in the Flint Hills, which may begin as early as mid-March in the southern Flint Hills, is typically performed in mid-April (8-year average = 12 April for years 1997–2004; KASS Bluestem Pasture Reports) to control brush and to improve the distribution and quality of forage for cattle (Ohlenbusch and Hartnett, 2000). Since the Bluestem Pasture Reports were not available in 2005, we applied land-management data from 2004 to both years, as sites were unlikely to convert from one management type to another in that timeframe; instead,

Table 1 – Managed grasslands in the Flint Hills and their use by three grassland birds, the Dickcissel (DICK), Grasshopper Sparrow (GRSP) and Eastern Meadowlark (EAME)

Management type	Grassland area ^a		Habitat use (% sites occupied)					
	ha	%	2004			2005		
			DICK	GRSP	EAME	DICK	GRSP	EAME
Restored grassland under conservation reserve program, burned (CRPB, n = 4)	17136.2	0.9	100	0	25 (0) ^b	100	0	25 (0) ^b
Restored grassland under conservation reserve program, unburned (CRPU, n = 4)	34272.3	1.9	100	25 (0) ^b	25 (0) ^b	100	0	0
Native tallgrass hayfield, burned (HAYB, n = 5)	30511.3	1.7	80	40	60	80	60	80
Native tallgrass hayfield, unburned (HAYU, n = 5)	91534.1	5.0	80	40	80	80	60	100
Intensive early-stocked grazed pasture, burned (IESB, n = 6)	460418.8	25.0	83	100	67	67	100	83
Season-long stocked grazed pasture, burned (SLSB, n = 6)	731766.8	39.8	83	67	33	83	83	83
Season-long stocked grazed pasture, unburned (SLSU, n = 6)	475512.2	25.8	83	83	83	67	100	83
Total managed grassland	1841151.7	–	–	–	–	–	–	–
Total grazed grassland	–	90.6	–	–	–	–	–	–
Total burned grassland	–	67.4	–	–	–	–	–	–

^a Land-use estimates based on total grassland acreage for the grassland-related categories of “range” (pastureland and rangeland other than cropland and woodland pastured), “wild hay” (native pasture that is mowed for forage), and Conservation Reserve Program (CRP) land in the 16-county region encompassing the Flint Hills (USDA 2002). In addition, data obtained from the Kansas Agricultural Service “Bluestem Pasture Reports” and other sources were used to estimate burned acreage within each management type, as explained in text.

^b GRSP and EAME were present at low occupancy in CRP fields (<2 sites) and nest density within these fields did not meet the criterion for estimating nest survival and fecundity on a given study site ($n_{\min} = 3$ nests), and thus these species were considered not to use these habitats for the purposes of this analysis (CRPB and CRPU use = 0%).

burning is the more variable practice among years. Two Flint Hills counties were not included in the reporting by the KASS (Riley Co., KS and Osage Co., OK), and thus we applied information on grazing contracts from neighboring counties to them (the average of Pottawatomie and Geary Cos. for Riley Co., and Cowley Co., KS for Osage Co.).

In the Flint Hills, most grasslands restored under the Conservation Reserve Program (CRP) are seeded to native warm-season grasses (e.g., *A. gerardii*, *S. nutans*, *P. virgatum*, and *S. scoparium*; CP2 plantings). The CRP is a federal program under the United States Department of Agriculture that provides incentives to landowners to remove highly erodible cropland out of production and manage it instead for wildlife conservation. The Kansas state office of the USDA Farm Service Agency recommends annual or biennial burning of CRP fields to control weeds and invasion by woody plants. In practice, CRP fields appear to be burned about every two to three years (Robel et al., 1998), with three or more years between burns more likely. We therefore assumed that the probability that a CRP field would be burned in a given year was 0.33 (one year in three). Prescribed burning for native hayfields is recommended every 2–3 years (Towne and Ohlenbusch, 1992), although in practice these may be burned two or more consecutive years, and then may not be burned for a few years (2–4 years) until needed again (Ohlenbusch and Hartnett, 2000). Thus, we assumed that the probability that a native hayfield will be burned is 0.33 (e.g., burned 2 years out of 6, if landowner waits 4 years after 2 years of consecutive burns). Unlike elsewhere in the Midwest, native prairie hayfields in the Flint Hills are mowed late in the season (mid-July), thus enabling birds breeding within hayfields to get off 1–2 nesting attempts before mowing renders this habitat unsuitable for nesting.

2.3. Nest searching and monitoring

We conducted nest searches weekly on our study plots throughout the breeding season (late April–early August) in 2004 and 2005. Nests were found through a combination of rope-dragging to flush incubating females, behavioral observations of adults and incidental to other field activities. For each nest, we recorded the number of eggs or nestlings, and re-checked nests every 3–4 days to determine nest fate. Nest failure was evidenced by egg shells, nest disturbance (nest lining pulled up, nest trampled), or the absence of nestlings before young could have fledged. Nests were successful if at least one young fledged. A nest was a failure if it only fledged cowbird young.

2.4. Seasonal fecundity estimates

Seasonal fecundity, b , is the production of female young per adult female in a given season summed across all nesting attempts per adult female (f_i), including re-nesting following earlier failed attempts and double-brooding after an earlier successful attempt, d . Thus, $b = \sum(f_i, d)$. We estimated seasonal fecundity from our empirical data on nest survival and brood size (below), and the maximum reported re-nesting and re-brooding attempts for each species, following the approach of McCoy et al., (1999). For each nesting attempt (n_i), we assessed the probability of nest survival (S), mean brood size (m), and the ratio of female offspring within clutches (0.5 assumed). We estimated nest survival probabilities (S) within each management type using Mayfield logistic regression, which adjusts for days of exposure (Hazler, 2004). Each day was treated as an individual Bernoulli trial, in which a

nest either survived (0) or failed (1), beginning when the first egg was laid. For failed nests, we assumed failure occurred at the midpoint between visits, an assumption that has been shown to produce the least bias in the calculation of the Mayfield estimate of daily nest survival (Manolis et al., 2000). We used logistic regression to model daily nest survival as a function of management type, with subregion within the Flint Hills (northern, central or southern) as a fixed effect, for each species (Rahmig et al., in press). We estimated mean brood

size (m) for each habitat type empirically based on the number of young present at the nest visit prior to fledging. As defined, our brood size estimate also accounts for partial clutch or brood loss (e.g., through incomplete predation or removal of eggs by cowbirds). We set a minimum criterion of three nests per species per plot for the estimation of nest survival and thus fecundity (Table 2). Each species was assumed to attempt the maximum number of nests after subsequent nest failure: three for Dickcissel and four for Eastern Meadowlark

Table 2 – Seasonal fecundity estimates (b) for three grassland birds in grasslands managed under different land-management practices in the Flint Hills

Species	2004	2005	2004–2005
Management practice ^b			
<i>Dickcissel</i>			
CRPB	1.07 (0.149) n = 90	0.52 (0.415) n = 57	0.79 (0.410) n = 147
CRPU	0.99 (0.218) n = 181	0.38 (0.244) n = 86	0.69 (0.393) n = 267
HAYB	0.43 (0.227) n = 64	0.34 (0.234) n = 40	0.38 (0.219) n = 104
HAYU	1.30 (0.084) n = 50	0.20 (0.156) n = 53	0.75 (0.595) n = 103
IESB	0.56 (0.388) n = 57	0.46 (0.416) n = 57	0.52 (0.378) n = 114
SLSB	0.54 (0.537) n = 73	0.33 (0.293) n = 81	0.44 (0.422) n = 154
SLSU	0.81 (0.289) n = 43	0.26 (0.204) n = 40	0.56 (0.376) n = 83
<i>Grasshopper Sparrow</i>			
CRPB	–	–	–
CRPU	–	–	–
HAYB	1.86 (0.395) n = 22	0.36 (0.178) n = 12	0.96 (0.857) n = 34
HAYU	0.82 (0.720) n = 11	0.18 (0.115) n = 21	0.43 (0.507) n = 32
IESB	0.72 (0.567) n = 65	0.46 (0.560) n = 63	0.59 (0.554) n = 128
SLSB	0.82 (0.576) n = 31	0.43 (0.315) n = 31	0.60 (0.467) n = 62
SLSU	0.74 (0.422) n = 48	0.37 (0.376) n = 38	0.54 (0.424) n = 86
<i>Eastern Meadowlark</i>			
CRPB	–	–	–
CRPU	–	–	–
HAYB	1.50 (0.343) n = 14	0.28 (0.245) n = 23	0.80 (0.701) n = 37
HAYU	0.62 (0.424) n = 24	0.41 (0.486) n = 51	0.50 (0.446) n = 75
IESB	1.04 (0.605) n = 26	0.61 (0.323) n = 29	0.80 (0.490) n = 55
SLSB	0.44 (0.459) n = 17	0.49 (0.378) n = 19	0.47 (0.358) n = 36
SLSU	1.10 (0.510) n = 35	0.48 (0.244) n = 26	0.80 (0.502) n = 61

a Values are $\bar{x} \pm 1SD$, averaged across plots within each management type (cf. Table 1). Sample sizes (n) are the total number of nests (across all plots of a given management type). Estimates in boldface are those that meet the viability criterion ($b = 1.33$ if $s_a = 0.6$ and $s_0 = 0.3$) for a stationary population ($\lambda = 1.0$). Missing values for treatments are where the number of nests did not meet the minimum for calculating nest survival ($n_{\min} = 3$ nests) on a study site or site occupancy < 2 sites, and thus represents habitat where the species effectively did not breed.

