

1 **Changing precipitation regime threatens population growth and persistence of a declining**
2 **grassland songbird**

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10

11 **Abstract**

12 Populations of grassland songbirds are rapidly declining across North America.

13 Although large swathes of natural grasslands have been lost, habitat loss alone does not fully
14 explain these population declines, and a portion of these losses may be due to changing

15 environmental conditions. Using detailed demographic data collected between 2013-2021 from
16 grasshopper sparrows (*Ammodramus savannarum*) at the Konza Prairie Biological Station,

17 Kansas, USA, we first developed an integrated population model (IPM). Then, using the vital

18 rates from the IPM, we conducted sensitivity analyses and a path analysis to assess the effect of

19 variability in weather on individual vital rates including survival, immigration, and fecundity and

20 overall population growth. Average annual apparent survival of males (adult: 58%, juvenile:

21 21%) was higher than females (adult: 51%, juvenile: 20%), while the average number of young

22 produced per female was 2.4. Population growth rate was over twice as sensitive to changes in

23 adult apparent survival than other vital rates and declined following wetter years. Because adult

24 apparent survival in this system is shaped more by emigration than mortality, these results

25 suggest population declines are largely mediated by adults dispersing away from the study site.

26 Projections of population size under forecasted precipitation predict that grasshopper sparrows

27 may be locally extirpated in the next century under future climate scenarios. Our study shows
28 that combining sophisticated modelling with detailed demographic data is critical for predicting
29 trends in population growth and guiding conservation approaches in declining species.

30

31 **Keywords:** drought, fecundity, IPM, population dynamics, population projection, rainfall,
32 sensitivity, survival

33

34 **Introduction**

35 Understanding the external drivers that limit or regulate population growth is a fundamental goal
36 of ecology (May 1999). Studies of animal populations commonly involve species that live in
37 relatively stable and predictable environments where populations can approach carrying capacity
38 and are thought to be shaped by food availability and competition (Caughley & Gunn, 1993;
39 Holmes, 2007). However, the drivers of population dynamics of species living in more
40 climatically variable environments are less understood. Theory predicts that the drivers of
41 population dynamics should be increasingly important for fitness as temporal variability in
42 environmental drivers increases (Andrewartha & Birch, 1954; Drake & Lodge, 2004; Jenouvrier
43 et al., 2015). In response to this variability, populations may evolve low sensitivity to highly
44 variable vital rates to minimize the negative fitness impacts of environmental heterogeneity (e.g.,
45 demographic buffering: Pfister, 1998). Demographic buffering could dampen the effects of
46 environmental variability on individual vital rates, but increased variability in population growth
47 rate will lead to lower geometric or stochastic population growth rates (Boyce, 1977; Tuljapurkar
48 & Orzack, 1980). Currently, it is unknown whether climate-induced variability in vital rates and

49 population growth rate is sufficient enough to generate meaningful change in and significantly
50 affect population persistence.

51 Climatic conditions can have diverse and substantial effects on vital rates at multiple
52 phases of the annual cycle (Woodworth et al., 2017; Sutton et al., 2021) and influence survival,
53 fecundity, and immigration (e.g., Halkka et al., 2006; Chen et al., 2015) in animals. Responses to
54 temperature are mediated via well understood physiological processes; animals are constrained
55 by thermal tolerance thresholds (Araújo et al., 2013) that have direct effects on survival and
56 population persistence (insects: Addo-Bediako et al., 2000; birds: Albright et al., 2017). Far less
57 is known about how precipitation drives population growth. Precipitation can influence
58 physiology (Freeman et al., 2023), behaviour (Wingfield et al., 2017), and survival (Shogren et
59 al., 2019), with precipitation extremes appearing to have substantial direct and indirect effects on
60 demographic rates (Tinkle et al., 1993; Ryder & Sillett, 2016). As climates continue to shift and
61 increase in variability, understanding how both temperature and precipitation impacts
62 populations, and the specific demographic processes most strongly influenced will be of
63 increasing importance.

64 The grasslands of mid-continental North America are highly climatically variable (Knapp
65 & Smith, 2001) and are one of the most threatened biomes in the world (Hoekstra et al., 2005;
66 Scholtz & Twidwell, 2022). The region experiences tremendous swings in both temperature and
67 precipitation within and between seasons (Borchert, 1950). Within the next century, temperatures
68 in the Great Plains are projected to increase by 4.4–6.6°C (Vose et al., 2017) with mean annual
69 precipitation predicted to decline by 5–10% (Easterling et al., 2017). Precipitation plays a
70 particularly important role in grasslands because it is the strongest driver of plant productivity
71 (Petrie et al., 2018) and affects plant, invertebrate, and vertebrate communities (Barnett & Facey,

72 2016; Deguines et al., 2017; Welte et al., 2020). Furthermore, precipitation often has delayed
73 effects on grassland communities (e.g., total rainfall in the prior year affecting plant composition;
74 Dudney et al., 2017). Grassland birds exhibit large fluctuations in local population sizes (Dornak
75 et al., 2013), and are subject to multiple direct and indirect climatic effects via food availability,
76 habitat structure, and predator abundance (Ockendon et al., 2014; Correll et al., 2019;
77 Baltensperger et al., 2020). These effects may be driven by temperature, precipitation, or both;
78 therefore, elucidating the effects of climate on avian demographics and identifying contributions
79 of individual vital rates to population growth will contribute to directed conservation efforts for
80 declining grassland birds.

81 Here, we used nine years of demographic data of grasshopper sparrows breeding in a
82 tallgrass prairie of the central USA to address key gaps in our knowledge of animal population
83 regulation in a dynamic environment. First, we constructed an integrated population model to
84 estimate annual population growth and vital rates (survival, fecundity, and immigration), and
85 conducted sensitivity analyses to determine how the annual rate of population growth responds
86 to shifts in each vital rate. Then, using path analysis, we distinguished between putative direct
87 and indirect effects of local weather and global change on population dynamics in our system.
88 We hypothesized that temperature and precipitation would affect population growth of
89 grasshopper sparrows via one or more vital rates due to multiple underlying physiological and
90 ecological mechanisms. Local storms and spells of excessive heat are energetically costly to
91 survive, and could have downstream consequences on survival, fecundity, and immigration via
92 death, nest abandonment and failure, and potentially impeding movement. Additionally or
93 alternatively, at regional scales, temperature and precipitation cycles may have bottom-up effects
94 on survival, fecundity and immigration via vegetation structure and prey availability (Flanagan

95 & Adkinson, 2011; Silber et al., 2023). A complete description of the predictions and
96 mechanisms underlying the relationships between the weather metrics and vital rates are in the
97 supporting materials (Table S1). Finally, we forecast population counts at our site based on
98 multiple projected climatic models to estimate local population persistence under future climate
99 regimes.

100

101 **Methods**

102 *Study Site and Species*

103 We collected data on grasshopper sparrows (*Ammodramus savannarum*) at the Konza Prairie
104 Biological Station (39°05' N, 96°35' W), a 3487-ha tallgrass prairie in NE Kansas, USA. Konza
105 Prairie is composed of pastures managed with replicated experimental grazing (grazed by bison
106 or cattle, or ungrazed) and fire frequency (1, 2, 3, 4, or 20 year interval) treatments (Collins et
107 al., 2021). In addition, we collected data at the Rannell's Preserve which is a 1175-ha grassland
108 adjacent to Konza Prairie with pastures that are grazed by cattle and burned annually (Owensby
109 et al., 2008).

110 The grasshopper sparrow is a small, migratory songbird that breeds in grasslands
111 throughout North America. On the breeding grounds, grasshopper sparrows occupy patchy
112 grasslands with heterogenous vegetation but few shrubs (Powell, 2008; Vickery, 2020). At our
113 site, grasshopper sparrows are present from mid-April through September, and during the study
114 period, were most abundant in grazed pastures that are burned every 2–3 years. Grasshopper
115 sparrows may attempt multiple nests each breeding season and can raise up to three broods per
116 season at this site (W.A.B. unpublished data). They construct domed ground nests of grasses and
117 litter (Vickery, 2020). Females lay and incubate 1–7 eggs and feed nestlings with the assistance

118 of males until fledging at 7–8 days old (Vickery, 2020; Winnicki, 2019). Nest success (i.e., at
119 least one sparrow fledging the nest) at the site is low with an average of 0.18 host fledglings
120 produced per nest attempt (Verheijen et al., 2022). Nests fail due to predation by snakes,
121 mammals, or other species of birds, abandonment, being trampled by large grazers, and flooding
122 or other extreme weather events. Additionally, grasshopper sparrows are frequent hosts for
123 brown-headed cowbirds (*Molothrus ater*), an obligate brood parasite. Brown-headed cowbirds
124 lay eggs in host nests, sometime removing a host egg, or removing all host eggs triggering
125 relaying by the host female (Arcese et al., 1996). At the Konza Prairie, female brown-headed
126 cowbirds deposited 1–5 eggs in 41.7% of the 240 nests we monitored between 2014–2019 (Sroor
127 et al., *in review*).

128 Grasshopper sparrows are highly mobile, frequently dispersing within and between
129 seasons. Within season, ~75% of males changed territories with known dispersal distances
130 reaching 8.9 km (Williams and Boyle, 2018). Furthermore, each month 52% of territories were
131 occupied by a new territorial male (Williams and Boyle, 2018); the limited data on female
132 movement suggests that they also frequently disperse, but their dispersal rates are unknown.
133 Grasshopper sparrows migrate annually, wintering in the southern United States and Mexico
134 with the NE Kansas population wintering in Texas and northern Mexico (Hill and Renfrew,
135 2019). In Texas, grasshopper sparrows have an overwinter survival probability ranging from
136 0.47 to 0.87 (Pérez-Ordoñez et al., 2022). Raw recapture or resight of males in any subsequent
137 year at the Konza Prairie is 26% (Silber et al., 2023) and the proportion of individuals resighted
138 from the previous year ranges from 13.7–2.5%, which is consistent with the 0% to 57% return
139 rates to the breeding grounds throughout North America (Gill et al., 2006; Jones et al., 2007).
140

141 *Field Methods*

142 Throughout each breeding season of 2013–2021, we captured grasshopper sparrows in mist nets
143 baited with a speaker playing a territorial male’s song and marked them with a unique
144 combination of one numbered, aluminum United States Geological Survey and three colored leg
145 bands. We determined sex based on the presence of a cloacal protuberance (male) or a brood
146 patch (female). We classified individuals as juveniles or adults based on plumage. Juveniles were
147 born in the year of capture while adults were born in any year prior to capture. Most juveniles
148 were marked as nestlings, and as a result, sex was unknown unless they were molecularly sexed
149 for another project.

150 Field crews surveyed 18 pastures totalling 1643.8 ha every 10 days from mid-April
151 through late-August so that each pasture was surveyed 8–10 times per breeding season. The
152 pastures surveyed ranged in size from 27.9–226.3 ha and included three ungrazed x annual burn,
153 three ungrazed x 2-year burn, two bison grazed x annual burn, two bison grazed x 2-year burn,
154 two cattle grazed x annual burn pastures, and six cattle grazed x 3-year patch burn pastures. Each
155 survey was conducted by one or two observers and routes varied between each survey to ensure
156 all areas within each pasture were surveyed multiple times throughout the season. Using
157 binoculars, scopes, and cameras, observers counted and recorded the identify of individuals
158 based on their unique color-band combinations or recorded that they were unmarked, which
159 triggered subsequent capture efforts.

