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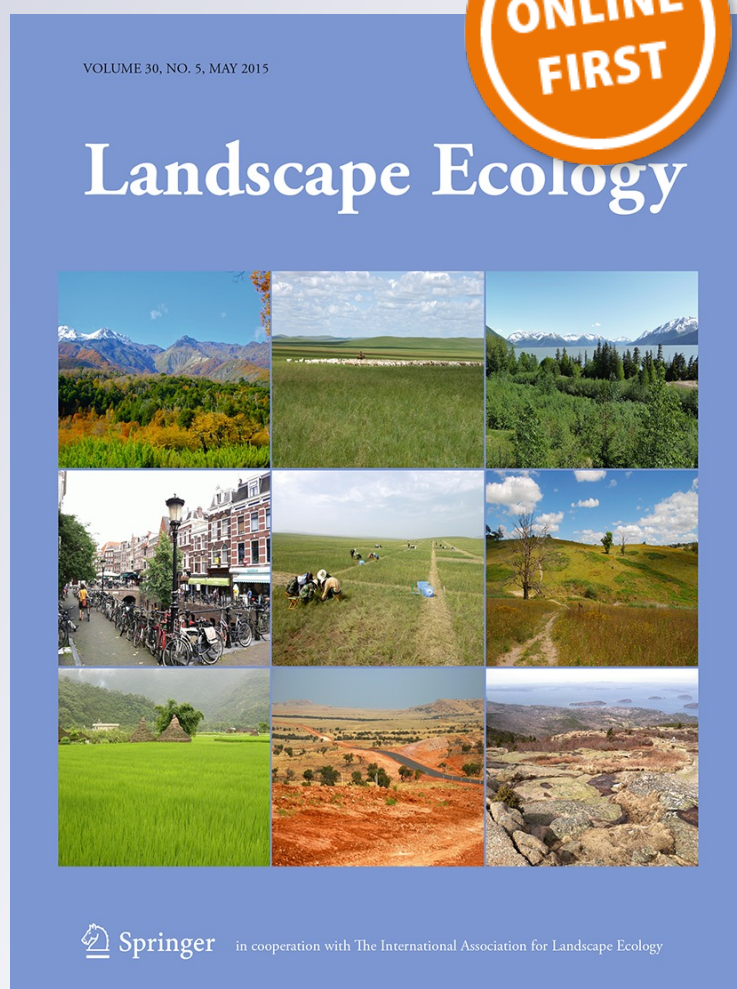
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The importance of range edges for an irruptive species during extreme weather events

Brooke L. Bateman  · Anna M. Pidgeon · Volker C. Radeloff · Andrew J. Allstadt · H. Resit Akçakaya · Wayne E. Thogmartin · Stephen J. Vavrus · Patricia J. Heglund

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Abstract

Context Threats to wildlife species from extreme events, such as droughts, are predicted to increase in frequency and magnitude with climate change. Extreme events can cause mortality and community-level changes, but for some mobile species, movement away from areas affected may be a viable option.

Objectives We examined the effect of extreme weather on spatial patterns of abundance for an irruptive grassland bird species, the Dickcissel (*Spiza americana*).

Methods We calculated route-level annual abundances and abundance anomalies from 1980 to 2012 from North American Breeding Bird Survey data, and classified the Dickcissel's range into core and edge regions using these abundances. We then compared

abundances in the core and edge regions to the standardized precipitation evapotranspiration index, a measure of drought, in linear regressions.

Results We found that Dickcissel irruptions in the northern range edges were related to drought conditions in the range core, potentially a consequence of birds being 'pushed' to the range edge when weather was unsuitable. Specifically, Dickcissels moved into refuge sites containing a high proportion of cultivated crops, with higher vegetation greenness, than those areas they leave during drought years.

Conclusions In a changing climate where more frequent extreme weather may be more common, conservation strategies for weather-sensitive species may require consideration of habitat in the edges of species' ranges, even though non-core areas may be unoccupied in 'normal' years. Our results highlight the conservation importance of range edges in providing refuge from extreme events, such as drought, and climate change.

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B. L. Bateman (✉) · A. M. Pidgeon · V. C. Radeloff · A. J. Allstadt
SILVIS Lab, Department of Forest and Wildlife Ecology,
University of Wisconsin-Madison, Madison, WI, USA
e-mail: brooke.bateman@gmail.com

H. Resit Akçakaya
Department of Ecology and Evolution, Stony Brook
University, Stony Brook, NY, USA

W. E. Thogmartin
Upper Midwest Environmental Sciences Center, United
States Geological Survey, La Crosse, WI, USA

S. J. Vavrus
Center for Climate Research, University of Wisconsin-
Madison, Madison, WI, USA

P. J. Heglund
Upper Midwest Environmental Sciences Center, United
States Fish and Wildlife Service, La Crosse, WI, USA

Keywords Drought · Extreme weather · Grassland birds · Range edge · Range core · Refuges

Introduction

Numerous species across many taxa are responding to recent changes in climate, shifting their ranges towards the poles and higher altitudes (Thomas and Lennon 1999; Parmesan and Yohe 2003; Root et al. 2003; Hitch and Leberg 2007; Chen et al. 2011). However, short-term processes such as climate variability or extreme weather events are likely to have immediate consequences for organisms (Thompson et al. 2013). These short-term climate and weather conditions can have a strong influence on overall population persistence (Gutschick and BassiriRad 2003; Bateman et al. 2012b; Thompson et al. 2013) and affect species' population dynamics and spatial distribution (Parmesan et al. 2000; Jentsch et al. 2007; Jentsch and Beierkuhnlein 2008). However, the effects of extreme weather on species at broad scales are not well understood. How these events influence species occurrence and persistence throughout the landscape is of particular concern for conservation planners.

Climate change projections forecast increasing mean temperatures, and also a more variable climate causing an increase in the frequency and magnitude of extreme weather events (Räisänen 2002; Salinger 2005; Jentsch et al. 2007; Rummukainen 2012; Goodess 2013). This heightened variability may include multi-year droughts, increased regional variability in weather patterns, and short-term extreme weather events such as weeklong heat waves, single-day high rainfall events, and spring cold snaps (IPCC 2007; Kunkel et al. 2008; Rahmstorf and Coumou 2011; Coumou and Rahmstorf 2012; IPCC 2012). Insights into both the role of changes in climate (e.g. long-term means) and of that of short-term variability (e.g., extreme weather) can provide a more complete picture of how climate change affects bird species.

For North America, a strong increase in the frequency and severity of widespread droughts is predicted (Wehner et al. 2011; Dai 2013). Species responses to such extreme events may occur locally, where changes may be reflected in adult survival or reproductive success or even cause population-level extirpations (Cormont et al. 2011; Bateman et al.