b CRPB = restored grassland under the Conservation Reserve Program, burned that year; CRPU = CRP field, unburned; HAYB = native hayfield, burned; HAYU = native hayfield, unburned; IESB = intensive early-stocked burned pasture (cattle-grazed); SLSB = season-long stocked pasture, burned; SLSU = season-long stocked pasture, unburned.

and Grasshopper Sparrow (McCoy et al., 1999), with the exception of one less nesting attempt for all species in hayfields that were mowed in mid-July. For hayfields, failure was additionally assessed for those nests that could not have fledged prior to mowing (i.e., were still in the incubation or early nesting stage). The number of re-nesting attempts, n , is therefore related to the probability of nest failure ($1 - S$) on previous attempts. Thus, seasonal fecundity (b) is assayed as the sum of

$$f_i = (1 - S)^{i-1} S * m(0.5) \quad (1)$$

for $i = 1, n$, where i is the individual nesting attempt, and

$$d = S^2 * m(0.5) \quad (2)$$

because only birds with successful nest attempts can double-brood. Among our study species, only Eastern Meadowlarks (Lanyon, 1995) and Grasshopper Sparrows (Vickery, 1996) are reported to be double-brooded. Our assumption of maximum nesting effort might thus be viewed as a “best-case scenario,” if our assessment demonstrates that grassland birds are not viable even under this assumption of maximum nesting effort, then they would not be viable under any more conservative estimate of nesting effort either.

2.5. Estimation of regional viability and translation bias

The expected annual growth rate of a population (λ) is given by

$$\lambda^\alpha - s_a \lambda^{\alpha-1} - b l_x = 0 \quad (3)$$

where b is fecundity, $\alpha \geq 1$ is the age of sexual maturity, s_a is annual adult survivorship ($0 < s_a < 1$), and l_x is the probability of an individual surviving to first reproduction (Lande, 1988). This assumes that there is no further age-dependent fecundity or survivorship once sexual maturity has been reached. With sexual maturity reached in year 1 ($\alpha = 1$) for all the species in this study, Eq. (3) reduces to

$$\lambda = s_a + b s_0 \quad (4)$$

where s_0 is annual juvenile survivorship.

We defined adult and juvenile survivorship as species-specific parameters and initially set $s_a = 0.6$ and $s_0 = 0.3$ (“baseline” scenarios) based on reported survivorship estimates for the three species (e.g., Vickery, 1996; McCoy et al., 1999). We had no *a priori* information to suggest that survivorship would be habitat-dependent for these species. Empirical estimates of survivorship are notoriously difficult to obtain for migratory songbirds, particularly for grassland birds that do not exhibit strong site fidelity either within or among years and thus have low recapture or resighting rates from which to estimate even local or apparent survival rates. For migratory songbirds, most adult mortality is believed to occur during migration, rather than on the breeding or wintering grounds, however. For example, 85% of the apparent annual mortality of Black-throated Blue Warblers (*Dendroica caerulescens*), a Neotropical migrant that breeds in eastern forests of North America, occurred during migration (Silllett and Holmes, 2002). Lower juvenile survivorship is expected because of high post-fledging mortality, when young are inept at escaping predators or are in poor body condition to survive extreme conditions (e.g., prolonged wet, cool periods; heat

waves) until they become proficient foragers. Post-fledging survival rates for Dickcissels have been variously reported at 0.22–0.33 (in Iowa and Nebraska; Berkeley 2004 cited in Suedkamp Wells et al., 2007) and 0.56 (in Missouri; Suedkamp Wells et al., 2007); for Eastern Meadowlarks, post-fledging survival was estimated at 0.63 (Suedkamp Wells et al., 2007). The addition of mortality incurred during migration and on the wintering grounds would thus contribute to an even lower overall rate of juvenile survivorship. Given our uncertainty regarding adult and juvenile survivorship, we varied s in a sensitivity analysis to explore how our uncertainty in this parameter estimate affected model results, as well as to identify what critical level of survival would be necessary to offset reproduction to sustain a viable population. If, for example, we find that an unrealistically high level of survivorship (e.g., $s_0 > 0.5$ or $s_a > 0.8$) is ultimately required for population viability, we could reasonably conclude that lower levels would not be sufficient either.

Fecundity (b), on the other hand, was modeled as both a species- and habitat-dependent parameter, since previous research has documented habitat effects on nest success in these species (e.g., Hughes et al., 1999; Shochat et al., 2005; Rahmig et al., in press). To integrate our local estimates of b across a broad heterogeneous landscape and thus extrapolate to a region-wide assessment of viability, we needed to (1) explicitly account for heterogeneity in the distribution of b , which we did by using Monte Carlo simulation to generate a distribution of expected regional population growth rates (λ_R) for each species that were drawn from species- and habitat-specific probability distributions of b , and (2) assess the scaling bias or translation error associated with scaling-up our estimates of fecundity from local to regional scales. We discuss each of these challenges in turn.

To integrate spatial heterogeneity in fecundity among sites within a habitat type for a given species, the estimates of b used in Eq. (4) were obtained from probability distributions defined by the statistics of our seasonal fecundity estimates (Table 2). For a given habitat type, fecundity may be distributed unimodally around some mean value (i.e., a Gaussian or normal distribution). Alternatively, fecundity may vary uniformly across a range of values; fecundity is just as likely to be “high” as “low” (or something in-between) across sites for a given habitat type. Because our sampling was insufficient for gauging the shape of these distributions, we defined both Gaussian and uniform distributions of b , with minimum and maximum values of the uniform distribution defined by the mean \pm 3SD (Table 2). Thus, instead of using a single estimate of b (e.g., the mean), we modeled the distribution of bs (either random or uniform) obtained from our habitat-based statistics.

To scale up from site-based estimates to the regional Flint Hills population (i.e., to integrate across habitat types), we used Monte Carlo simulation to generate a distribution of expected regional population growth rate (λ_R) for each species. Values of b were first drawn randomly from the habitat-specific distributions for each species, with the number of draws from each weighted by habitat area and the probability of species occurrence within the Flint Hills (Table 1). A sample of 1000 values of b was drawn from the management type of smallest area used least frequently by the species (i.e., site

occupancy; Table 1). Proportionally larger samples were drawn from the types with larger area and greater use, which were combined to build a species-specific regional frequency distribution of several thousand b values (thus effectively increasing our sample size from four-dozen to many thousands of plots). This regional b distribution was then used in calculating a regional distribution of λ s (Eq. (4), under different conditions of s), which again we modeled as either a random or uniform distribution.

Deriving a region-wide estimate of population viability (λ_R) ultimately requires an assumption about nesting density across sites. The fecundity (b) of a closed population occupying a region R is the total number of female fledglings (f) produced in the region divided by the total number of reproductive females (F) in the region:

$$b_R \equiv \frac{\sum_{i=1}^n f_i}{\sum_{i=1}^n F_i} \quad (5)$$

where i is a site within the region, and n is the total sites. If the number of reproductive females is the same at all sites in the region, $F_i = F$ for all sites i , then

$$b_R \equiv \frac{\sum_{i=1}^n f_i}{\sum_{i=1}^n F_i} = \frac{\sum_{i=1}^n f_i}{nF} = \frac{1}{n} \frac{\sum_{i=1}^n f_i}{F} = \frac{1}{n} \sum_{i=1}^n \frac{f_i}{F} = \frac{1}{n} \sum_{i=1}^n b_i = \bar{b}_i \quad (6)$$

That is, when the number of females is the same at all sites, the regional b_R is the mean \bar{b}_i of the local, site-specific b_i . With age of sexual maturity at 1 year, λ is a simple linear transformation of b (Eq. (4)). Therefore, the probability distribution of λ or the $E(\lambda)$ is a linear translation of the distribution for b_i and the value of $E(b)$. Thus, when the number of reproductive females is the same at all sites within the region, the regional λ (λ_R) is the expected value of the regional probability distribution of local λ_i :

$$\lambda_R = E(\lambda_i) \quad (7)$$

In other words, the mean of the probability distribution of λ for the region is the regional population-level λ translated or scaled-up from the local field estimates of b , but only when the number of reproductive females is the same at all sites in the region. Alternatively, $\lambda_R = E(\lambda_i) + \epsilon$, where ϵ is an error

term, a translation or scaling error that is a function of the deviation from a common number of reproductive females at all sites.