160 We searched for nests throughout the breeding season in areas where males were
161 defending territories. We located nests by observing adults carrying food and by flushing females
162 off nests, either incidentally or by dragging a weighted rope over the top of the vegetation
163 (Higgins et al., 1969). We visited nests every 2–3 days and recorded the number of grasshopper

164 sparrow and brown-headed cowbird eggs or nestlings present until the nest successfully fledged
165 young or failed. We marked nestlings at approximately day 4 post hatch with a single, numbered
166 metal band to enable identification post-fledge. For each nest, we attempted to identify the
167 female and the social male using a combination of behavioural observations (e.g., if they took
168 food to the nest to feed nestlings) and captures at the nest. We captured females by placing a
169 mist-net immediately in front of the nest opening and, after allowing her to return to the nest,
170 flushed her into the net. Identifying the females by band combination was difficult because they
171 are secretive and can evade both capture and resight by running through the tall grasses.
172 Therefore, some nests had an unknown parent, in which case we generated a unique parental ID
173 for that individual.

174 We followed all guidelines for the care and use of animals as well as institutional, state,
175 and federal regulations throughout our study (Kansas State University IACUC permits #3260,
176 3733, and 4250 and North American Bird Banding Laboratory permit #23836).

177

178 *Integrated Population Model*

179 We collated the demographic data collected during the surveys, capture events, and nest
180 monitoring into three data sets: annual population counts, a capture-recapture/resighting matrix,
181 and annual measures of productivity. To get annual population counts of adult and juvenile
182 males and females, we summed the number of unique individuals observed at least once each
183 year. Similarly, we included all individuals in the capture-recapture/resighting matrix if they
184 were observed at least once within a breeding season. Individuals with unknown IDs or sex were
185 excluded from the counts and matrix except for juveniles whose sexes are unknown due to lack
186 of secondary sex characteristics. Juveniles of unknown sex were randomly assigned a sex based

187 on a 1:1 offspring sex ratio common in passerines (Gowaty, 1993). The productivity data set
188 included the total count of females observed (including females of nests with generated IDs) and
189 the number of grasshopper sparrow juveniles in each year. To estimate annual vital rates and
190 population growth rates from these three datasets, we fit an integrated population model (IPM;
191 Schaub et al., 2007). In an IPM, a state-space model describes the population count data (Schaub
192 and Kéry, 2021). The state process represented a population projection model that considered
193 two sexes and three stages (recruits, surviving adults, and immigrants). Recruits were individuals
194 born in the study area in the year prior that returned to their natal site to breed. Surviving adults
195 were ≥ 2 -years old that had bred in the study area in previous years while immigrants were
196 individuals that were not known to have been born or have bred in the study area in previous
197 years. We projected stage-specific abundance using binomial and Poisson distributions to
198 account for demographic stochasticity (Schaub and Kéry, 2021).

199 We estimated apparent survival of both sexes and two age classes (juvenile and adult)
200 using the capture-recapture/resight data set and a Cormack-Jolly-Seber model (Schaub and Kéry,
201 2021). We estimated both apparent survival, which is the probability of an individual surviving
202 and returning in the next year, and recapture/resight, which is the probability of detecting an
203 individual the following year given the individual is alive and present in the study area (Schaub
204 and Kéry, 2021).

205 We estimated fecundity, or annual productivity of the population, using a regression
206 model with a Poisson distribution fitted to the number of juveniles and females each breeding
207 season (Schaub and Kéry, 2021). We included a parameter dividing fecundity in the regression
208 model to account for known underestimation of the number of offspring produced each year. We
209 included this parameter because when studying post-fledge survival in 2021 and 2022, only

210 0.04% of juveniles caught at the end of the breeding season were recaptures (i.e., birds banded as
211 nestlings). This underestimation was a result of several methodological and biological factors
212 including the amount of land surveyed relative to the number of observers, the difficulty of
213 finding ground nests in grasslands, and rapid pace of embryonic and nestling development in this
214 species. A uniform prior was specified for the parameter with support from 1 to 3, which
215 accounts for finding between 33% and 100% of all nests each year.

216 We used results from other studies on grasshopper sparrows and knowledge of the local
217 system to inform priors. We specified a uniform prior with support from 0.3 to 0.9 for the adult
218 male and female apparent survival parameters based on a published range of adult male survival
219 estimates (0.4 to 0.9; Bernath-Plaisted et al., 2021). We applied a uniform prior with support
220 from 0.1 to 0.5 for juvenile male and female apparent survival (i.e., young birds that survived
221 and returned to the site the following year) because juvenile survival is estimated to be
222 approximately half that of adults (Seigal, 2009). The prior for adult male recapture probability
223 was set as uniform with support from 0 to 1, reflecting the range of published return rates of 0%
224 (Kaspari and O’Leary, 1988) to 84% (Delany et al., 1995). Female and juvenile recapture rates
225 were expected to be less than the adults (Small et al. 2009), so the prior for juvenile male
226 recapture probability was specified as uniform with support 0 to 0.5, while the priors applied to
227 juvenile and adult female recapture probabilities were uniform with support from 0 to 0.3. The
228 number of immigrants into a population is likely site specific and immigration rates have not
229 been well characterized in grasshopper sparrows, so we set the limits of the immigration prior to
230 be broad. Both priors for male and female immigration were uniform with support 0 to 175
231 individuals. Because grasshopper sparrows can have as many as 4.2 fledglings per nest (Davis et
232 al., 2016) and have multiple nest attempts per year (e.g., 3.5–4.8 nest attempts per year; Wray et

233 al., 1982), we specified the prior for fecundity to be uniform with support from 0 to 14 offspring.
234 We estimated the initial population size to be between 80 and 350 individuals. These estimates
235 are ~2x the lowest and highest number of individuals counted within the previous five years
236 from line transects conducted throughout the field site prior to 2013 (Boyle, 2023a; Boyle,
237 2023b). We doubled the counts because almost all individuals counted were territorial males. We
238 used Markov chain Monte Carlo (MCMC) to fit the model to the data, using three independent
239 chains for 1,500,000 iterations (burn in = 750,000 and thin = 100). We fit the IPM and performed
240 MCMC-based diagnostics using the package *jagsUI* (Kellner, 2021) in R version 4.1.1.

241

242 *Sensitivity analyses*

243 Using the annual vital rates derived from the integrated population model, we constructed a
244 simple stage-based population model. We estimated population size (N) as

$$245 \quad N_t = I_t + (N_{t-1} * \phi_{a,t}) + (N_{t-1} * F_t) * \phi_{j,t},$$

246 Using estimates of juvenile apparent survival ($\phi_{j,t}$) and adult apparent survival ($\phi_{a,t}$), immigration
247 estimates (I_t), and fecundity estimates (F_t) at year t . We calculated the annual population growth
248 as $\lambda_t = \frac{N(t+1)}{N(t)}$. We then calculated the geometric mean of λ_t across the seven annual transitions
249 (i.e., $\lambda_1 \lambda_2 \dots \lambda_7^{1/7}$), to estimate the mean annual population growth rate throughout the entire
250 study period (Morris & Doak, 2002).

251 We then used a perturbation approach (as in Vélez-Espino 2005 and Dahlgren et al.
252 2016) to estimate sensitivity and elasticity of population growth to each of the vital rates (sex-
253 specific juvenile and adult apparent survival, male and female immigration, and fecundity). We
254 perturbed the annual estimates of each vital rate by 5%, one vital rate at a time, and then
255 recalculated the population growth rate across the seven annual transitions, estimating the

256 sensitivity of the annual population growth rate to each vital rate by averaging the changes in the
257 population growth rate across transitions. To estimate elasticity, we calculated the proportional
258 change in the population growth rate for each vital rate (i.e., change in annual population growth
259 rate divided by the change in vital rate; Morris & Doak, 2002).

260

261 *Weather Metrics*

262 To assess the relationships between weather, vital rates, and population growth, we calculated
263 three weather variables previously shown to be associated with grasshopper sparrow physiology
264 (Freeman et al., 2023) and demography (Silber et al., 2023) that encompass local measures of
265 temperature, humidity, and rainfall, as well as a regional, integrative measure of weather patterns
266 based on rainfall anomalies related to the El Niño cycles. First, we extracted local data from the
267 Gridded Surface Meteorological (gridMET) dataset that consists of high resolution (~4 km)
268 meteorological data (Abatzoglou, 2013). We extracted the maximum daily temperature (°C) and
269 maximum daily relative humidity (%) for the duration of the breeding season (May 1 – August
270 31) and used an equation derived by Stull (2011) to calculate the average daily high wet bulb
271 temperature (°C) for each breeding season. Wet bulb temperature incorporates both air
272 temperature and humidity, is always lower than the measured dry bulb temperatures, and is
273 biologically relevant because the thermoregulatory costs of high air temperature increase with
274 high humidity (Gerson et al., 2014). Second, we calculated the number of storms within each
275 breeding season because storms can have both direct and indirect consequences on survival,
276 movement, and reproduction (Wingfield et al., 2017). We classified rainfall as a storm event if
277 more than 18.21 mm of precipitation fell within a day (i.e., if rainfall exceeded one standard
278 deviation above the mean, Freeman et al., 2023), and summed the number of storms per breeding

279 season using daily rainfall (mm) from gridMET. Lastly, we included a broad, regional metric of
280 breeding season temperature and precipitation: the El Niño-Southern Oscillation Precipitation
281 Index (ESPI). The ESPI is a normalized index that incorporates El Niño and La Niña
282 precipitation indices which are measures of the precipitation anomalies in the tropical eastern
283 Pacific and the Maritime Continent (Curtis & Adler, 2000). In Kansas, positive values indicate a
284 wet and cold El Niño year while negative values indicate dry and warm La Niña summer (Curtis
285 & Adler, 2003). We obtained monthly ESPI data from the University of Maryland Global
286 Precipitation Climatology Project (2020) and to calculate an overall value for each breeding
287 season, we summed ESPI across May to August and lagged it by two years. We lagged ESPI
288 because, in previous work, ESPI lagged by two years was curvilinearly related to grasshopper
289 sparrow emigration rates (Silber et al., 2023).

290

291 *Path Analysis*

292 We quantified the relative effects of weather on annual population growth rates via the annual
293 vital rates using a path analysis following the approach developed by Woodworth et al. (2017).
294 We modeled all hypothesised linkages between the weather metrics, the sex and age specific
295 vital rates, and the annual population growth rates using multiple linear regressions (supporting
296 materials Fig. S1). In total, the path analysis was composed of seven linear regressions: one for
297 each vital rate with annual weather metrics as predictors and one for the annual population
298 growth rates with annual vital rates as predictors. We modeled vital rate-weather regressions
299 using linear relationships due to lack of statistical power to fit more complex models. We scaled
300 all variables included within the path by subtracting the mean and dividing by the standard
301 deviation. We fitted each model to each sample of the posterior distribution generated by the

302 IPM which allowed for the uncertainty within the IPM to be carried forward (Woodworth et al.,
303 2017). We ran each model within the path for 225,000 iterations, once for each value of the
304 posterior distributions generated by the IPM, after which we calculated the mean estimate and
305 the 95% credible intervals. We estimated the indirect effects of weather on the annual population
306 growth rate by calculating the product of the direct effects of each weather metric on a vital rate
307 and that vital rate on population growth. We then summed these indirect effects across the vital
308 rates to obtain a cumulative indirect effect of a weather metric across all vital rates on annual
309 population growth rates.