2012b). Extreme weather can also cause changes in abundance, and ultimately communities (Thibault and Brown 2008; Albright et al. 2010a, b). Whether these abundance changes reflect movement or mortality is difficult to determine because weather events can have different effects on different species, depending on their life history traits (Jiguet et al. 2006; Albright et al. 2011; Cormont et al. 2011). For highly mobile species, such as most birds, movement away from threat during extreme events may be a viable response, even in the case of species that normally exhibit high site fidelity (Martin et al. 2007). Movement may be an especially effective response for slowly evolving extreme events, such as droughts. Highly mobile bird species could thus have an advantage during extreme conditions because they can move away from adversely affected areas.

Individuals that do move in response to extremes must decide not just *when* but also *where* to go (Dean et al. 2009). The 'push-pull' hypothesis, originally developed to explain human migration (Fuguitt 1959), provides a useful framework to conceptualize the responses of mobile species to extreme weather. Movement of a species outside of its core range could be caused either by 'push' factors, with individuals dispersing in response to poor conditions within their core range, or by 'pull' factors that attract individuals into areas of better conditions, or by both. In migratory birds, the processes involved in the 'push-pull' hypothesis can be seen during molt-migration, a phenomenon in which birds molt at a location in between their breeding and wintering range. This is where poor weather conditions causing low productivity on the breeding grounds appear to 'push' birds out, leading to a staged migration as birds are 'pulled' to areas with better productivity (Barry et al. 2009; Fox and Walsh 2012). Movement of species that require resources or habitats that are especially dependent on suitable weather conditions, such as seasonal or semi-permanent water sources, may respond more to 'push' pressures by moving away from sub-optimal conditions. Such 'push' pressures have been suggested as a mechanism for post-spring-migratory movement in relation to weather and extreme events in songbirds (Albright et al. 2010b) and waterfowl (Smith 1970; van Wijk et al. 2012). When 'push' pressures occur, birds may be pushed across large areas, especially when the pressures themselves are widespread. Alternatively, species may

concentrate in areas of higher-quality habitat within a matrix of lower quality habitat. For example, Snail Kites (*Rostrhamus sociabilis*) concentrate in 'refuge' areas that have better water conditions than the surroundings (Martin et al. 2007). To best conserve species facing extreme weather events, it is necessary to identify conditions 'pushing' species, and, more importantly, to identify the refuge sites to which individuals move.

Irruptive species, which exhibit high variability in abundance and spatial distribution, are ideal organisms to test the 'push-pull' hypothesis in connection to their response to extreme conditions. Irruptive species irregularly occur in large numbers outside of their normal range, moving vast distances into new habitats (Koenig 2001; Koenig and Knops 2001). The Dickcissel (*Spiza americana*) is a classic example of an irruptive species (Sealy 1976). It is a member of the grassland bird assemblage breeding in the U.S., an assemblage that has experienced dramatic declines in recent years (Peterjohn and Sauer 1999). As a Neotropical migrant, the Dickcissel is highly mobile and capable of moving long distances, and as a species, it is remarkably opportunistic in its habitat use (Sealy 1976). Although the Dickcissel displays some measure of site fidelity in the core of its range, the species is known for exhibiting high inter-annual variability in occurrence and abundance at the edge of its range (Temple 2002). The Dickcissel is strongly density-dependent (Zimmerman 1971) and thus, when the most suitable habitat is occupied, individuals without territories seek suitable habitat in other locations (Sealy 1976). In addition, nesting females are more likely to disperse after nest failure because of poor conditions than when habitat conditions are average to good (Walk et al. 2004). Movement outside of core breeding range by both male and females, especially later in the season, can be a response to poor conditions.

These irruptions may be linked to both land use changes and adverse weather (Temple 2002), and many have speculated that drought conditions in the species core range are a key factor (Wooster 1935; Taber 1947; Emlen and Wiens 1965; Igl 1991; Temple 2002; Post et al. 2009; Prestby and Anich 2013). Irruptions on the northern range edge have been noted when drought conditions occurred elsewhere in the species' range. Irruption events of Dickcissels have been documented for over 80 years. In the early

1930s, Dickcissel irruptions in the northern range edge (e.g. southern Wisconsin) coincided with the dustbowl drought years (Taber 1947), and Dickcissels simultaneously became scarce in the range core (i.e., Kansas) where this species is commonly abundant during non-drought periods (Wooster 1935). In 1964, a Dickcissel irruption in Wisconsin included an increase in density of up to 50-fold (Emlen and Wiens 1965). Movement of individuals towards the northern range edge was also apparent in association with the 1988, 2006 and 2012 droughts (Prestby and Anich 2013), further evidence for the link between drought in the core of the species range and irruptions outward from the core. In the 1988 drought, Dickcissel abundance on the range edge areas of southwest Wisconsin was positively related to drier April soil moisture conditions in southwest Iowa, where the species is common in most years (Igl 1991). This may indicate that irruptions on the northern range edge are linked to spring conditions in the core and southern portions of its breeding range, and that precipitation may play a key role in Dickcissel habitat quality (Fretwell 1986; Igl 1991). Thus, Dickcissel irruptions in the range edge may be seen as a drought displacement (facultative) migration, in which long-distance movement outweighs the risk of staying on the core breeding grounds where conditions are poor (Igl 1991).

Although there is qualitative evidence that drought plays a key role in Dickcissel irruptions, no study has explicitly studied the relationship between Dickcissel irruptions and drought conditions in a quantitative framework across the entire range. Our goal was to examine how irruptions in the abundance of Dickcissels are related to drought. Specifically we asked the following questions:

- (1) How does drought affect abundance patterns of Dickcissels;
- (2) Does drought in the species' core range 'push' individuals to move elsewhere;
- (3) If so, are there specific regions (refuges) to which individuals move during the drought, and within these regions are there specific characteristics of sites used as refuges by the Dickcissel?

We tested the hypothesis that during extreme drought, Dickcissels abundance patterns are altered, and that individual birds are 'pushed' out of the core range in search of better habitat conditions. We

expected to find that regions with wetter conditions serve as refuge during droughts, and that specific sites that ‘gain’ individuals contain high percentages of grassland landcover.

Methods

Bird data

We obtained Dickcissel abundance data from the North American Breeding Bird Survey (BBS; Sauer et al. 2012) for 1980–2012 ($t = 33$). The BBS is an annual bird survey conducted during the breeding season on routes that are ~ 39.4 km long and located on secondary roads throughout the conterminous United States and parts of Canada (Pidgeon et al. 2007). Some routes have been added or dropped over time, so for consistency, we included only routes that were run in 22 or more ($>2/3$) years of our study. We calculated raw abundance per route per year, defined as the total number of Dickcissels detected along the route in that year.