Although the assumption of uniform female density across sites is violated in the Flint Hills because of species-specific habitat preferences that result in uneven settlement across the landscape, we explored the scaling error (ϵ) associated with this assumption by analyzing the impact on λ_R of deviations from an even nesting density. In simulations, we measured $\epsilon < \pm 15\%$ for deviations in female density as great as 100% among sites (Fig. 2). Field observations indicate that variation in female density was no greater (and generally far less) than 100% (Rahmig et al., in press). Thus, we view the mean of the λ distribution as a reasonable estimate of λ_R ($\bar{\lambda} = \lambda_R$). We can therefore assess the regional viability of these species across the Flint Hills ($\lambda_R \geq 1.0$), as well as the probability that species are viable [$P(\lambda > 1.0)$], using this modeling approach that explicitly accounts for heterogeneity, uncertainty in parameter estimates, and scaling issues (e.g., Fig. 3).

2.6. Sensitivity to total grassland burned

In an independent analysis of remotely sensed imagery from the Flint Hills, the total grassland burned was estimated at 32.2% for 2004 and 49.3% for 2005 (Fig. 1; Mohler and Goodin, unpublished data). This differs from our estimate of burned grassland (67.4%) in 2004, which could result from biases in reporting (i.e., not all acreage within a pasture reported as “burned” actually burns and ranchers may not burn all land-holdings), producing an overestimate in the acreage burned. Conversely, the analysis based on remotely sensed imagery may have underestimated burned acreage owing to the rapid regrowth of vegetation (“green-up”) following a burn. Interestingly, our estimates are more in-line with another GIS-based analysis of burning in the southern Flint Hills (across 45,000 ha in Osage Co.), in which 60–80% of the region was burned annually during a 3-year period (1998–2000; Patten et al., 2007). Given the uncertainty regarding the extent of burning in the Flint Hills, however, we conducted a sensitivity analysis by reducing the total grazed area burned in our original estimates of regional land use by 50% (i.e., total burned area = 35%). This was done by reducing the acreage within each of the burned, grazed categories (IESB, SLSB) by half and allocating that area to SLSU so as to preserve the total grazed area within the Flint Hills (91%). The demographic model was then run on this new landscape as described above to assess the effect on regional viability.

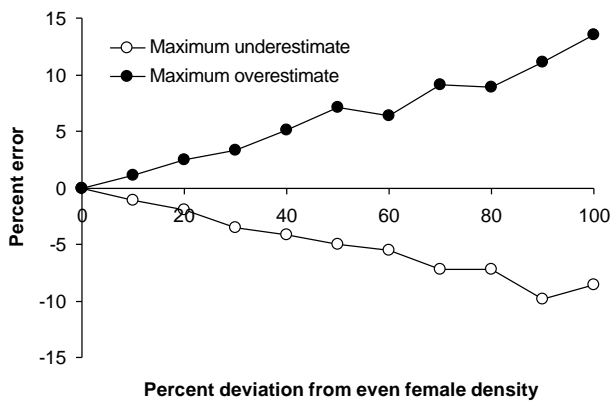


Fig. 2 – Translation error associated with departures from an assumption of even female density among sites in calculating region-wide fecundity (b_R). The translation error (ϵ) is the effect (expressed as a percentage) that deviations in female density have on b_R (or equivalently, λ_R).

3. Results

3.1. Use of managed grasslands

Grasslands restored under the CRP were virtually unused by all species but Dickcissels, which nested in every CRP field we surveyed (100% site occupancy, $n = 8$ fields). Dickcissels were ubiquitous across the Flint Hills, and generally nested in >80% of study sites whatever the management type (Table 1). In contrast, Grasshopper Sparrows occurred with highest frequency in grazed pastures, especially those that were in-

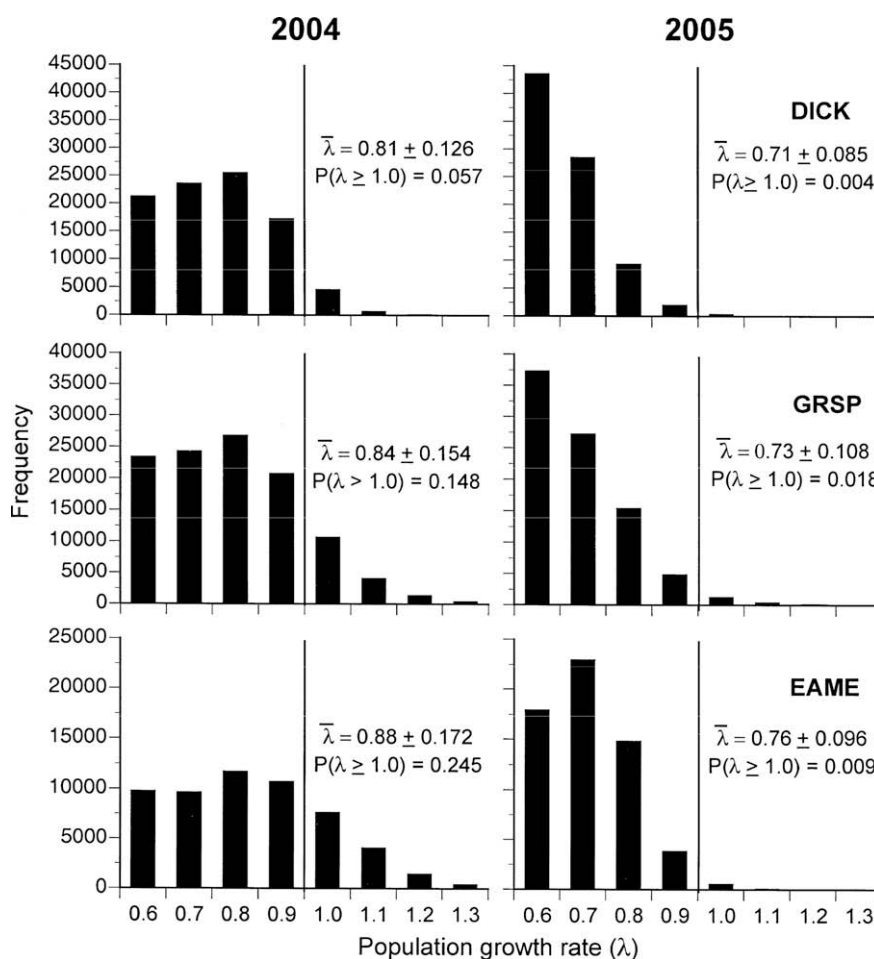


Fig. 3 – Probability distribution of population growth rates (λ) for three grassland birds in the Flint Hills (DICK = Dickcissel, GRSP = Grasshopper Sparrow, EAME = Eastern Meadowlark), assuming regional fecundity (b_R) is normally distributed, and baseline juvenile and adult survivorship values ($s_0 = 0.3$ and $s_a = 0.6$, respectively). Vertical line is the viability threshold ($\lambda \geq 1.0$).

tensely grazed and burned (IESB: 100% site occupancy, $n = 6$). Eastern Meadowlarks also occurred with high frequency in grazed pastures, but had their highest occurrence in unburned hayfields (80–100% site occupancy, $n = 5$). In general, use patterns did not differ much between years, except for Eastern Meadowlarks, which increased their use of SL5B in 2005 (Table 1).

3.2. Local management effects on fecundity

Seasonal fecundity (b) was substantially higher (up to 5–6× greater) in 2004 than in 2005 for all species in virtually all habitat types (Table 2). Fecundity was uniformly low across the region in 2005 for all species (Table 2). In 2004, fecundity for all three species was highest in native hayfields that were either burned (Grasshopper Sparrow, Eastern Meadowlark) or unburned (Dickcissel) that year (Table 2). The fecundity necessary to support a given rate of population change within a homogeneous habitat (plot), assuming reproduction after 1 year of age, is $b = (\lambda - s_a)/s_0$ (from Eq. (4)). If we assume $s_0 = 0.3$ and $s_a = 0.6$, the critical fecundity necessary to achieve a stationary population ($\lambda = 1.0$) is $b = 1.33$. This critical fecundity was only observed for Grasshopper Sparrows and Eastern

Meadowlarks in burned native hayfields, and then only in 2004 (Table 2).