310

311 *Population Projections*

312 Because the path analysis revealed lagged breeding season ESPI to have a 5x and 10x greater
313 effect on the annual population growth rate than the other two weather metrics, we aimed to use
314 this regional index to estimate the population size under future climate scenarios. However,
315 because ESPI is a record of ongoing weather patterns and thus does not support climate
316 projections, as a proxy we used lagged precipitation extracted at our study site from the gridMET
317 dataset for climate projections. We extracted and summed the daily rainfall (mm) from May 1 –
318 August 31 then lagged these totals by two years to match the two-year lagged ESPI. The
319 gridMET lagged precipitation data were highly correlated with the lagged ESPI index (Pearson’s
320 correlation: $r = 0.53$, supporting materials: Table S2), indicating that it was a good proxy for this
321 variable in population projections. We then fit a regression to predict changes in the annual
322 population growth rate in our study area as a function of lagged precipitation. To project
323 population change under future climate conditions, we predicted the population growth rate with
324 all the 18 available Multivariate Adaptive Constructed Analogs (MACA) global climate models

325 from the Climatology Lab (Abatsoglou & Brown, 2012). We projected annual population growth
326 rates from the regression under each of the MACA model-predicted climate scenarios and used
327 these growth rates to project annual population size at our site from 2021–2100.

328

329 **Results**

330 *Integrated Population Model*

331 From 2013–2021, we captured 2898 unique individuals comprising 1640 adult males, 277 adult
332 females, 36 juvenile males, 20 juvenile females, and 925 juveniles of unknown sex. Across the
333 nine years we recaptured or resighted 2445 individuals at least once for a total of 3641
334 recaptures/resights. Average annual probability of apparent survival varied by sex and age class
335 (adult male = 58%, adult female = 51%, juvenile male = 21%, juvenile female = 20%, Fig. 1A
336 and 1B). Immigration into the study area was high and varied by sex, with an estimated average
337 of 79 males and 40 females joining the population each year (Fig. 1D). Overall, the estimated
338 number of individuals in the population fluctuated from a high of 810 in 2014 to a low of 369 in
339 2020 (Fig. 1F) with no clear directional change over time. The estimated annual population
340 growth rate was relatively high in the first year of the study (population growth rate in 2013=
341 1.71) after which it oscillated around 1 (range for remaining years = 0.89–1.20, Fig. 1C).

342 We located and monitored 498 nests over the nine years of the study, 206 of which had
343 known females. Females attempted 1–3 known clutches per year at the site, and nests contained
344 an average of 3.32 grasshopper sparrow eggs (range = 0–7) with an average of 0.85 grasshopper
345 sparrow nestlings successfully reaching fledge (range = 0–6). The total clutch size (grasshopper
346 sparrow and brown-headed cowbird eggs combined) ranged from 0–10 eggs and the total brood
347 size (grasshopper sparrow and brown-headed cowbird nestlings combined) ranged from 0–6

348 nestlings. The number of grasshopper sparrow juveniles known to be produced each breeding
349 season ranged from 17 to 120 and the average number of juveniles produced per female per
350 breeding season (i.e., fecundity) was estimated at 2.40 (Fig. 1E).

351

352 *Sensitivity Analyses*

353 The population growth rate was most sensitive to changes adult male apparent survival
354 (supporting materials: Fig. S2). Sensitivity was highest for adult male apparent survival (0.13),
355 moderate for adult female apparent survival (0.08) and juvenile survival (male = 0.06, female =
356 0.08), and lowest for fecundity (0.03) and immigration (male and female < 0.01). The elasticity
357 (i.e., proportional change in population growth rate) was also higher for adult apparent survival
358 (0.08) than for adult female apparent survival (0.04), fecundity (0.03), juvenile survival (male =
359 0.01, female = 0.02), and immigration (male and female = 0.02).

360

361 *Path Analysis*

362 Weather metrics were highly variable among the nine years of study (supporting materials: Fig.
363 S3). During the breeding season, average daily highs for wet bulb temperature stayed
364 consistently around 27°C (range = 26.1 to 28.8°C). Total rainfall across the breeding seasons was
365 highly variable, ranging from 347 mm in 2017 to 847 mm in 2019. Grasshopper sparrows were
366 exposed to 4 (2018) to 16 (2019) storms (i.e., rainfall events exceeding 18.2 mm) between May
367 and August each breeding season. ESPI was lowest in 2015 (-1.10) and highest in 2017 (2.68),
368 which when lagged by two years, matched the extremes of the total rainfall.

369 The path analysis revealed that immigration had the largest direct effect on the annual
370 population growth rate (mean estimate = 0.63, 95% credible interval (CI) = -0.64, 1.98) followed

371 by adult male apparent survival (mean = 0.39, 95% CI = -0.83, 1.59) where more immigrants and
372 higher apparent survival increased the annual population growth rate. All direct relationships
373 including effects of weather on vital rates and the effect of vital rates on the annual population
374 growth rate had credible intervals that substantially overlapped zero (Fig. 2A and 2B, supporting
375 materials: Table S3).

376 Combining the direct effects of weather on vital rates and vital rates on the annual
377 population growth rate we also estimated the indirect effects that the average daily high wet bulb
378 temperature, number of storms, and lagged ESPI had on the annual population growth rate.
379 Lagged ESPI had the strongest effect on annual rates of population growth (mean estimate = -
380 0.21, 95% CI = -0.63, 0.23) where the annual population growth rate was highest two years after
381 a hot and dry year. Locally measured temperature and storms were less strongly related to annual
382 rates of population growth than lagged ESPI (Fig. 2C, supporting materials: Table S4).

383

384 *Population Projections*

385 We projected annual population growth rate and size through 2100 using precipitation lagged by
386 two years in 18 GCMs. The mean annual population growth rate over the 2021–2100 period was
387 projected to be 0.98 (95% CI = 0.86, 1.11; supporting materials: Fig. S4). The projected
388 population size declined under all climate scenarios (Fig. 3). The median population estimate
389 declined from the 2013 estimate of 539 individuals to 87 individuals by 2100, with two GCMs
390 predicting the population size to dropping below 100 individuals as early as 2055. Projected
391 grasshopper sparrow population sizes remained relatively stable under climate models with
392 lower mean annual rainfall (<425 mm), while projected population sizes decreased more under
393 climate projections with higher mean annual rainfall (Fig. 4).

394

395 **Discussion**

396 In the eastern tallgrass prairies of the central Great Plains, climate variability strongly influences
397 the demography of an imperiled grassland songbird. Furthermore, grasshopper sparrows are
398 expected to decline under future climate scenarios and may be locally extirpated within the next
399 century. Importantly, our population projection is conservative and does not take into account
400 other factors that are known to drive declines in grassland birds observed since the 1970s
401 (Rosenberg et al., 2019). While grasshopper sparrow declines at our local site are predicted given
402 future precipitation trends, many grassland birds exhibit sharp declines in response to habitat
403 loss, habitat degradation, and habitat fragmentation across their ranges (Herkert, 1998, Stanton et
404 al., 2018). Thus, the changing climate will likely exacerbate ongoing declines. By investigating
405 the drivers of population growth we may be able to mitigate threats to the population.

406 Over this nine-year study, estimated annual population growth rates fluctuated around 1
407 suggesting that the population remained relatively stable. Despite this, the population is projected
408 to decline over the coming century, which with temporal changes in the climate, is likely due to
409 high interannual variation. The annual population growth rates were highly variable and
410 exceeded the common bounds of long-term variation in population growth rates (annual
411 population growth rates in our population: 0.89–1.71, common bounds: 0.95–1.05, Koons et al.,
412 2006). We would expect species that are highly mobile such as the grasshopper sparrow to have
413 higher variation in local population growth because they have a higher propensity to move in and
414 out of a local site. This variability in population growth rates and individual vital rates often
415 leads to declines when compared to a population with more stable growth and vital rates (Morris
416 & Doak, 2002). The variation we observed is consistent with regional analyses that predict

417 grasshopper sparrows are not regionally viable (With et al., 2008). Therefore, while high
418 dispersal propensity means that populations can easily be "rescued" by immigrants from
419 elsewhere, the stochastic nature of the climate and the links between climate and population
420 growth expose these birds to regional-scale risks.

421 Interannual variation in the annual population growth rate was most sensitive to changes
422 in adult apparent survival (i.e., the product of true survival and movement), which in this
423 population is shaped more by emigration than true survival (Silber et al., 2023). Species with low
424 breeding site fidelity are often responsive to spatial variation in rainfall so we expected
425 precipitation metrics to play an important role in shaping vital rates and population growth.
426 Based on evidence from this and other studies (Silber et al., 2023; *in review*), it seems likely that
427 the causal links between lagged ESPI and grasshopper sparrow demography are mediated by
428 vegetation structure for several reasons. (1) Grasshopper sparrows select quite specific structural
429 attributes for breeding territories, and those attributes are linked by lagged rainfall (Silber et al.,
430 2023; *in review*). (2) Nest success in grasshopper sparrows is associated with vegetation
431 structure, mediated, in part, by precipitation in previous years (Ruth & Skagen, 2018), and
432 juveniles move to areas with higher vegetation cover (Small et al., 2015; Guido, 2020). (3)
433 Vegetation structure is associated with multiple vital rates in this species and their communities
434 (e.g., Anderson et al., 2015; Giovanni et al., 2015). Overall, in this study, lagged ESPI had a 5–
435 10 times larger indirect effect on the population growth rate than the other weather variables we
436 included. But, unlike previous work, we uncovered a stronger relationship of lagged ESPI with
437 fecundity than emigration of adult males (Silber et al., 2023), likely reflecting differences in
438 modeling framework of the two studies. Combined, these studies highlight the need for large

439 scale, regional analyses to determine why and where birds are moving to elucidate the
440 mechanisms underlying meta-population dynamics.

441 Despite a massive effort covering many hectares, our study is limited by a relatively short
442 temporal extent of 9 years, and the difficulties of locating females and their nests. First, because
443 the habitat, weather, and population are highly dynamic in this system, nine years may not
444 provide enough data to explore fine scale relationships between environmental conditions and
445 individual performance. Second, due to the secretive nature of females, and the unachievable
446 amounts of time and manpower required to find all re-nests, considerable uncertainty remains
447 around fecundity estimates. Nevertheless, this combination of an IPM, sensitivity and path
448 analyses, and population projection is the most comprehensive study of the population dynamics
449 of a grassland bird at a single site to date, and represents a significant advancement in the road to
450 recovery of a declining species. Our incorporation of informative priors is also an important step
451 forward when compared to other demographic studies (e.g. Woodworth et al., 2015) and draws
452 on years of in-depth knowledge to strengthen inference.

453 Developing IPMs is a critical step in guiding effective conservation efforts (Zipkin &
454 Saunders, 2018). Often, the focus of applied studies is on local habitat selection; although it is
455 important to understand local conditions most strongly associated with occupancy, we need a
456 broader perspective on species' relationships with their environment. Demographic models such
457 as this one aid in understanding which vital rates are most important for persistence which
458 represents a key step in recovering North American birds (Road to Recovery, 2022). Such work
459 paves the way for the next step which is to implement targeted conservation actions. In this
460 population we recommend mitigating climatic drivers through careful, and year-specific habitat
461 management in ways that will increase fecundity, promote immigration, and suppress

462 emigration (Silber et al. *in review*). Given the propensity for movement in grassland birds (Jones
463 et al., 2007), and the ultimate effects on local population persistence, management plans and
464 action at regional scales are imperative. Pastures with heterogenous vegetation and suppression
465 of woody encroachment best support diverse communities of grassland-dependent species
466 (Wiens, 1969, Bakker, 2003). Furthermore, combining land management efforts on the breeding
467 grounds with ongoing work at grasshopper sparrow overwintering sites (e.g. Macías-Duarte et al.
468 2017, Pérez-Ordoñez et al. 2022) will be an important step in the recovery of the population.