To identify the core breeding range of the Dickcissel, we calculated mean proportional abundance, i.e., the average abundance on a given route across all years relative to the number of Dickcissels observed on all routes and all years $\left(\frac{\sum_{1980}^{2012} x}{33} / \left(\sum_{i=1}^n \frac{\sum_{1980}^{2012} x}{33} \right) \right)$, where n was the number of routes and x was the observed count. We defined core range as routes with mean proportional abundance values above or equal to the median, and edge range as routes with mean proportional abundance below the median among routes, which was 3.37 Dickcissels/route/year (Fig. 1). Based on this definition, in the core range, there were on average 33.89 Dickcissels/route/year while in the edge range, there were on average 0.78 Dickcissels/route/year over our time period. Lastly, we selected 95°E longitude as the dividing line between northeast and northwest edge of range, based on initial results indicating that drought responses varied in East–West direction.

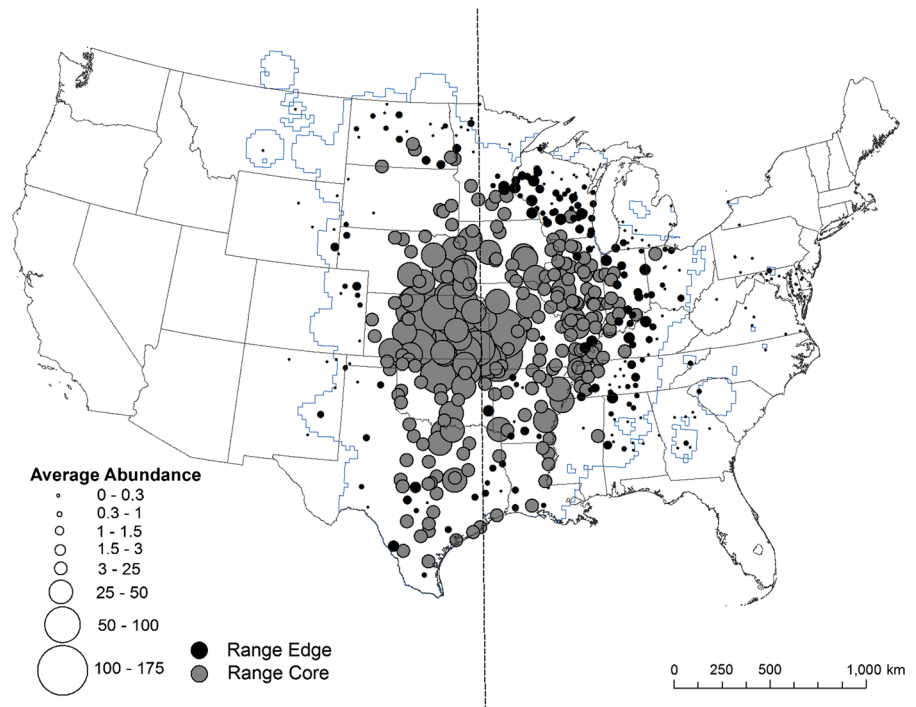
To assess the effect of drought on Dickcissel abundance across the species’ range, we calculated the raw anomaly in abundance for each year from the

long-term average abundance $\left(x_i - x \right)$, where positive measures indicated higher-than-average abundance, and negative numbers indicated lower-than-average abundance. Abundance anomalies can indicate movement when, for example, a low abundance anomaly in one location is associated with a high abundance anomaly elsewhere (Taylor and Taylor 1977; Taylor et al. 1983). We calculated the raw abundance anomaly for each BBS route, as well as an overall measure of raw abundance anomalies for the core of the species range and its northeastern and northwestern range edges. We also calculated the absolute anomaly in abundance for each year, i.e., the absolute annual deviance in abundance from the long-term average abundance for each route, and then summed this across the entire range $\left(\sum_{i=1}^n (|x_i - x|) \right)$, where x is the denominator of the previous equation. This provided a measure of overall change in abundance from normal for a given year, regardless of whether this change was positive or negative.

Extreme weather data

Climate conditions vary widely over the large range of the Dickcissel, making absolute measures of drought difficult to compare among locations. However, standardized indices, like the standardized precipitation evapotranspiration index (SPEI), measure deviation from local climatic conditions and can therefore be compared over large areas (McKee et al. 1993; Vicente-Serrano et al. 2010). SPEI models local water availability as the difference between total precipitation and atmospheric demand for moisture, or potential evapotranspiration (PET) (Beguería et al. 2014). For our study, the SPEI has two main advantages over other drought measures. First, the SPEI can be calculated for a specific time window within each year, in our case the Dickcissel breeding season, while the better-known Palmer Drought Severity Index is calculated continuously and has an implicit 9–12 month timescale (Guttman 1998). Second, because PET calculations incorporate temperature (Allen et al. 1998), SPEI may be better suited to study drought under climate change than precipitation-only indices (Beguería et al. 2010; Vicente-Serrano et al. 2010).

Fig. 1 Dickcissel range core (grey) and range edge (black) mean proportional abundance for the period 1980–2012. Each circle represents the long-term mean proportional abundance for that BBS route. Average abundance of Dickcissels (1980–2012) of 1, 10 and 50 individuals on a route with coincide with a given mean proportional abundance value). The dotted line represents the 95°E longitude as the dividing line between northeast and northwest edge of range. Summer breeding distribution map is superimposed as a blue polygon (from Sauer et al. 2012)



SPEI calculation begins with the selection of a time window of interest within each year, e.g., May–July. At each location, the total precipitation deficit during this time period is calculated for each year. An appropriate statistical distribution is fit to these yearly totals, and the yearly values are converted into percentiles from this distribution. Finally, these yearly percentiles are converted into standard deviations from a standard normal distribution, which users are familiar with and which have desirable statistical qualities. These final SPEI values in our example represent the deviation of May–July water availability in that year relative to normal conditions at that location, with negative deviations indicating drier conditions (Vicente-Serrano et al. 2010).

Our SPEI calculations were based on precipitation and potential evapotranspiration totals from the North American Land Data Assimilation System-2 (NLDAS-2) forcing dataset from 1980–2012. The NLDAS-2 dataset incorporates land-surface models, remote sensing products, and weather station data into a 1/8th degree (~ 12 km), gridded product covering the contiguous US and portions of Canada, northern Mexico, and the Caribbean (Mitchell et al. 2004). For each grid cell, we calculated SPEI for the 90-day

period from May–July, encompassing the Dickcissel breeding season. We used a generalized-logistic distribution in our calculations because we found that it fit our data better than the log-logistic distribution used in Vicente-Serrano et al. (2010). For each year from 1980 to 2012, we extracted summer SPEI data for each BBS route (summer SPEI value of the grid cell overlapping the center of a BBS route), and averaged these values for the entire Dickcissel range to determine the mean summer SPEI for all routes where Dickcissels had ever been recorded. We also calculated the average SPEI value for BBS routes within the core Dickcissel range.