3.3. Regional viability of grassland birds

Based on our regional demographic analysis, none of the three grassland bird species was assessed as being viable in the Flint Hills over the two years studied. Assuming a normal probability distribution in fecundity and “baseline” survivorship estimates (Fig. 3), Eastern Meadowlarks are estimated to be declining by 12–24%/year [% decline/year = $(1 - \lambda) * 100$] (Fig. 4). The likelihood that Eastern Meadowlarks are regionally viable is <25% (Fig. 4). Grasshopper Sparrows are declining by 16–27%/year, with <15% probability that the Flint Hills supports viable populations of this species. The Dickcissel is exhibiting the most rapid rate of decline in this region, with an estimated loss of 19–29%/year. It is therefore unlikely that this species is viable within the Flint Hills (<5% probability), at least during the years of this study. From the sensitivity analysis for adult survivorship (s_a), we found viable populations can only be assured, assuming a normal distribution of fecundity, if 80% of adults survive between years, and then only in 2004 (Fig. 4). For the sensitivity analysis of juvenile survivor-

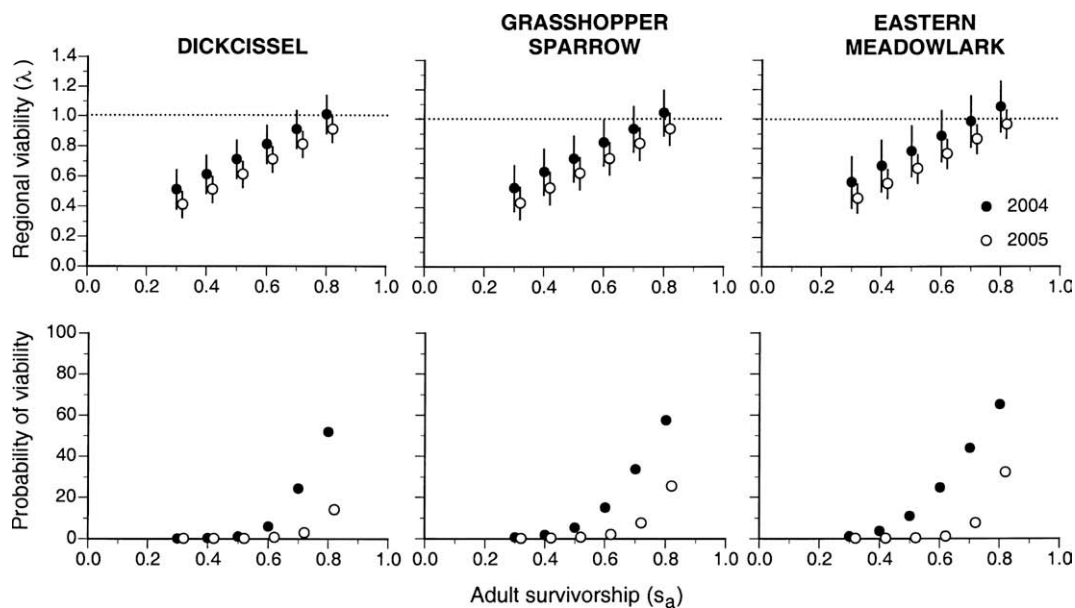


Fig. 4 – Regional viability (top) and the probability of viability [$P(\lambda_R \geq 1.0)$, bottom] for three grassland birds in the Flint Hills. Analysis assumes regional fecundity (b_R) is normally distributed. We explored the sensitivity of the model to adult survivorship (s_a), but considered $s_a = 0.6$ as the baseline in our regional analysis (cf. Fig. 3). Horizontal line is the viability threshold ($\lambda \geq 1.0$). Symbols represent means (± 1 SD) for λ_R .

ship (s_0), viable populations were attained if 50–60% of juveniles survived, but again only in 2004 (Table 3).

If we instead assume a uniform distribution in regional fecundity, along with baseline survivorship (Fig. 5), all three species are still predicted to be declining, albeit less rapidly (Fig. 6). Eastern Meadowlarks are declining by 3–17%/year, with a <45% probability of regional viability. Similarly, Grasshopper Sparrows are declining 4–16%/year, with a <43% likelihood that populations are regionally viable in the Flint Hills. Dickcissels, however, are still predicted to be experiencing significant declines of 11–21%/year, with a <29% probability that the Flint Hills supports viable populations of this species. In all cases, adult survivorship would still have to be greater than 70% to affect regional viability (Fig. 5). In 2004, regional viability required at least 40% juvenile survivorship, but at least 60% juvenile survivorship would have been required for regional viability in 2005 (Table 3).

3.4. Sensitivity to total grassland burned

Despite the uncertainty regarding how much of the Flint Hills is burned in a given year, this ultimately had little effect on our assessment of regional viability. If we assume that at least a third of the Flint Hills was burned, which is consistent with the lower estimate derived from an analysis of remotely sensed imagery from 2004 (Fig. 1), the expected rates of decline for each species are only marginally affected (Table 4), regardless of year or what assumptions we made regarding how fecundity is distributed (i.e., normally or uniformly).

4. Discussion

Despite its size and presumed conservation importance for grassland birds, the Flint Hills does not appear to be function-

ing as either a secure regional population base or population source (*sensu* Pulliam, 1988) for grassland birds, at least for the Dickcissel, Grasshopper Sparrow and Eastern Meadowlark. These species are estimated to be declining by 3–29%/year with a 0–45% probability of regional viability, depending upon assumptions. To what extent might this be a temporary decline, the result of a couple of “bad” or anomalous years, however? As will be discussed, the second year of our study was marked by a near-record drought during the early spring (March–May 2005), which may have affected productivity and thus avian nesting success later in the season (Rahmig et al., in press). That would not account for the declining trend for these species the previous year, a year of normal rainfall, however. Further, it appears that grassland birds in the Flint Hills have been declining for at least a decade. All three species were documented to have low nest success within burned, grazed pastures in the southern Flint Hills more than a decade prior to our study (1992–1996; Patten et al., 2006; Appendix A). It is unlikely that these low rates of nest success (comparable to those we observed in our study, if we convert our nest fate data to apparent nest success as used in that study) would have been sufficient to sustain viable populations. In all cases where fecundity exceeded the threshold for viability ($b = 1.33$), our related estimates based on daily nest survival fell below that critical threshold (Appendix A). Bear in mind that our estimates of fecundity assumed maximum nesting effort (i.e., the maximum number of re-nesting and re-brooding attempts reported for each species), thus possibly inflating our estimates of fecundity, and yet the resulting value still fell below the viability threshold (i.e., estimates of fecundity involving less-than-maximum reproductive effort could only result in lower values that would translate into even greater rates of decline, and therefore would not qualitatively alter our main conclusion). Sim-

Table 3 – Sensitivity analysis of juvenile survivorship (s_0) on regional viability estimates (λ_R) for three grassland birds in the Flint Hills^a

Year/distribution ^b /species	Juvenile survivorship (s_0)			
	0.3	0.4	0.5	0.6
2004				
<i>Normal distribution</i>				
Dickcissel	0.81 (0.126) 0.6, 1.40 5.7%	0.89 (0.172) 0.6, 1.67 28.0%	0.96 (0.215) 0.6, 1.93 44.6%	1.03 (0.258) 0.6, 2.20 55.9%
Grasshopper Sparrow	0.84 (0.154) 0.6, 1.63 14.8%	0.92 (0.203) 0.6, 1.97 34.3%	1.01 (0.254) 0.6, 2.32 48.8%	1.09 (0.305) 0.6, 2.66 59.1%
Eastern Meadowlark	0.88 (0.172) 0.6, 1.62 24.5%	0.95 (0.223) 0.6, 1.84 39.9%	1.03 (0.279) 0.6, 2.16 53.0%	1.12 (0.335) 0.6, 2.47 61.5%
<i>Uniform distribution</i>				
Dickcissel	0.89 (0.164) 0.6, 1.25 28.7%	1.00 (0.224) 0.6, 1.46 51.0%	1.10 (0.280) 0.6, 1.68 61.1%	1.20 (0.336) 0.6, 1.89 67.9%
Grasshopper Sparrow	0.96 (0.210) 0.60, 1.55 43.2%	1.07 (0.280) 0.6, 1.87 56.8%	1.19 (0.350) 0.6, 2.19 65.5%	1.31 (0.420) 0.6, 2.51 71.3%
Eastern Meadowlark	0.97 (0.225) 0.6, 1.46 44.5%	1.07 (0.281) 0.6, 1.72 55.7%	1.18 (0.352) 0.6, 2.00 64.7%	1.30 (0.422) 0.6, 2.27 70.6%
2005				
<i>Normal distribution</i>				
Dickcissel	0.71 (0.085) 0.6, 1.23 0.4%	0.73 (0.097) 0.6, 1.40 0.8%	0.76 (0.121) 0.6, 1.60 3.6%	0.79 (0.145) 0.6, 1.81 8.8%
Grasshopper Sparrow	0.73 (0.108) 0.6, 1.40 1.8%	0.76 (0.121) 0.6, 1.34 3.6%	0.81 (0.152) 0.6, 1.52 11.5%	0.85 (0.182) 0.6, 1.71 21.0%
Eastern Meadowlark	0.76 (0.096) 0.6, 1.25 0.9%	0.80 (0.127) 0.6, 1.46 5.9%	0.84 (0.158) 0.6, 1.68 16.3%	0.89 (0.190) 0.6, 1.89 28.1%
<i>Uniform distribution</i>				
Dickcissel	0.78 (0.119) 0.6, 1.13 5.2%	0.82 (0.132) 0.6, 1.31 10.9%	0.87 (0.166) 0.6, 1.48 23.8%	0.92 (0.199) 0.6, 1.66 35.7%
Grasshopper Sparrow	0.84 (0.153) 0.6, 1.24 15.1%	0.88 (0.166) 0.6, 1.20 28.0%	0.95 (0.207) 0.6, 1.35 41.2%	1.01 (0.249) 0.6, 1.50 50.2%
Eastern Meadowlark	0.83 (0.135) 0.6, 1.16 12.8%	0.90 (0.179) 0.6, 1.35 31.0%	0.97 (0.224) 0.6, 1.53 44.8%	1.05 (0.269) 0.6, 1.72 54.0%