469 Overall, this study supports the idea that in climatically variable environments, animal
470 populations are regulated by environmental conditions (Andrewartha & Birch, 1954; Drake &
471 Lodge, 2004; Jenouvrier et al., 2015). Unlike animals living in more stable environments, the
472 lives and vital rates of grassland-obligate birds appear to be shaped to a large degree by
473 interannual variation in rainfall that affects both individual vital rates and population growth
474 rates. By revealing the nature of those associations and the magnitude of responses, our study
475 helps identify the mechanistic links between environmental conditions and demographic
476 responses. Our work provides an example of how such insight paves the way for action that
477 mitigates the future predicted for birds under anticipated climate scenarios. Because animal
478 population growth is likely mediated by vegetation responses, management can compensate in
479 other ways to mitigate changes driven by climate.

480

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488

489 **Literature Cited**

490 Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological
491 applications and modelling. *International Journal of Climatology*, *131*, 121–131.
492 <https://doi.org/10.1002/joc.3413>

493

494 Abatzoglou, J. T., & Brown, T. J. (2012). A comparison of statistical downscaling methods
495 suited for wildfire applications. *International Journal of Climatology*, *780*, 772–780.
496 <https://doi.org/10.1002/joc.2312>

497

498 Addo-Bediako, A., Chown, S. L., & Gaston, K. J. (2000). Thermal tolerance, climatic variability
499 and latitude. *Proceedings of the Royal Society of London. Series B: Biological*
500 *Sciences*, *267*(1445), 739–745. <https://doi.org/10.1098/rspb.2000.1065>

501

502 Albright, T. P., Mutiibwa, D., Gerson, Alexander. R., Smith, E. K., Talbot, W. A., O’Neill, J. J.,
503 McKechnie, A. E., & Wolf, B. O. (2017). Mapping evaporative water loss in desert
504 passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National*
505 *Academy of Sciences of the United States of America*, *114*(9), 2283–2288.
506 <https://doi.org/10.1073/pnas.1613625114>

507

508 Anderson, L. C., Powell, L. A., Schacht, W. H., Lusk, J. J., & Vodehnal, W. L. (2015). Greater
509 prairie-chicken brood-site selection and survival in the Nebraska sandhills. *The Journal*
510 *of Wildlife Management*, *79*(4), 559–569. <https://doi.org/10.1002/jwmg.876>

511

512 Andrewartha, H. G., & Birch, L. C. (1954). *The distribution and abundance of animals*.
513 University of Chicago Press.

514

515 Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L.
516 (2013). Heat freezes niche evolution. *Ecology Letters*, *16*(9), 1206–1219.
517 <https://doi.org/10.1111/ele.12155>

518

519 Arcese, P., Smith, J. N., & Hatch, M. I. (1996). Nest predation by cowbirds and its consequences
520 for passerine demography. *Proceedings of the National Academy of Sciences*, *93*(10),
521 4608–4611. <https://doi.org/10.1073/pnas.93.10.4608>

522

- 523 Bakker, K. K. (2003). A synthesis of the effect of woody vegetation on grassland nesting birds.
524 In *Proceedings of the South Dakota Academy of Science* (Vol. 82, pp. 119–141). South
525 Dakota Academy of Sciences.
526
- 527 Baltensperger, A. P., Dixon, M. D., & Swanson, D. L. (2020). Implications of future climate-
528 and land-change scenarios on grassland bird abundance and biodiversity in the Upper
529 Missouri River Basin. *Landscape Ecology*, 35(8), 1757–1773.
530 <https://doi.org/10.1007/s10980-020-01050-4>
531
- 532 Barnett, K. L., & Facey, S. L. (2016). Grasslands, invertebrates, and precipitation: a review of
533 the effects of climate change. *Frontiers in Plant Science*, 7.
534 <https://www.frontiersin.org/articles/10.3389/fpls.2016.01196>
535
- 536 Bernath-Plaisted, J., Panjabi, A., Guido, N., Bell, K., Drilling, N., Strasser, E., Johnson, S. K., &
537 Correll, M. (2021). Quantifying multiple breeding vital rates in two declining grassland
538 songbirds. *Avian Conservation and Ecology*, 16(1). [https://doi.org/10.5751/ACE-01875-](https://doi.org/10.5751/ACE-01875-160119)
539 [160119](https://doi.org/10.5751/ACE-01875-160119)
540
- 541 Borchert, J. R. (1950). The climate of the central North American grassland. *Annals of the*
542 *Association of American Geographers*, 40(1), 1–39. <https://doi.org/10.2307/2561016>
543
- 544 Boyce, M. S. (1977). Population growth with stochastic fluctuations in the life table. *Theoretical*
545 *Population Biology*, 12(3), 366–373. [https://doi.org/10.1016/0040-5809\(77\)90050-8](https://doi.org/10.1016/0040-5809(77)90050-8)
546
- 547 Boyle, W. (2023a). CBP01 Variable distance line-transect sampling of bird population numbers
548 in different habitats on Konza Prairie. Environmental Data
549 Initiative. <http://dx.doi.org/10.6073/pasta/17b63f19967d13ba55acb5ed4d9601de>.
550
- 551 Boyle, W. (2023b). CBS06 Line transects surveys of breeding birds throughout Konza Prairie.
552 Environmental Data
553 Initiative. <http://dx.doi.org/10.6073/pasta/15dd6cd7e150acd8b13490f060d0ac2e>.
554
- 555 Caughley, G., & Gunn, A. (1993). Dynamics of large herbivores in deserts: kangaroos and
556 caribou. *Oikos*, 67(1), 47–55. <https://doi.org/10.2307/3545094>
557
- 558 Chen, L., Wang, G., Wan, X., & Liu, W. (2015). Complex and nonlinear effects of weather and
559 density on the demography of small herbivorous mammals. *Basic and Applied Ecology*,
560 16(2), 172–179. <https://doi.org/10.1016/j.baae.2014.12.002>
561
- 562 Collins, S. L., Nippert, J. B., Blair, J. M., Briggs, J. M., Blackmore, P., & Ratajczak, Z. (2021).
563 Fire frequency, state change and hysteresis in tallgrass prairie. *Ecology Letters*, 24(4),
564 636–647. <https://doi.org/10.1111/ele.13676>
565
- 566 Correll, M. D., Strasser, E. H., Green, A. W., & Panjabi, A. O. (2019). Quantifying specialist
567 avifaunal decline in grassland birds of the Northern Great Plains. *Ecosphere*, 10(1),
568 e02523. <https://doi.org/10.1002/ecs2.2523>

569
570 Curtis, S., & Adler, R. (2000). ENSO indices based on patterns of satellite-derived precipitation.
571 *Journal of Climate*, 13(15), 2786–2793. <https://doi.org/10.1175/1520->
572 0442(2000)013<2786:EIBOPO>2.0.CO;2
573

574 Dahlgren, D. K., Guttery, M. R., Messmer, T. A., Caudill, D., Elmore, R. D., Chi, R., & Koons,
575 D. N. (2016). Evaluating vital rate contributions to greater sage-grouse population
576 dynamics to inform conservation. *Ecosphere* 7(3): e01249
577 <https://doi.org/10.1002/ecs2.1249>
578

579 Davis, C. A., Churchwell, R. T., Fuhlendorf, S. D., Engle, D. M., & Hovick, T. J. (2016). Effect
580 of pyric herbivory on source–sink dynamics in grassland birds. *Journal of Applied*
581 *Ecology*, 53(4), 1004–1012. <https://doi.org/10.1111/1365-2664.12641>
582

583 Deguines, N., Brashares, J. S., & Prugh, L. R. (2017). Precipitation alters interactions in a
584 grassland ecological community. *Journal of Animal Ecology*, 86(2), 262–272.
585 <https://doi.org/10.1111/1365-2656.12614>
586

587 Delany, M. F., Moore, C. T., & Progulsk Jr, D. R. (1995). Territory size and movements of
588 Florida grasshopper sparrows. *Journal of Field Ornithology*, 305–309.
589 <https://www.jstor.org/stable/4514021>
590

591 Dornak, L. L., Barve, N., & Peterson, A. T. (2013). Spatial scaling of prevalence and population
592 variation in three grassland sparrows. *The Condor*, 115(1), 186–197.
593 <https://doi.org/10.1525/cond.2013.120055>
594

595 Drake, J. M., & Lodge, D. M. (2004). Effects of environmental variation on extinction and
596 establishment. *Ecology Letters*, 7(1), 26–30. <https://doi.org/10.1046/j.1461->
597 0248.2003.00546.x
598

599 Dudney, J., Hallett, L. M., Larios, L., Farrer, E. C., Spotswood, E. N., Stein, C., & Suding, K. N.
600 (2017). Lagging behind: have we overlooked previous-year rainfall effects in annual
601 grasslands? *Journal of Ecology*, 105(2), 484–495. <https://doi.org/10.1111/1365->
602 2745.12671
603

604 Easterling, D. R., Arnold, J. R., Knutson, T., Kunkel, K. E., LeGrande, A. N., Leung, L. R.,
605 Vose, R. S., Waliser, D. E., & Wehner, M. F. (2017). *Ch. 7: Precipitation Change in the*
606 *United States. Climate Science Special Report: Fourth National Climate Assessment,*
607 *Volume I.* U.S. Global Change Research Program. <https://doi.org/10.7930/J0H993CC>
608

609 Flanagan, L. B., & Adkinson, A. C. (2011). Interacting controls on productivity in a northern
610 Great Plains grassland and implications for response to ENSO events. *Global Change*
611 *Biology*, 17(11), 3293–3311. <https://doi.org/10.1111/j.1365-2486.2011.02461.x>
612

613 Freeman, N. E., Gustafson, M., Hefley, T. J., & Boyle, W. A. (2023). Riding out the storm:
614 depleted fat stores and elevated hematocrit in a small bodied endotherm exposed to

615 severe weather. *Conservation Physiology*, 11(1), coad011.
616 <https://doi.org/10.1093/conphys/coad011>
617

618 Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E., & Wolf, B. O. (2014). The impact of
619 humidity on evaporative cooling in small desert birds exposed to high air
620 temperatures. *Physiological and Biochemical Zoology*, 87(6), 782–795.
621 <https://doi.org/10.1086/678956>
622

623 Gill, D. E., Blank, P., Parks, J., Guerard, J. B., Lohr, B., Schwartzman, E., Gruber, J. G., Dodge,
624 G., Rewa, C. A., & Sears, H. F. (2006). Plants and breeding bird response on a managed
625 Conservation Reserve Program grassland in Maryland. *Wildlife Society Bulletin*, 34(4),
626 944–956. [https://doi.org/10.2193/0091-7648\(2006\)34\[944:PABBRO\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2006)34[944:PABBRO]2.0.CO;2)
627

628 Giovanni, M. D., Powell, L. A., & Schacht, W. H. (2015). Habitat preference and survival for
629 western meadowlark (*Sturnella neglecta*) fledglings in a contiguous prairie system.
630 *Wilson Journal of Ornithology*, 127(2), 200–211. [https://doi.org/10.1676/wils-127-02-](https://doi.org/10.1676/wils-127-02-200-211.1)
631 [200-211.1](https://doi.org/10.1676/wils-127-02-200-211.1)
632