In addition to SPEI, we also tested both the standardized precipitation index (SPI) (McKee et al. 1993), and a standardized temperature anomaly as potential predictors of irruptions in Dickcissel abundances. SPEI clearly had the strongest relationship with abundance anomalies, so we present only those results here.

Analysis

Our first objective was to determine the effect of extreme drought on Dickcissel abundance across the

entire species' range. To do this, we fit a linear regression model of 1980–2012 annual Dickcissel absolute abundance anomalies (summed across all routes) as a function of mean summer SPEI in the Dickcissel range as the sole parameter. We only included SPEI in these analysis because we were interested in short-term (1 year) variation in Dickcissel abundance (i.e., irruptions). Other processes cause longer term changes in abundance, and therefore we did not include potential covariates such as land cover. Land cover is a key variable in explaining distribution patterns of bird species that have strong habitat affiliations such as Dickcissels, especially long-term abundance trends in areas where landcover changed gradually, or where a permanent change in abundance (e.g. high for several years, then declining after conversion) is related to a permanent change in landcover. However, landcover data for the conterminous U.S. is not available for our entire study period. Therefore we left landcover out of initial models, and examined landcover on BBS routes post hoc (see below).

Our second objective was to determine if irruptions in range edges were related to a 'push' from drought in the species' core. We parameterized linear regression models of 1980–2012 raw abundance anomaly within the northern range edges (northeastern and northwestern edges analyzed separately) as a function of summer SPEI in core BBS route locations. We then repeated the same regression, this time for each individual BBS route over the same time frame. We assessed R^2 values, the slopes of the two regression lines, and F test scores and their p values to determine if irruptions were related to drought in the range core. Because neither SPEI nor abundance anomalies were bounded at zero, negative values for each indicate below-average values (drought for SPEI, and fewer than average individuals), and positive values indicate above-average values. In the regression this means that if increases in abundance (positive anomaly) co-occurred with drought conditions in the core range (negative anomaly), then the slope of the regression line would be negative. On the other hand, if a decline in abundance (negative anomaly) co-occurred with drought conditions in the core range (negative anomaly), then the slope of the regression line would be positive. Individual routes with a positive regression slope therefore represent a 'loss' of individuals during

drought, and routes with negative regression slope represent a 'gain' of individuals during drought.

We conducted a sensitivity analysis of our regression analysis to determine if the results were robust to the break point that we selected to define core and edge range. To do this, we sequentially changed the core and edge breakpoint from our initial definition of the median mean proportional abundance to 25th, 62.5th, and the 75th percentiles, and then repeated the linear regression models of abundance in the northern range edge as predicted by summer SPI in the core, under each of these definitions.

We also quantified the percent population change in relation to the long-term average for each year in the range edge, and calculated population centroids for each year to characterize the shift in Dickcissel abundance in normal and drought years. To calculate population centroids, we applied the center of gravity (COGravity, or COG) function in the R package, *SDMTools* (<http://cran.r-project.org/web/packages/SDMTools/>). As our spatial weighting measure we used annual abundance values on each BBS route that met our criteria for inclusion in the analysis, i.e., those on which Dickcissels occurred in at least 2/3 of the years that we analyzed, from 1980 to 2012.

Our third objective was to determine which locations were favored by Dickcissels during drought events. To do this, we assessed individual BBS routes to identify which routes had high Dickcissel abundance (i.e., experienced 'gain') only during extreme drought, potentially serving as refuges. Finally, we post hoc selected 3 years, 1988, 2006 and 2012, to highlight how extreme drought within the core range related to changes in abundance per route.

To examine the characteristics of routes which act as refuges during drought related irruption years in further detail, we obtained landcover and measures of habitat heterogeneity (image texture), for Dickcissel habitat on BBS routes (Culbert et al. 2012, 2013). Landcover variables included proportion of landcover (from National Landcover Database (NLCD) 2001; Vogelmann et al. 2001; Homer et al. 2007) of grassland, pasture, cultivated crops, and the sum of all of these classes, the area of grassland core and edge habitat. Image texture measures represent the heterogeneity of the reflectance values in a remotely sensed image, and are well suited to capture vegetation variability and structure (Harlick et al. 1973; St-Louis

et al. 2006; Bellis et al. 2008). Texture measures were derived from Landsat TM/ETM+ satellite imagery and included first order mean of each of the spectral bands 2–5 calculated in a 5×5 moving window across the study area, and second order entropy, also calculated for each of bands 2–5 in a moving window (Baraldi and Parmiggiani 1995; Bellis et al. 2008). Bands 2–5 are useful for distinguishing various aspects of vegetation because of the differences in how they reflect irradiative energy. Band 2 senses green light (wavelength 0.52–0.60) and is related to plant vigor, Band 3 is red (wavelength 0.63–0.69) and discriminates chlorophyll absorption among different species and dead foliage, Band 4 senses Near Infrared (NIR; wavelength 0.77–0.90) and represents vegetation biomass, and Band 5 is Short-wave Infrared (SWIR-1; wavelength 1.55–1.75) and discriminates soil and vegetation moisture. Mean texture represents the average reflectance values for a given 5×5 window, without accounting for spatial arrangement of pixels (Baraldi and Parmiggiani 1995; Bellis et al. 2008). Entropy represents the disorder of an image and takes into account the spatial relationship of pixels within a 5×5 pixel window, and characterizes variation in vegetation structure (Bellis et al. 2008). Therefore, mean texture values for each band provide an estimate of the average reflectance within a given spectral band within an analysis window, whereas entropy identifies the degree of spatial heterogeneity in reflectance of a band for a given area. We chose these image texture variables because they have been found to characterize bird habitat in other ecosystems with a variety of herbaceous and woody cover types (e.g., St-Louis et al. 2006; Bellis et al. 2008; Wood et al. 2013).

We summarized landcover proportion and image texture variables within a 19.7 km circle surrounding each BBS route centroid. We chose this radius because it ensures that the entire BBS route is included, regardless of route path, and a circle has the advantage that it is of uniform area and shape, and is commonly used studies linking BBS data to landcover (e.g., Flather and Sauer 1996; Pidgeon et al. 2007; Culbert et al. 2013; Pidgeon et al. 2014). We also calculated SPEI of the 2012 drought year for each route separately. We included these data for all routes on which Dickcissels occurred in at least 2/3 of years between 1980 and 2012. We compared landcover data on core versus edge routes, as well routes that showed

overall ‘gain’ or ‘loss’ (based on regression results) of Dickcissels during drought for the entire study period (1980–2012). In addition, for the year 2012, we inspected the proportion of landcover type on each route that gained or lost Dickcissels relative to 2011.