^a Values represent the regional population growth rate ($\lambda \pm 1$ SD, min, max) and likelihood of regional viability [$P(\lambda \geq 1.0)$], assuming annual adult survivorship (s_a) is 0.6 and the observed habitat-specific fecundity (b) for each species and year (cf. Table 2).

^b Distribution refers to the assumption of how fecundity is distributed across the region.

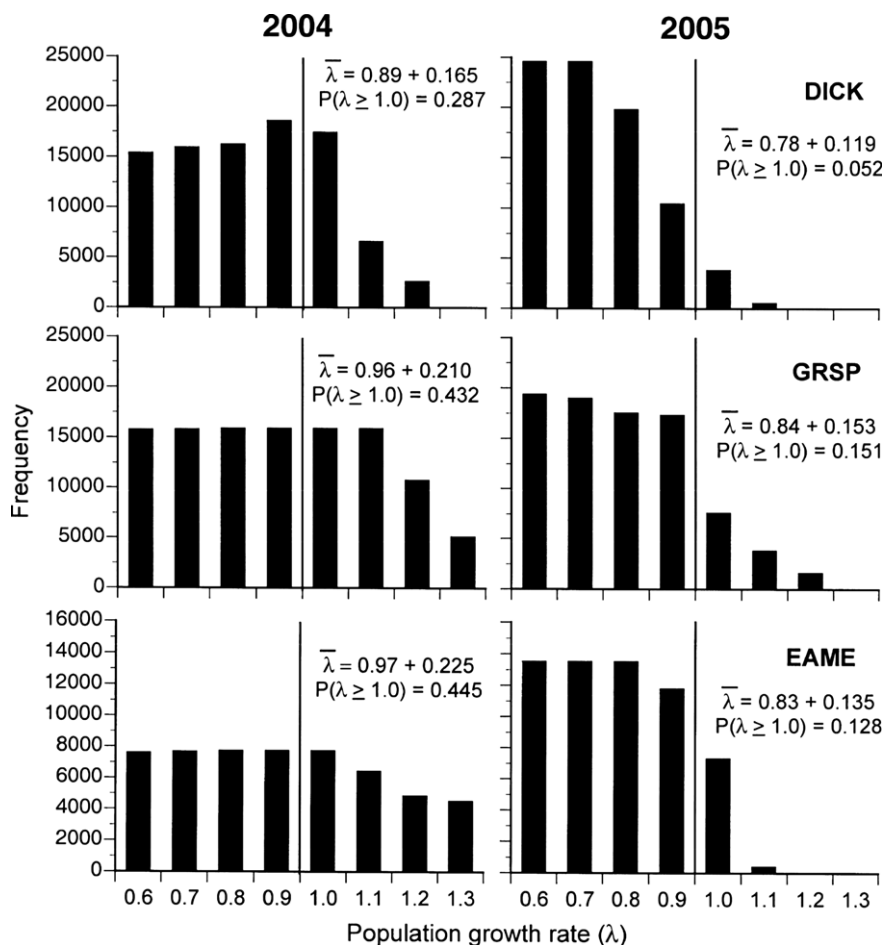


Fig. 5 – Probability distribution of population growth rates (λ) for three grassland birds in the Flint Hills (DICK = Dickcissel, GRSP = Grasshopper Sparrow, EAME = Eastern Meadowlark), assuming regional fecundity (b_R) is uniformly distributed, and baseline juvenile and adult survivorship values ($s_0 = 0.3$ and $s_a = 0.6$, respectively). Vertical line is the viability threshold ($\lambda \geq 1.0$).

ilarly, although we also lack direct estimates of survivorship, we have demonstrated analytically that unrealistically high levels of survivorship ($s_0 > 0.5$ or 0.6 ; $s_a > 0.7$ or 0.8) would generally be necessary to offset such low reproduction to achieve a regionally viable population. Such a high rate of adult survivorship has never been reported for these species (Lanyon, 1995; Vickery, 1996; Temple, 2002), or in general for any small migratory songbird (Martin, 1995). Although post-fledging survival (in the month following fledging) for some of these species has been reported to be as high as 0.56 or 0.63 (Suedkamp Wells et al., 2007), the cumulative effects of mortality accrued during migration and over the winter would surely reduce juvenile survivorship to levels below this. Thus, although empirical estimates of survivorship would give us a more precise estimate of by how much these grassland birds might be declining, the main conclusion is the same: grassland bird populations do not appear to be regionally viable within the largest remaining tallgrass prairie landscape.

Our finding that none of these species is regionally viable is consistent with other demographic analyses of grassland birds at more local scales elsewhere in the Midwest, as well as the continent-wide declines exhibited by these species over the past four decades (Butcher and Niven, 2007). Beyond

the Flint Hills, Dickcissel populations were not viable within small, restored grasslands in either Missouri or Iowa, where little else in the way of native grassland remains (McCoy et al., 1999; Fletcher et al., 2006). In Iowa, Dickcissels were declining by about 40%/year ($\lambda = 0.58$; Fletcher et al., 2006), which is even higher than the 20–30% decline/year we assessed for this species across the entire Flint Hills region, as might be expected for populations occupying smaller grassland fragments, especially those embedded in an agricultural context. Nevertheless, these studies, conducted across a range of scales, paint a consistent picture of grassland bird declines that is becoming increasingly difficult to ignore in light of the extent and magnitude of continent-wide declines over the past several decades (Peterjohn and Sauer, 1999; Butcher and Niven, 2007). At this point, the question is not whether grassland birds are declining, but by how much.

Our estimates of decline for these three species (3–29% decline/year) are higher than the 2–3%/year decline reported in the analysis of the Breeding Bird Survey data (Dickcissel: $r = -0.021$, $\lambda = 0.979$; Grasshopper Sparrow: $r = -0.026$, $\lambda = 0.974$; Eastern Meadowlark: $r = -0.031$; $\lambda = 0.969$; Appendix A in Butcher and Niven, 2007). There are two possible reasons for this discrepancy. First, the scale of the analysis differs: our