633 Gowaty, P. A. (1993). Differential dispersal, local resource competition, and sex ratio variation
634 in birds. *The American Naturalist*, 141(2), 263–280. <https://doi.org/10.1086/285472>
635

636 Guido, N. A. (2020). *Habitat Selection Across the Reproductive Cycles of Grassland Songbirds*
637 *in the Northern Great Plains* [Thesis]. University of Maine.
638

639 Halkka, A., Halkka, L., Halkka, O., Roukka, K., & Pokki, J. (2006). Lagged effects of North
640 Atlantic Oscillation on spittlebug *Philaenus spumarius* (Homoptera) abundance and
641 survival. *Global Change Biology*, 12(12), 2250–2262. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2486.2006.01266.x)
642 [2486.2006.01266.x](https://doi.org/10.1111/j.1365-2486.2006.01266.x)
643

644 Herkert, J. R. (1998). The influence of the CRP on grasshopper sparrow population trends in the
645 mid-continental United States. *Wildlife Society Bulletin*, 227–231.
646 <https://www.jstor.org/stable/3784041>
647

648 Higgins, K. F., Kirsch, L. M., & Ball Jr, I. J. (1969). A cable-chain device for locating duck
649 nests. *The Journal of Wildlife Management*, 1009–1011. <https://doi.org/10.2307/3799339>
650

651 Hill, J. M., & Renfrew, R. B. (2019). Migratory patterns and connectivity of two North
652 American grassland bird species. *Ecology and Evolution*, 9(1), 680–692.
653 <https://doi.org/10.1002/ece3.4795>
654

655 Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome
656 crisis: global disparities of habitat loss and protection. *Ecology Letters*, 8(1), 23–29.
657 <https://doi.org/10.1111/j.1461-0248.2004.00686.x>
658

- 659 Holmes, R. T. (2007). Understanding population change in migratory songbirds: long-term and
660 experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis*,
661 149(s2), 2–13. <https://doi.org/10.1111/j.1474-919X.2007.00685.x>
662
- 663 Jenouvrier, S., Péron, C., & Weimerskirch, H. (2015). Extreme climate events and individual
664 heterogeneity shape life-history traits and population dynamics. *Ecological Monographs*,
665 85(4), 605–624. <https://doi.org/10.1890/14-1834.1>
666
- 667 Jones, S. L., Dieni, J. S., Green, M. T., & Gouse, P. J. (2007). Annual return rates of breeding
668 grassland songbirds. *The Wilson Journal of Ornithology*, 119(1), 89–94.
669 <https://doi.org/10.1676/05-158.1>
670
- 671 Kaspari, M., & O'Leary, H. (1988). Nonparental attendants in a north-temperate migrant. *The*
672 *Auk*, 105(4), 792–793.
673
- 674 Kellner, K. (2021). jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS' Analyses. R package
675 version 1.5.2. <https://CRAN.R-project.org/package=jagsUI>
676
- 677 Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of
678 aboveground primary production. *Science*, 291(5503), 481–484.
679 <https://doi.org/10.1126/science.291.5503.481>
680
- 681 Koons, D. N., Rockwell, R. F., & Grand, J. B. (2006). Population momentum: implications for
682 wildlife management. *The Journal of Wildlife Management*, 70(1), 19–26.
683 [https://doi.org/10.2193/0022-541X\(2006\)70\[19:PMIFWM\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[19:PMIFWM]2.0.CO;2)
684
- 685 Lindenmayer, D. B., Lane, P., Foster, C. N., Westgate, M. J., Sato, C., Ikin, K., Crane, M.,
686 Michael, D., Florance, D., & Scheele, B. C. (2019). Do migratory and resident birds
687 differ in their responses to interacting effects of climate, weather and
688 vegetation?. *Diversity and Distributions*, 25(3), 449–461.
689 <https://doi.org/10.1111/ddi.12874>
690
- 691 Macías-Duarte, A., Panjabi, A. O., Strasser, E. H., Levandoski, G. J., Ruvalcaba-Ortega, I.,
692 Doherty, P. F., & Ortega-Rosas, C. I. (2017). Winter survival of North American
693 grassland birds is driven by weather and grassland condition in the Chihuahuan
694 Desert. *Journal of Field Ornithology*, 88(4), 374–386. <https://doi.org/10.1111/jfo.12226>
695
- 696 May, R. (1999). Unanswered questions in ecology. *Philosophical Transactions of the Royal*
697 *Society of London. Series B: Biological Sciences*, 354(1392), 1951–1959.
698 <https://doi.org/10.1098/rstb.1999.0534>
699
- 700 Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology: theory and practice of*
701 *population viability analysis*. Sinauer Associates, Sunderland, Massachusetts.
702
- 703 Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E.,
704 Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C.,

705 Green, R. E., Sutherland, W. J., Tanner, E. V. J., & Pearce-Higgins, J. W. (2014).
706 Mechanisms underpinning climatic impacts on natural populations: altered species
707 interactions are more important than direct effects. *Global Change Biology*, 20(7), 2221–
708 2229. <https://doi.org/10.1111/gcb.12559>
709

710 Owensby, C. E., Auen, L. M., Berns, H. F., & Dhuyvetter, K. C. (2008). Grazing systems for
711 yearling cattle on tallgrass prairie. *Rangeland Ecology & Management*, 61(2), 204–210.
712 <https://doi.org/10.2111/07-034.1>
713

714 Pérez-Ordoñez, D. J., Titulaer, M., Correll, M. D., Strasser, E. H., Baeza-Tarin, F., Martin, R. L.,
715 & Harveson, L. A. (2022). The role of temperature and microclimate in the survival of
716 wintering grassland birds. *Avian Conservation and Ecology*, 17(1), 1.
717 <https://doi.org/10.5751/ACE-02010-170101>
718

719 Petrie, M. D., Peters, D. P., Yao, J., Blair, J. M., Burruss, N. D., Collins, S. L., Derner, J. D.,
720 Gherardi, L. A., Hendrickson, J. R., Sala, O. E., Starks, P. J., & Steiner, J. L. (2018).
721 Regional grassland productivity responses to precipitation during multiyear above-and
722 below-average rainfall periods. *Global Change Biology*, 24(5), 1935–1951.
723 <https://doi.org/10.1111/gcb.14024>
724

725 Pfister, C. A. (1998). Patterns of variance in stage-structured populations: evolutionary
726 predictions and ecological implications. *Proceedings of the National Academy of*
727 *Sciences*, 95(1), 213–218. <https://doi.org/10.1073/pnas.95.1.213>
728

729 Powell, A. F. L. A. (2008). Responses of breeding birds in tallgrass prairie to fire and cattle
730 grazing. *Journal of Field Ornithology*, 79(1), 41–52. <https://doi.org/10.1111/j.1557-9263.2008.00144.x>
731
732

733 Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A.,
734 Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the
735 North American avifauna. *Science*, 366(6461), 120–124.
736 <https://doi.org/10.1126/science.aaw1313>
737

738 Ruth, J. M., & Skagen, S. K. (2018). Reproductive response of Arizona grasshopper sparrows to
739 weather patterns and habitat structure. *The Condor*, 120(3), 596–616.
740 <https://doi.org/10.1650/CONDOR-17-128.1>
741

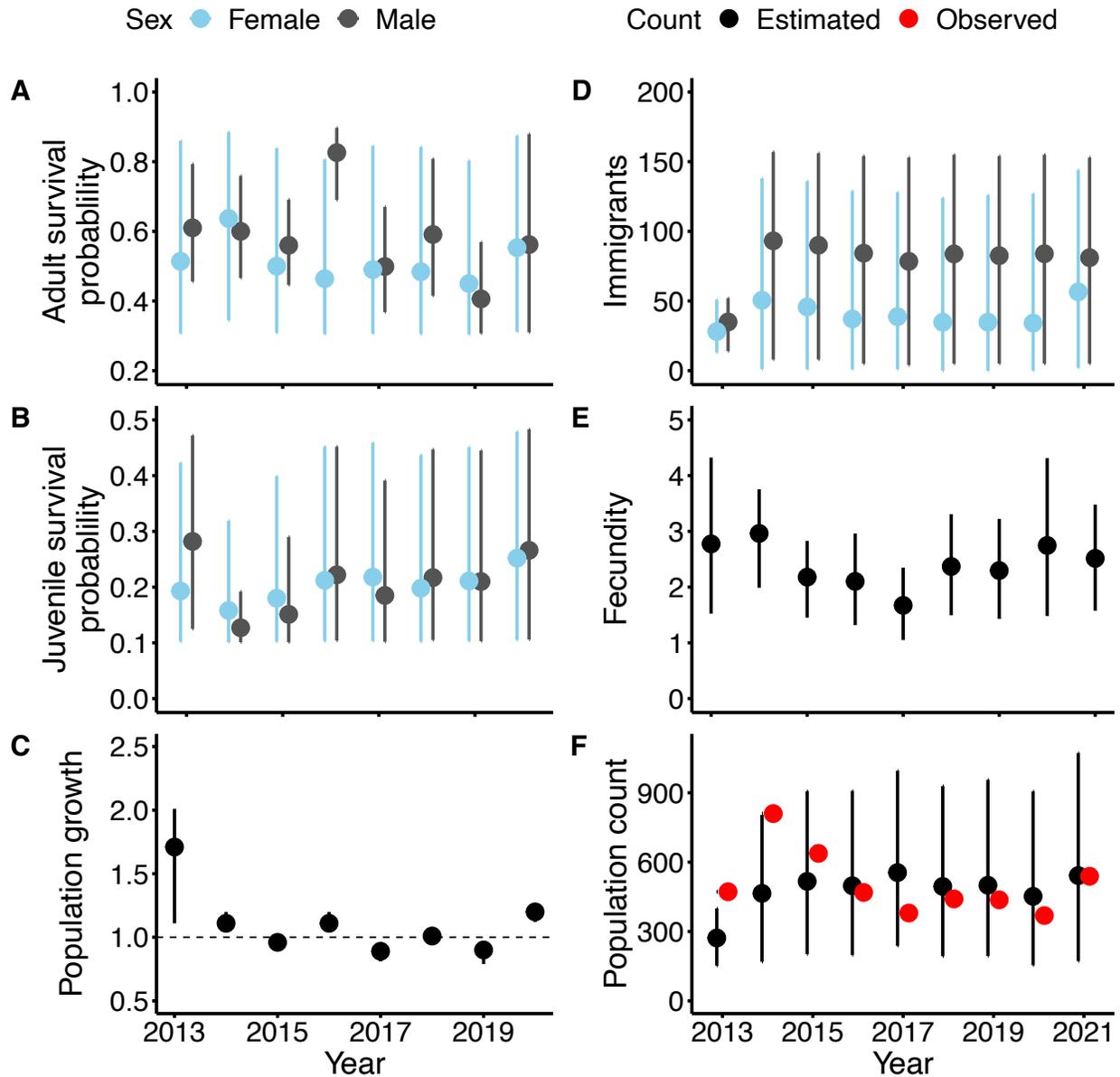
742 Ryder, T. B., & Sillett, T. S. (2016). Climate, demography and lek stability in an Amazonian
743 bird. *Proceedings of the Royal Society B: Biological Sciences*, 283(1823), 20152314.
744 <https://doi.org/10.1098/rspb.2015.2314>
745