Results

The core of Dickcissel range throughout our study period (1980–2012) was centered on Kansas (Fig. 1). We found a significant negative relationship between the absolute Dickcissel abundance anomaly and summer SPEI over the entire range [$R^2 = 0.19$, $F_{1,31} = 7.04$, p value = 0.01, slope = -0.42 ± 0.16 SE (95 % CI [-0.75, -0.10]); Fig. 2]. We also found greater deviance from average abundance, that is larger differences from normal abundances across all routes, when drought conditions were experienced throughout the species’ range.

We found significant negative relationships between Dickcissel abundance anomalies in the northern edge of the range and SPEI in the range core. This pattern was similar for the northwest range edge [$R^2 = 0.43$, $F_{1,31} = 23.64$, p value ≤ 0.0001 , Slope = -0.92 ± 0.19 SE (95 % CI [-1.30, -0.53]); Fig. 3a] and the northeast range edge [$R^2 = 0.49$, $F_{1,31} = 29.16$, p value ≤ 0.0001 , Slope = -0.88 ± 0.16 SE (95 % CI [-1.22, -0.55]); Fig. 3b], with both exhibiting clear negative relationships between SPEI and Dickcissel abundance. That is, when the range core experienced a drought, Dickcissel abundance was anomalously high in the northern range edges (i.e., an irruption).

The sensitivity analysis showed that the relationship between abundance anomalies in the edge of range to SPEI in the core of range was robust to different definitions of the code/edge regions. The same relationship was found when the core of range was defined as the top 75 % of routes by abundance [e.g. 25 % of routes were in edge range; $R^2 = 0.49$, $F_{1,31} = 32.51$, p value ≤ 0.0001 , Slope = -0.70 ± 0.12 SE (95 % CI [-0.95, -0.45])] and the top 50 % of abundance [e.g. 50 % edge or the median; $R^2 = 0.47$, $F_{1,31} = 30.57$, p value ≤ 0.0001 , Slope = -0.63 ± 0.12 SE (95 % CI [-0.87, -0.40])]. However, the relationship began to degrade as the number of routes in the edge exceeded the number in the core: 62.5 % edge routes [$R^2 = 0.31$, $F_{1,31} = 15.86$, p value = 0.0004, Slope = -0.66 ± 0.17 SE (95 % CI [-0.99, -0.32])] and 75 % edge

Fig. 2 Relationship between Dickcissel abundance anomaly and summer SPEI across entire range between 1980 and 2012. Abundance anomaly here indicates the absolute value of change from normal in a given year, regardless if change was a loss or a gain in individuals

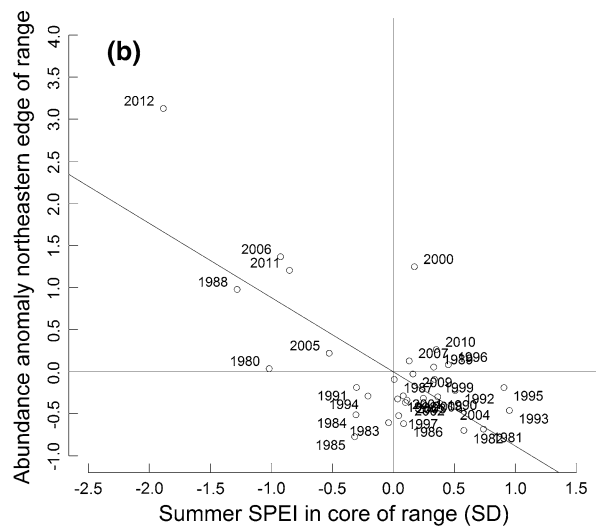
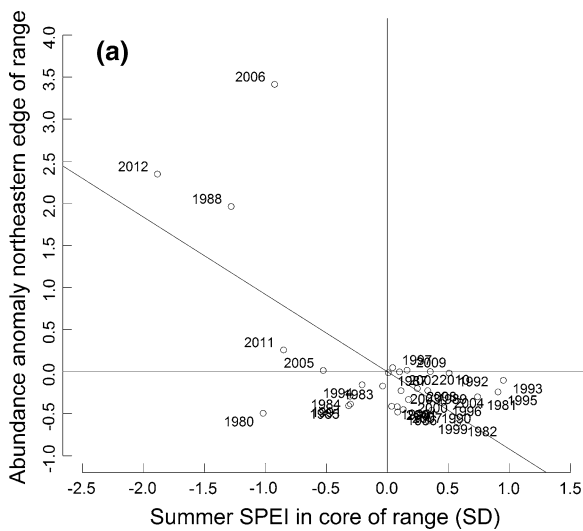
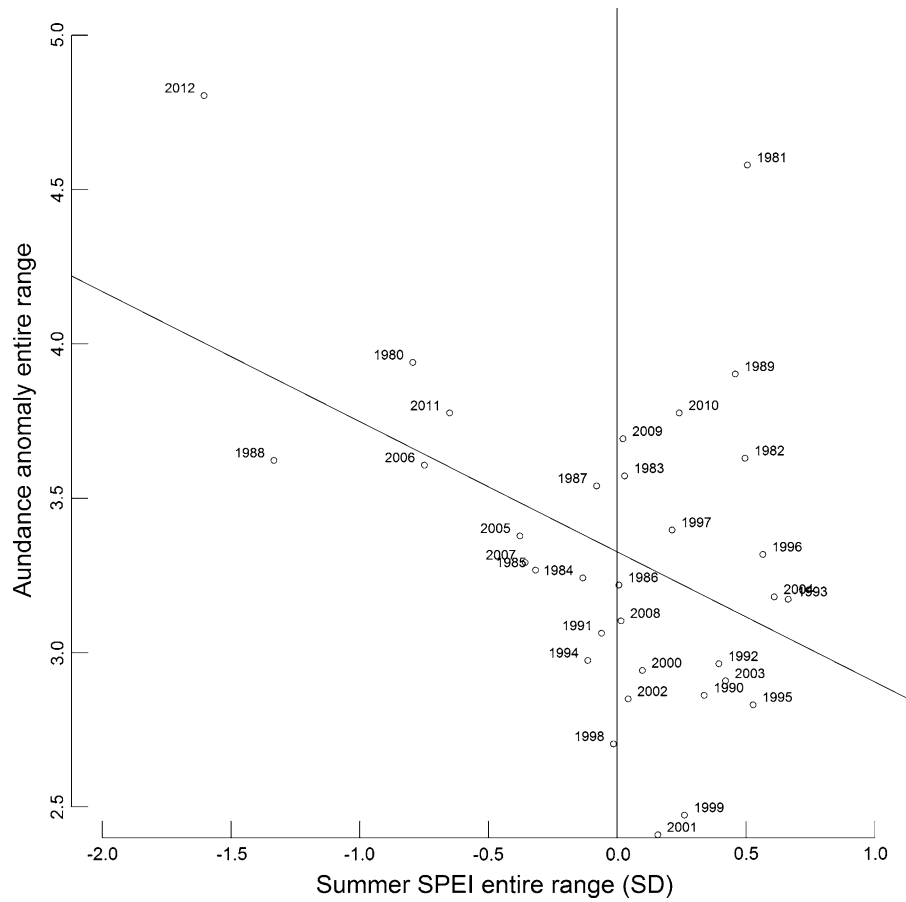


Fig. 3 Relationship between Dickcissel abundance anomaly **a** in the northwestern range edge and summer SPEI in the range core and **b** in the northeastern range edge and summer SPEI in

the range core between 1980 and 2012. Abundance anomaly here indicates the raw value of change from normal in a given year, indicating change was a loss or a gain in individuals

routes [$R^2 = 0.18$, $F_{1,31} = 8.28$, p value = 0.007, Slope = -0.57 ± 0.20 SE (95 % CI [-0.97, -0.17])].