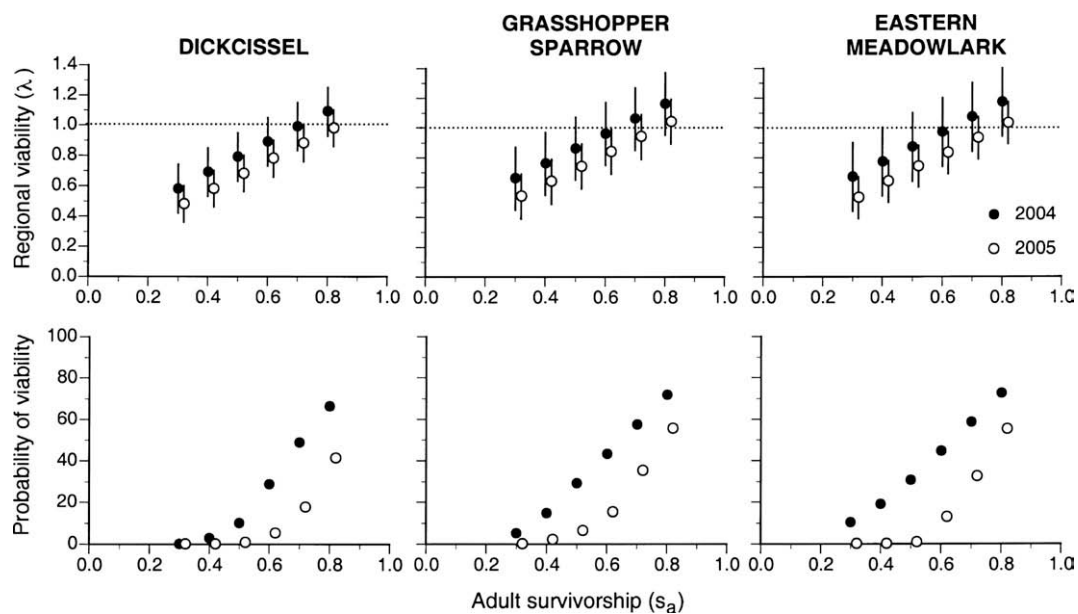


Fig. 6 – Regional viability (top) and the probability of viability [$P(\lambda_R \geq 1.0)$, bottom] for three grassland birds in the Flint Hills. Analysis assumes regional fecundity (b_R) is uniformly distributed. We explored the sensitivity of the model to adult survivorship (s_a), but considered $s_a = 0.6$ as the baseline in our regional analysis (cf. Fig. 5). Horizontal line is the viability threshold ($\lambda \geq 1.0$). Symbols represent means (± 1 SD) for λ_R .

assessment is regional, whereas the BBS analysis involves a nationwide assessment of population trends. Negative trends within a particular region could be offset by positive trends elsewhere that would reduce the overall magnitude of decline at a broader, continent-wide scale. Second, these assessments of population trends are founded on different types of data and analysis. Our approach employs demographic analysis, which assesses population viability in terms of the relative difference between birth (b) and death rates (s). In contrast, the BBS analysis assesses trends in bird count data, as the difference in the number of birds observed from one year to the next. Count or census data may not reflect how well (or poorly) a population is doing demographically. For example, migratory songbirds such as these are hypothesized to exhibit source-sink population dynamics at broad regional or even continental scales (Donovan et al., 1995; With and King, 2001; Tittler et al., 2006; With et al., 2006). Populations that are not demographically viable may appear stable (or even increasing) owing to an influx of individuals from source populations elsewhere (Brawn and Robinson, 1996). This may explain why trend estimates based on count data (e.g., BBS) can give different, and sometimes contradictory, results to estimates obtained from demographic analysis. This is particularly likely if birds are attracted to a region (because of its size or habitat characteristics) in which they ultimately suffer poor demographic performance (i.e., the region is an ecological trap; Shochat et al., 2005). Given its size, the Flint Hills was assumed to represent a landscape source for grassland birds, but that status is now questionable in light of our regional demographic analysis.

Although the reason for the continued decline of grassland birds is likely multifaceted, degradation of remaining large grassland remnants may be a contributing factor. The combination of grazing and frequent burning is known to be detri-

mental to many grassland birds (Zimmerman, 1997; Fuhlendorf et al., 2006). These practices are widespread throughout the Flint Hills, and may effectively degrade and homogenize habitat, which has led to calls for patch-burning (where only a portion of pastures are burned), decreased fire frequency, shifts in the timing of burns (from spring to fall or winter), reduced grazing intensity or rest-rotational grazing, and landscape-scale management that would increase overall habitat heterogeneity (Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2006). Alternatives to grazing, where economically feasible, may indeed prove beneficial, given that all species in our study had highest nesting success in native hayfields (in 2004), which may also mimic the structure of rested pasture. Native warm-season grasses are the predominant hay crop in the Flint Hills (USDA, 2002), which is mowed later (mid-July) than elsewhere in the Midwest (where cool-season grasses dominate and are cut multiple times per growing season), enabling birds to complete at least one nesting attempt. Interestingly, grasslands restored under the CRP did not afford nesting habitat except for Dickcissels, although nest success was low in this habitat and thus did not appear capable of supporting viable populations (Table 2). Although the CRP has been credited with stabilizing or reversing declining population trends in grassland birds elsewhere (e.g., Johnson and Schwartz, 1993; Reynolds et al., 1994; Best et al., 1997), its importance for the Flint Hills region may be nominal given the different landscape context (i.e., grazed native prairie vs. rowcrop agriculture) and widespread availability of other grassland habitats (Rahmig et al., in press).

Current land-management practices may not be solely to blame for declining bird populations in the Flint Hills, however. Grassland birds experienced near complete reproductive failure across the region in 2005 (Table 2). Was this due to changes in land management or some other factor? Indepen-

Table 4 – Sensitivity analysis of the extent of burning on regional viability estimates for three grassland birds in the Flint Hills, in which regional viability under the current land-use assumptions (“Current landscape”, Table 1) is compared to a scenario involving a 50% reduction in the total grazed area burned (IESB, SLSB). The total area grazed remains constant (91%) in both scenarios

Distribution ^b /Land-management scenario (proportion of managed grasslands)	Dickcissel		Grasshopper Sparrow		Eastern Meadowlark	
	2004	2005	2004	2005	2004	2005
<i>Normal distribution</i>						
Current landscape (CRPB = 0.01, CRPU = 0.02, HAYB = 0.02, HAYU = 0.05, IESB = 0.25, SLSB = 0.40, SLSU = 0.26)	0.81 (0.126)	0.71 (0.085)	0.84 (0.154)	0.73 (0.108)	0.88 (0.172)	0.76 (0.096)
Total burned = 68%, Total grazed = 91%	0.6, 1.40	0.6, 1.23	0.6, 1.63	0.6, 1.40	0.6, 1.62	0.6, 1.25
Reduce total grazed area burned by 50% (CRPB = 0.01, CRPU = 0.02, HAYB = 0.02, HAYU = 0.05, IESB = 0.12, SLSB = 0.20, SLSU = 0.58)	0.81 (0.137)	0.69 (0.074)	0.85 (0.170)	0.73 (0.102)	0.91 (0.164)	0.75 (0.087)
Total burned = 35%, Total grazed = 91%	0.60, 1.39	0.60, 1.20	0.60, 1.63	0.60, 1.34	0.60, 1.56	0.60, 1.25
<i>Uniform distribution</i>						
Current landscape (CRPB = 0.01, CRPU = 0.02, HAYB = 0.02, HAYU = 0.05, IESB = 0.25, SLSB = 0.40, SLSU = 0.26)	0.89 (0.164)	0.78 (0.119)	0.96 (0.210)	0.84 (0.153)	0.97 (0.225)	0.83 (0.135)
Total burned = 68%, Total grazed = 91%	0.6, 1.25	0.6, 1.13	0.60, 1.55	0.6, 1.24	0.6, 1.46	0.6, 1.16
Reduce total grazed area burned by 50% (CRPB = 0.01, CRPU = 0.02, HAYB = 0.02, HAYU = 0.05, IESB = 0.12, SLSB = 0.20, SLSU = 0.58)	0.90 (0.164)	0.75 (0.090)	0.98 (0.222)	0.81 (0.128)	0.98 (0.227)	0.80 (0.123)
Total burned = 35%, Total grazed = 91%	0.60, 1.25	0.60, 1.13	0.60, 1.55	0.60, 1.05	0.60, 1.46	0.60, 1.16

a Values represent the regional population growth rate ($\lambda \pm 1SD$, min, max) and likelihood of regional viability [$P(\lambda \geq 1.0)$], assuming annual adult survivorship (s_a) is 0.6 and juvenile survivorship (s_0) is 0.3 and habitat-specific seasonal fecundity (b) for each species (cf. Table 2).

b Distribution refers to the assumption of how fecundity is distributed across the region.

dent analysis of remotely sensed imagery suggests that more grassland area may have burned in 2005 than 2004 (49% vs. 32%, respectively; Fig. 1). Although these estimates of burned grassland are lower than that (67%) used in our regional viability analysis, varying the total grassland burned in a sensitivity analysis did not alter our results. Even if only a third of the grassland was burned (a reduction of 50%), all three species are still predicted to be declining, by about the same amount or slightly less (in 2004) than original estimates (Table 3). Although this gives us an idea of the sensitivity of our results to the amount of burning on the landscape, this should not be interpreted as the effect of prescribed burning on grassland birds (i.e., that decreasing the extent of burning in the Flint Hills would not affect population viability in grassland birds). We do not know to what extent altering the landscape at such a broad scale (e.g., reducing the amount of grazing or burning across the region) would alter the types or abundance of predators and thus nest predation rates within habitats, for example, which could complicate translating our current estimates to different landscape configurations representing different management scenarios.