746 Schaub, M., Gimenez, O., Sierro, A., & Arlettaz, R. (2007). Use of integrated modeling to
747 enhance estimates of population dynamics obtained from limited data. *Conservation*
748 *Biology*, 21(4), 945–955. <https://doi.org/10.1111/j.1523-1739.2007.00743.x>
749

- 750 Schaub, M., & Kéry, M. (2021). *Integrated population models: Theory and ecological*
751 *applications with R and JAGS*. Academic Press.
- 752
- 753 Scholtz, R., & Twidwell, D. (2022). The last continuous grasslands on Earth: identification and
754 conservation importance. *Conservation Science and Practice*, 4(3), e626.
755 <https://doi.org/10.1111/csp2.626>
- 756
- 757 Seigel, A. B. (2009). *Maximizing the effectiveness of grassland management for a Grasshopper*
758 *Sparrow (Ammodramus savannarum) metapopulation* [Thesis]. Rutgers The State
759 University of New Jersey, School of Graduate Studies.
- 760
- 761 Shogren, E. H., Jones, M. A., Sandercock, B. K., & Boyle, W. A. (2019). Apparent survival of
762 tropical birds in a wet, premontane forest in Costa Rica. *Journal of Field*
763 *Ornithology*, 90(2), 117-127. <https://doi.org/10.1111/jofo.12290>
- 764
- 765 Silber, K. M., Mohankumar, N. M., Hefley, T. J., & Boyle, W. A. (2023). Emigration and
766 survival correlate with different precipitation metrics throughout a grassland songbird's
767 annual cycle. *The Journal of Wildlife Management*, 87(3), e22371.
768 <https://doi.org/10.1002/jwmg.22371>
- 769
- 770 Silber, K., Hefley, T.J., Castro-Miller, H., Ratajczak, Z., & Boyle., W.A. (*In review*). The long
771 shadow of woody encroachment: an integrated approach to modeling grassland songbird
772 habitat. *Ecological Applications*.
- 773
- 774 Small, D. M., Blank, P. J., & Lohr, B. (2015). Habitat use and movement patterns by dependent
775 and independent juvenile Grasshopper Sparrows during the post-fledging period. *Journal*
776 *of Field Ornithology*. 86(1), 17–26. <https://www.jstor.org/stable/24617828>
- 777
- 778 Small, D. M., Parks, J., Gruber, J. G., & Gill, D. E. (2009). Grasshopper sparrow (*Ammodramus*
779 *savannarum*) longevity record. *North American Bird Bander*, 33, 186–187.
- 780
- 781 Sroor, E. N., Boyle, W. A., Castro-Miller, H. N., Hobbs, K. S., Reynaldo, M. D., Silber, K.,
782 Mohankumar, N. M., Wright, N. A., & Freeman, N. E. (*In review*). Environmental drivers
783 of female reproductive investment in quantity versus quality. *IBIS*.
- 784
- 785 Stanton, R. L., Morrissey, C. A., & Clark, R. G. (2018). Analysis of trends and agricultural
786 drivers of farmland bird declines in North America: A review. *Agriculture, Ecosystems &*
787 *Environment*, 254, 244–254. <https://doi.org/10.1016/j.agee.2017.11.028>
- 788
- 789 Stull, R. (2011). Wet-bulb temperature from relative humidity and air temperature. *Journal of*
790 *applied meteorology and climatology*, 50(11), 2267–2269.
791 <https://doi.org/10.1175/JAMC-D-11-0143.1>
- 792
- 793 Sutton, A. O., Strickland, D., Freeman, N. E., & Norris, D. R. (2021). Climate-driven carry-over
794 effects negatively influence population growth rate in a food-caching boreal passerine.
795 *Global Change Biology*, 27(5), 983–992. <https://doi.org/10.1111/gcb.15445>

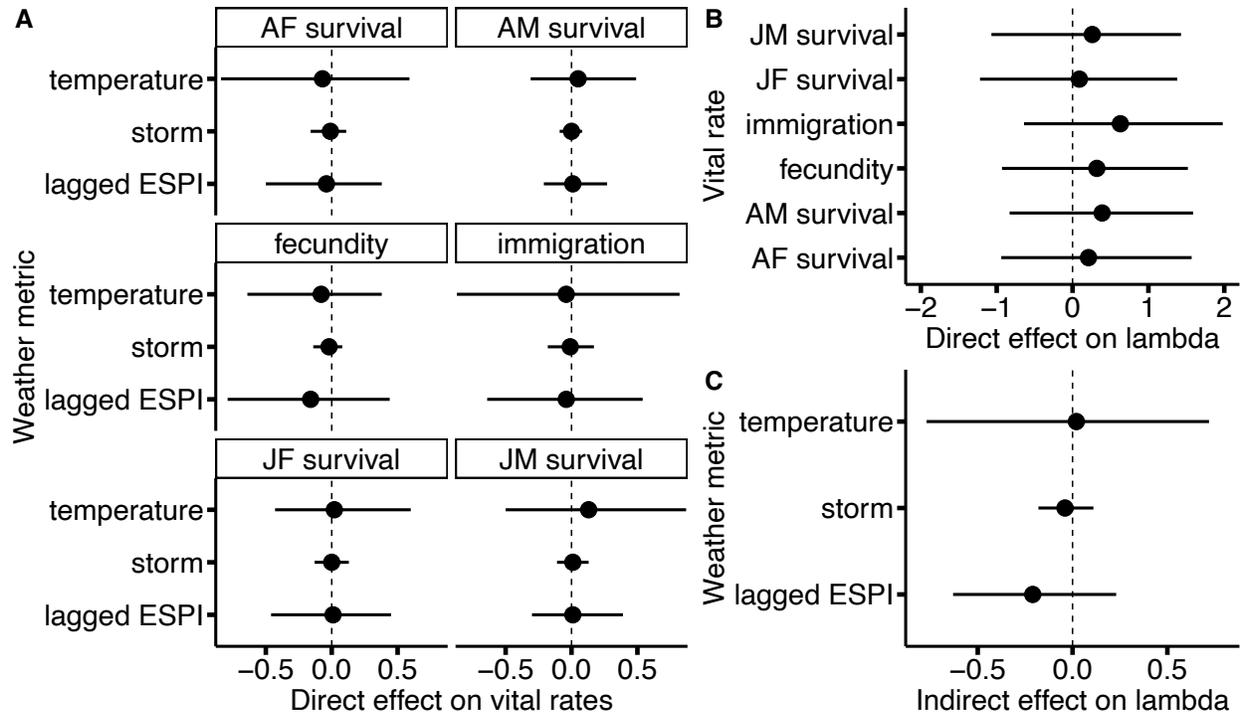
796
797 Tinkle, D. W., Dunham, A. E., & Congdon, J. D. (1993). Life history and demographic variation
798 in the lizard *Sceloporus graciosus*: a long-term study. *Ecology*, 74(8), 2413–2429.
799 <https://doi.org/10.2307/1939592>
800
801 Tuljapurkar, S. D., & Orzack, S. H. (1980). Population dynamics in variable environments I.
802 Long-run growth rates and extinction. *Theoretical Population Biology*, 18(3), 314–342.
803 [https://doi.org/10.1016/0040-5809\(80\)90057-X](https://doi.org/10.1016/0040-5809(80)90057-X)
804
805 University of Maryland Global Climate Project. (2020). *El Nino-Southern Oscillation*
806 *Precipitation Index, 1979-present*. Retrieved from <http://gpcp.umd.edu/espi.htm>
807
808 Vélez-Espino, L. A. 2005. Population viability and perturbation analyses in remnant populations
809 of the Andean catfish *Astroblepus ubidiai*. *Ecology of Freshwater Fish* 14: 125–138.
810
811 Verheijen, B. H. F., Erickson, A. N., Boyle, W. A., Leveritte, K. S., Sojka, J. L., Spahr, L. A.,
812 Williams, E. J., Winnicki, S. K., & Sandercock, B. K. (2022). Predation, parasitism, and
813 drought counteract the benefits of patch-burn grazing for the reproductive success of
814 grassland songbirds. *Ornithological Applications*, 124(2), duab066.
815 <https://doi.org/10.1093/ornithapp/duab066>
816
817 Vickery, P. D. (2020). *Grasshopper Sparrow (Ammodramus savannarum), version 1.0*. In *Birds*
818 *of the World (AF Poole and FB Gill, Editors)*. Cornell Lab of Ornithology, Ithaca, NY,
819 USA.
820
821 Vose, R. S., Easterling, D. R., Kunkel, K. E., LeGrande, A. N., & Wehner, M. F. (2017). *Ch. 6:*
822 *Temperature Changes in the United States. Climate Science Special Report: Fourth*
823 *National Climate Assessment, Volume I*. U.S. Global Change Research Program.
824 <https://doi.org/10.7930/J0N29V45>
825
826 Welte, E. A., Roeder, K. A., De Beurs, K. M., Joern, A., & Kaspari, M. (2020). Nutrient dilution
827 and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the*
828 *National Academy of Sciences*, 117(13), 7271–7275.
829 <https://doi.org/10.1073/pnas.1920012117>
830
831 Wiens, J. A. (1969). An approach to the study of ecological relationships among grassland birds.
832 *Ornithological Monographs*, 8, 1–93. <https://doi.org/10.2307/40166677>
833
834 Williams, E. J., & Boyle, W. A. (2018). Patterns and correlates of within-season breeding
835 dispersal: a common strategy in a declining grassland songbird. *The Auk: Ornithological*
836 *Advances*, 135(1), 1–14. <https://doi.org/10.1642/AUK-17-69.1>
837
838 Wingfield, J. C., Pérez, J. H., Krause, J. S., Word, K. R., González-Gómez, P. L., Lisovski, S., &
839 Chmura, H. E. (2017). How birds cope physiologically and behaviourally with extreme
840 climatic events. *Philosophical Transactions of the Royal Society B: Biological*
841 *Sciences*, 372(1723), 20160140. <https://doi.org/10.1098/rstb.2016.0140>

842
843 Winnicki, S. (2019). *Growing up prairie: ecological drivers of grassland songbird nestling*
844 *development* [Thesis]. <https://krex.k-state.edu/dspace/handle/2097/40070>
845
846 With, K. A., King, A. W., & Jensen, W. E. (2008). Remaining large grasslands may not be
847 sufficient to prevent grassland bird declines. *Biological Conservation*, *141*(12), 3152–
848 3167. <https://doi.org/10.1016/j.biocon.2008.09.025>
849
850 Woodworth, B. K., Wheelwright, N. T., Newman, A. E., Schaub, M., & Norris, D. R. (2017).
851 Winter temperatures limit population growth rate of a migratory songbird. *Nature*
852 *Communications*, *8*(1), 14812. <https://doi.org/10.1038/ncomms14812>
853
854 Wray, T., Strait, K. A., & Whitmore, R. C. (1982). Reproductive success of grassland sparrows
855 on a reclaimed surface mine in West Virginia. *The Auk*, *99*(1), 157–164.
856 <https://doi.org/10.2307/4086032>
857
858 Zipkin, E. F., & Saunders, S. P. (2018). Synthesizing multiple data types for biological
859 conservation using integrated population models. *Biological Conservation*, *217*, 240–250.
860 <https://doi.org/10.1016/j.biocon.2017.10.017>
861