Dickcissel mean abundance for the study period averaged across all BBS routes in the edge of the species' range was 0.78 individuals per route, with large increases in percent change of the BBS route population in the drought years of 1988 (~100 % change, increase to 1.5 individuals per BBS route), 2006 (~150 % change, increase to 2 individuals per BBS route), 2011 (~100 % change, increase of 1.5 individuals per BBS route) and—in particular—2012 (~300 % change, increase to 3 individuals per BBS route; Table S1). The analysis of population centroids in each year revealed a northeasterly shift in abundance during drought years, which is most notable in years with stronger droughts (Fig. S1).

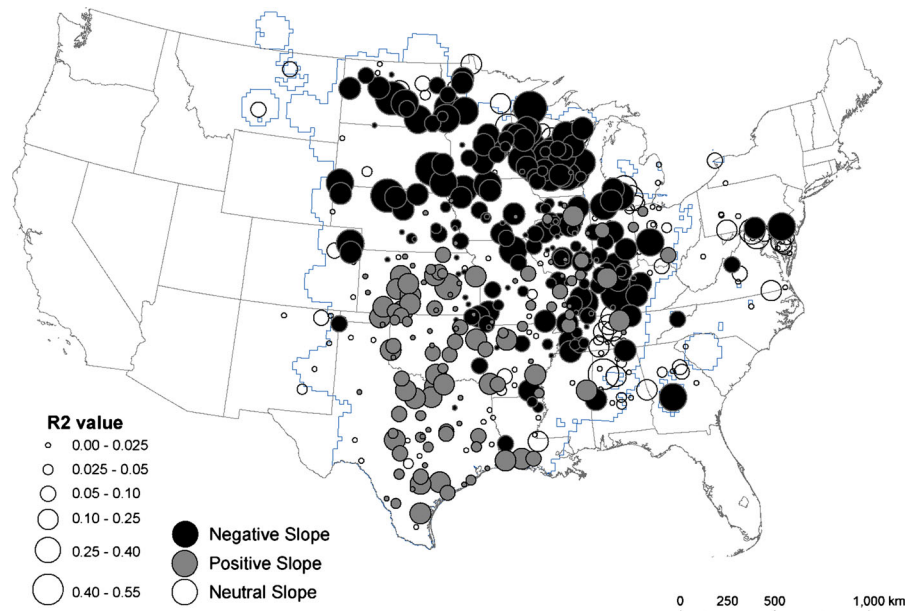
Route-level regressions also showed that, for the majority of routes, when the core range experienced drought, Dickcissel abundance was anomalously high in the northern range edge and anomalously low in the range core (Fig. 4). In 2012, BBS routes within the range core generally experienced lower abundance, while routes in the northern range edge experienced greater abundance than average (Fig. 5). We identified individual routes that consistently had positive abundance anomalies during drought within the range core for the entire study period (Fig. 4), and for specific years (e.g., Fig. 5, S2, S3). Across all drought years,

individual routes north of the breeding range core in states including Nebraska, North Dakota, South Dakota, Iowa, Minnesota and Wisconsin were important for the Dickcissel. Eastern states such as Illinois, Indiana and Kentucky also contained important routes, though in lower density than states north of the breeding range core. There were interesting differences among specific years of extreme droughts (1988, 2006, and 2012) though, when different edge routes were important during extreme conditions in the core (Figs. 5, S2, S3). In the severe drought of 2012, northern routes in South Dakota, Iowa, Wisconsin and Illinois experienced the highest gains in abundance relative to the 32-year average. In 1988 the pattern was similar (Fig. S2), while in 2006 the abundance gains were more broadly spread across northern BBS routes, including routes in western-most North Dakota (Fig. S3).

Landcover around core BBS routes had a higher percentage of grassland and agriculture (16 and 40 % respectively) than routes in the edge of the range (9 and 23 % respectively, Table 1a). However, during drought years birds left grassland areas and moved to locations with a high percentage of cultivated crops (Table 1a) in edge habitat. The areas experiencing a loss of Dickcissels had more core grassland habitat than areas that gained Dickcissels during drought (17 vs. 9 %).

Mean reflectance values of most Landsat bands were higher in areas that lost Dickcissels, with the exception of band 4, which is related to vegetation

Fig. 4 Dickcissel abundance anomaly versus summer SPEI in core of range for each BBS route between 1980 and 2012 (All routes). Circle size is related to R^2 value, with larger circles indicating stronger associations. Greyscale colors indicate the nature of the relationships, as indicated by the slope of the regression line [black negative slope, grey positive slope, open neutral (slope between -0.5 and 0.5)]. Summer breeding distribution map is superimposed as a blue polygon