Coupled with land management, climatic conditions may be exacerbating grassland bird declines in this region. The tallgrass prairie is an extremely dynamic system with annual precipitation and other climatic factors interacting with grazing and fire to influence primary productivity and trophic interactions (Knapp et al., 1998). Precipitation patterns vary greatly among years. For example, March–May 2005 was one

of the driest springs on record for the northern Flint Hills (28–52% of normal), and this below-average precipitation at such a critical point, which has been shown to be a good predictor of seasonal grassland productivity (Briggs and Knapp, 1995), may explain decreased avian nesting success and fecundity across the region that year. In the coastal sage scrub of California, widespread reproductive failure was documented for several passerine birds during an exceptionally dry year (30% of normal), resulting in low prey abundance and reduced primary productivity (Bolger et al., 2005). Changes in precipitation patterns, with less frequent but more severe precipitation events, are an expected consequence of global climate change in the Great Plains (Knapp et al., 2002). Droughts may therefore become more common, and coupled with current land-management practices, may further exceed the ability of birds to persist in the face of such widespread environmental changes.

Declining grassland bird populations may also reflect the legacy of past land-use change. Despite the fact that the widespread conversion of grasslands to agricultural-production landscapes across the American Great Plains was completed some 70–100 years ago (Waisanen and Bliss, 2002), grassland bird populations have continued to decline (Butcher and Niven, 2007). Delayed population responses to environmental or landscape change are likely to occur when the rate of change exceeds the demographic potential of the population, thereby decoupling population dynamics from landscape dynamics (Schrott et al., 2005). Songbirds may continue to

breed in highly disturbed or degraded landscapes, but may suffer low reproductive success owing to higher rates of nest predation or brood parasitism by Brown-headed Cowbirds in remaining habitat (Robinson et al., 1995; Herkert et al., 2003). However, because individuals continue to immigrate to these landscapes, despite poor reproductive performance, it may take many generations (years) before such changes in demographic measures (e.g., fecundity, b) are reflected in significant changes in population-wide measures of density (e.g., bird count data) or performance (e.g., population growth rates, λ) (Schrott et al., 2005). Thus, populations may appear resistant to landscape change for many years or decades before inexorably declining.

This raises the possibility that ongoing declines in grassland birds reflect an extinction debt (Tilman et al., 1994), incurred during the era of rapid agricultural transformation nearly a century ago, and which may now be exacerbated by degradation of remaining grasslands. If the North American grasslands have been reduced in area below some critical habitat threshold, theory predicts that it may take many decades for an extinction debt to pay out, especially if this coincides with the individual extinction thresholds of many species (Hanski and Ovaskainen, 2002). If this is the case with grassland birds, then we may be witnessing an unfolding conservation crisis (Brennan and Kuvlesky, 2005). Degradation of habitat within remaining large grasslands, such as the Flint Hills, may be eroding the source potential of these regions, thereby reducing connectivity among other landscape populations by providing fewer immigrants that can supplement declining populations elsewhere (i.e., a disruption of meta-landscape connectivity; With et al., 2006). If that is the case,

remaining large grasslands, which tend to be managed for agricultural or livestock production, will not be sufficient by themselves to prevent declining grassland bird populations.

Acknowledgements

This research was funded by a grant from the USDA CSREES NRI Managed Ecosystems Program to K.A.W. (#2003-35101-13714). We thank R. Mohler and D. Goodin for sharing their analysis of burned grassland in the Flint Hills, M. Patten for data on nest success in the 1990s from Oklahoma, J. Koellicker for precipitation data from Manhattan and the Konza Prairie Biological Station, B. Hamilton for support at the Tallgrass Prairie Preserve (OK), G. Smith for support at the Ross Natural History Reserve (KS), the dozens of landowners in the Flint Hills who kindly granted property access, and the two dozen students and research technicians who assisted with data collection in the field. We also thank M. Patten and two anonymous reviewers for their comments and suggestions on the manuscript.

Appendix A

Seasonal fecundity estimates (b) for several grassland birds in grasslands managed under different grazing regimes from the southern Flint Hills (Osage Co., Oklahoma) at different time periods. Fecundity estimates for the entire Flint Hills for the combined 2004–2005 period (this study) are provided for comparison. Values in boldface are those estimates that meet or exceed the viability criterion ($b = 1.33$ if $s_a = 0.6$ and $s_0 = 0.3$) for a stationary population ($\lambda = 1.0$).

Species	1992–1996 ^b		2004 South ^c		2005 South ^d		2004–2005 South		2004–2005 Total Flint Hills	
	Management type ^a	Apparent	Apparent	Logistic-exposure method	Apparent	Logistic-exposure method	Apparent	Logistic-exposure method	Apparent	Logistic-exposure method
<i>Dickcissel</i>										
IESB		1.05	0.98 (0.112)	0.43 (0.070)	1.00 (0.655)	0.63 (0.594)	0.99 (0.384)	0.53 (0.364)	0.84 (0.401)	0.52 (0.378)
SLSB		–	0	0.05	0.93 (0.476)	0.51 (0.483)	0.62 (0.635)	0.36 (0.434)	0.79 (0.416)	0.44 (0.422)
SLSU		1.00	1.34 (0.189)	0.88 (0.122)	0	0.11	0.89 (0.783)	0.62 (0.448)	0.87 (0.464)	0.56 (0.376)
<i>Grasshopper Sparrow</i>										
IESB		1.72	1.71 (0.797)	1.18 (0.850)	1.03 (0.055)	0.39	1.37 (0.603)	0.78 (0.693)	0.99 (0.796)	0.59 (0.554)
SLSB		–	1.87	1.36	0.95	0.67	1.41 (0.650)	1.02 (0.487)	0.92 (0.63)	0.60 (0.467)
SLSU		1.52	1.07	0.83	0.34 (0.477)	0.21 (0.285)	0.58 (0.543)	0.41 (0.411)	1.08 (0.774)	0.54 (0.424)
<i>Eastern Meadowlark</i>										
IESB		1.00	1.35 (0.672)	1.17 (0.835)	1.25 (0.231)	0.81 (0.060)	1.30 (0.41)	0.99 (0.526)	1.28 (0.319)	0.80 (0.320)
SLSB		–	0	0.11	0	0.12	0	0.12 (0.007)	0.83 (0.736)	0.47 (0.358)
SLSU		1.39	1.92 (0.198)	1.26 (0.544)	1.74 (1.18)	0.65 (0.037)	1.83 (0.696)	0.95 (0.473)	1.23 (0.902)	0.80 (0.502)

a Management type: IESB = intensive early-stocked pastures, burned that year; SLSB = season-long stocked pastures, burned; SLSU = season-long stocked pastures, unburned. See Table 1 for additional description of grazing regimes (e.g., stocking densities).

b Fecundity data from the 1990s (Patten et al., 2006) were only available as apparent nest success (total young fledged/total nests), which tends to produce a positive bias in nest success (nests that failed early in the nesting cycle are not accounted for by this approach). Our data from 2004 and 2005 are therefore also presented as apparent nest success to facilitate comparisons. Burned season-long grazed pasture (SLSB) was not a treatment studied by Patten et al. (2006).

c Mean fecundity estimates given for those nests located in the southern range of the Flint Hills (Osage Co.), averaged over study sites. Sample sizes (2004): IESB = 2 sites, SLSB = 1 sites, and SLSU = 2 sites. Values lacking (SD) are for SLSB ($n = 1$ study site in southern Flint Hills) or where species only occurred in one site.

d Sample sizes (2005): IESB = 2 sites, SLSB = 2 sites, and SLSU = 2 sites. Values lacking (SD) are for species that only occurred in one site or failed to nest successfully.