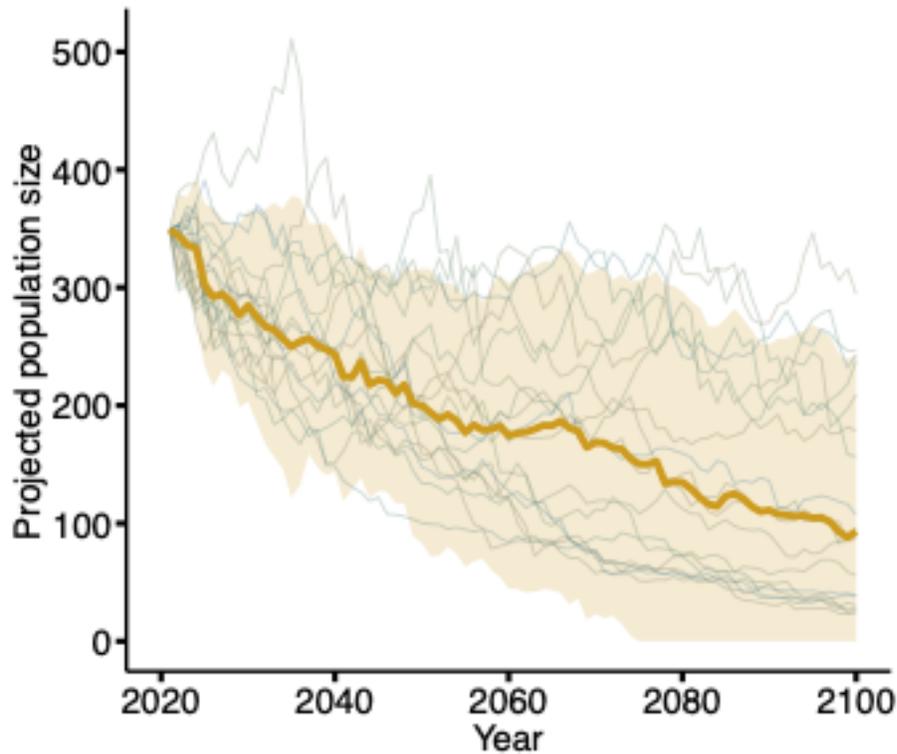
863 **Fig.1.** Annual estimates of vital rates and population counts of grasshopper sparrows
 864 (*Ammodramus savannarum*) including survival probabilities of adults (A) and juveniles (B),
 865 annual population growth rates (C), the number of immigrants (D), fecundity (i.e., the number of
 866 juveniles produced per female, E), and population counts (F). Dots represent the mean estimate
 867 and the error bars represent the 95% credible intervals.

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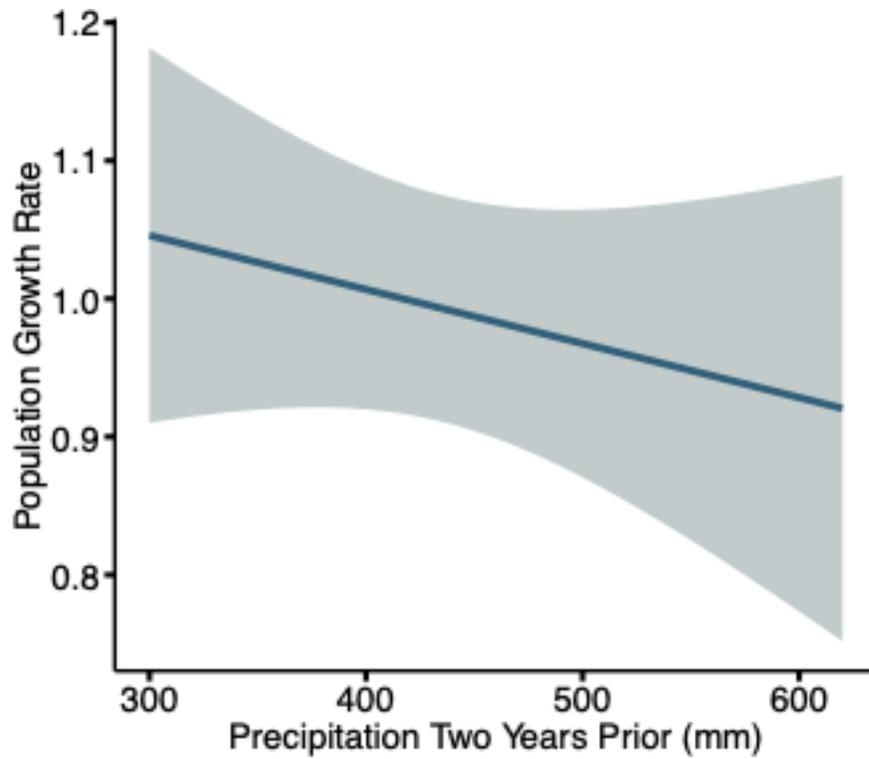
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872 **Fig.2.** Estimates of the direct (A, B) and indirect (C) effects of weather and vital rates on annual
 873 population growth rate of a population of grasshopper sparrows (*Ammodramus savannarum*) at
 874 Konza Prairie Biological Station, KS, USA. ESPI = El Niño-Southern Oscillation Precipitation
 875 Index, AF = adult female, AM = adult male, JF = juvenile female, and JM = juvenile male. Dots
 876 represent the mean estimate and the error bars represent the 95% credible intervals.



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 878 **Fig.3.** Projected population size of a population of grasshopper sparrows (*Ammodramus*
 879 *savannarum*) at Konza Prairie Biological Station, KS, USA (2021–2100). Future population
 880 sizes were calculated using projected breeding season precipitation lagged two years, derived
 881 from global climate models (GCMs). Each gray line represents population projections derived
 882 from a different GCM’s climate projections. The yellow line and shaded region represent mean
 883 population size and 95% prediction interval for projected population size, respectively.

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886 **Fig.4.** Relationship between breeding season precipitation two years prior and the population
 887 growth rate of a population of grasshopper sparrows (*Ammodramus savannarum*) at Konza
 888 Prairie Biological Station, KS, USA (2014–2021). The population is expected to decrease
 889 following wetter conditions. The line represents the expected population growth rate and the
 890 shaded region represents the 95% credible intervals.

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Supplemental Materials

Changing precipitation regime threatens population growth and persistence of a declining grassland songbird

Tables

Table S1. Hypothesized relationships between weather and vital rates of a population of grasshopper sparrows (*Ammodramus savannarum*) in northeastern Kansas, USA during the breeding season (May to August). The weather metrics considered include the number of storms, the average daily high wet bulb temperature (°C), and the summed monthly El Niño-Southern Oscillation Precipitation Index (ESPI) lagged by two years.

Weather metric	Proposed hypotheses	Predicted response
storms	storms are energetically costly and could impact survival	more storms lower survival
	storms can lead to nest failure via flooding or abandonment	more storms lower fecundity
	storms may impede movement of individuals	more storms reduce immigration
temperature	excessive heat could impact survival if at thermoregulatory limits	hotter temperatures lower survival
	excessive heat is energetically costly and could impact provisioning and offspring survival	hotter temperatures lower fecundity
	excessive heat is energetically costly, could impact resources, and could impact movement and choice to settle	hotter temperatures reduce immigration
lagged ESPI	bottom-up effects of weather two years prior on vegetation and prey availability could alter exposure to predators and impact whether individuals choose to return	prior wet conditions increase survival by increasing concealment and site fidelity
	bottom-up effects of weather two years prior on vegetation and prey availability could impact nest placement and success	prior wet conditions increase fecundity by increasing nest concealment and prey availability
	bottom-up effects of weather two years prior on vegetation and prey availability could impact whether individuals choose to settle	prior wet conditions increase immigration via vegetation structure and increased prey availability

1 **Table S2.** Pearson’s correlation matrix of the weather variables included in analyses. Annual
 2 measures of the number of storms, the average daily high wet bulb temperature (°C), and the
 3 summed monthly El Niño-Southern Oscillation Precipitation Index (ESPI) lagged by two years
 4 were included in a path model fitted to assess the direct and indirect relationships between
 5 weather metrics, vital rates, and population growth rate. Total breeding season precipitation
 6 lagged by two years was used as a proxy for ESPI in the population projection models.

Variable	storms	temperature	lagged ESPI	lagged precipitation
storms	1			
temperature	-0.07	1		
lagged ESPI	-0.31	-0.17	1	
lagged precipitation	-0.29	0.08	0.53	1

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9 **Table S3.** Mean estimates and the lower and upper limits of the 95% credible interval from a
10 path model fitted to assess the direct relationships between annual weather metrics (the number
11 of storms, the average daily high wet bulb temperature (°C), and the summed monthly El Niño-
12 Southern Oscillation Precipitation Index (ESPI) lagged by two years), annual vital rates, and
13 annual population growth rates of a population of grasshopper sparrows (*Ammodramus*
14 *savannarum*) in northeastern Kansas, USA during the breeding season (May to August).

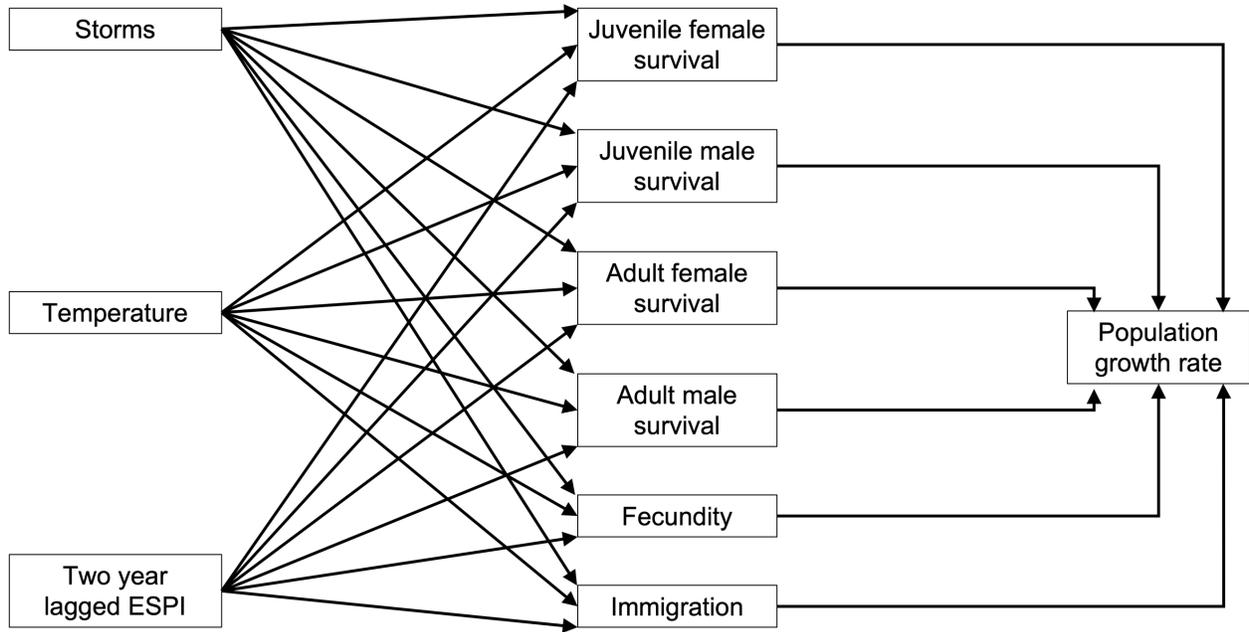
Predictor	Response	Mean	Lower	Upper
storm	juvenile female survival	0.00	-0.13	0.13
	adult female survival	-0.01	-0.16	0.11
	juvenile male survival	0.01	-0.11	0.13
	adult male survival	0.00	-0.09	0.08
	fecundity	-0.02	-0.14	0.08
	immigration	-0.01	-0.18	0.17
temperature	juvenile female survival	0.02	-0.43	0.60
	adult female survival	-0.07	-0.84	0.59
	juvenile male survival	0.13	-0.50	0.87
	adult male survival	0.05	-0.31	0.49
	fecundity	-0.08	-0.64	0.38
	immigration	-0.04	-0.87	0.82
lagged ESPI	juvenile female survival	0.01	-0.46	0.45
	adult female survival	-0.04	-0.50	0.38
	juvenile male survival	0.01	-0.30	0.39
	adult male survival	0.01	-0.21	0.27
	fecundity	-0.16	-0.79	0.44
	immigration	-0.04	-0.64	0.54
juvenile female survival	population growth rate	0.09	-1.22	1.38
adult female survival		0.21	-0.94	1.57
juvenile male survival		0.26	-1.07	1.43
adult male survival		0.39	-0.83	1.59
fecundity		0.32	-0.93	1.52
immigration		0.63	-0.64	1.98

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16 **Table S4.** Mean estimates and the lower and upper limits of the 95% credible interval from a
 17 path model fitted to assess the indirect relationships between annual weather metrics (the number
 18 of storms, the average daily high wet bulb temperature (°C), and the summed monthly El Niño-
 19 Southern Oscillation Precipitation Index (ESPI) lagged by two years) and the annual population
 20 growth rate of a population of grasshopper sparrows (*Ammodramus savannarum*) in northeastern
 21 Kansas, USA during the breeding season (May to August).