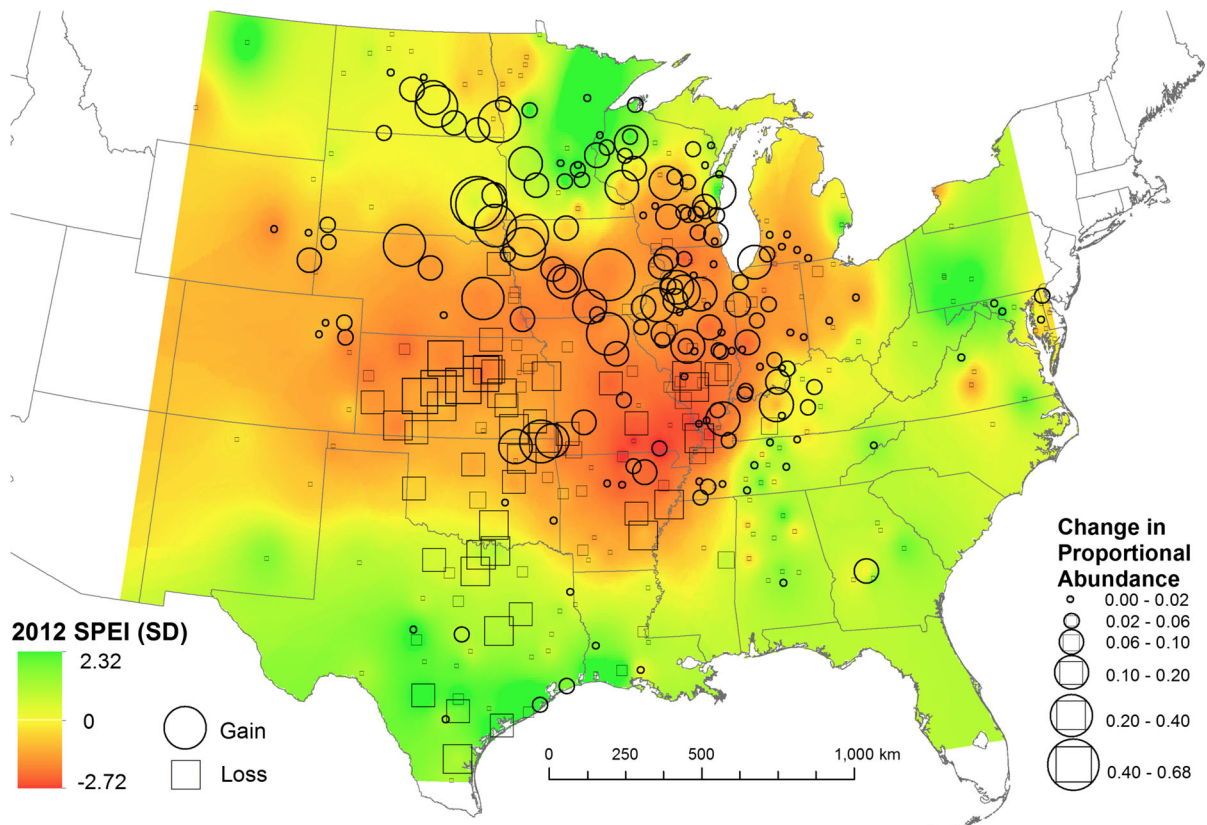


Fig. 5 Difference in 2012 Dickcissel abundance from the mean proportional abundance (1980–2012) for each BBS route, superimposed on the 2012 standardized precipitation evapotranspiration index. *Circles* represent greater abundance than mean, and *squares* represent lower abundance than the mean. The size

of *circle* or *square* indicates the relative size of the anomaly (i.e., the difference between 2012 route proportional abundance and the study-long mean proportional abundance value for that route). Summer breeding distribution map is superimposed as a *blue* polygon

biomass; and which had higher reflectance in the vicinity of routes that gained birds during drought (Table 1c). Areas that gained Dickcissels also appear to have had less standing dead vegetation than areas they left, as indicated by lower mean value of B3, (Table 1c). Areas experiencing a gain in Dickcissels contained habitat with more patchily distributed biomass (as indicated by entropy of B4; Table 1d). When looking at the single-year 2012 drought, we found that areas that gained Dickcissels also had a high proportion of cultivated crops compared to areas where Dickcissels were lost (Table 2).

Discussion

Our results indicate that drought plays an important role in shaping short-term changes in the spatial

distribution of Dickcissel populations. Dickcissel abundance varied greatly among years, and we found large abundance anomalies in years when core BBS route locations experienced drought conditions. Drought appears to have acted as a ‘push’ factor causing the Dickcissel population to become more dispersed, and this may be a major factor causing Dickcissel irruptions in range edges. Our findings support those of others that have found that species distributions, and particularly their range edges, are strongly affected by climate (Hardie and Hutchings 2010, for various taxa; Jiménez-Valverde et al. 2011, for birds).

Typically, range edges occur at or near a species’ physiological tolerance to environmental conditions, and that means living in peripheries is more physiologically stressful than living in the range core (Parmesan et al. 2000; Thuiller et al. 2008; Brook et al.

Table 1 Summary of landcover and image texture values within 19.7 km of each BBS route included in analysis

Landcover	Grassland	Pasture	Cultivated crops	Combination
(a)				
Core	0.16	0.12	0.40	0.68
Edge	0.09	0.13	0.23	0.46
Gain	0.08	0.14	0.41	0.63
Loss	0.24	0.12	0.27	0.62
All routes	0.13	0.13	0.31	0.57
Landcover; average		Core grassland		Edge grassland
(b)				
Gain		0.09		0.13
Loss		0.17		0.19
All routes		0.11		0.15
Mean texture; first order				
	B2	B3	B4	B5
(c)				
Gain	618	588	2990	2114
Loss	745	804	2794	2475
All routes	652	652	2879	2185
Entropy texture, second order				
	B2	B3	B4	B5
(d)				
Gain	3.38	3.45	3.63	3.57
Loss	3.47	3.64	3.39	3.69
All routes	3.4	3.49	3.54	3.61

Landcover combination is defined as the summed proportion of grassland, pasture and cultivated crop landcover. B2, B3, B4, and B5 represent Bands 2–5 in Landsat TM/ETM+ image. Band 2 is associated with vegetation vigor, Band 3 discriminates standing dead foliage, Band 4 is associated with vegetation biomass, and Band 5 is associated with soil and vegetation moisture, and may aid discrimination among vegetation types. ‘Gain’ and ‘loss’ are defined based on individual route regressions, with a gain in individuals occurring with a positive abundance anomaly and a loss with a negative abundance anomaly with drought in the core

(a) proportion of landcover in Grassland, Pasture or Cultivated Crops from NLCD 2001 (Vogelmann et al. 2001; Homer et al. 2007) on core and edge routes, as well as on routes that gained or lost Dickcissel abundance

(b) The grand averages for proportion of core habitat and edge habitat in grasslands, on routes that gained or lost Dickcissel abundance (including only routes on which Dickcissels occurred in 2/3rd of years 1980–2012). Image texture variables derived from remotely sensed data are also given

(c) First order mean

(d) Second order entropy

Table 2 Landcover and SPEI values in 2012, an extreme drought year

	Grassland	Pasture	Cultivated Crops	Combination	2012 SPEI
Gain	0.08	0.14	0.38	0.60	−1.65
Loss	0.21	0.15	0.20	0.57	−1.4

Average proportion of Dickcissel habitat (Grassland, Pasture or Cultivated Crops from NLCD 2001) within 19.7 km radius circle around the centroid BBS routes that gained or lost Dickcissel abundance for the 2012 drought year

2009). Peripheral habitats generally contain fewer individuals (Brown et al. 1995) and individuals living in range edges may result in higher exposure to environmental change than individuals living in the core of their range (Gutschick and BassiriRad 2003; Anderson et al. 2009). However, while this generalization may hold for less mobile species and ecological specialists (Bateman et al. 2012a), highly vagile and generalist species like the Dickcissel are likely better able to utilize their full range. Species distributions, or areas that meet the set of conditions in which a species can occur, are not static but can fluctuate in geographic space over time (Bateman et al. 2012b), and range edges may occasionally contain optimal conditions for a species. While used infrequently and often containing only few individuals during normal years, range edges may episodically serve as 'refuges' from extreme weather events or conditions such as drought (Magoulick and Kobza 2003; Pidgeon et al. 2003; Albright et al. 2010b). This appears to be the case for the Dickcissel, which occurs in low numbers—or not at all—in its range edges in most years, but occasionally uses these areas in high numbers when conditions are poor in its core range. Drought can lead to deteriorating conditions either due to lower than average vegetation productivity, fewer insects to prey upon, physiological stress, or combinations of these factors (Kingsolver 1989; Fay et al. 2003; Wang et al. 2003; Archaux and Wolters 2006). Vegetation structure changes brought on by drought conditions can also reduce the availability of nesting and perching sites needed for successful breeding (Igl 1991). Territoriality in Dickcissels likely intensifies the movement response during years of severe drought, and a large proportion of the breeding population is likely 'pushed' by such deteriorating conditions out of its core range.