REFERENCES

- Best, L.B., Campa III, H., Kemp, K.E., Robel, R.J., Ryan, M.R., Savidge, J.A., Weeks Jr., H.P., Winterstein, S.R., 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. *Wildlife Society Bulletin* 25, 864–877.
- Bolger, D.T., Patten, M.A., Bostock, D.C., 2005. Avian reproductive failure in response to an extreme climatic event. *Oecologia* 142, 398–406.
- Brawn, J.D., Robinson, S.K., 1996. Source-sink population dynamics may complicate the interpretation of longterm census data. *Ecology* 77, 3–12.
- Brennan, L.A., Kuvlesky Jr., W.P., 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69, 1–13.
- Briggs, J.M., Knapp, A.K., 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. *American Journal of Botany* 82, 1024–1030.
- Briggs, J.M., Hoch, G.A., Johnson, L.C., 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5, 578–586.
- Butcher, G.S., Niven, D.K., 2007. Combining Data from the Christmas Bird Count and the Breeding Bird Survey to Determine the Continental Status and Trends of North America Birds. National Audubon Society, New York, NY. <<http://www.audubon.org/bird/stateofthebirds/CBID/content/Report.pdf>> (accessed 08.09.08).
- Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London B* 268, 25–29.
- Donovan, T.M., Lamberson, R.H., Kimber, A., Thompson III, F.R., Faaborg, J., 1995. Modeling the effects of habitat fragmentation on source and sink demography of Neotropical migrant birds. *Conservation Biology* 9, 1396–1407.
- Fletcher Jr., R.J., Koford, R.R., Seamanc, D.A., 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management* 70, 145–157.
- Fuhlendorf, S.D., Engle, D.M., 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51, 625–632.
- Fuhlendorf, S.D., Engle, D.M., 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* 41, 604–614.
- Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., Leslie Jr., D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* 16, 1706–1716.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology* 9, 1425–1441.
- Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. *Conservation Biology* 16, 666–673.
- Hazler, K.R., 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. *Auk* 121, 707–716.
- Herkert, J.R., Reinking, D.L., Wiedenfeld, D.A., Winter, M., Zimmerman, J.L., Jensen, W.E., Finck, E.J., Koford, R.R., Wolfe, D.H., Sherrrod, S.K., Jenkins, M.A., Faaborg, J., Robinson, S.K., 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental US. *Conservation Biology* 17, 587–594.
- Hughes, J.P., Robel, R.J., Kemp, K.E., Zimmerman, J.L., 1999. Effects of habitat on Dickcissel abundance and nest success in conservation reserve program fields in Kansas. *Journal of Wildlife Management* 63, 523–529.
- Jensen, W.E., Cully Jr., J.F., 2005. Geographic variation in Brown-headed Cowbird (*Molothrus ater*) parasitism on Dickcissels (*Spiza americana*) in Great Plains tallgrass prairie. *Auk* 122, 648–660.
- Johnson, D.H., Schwartz, M.D., 1993. The conservation reserve program and grassland birds. *Conservation Biology* 7, 934–937.
- Knapp, A.K., Briggs, J.M., Hartnett, D.C., Collins, S.L. (Eds.), 1998. *Grassland Dynamics: Long-Term Research in Tallgrass Prairie*. Oxford University Press, New York.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. *Science* 298, 2202–2205.
- Knopf, F.L., 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15, 247–257.
- Lande, R., 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75, 601–607.
- Lanyon, W.E., 1995. Eastern Meadowlark. In: Poole, A. (Ed.), *The Birds of North America*. Academy of Natural Sciences, PA and American Ornithologists' Union, Washington, DC.
- Manolis, J.C., Andersen, D.E., Cuthbert, F.J., 2000. Uncertain nest fates in songbird studies and variation in mayfield estimation. *Auk* 117, 615–626.
- Martin, T.E., 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65, 101–127.
- McCoy, T.D., Ryan, M.R., Kurzejeski, E.W., Burger Jr., L.W., 1999. Conservation reserve program: source or sink habitat for grassland birds in Missouri? *Journal of Wildlife Management* 63, 530–538.
- National Audubon Society, 2004. State of the Birds, Watch List National Audubon Society, New York, NY. <<http://www.audubon.org/bird/stateofthebirds/grasslands.html>> (accessed 08.09.08).
- Ohlenbusch, P.D., Hartnett, D.C., 2000. Prescribed Burning as a Management Practice. Kansas State University Agricultural Experiment Station and Cooperative Research Extension Service L-815, Manhattan, Kansas. <<http://www.oznet.ksu.edu/library/crps12/l815.pdf>> (accessed 08.09.08).
- Patten, M.A., Shochat, E., Reinking, D.L., Wolfe, D.H., Sherrrod, S.K., 2006. Habitat edge, land management, and rates of brood parasitism in tallgrass prairie. *Ecological Applications* 16, 687–695.
- Patten, M.A., Shochat, E., Wolfe, D.H., Sherrrod, S.K., 2007. Lekking and nesting response of Greater Prairie-Chicken to burning of tallgrass prairie. *Proceedings of the Tall Timbers Fire Ecology Conference* 23, 149–155.
- Peterjohn, B.G., Sauer, J.R., 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966–1996. *Studies in Avian Biology* 19, 27–44.
- Pulliam, H.R., 1988. Sources, sinks, and population regulation. *American Naturalist* 132, 652–661.
- Rahmig, C.J., Jensen, W.E., With, K.A., in press. Grassland bird responses to land management in the largest remaining tallgrass prairie. *Conservation Biology*.
- Reynolds, R.E., Shaffer, T.L., Sauer, J.R., Peterjohn, B.G., 1994. Conservation Reserve Program: benefit for grassland birds in the Northern Plains. *Transactions of the North American Wildlife and Natural Resources Conference* 59, 328–336.
- Robel, R.J., Hughes, J.P., Hull, S.D., Kemp, K.E., Klute, D.S., 1998. Spring burning: resulting avian abundance and nesting in Kansas CRP. *Journal of Range Management* 51, 132–138.
- Robbins, M.B., Peterson, A.T., Ortega-Huerta, M.A., 2002. Major negative impacts of intensive-early cattle stocking on tallgrass

- prairies: the case of the Greater Prairie-chicken. *North American Birds* 56, 239–244.
- Robinson, S.K., Thompson III, F.R., Donovan, T.M., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267, 1987–1990.
- Samson, F., Knopf, F., 1994. Prairie conservation in North America. *BioScience* 44, 418–421.
- Shochat, E., Patten, M.A., Morris, D.W., Reinking, D.L., Wolfe, D.H., Sherrrod, S.K., 2005. Ecological traps in isodars: effects of tallgrass prairie management on bird nest survival. *Oikos* 111, 159–169.
- Schrott, G.R., With, K.A., King, A.W., 2005. On the importance of landscape history for assessing extinction risk. *Ecological Applications* 19, 493–506.
- Sillett, T.S., Holmes, R.T., 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71, 296–308.
- Smith, E.F., Owensby, C.E., 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills range. *Journal of Range Management* 31, 14–17.
- Suedkamp Wells, K.M., Ryan, M.R., Millspaugh, J.J., Thompson III, F.R., Hubbard, M.W., 2007. Survival of postfledging grassland birds in Missouri. *Condor* 109, 781–794.
- Temple, S.A., 2002. Dickcissel. In: Poole, A. (Ed.), *The Birds of North America*. Academy of Natural Sciences, PA and American Ornithologists' Union, Washington, DC.
- Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- Tittler, R., Fahrig, L., Villard, M.A., 2006. Evidence of large-scale source-sink dynamics and long-distance dispersal among Wood Thrush populations. *Ecology* 87, 2029–2036.
- Towne, G., Ohlenbusch, P.D., 1992. Native Hay Meadow Management. Kansas State University Agricultural Experiment Station and Cooperative Research Extension Service, MF-1042, Manhattan, Kansas. <<http://www.oznet.ksu.edu/library/crpls2/MF1042.pdf>> (accessed 08.09.08).
- United States Department of Agriculture, 2002. Census of Agriculture. USDA National Agricultural Statistics Service, Washington, DC. <http://www.nass.usda.gov/Census_of_Agriculture/index.asp> (accessed 08.09.08).
- Vickery, P.D., 1996. Grasshopper Sparrow. In: Poole, A. (Ed.), *The Birds of North America*. Academy of Natural Sciences, PA and American Ornithologists' Union, Washington, DC.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499.
- Waisanen, P.J., Bliss, N.B., 2002. Changes in population and agricultural land in conterminous United States counties, 1790 to 1997. *Global Biogeochemical Cycles* 16, 1137.
- White, R.P., Murray, S., Rohweder, M., 2000. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. World Resources Institute, Washington, DC. <http://pdf.wri.org/page_grasslands.pdf> (accessed 08.09.08).
- With, K.A., King, A.W., 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. *Biological Conservation* 100, 75–88.
- With, K.A., Schrott, G.R., King, A.W., 2006. The implications of metalandscape connectivity for population viability in migratory songbirds. *Landscape Ecology* 21, 157–167.
- Zimmerman, J.L., 1993. *The Birds of Konza Prairie: The Avian Ecology of the Tallgrass Prairie*. University of Kansas Press, Lawrence, Kansas.
- Zimmerman, J.L., 1997. Avian community responses to fire, grazing, and drought in the tallgrass prairie. In: Knopf, F., Samson, F.B. (Eds.), *Ecology and Conservation of Great Plains Vertebrates*. Springer-Verlag, New York, pp. 167–180.