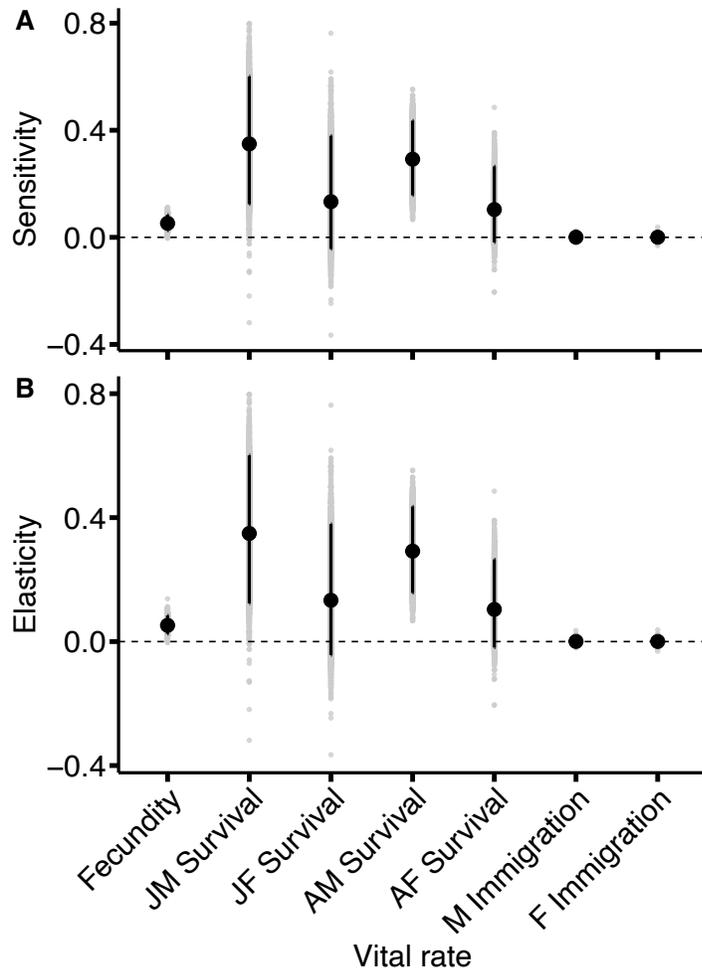
Predictor	Response	Mean	Lower	Upper
storm	population growth rate	-0.04	-0.18	0.11
temperature		0.02	-0.77	0.72
lagged ESPI		-0.21	-0.63	0.23

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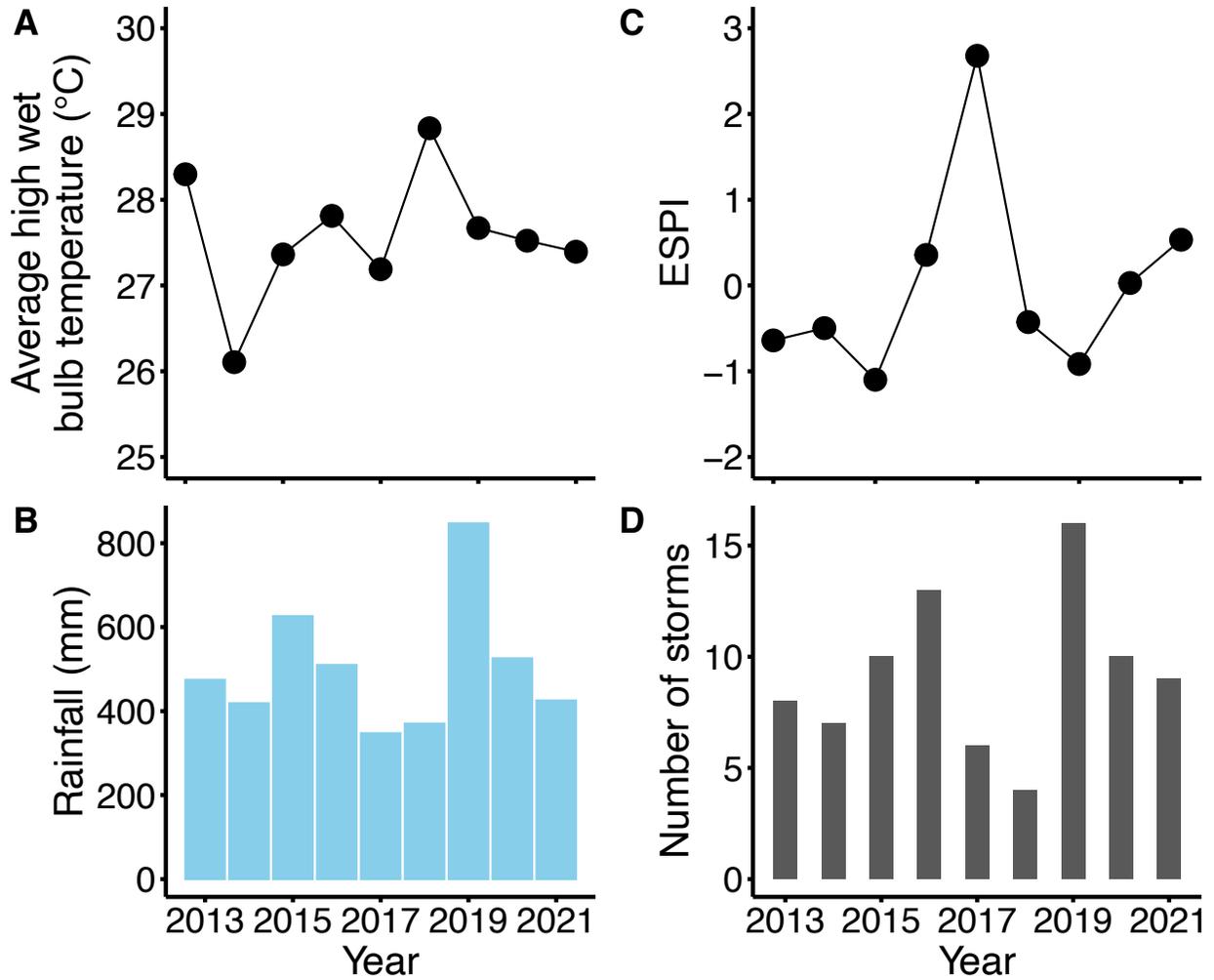
Fig.S1. Diagram of the path model fit to assess the direct and indirect relationships between annual weather metrics (the number of storms, the average daily high wet bulb temperature (°C), and the summed monthly El Niño-Southern Oscillation Precipitation Index (ESPI) lagged by two years), annual vital rates, and the annual population growth rate in a population of grasshopper sparrows (*Ammodramus savannarum*) in northeastern Kansas, USA during the breeding season (May to August).



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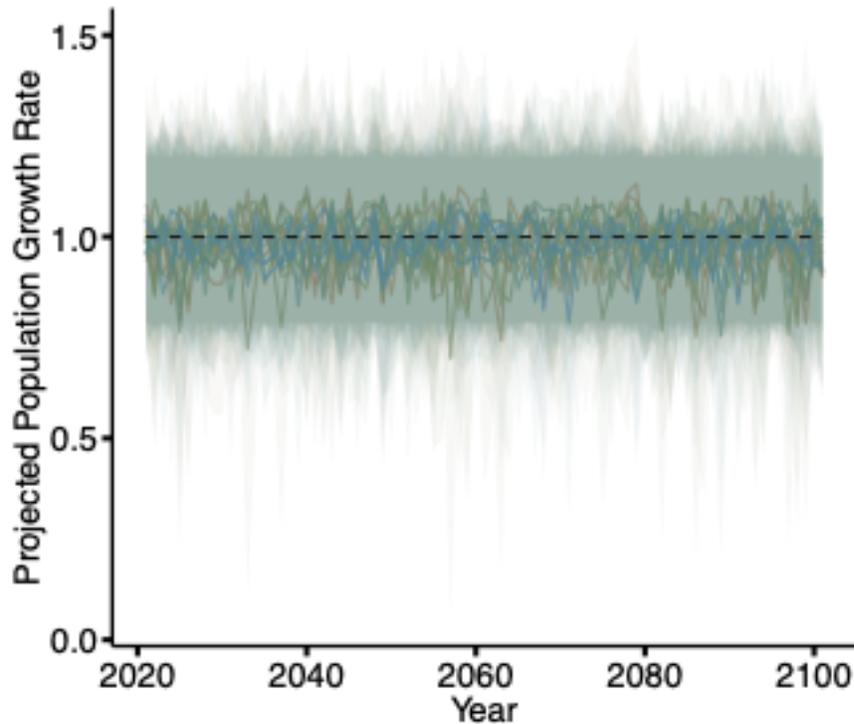
34 **Fig.S2.** Percent change in the population growth rate (λ) of grasshopper sparrows (*Ammodramus*
 35 *savannarum*) given a 5% change in each vital rate each year (i.e., sensitivity; A). The
 36 proportional contribution, or percent change scaled for vital rate units, in the population growth
 37 rate (B). The population growth rate changes more in response to adult survival than in response
 38 to changes in juvenile survival, fecundity, or immigration. JM = juvenile male, JF = juvenile
 39 female, AM = adult male, AF = adult female, M = male, and F = female.

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 42 **Fig.S3.** Change in average daily high wet bulb temperature (°C, A), total precipitation (mm, B),
 43 the monthly summed El Niño-Southern Oscillation Precipitation Index (ESPI) lagged by two
 44 years (C), and the number of storms (D) across the breeding seasons (May to August) of 2013–
 45 2021 at Konza Prairie Biological Station, KS, USA.

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48 **Fig.S4.** Projected population growth rates of a population of grasshopper sparrows
49 (*Ammodramus savannarum*) at the Konza Prairie Biological Station, KS, USA (2021–2100).
50 Future population growth rates were calculated using projected breeding season precipitation
51 lagged two years, derived from global climate models. Each line represents projections derived
52 from a different global climate model and shaded areas are 95% credible intervals around the
53 projected population growth rate.

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