With their high mobility and known movement away from failed breeding sites the fluctuations in abundance observed during drought conditions found in this study likely reflects a shift in the location of individuals, rather than an overall population change at a continental level (Prestby and Anich 2013). As movement is generally northward, with the population centroid shifting towards the northeast during drought, it appears that northern range edge offers refuge for individuals when drought conditions occur within this species' core range. During extreme conditions, grassland and cultivated crop habitats within the range

edges likely serve as a refuge where survival probability, reproductive success or both is higher than in the core of its range. Dickcissel abundance has been positively linked with haylands containing forbs and legumes and crops such as alfalfa and soybeans (Emlen and Wiens 1965; Hurley and Franks 1976; Frawley and Best 1991; Dechant et al. 2002; Quinn et al. 2012). Grass and alfalfa fields provide the principal nesting habitat for Dickcissels (Hurley and Franks 1976). Indeed it appears that range edge refuge sites contain high amounts of forbs and cultivated dicotyledons (i.e., these sites had a higher NIR reflectance), which is consistent with cultivated crop cover of alfalfa or soybean (Bellis et al. 2008). However, use of this habitat can be risky because an untimely harvest or hay cutting can cause a radical change in habitat suitability, and the loss of active nests.

From a climate change perspective, range edges may become increasingly important in the future as refugia (Keppel et al. 2012) if extreme weather becomes more frequent within the core of species' ranges. Sites that are important during extreme events at present can be movement sites, or stepping stones, along the potential northward range expansions (Maggini et al. 2011). Range edges may also become less peripheral, with range shifts causing these locations to become situated more centrally with increased warming (Thomas and Lennon 1999). This may be the case for the Dickcissel, as successful establishment at the northern range edge appears to be limited by the magnitude and duration of productive energy available for reproduction (a measurement of metabolized energy minus existence energy, based on air temperature and photoperiod, Zimmerman 1965). Historically, northern range edge sites may have only been able to support breeding during a few favorable years (Zimmerman 1965). However, recent climate change and increased temperatures may be pushing the range of this species northward (Prestby and Anich 2013). During the recent drought related Dickcissel irruption of 2012, there was evidence of successful breeding in the range edges in Wisconsin (Prestby and Anich 2013). However, how this reproductive output compares to that in the core grasslands during non-drought years is not known. Perhaps range edges are essential for survival during drought events, but are less suited for reproduction, explaining to some extent why abundances are low during non-drought years.

Regardless, increasing drought in the core range may lead to greater use of range edges, but with lower reproduction and possibly lower population performance here without management considerations.

These peripheral populations are crucial from an evolutionary and genetic diversity perspective (Lesica and Allendorf 1995; Hampe and Petit 2005; Gibson et al. 2009) and as effective complementarity hotspots for protected area networks (Araújo and Williams 2001). Here we show that range edges also have a buffering capacity for populations during extreme weather events when conditions become temporally sub-optimal within a species' core range. In a changing climate, with more erratic weather, conservation strategies for irruptive and weather-sensitive species may require more broadly distributed habitat instead of focusing all efforts on the core range, even though non-core areas may be unoccupied in 'normal' years.

It is important to note though that population viability of Dickcissel is not driven solely by weather and climate processes. Dickcissels are sensitive to loss of grassland habitat, cowbird parasitism, field mowing, grazing, and fires during breeding season (Dechant et al. 2002). In particular, early haying has been shown to be detrimental to Dickcissel breeding (Luscier and Thompson 2009; Prestby and Anich 2013). If drought or other extreme weather becomes a frequent occurrence in the core of the Dickcissel range during the breeding season, then it will become important that land managers in the current range edge adopt conservation strategies to ensure that habitat suitability is not compromised. Given that cultivated crops appear to be important during droughts, one possible conservation strategy could be to delay the mowing of fields while nests are active. Early mowing of crops such as alfalfa leads to declines in Dickcissel density, total abandonment and nest failure (Hurley and Franks 1976; Frawley and Best 1991), with recolonization occurring only after re-growth of vegetation (Frawley and Best 1991), and at lower densities. Thus for grassland birds such as Dickcissels, early haying or mowing of cultivated crops during the breeding season likely creates local population sinks (Sealy 1976; Igl 1991; Perlut et al. 2006). Fields mowed after nesting has concluded, less regularly, or in conservation-hayed areas, which are mowed in July to allow adequate vegetation cover during peak breeding season, are linked with higher Dickcissel densities (Igl 1991; Swengel 1996).

Cropland enrolled in federal programs such as Conservation Reserve Program (CRP), where timing of mowing can be regulated, may serve as vital refuges for Dickcissels and other grassland birds during drought.

We also note that in addition to breeding season threats, the Dickcissel is considered an agricultural pest within its wintering range in Central and South America where it may be subject to lethal control (Basili and Temple 1999; Temple 2002). In the early 1980s lethal control was common, and may be a large contributing factor to low Dickcissel abundances seen at the same time period across our sites (see Fig. 3). This highlights that abundances in a given year may reflect other factors beyond drought. In addition, the uneven coverage of BBS routes both temporally (some routes not covered in some years) and spatially (routes are not evenly distributed, vary in landcover types, and do not include all land cover types, e.g., no urban areas) posed some limitations for our study. However the BBS data provides the best data source for bird species associated with grassland areas (Niemuth et al. 2007) and BBS data are standardized, accounting for effort and using a uniform sampling technique which is not true for other spatially comprehensive data sets such as eBird (Sullivan et al. 2009).

Our results highlight the conservation importance of range edges in providing refuge during extreme events and climate change. Birds are already responding to recent climate change with non-homogenous shifts and movements (Tingley et al. 2012), which suggests that land managers need to be flexible and adaptable in identifying integral conservation sites for this highly mobile taxa. It is imperative that range edges be considered in conservation planning in order to maximize the likelihood that individuals will be able to find refuge in terms of suitable habitat, during extreme weather events and as climate trends evolve.

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