

2 **Phenology dictates the impact of climate change on geographic distributions of six co-**  
3 **occurring North American grasshoppers**

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22

**Biosketch**

24 Nathan Lemoine is an Assistant Professor in the Department of Biological Sciences at Mar-  
quette University. He studies the impact of climate change on plant-insect interactions and  
26 ecosystem function. His research couples physiology with large-scale patterns using statisti-  
cal and mathematical modeling.

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**Phenology dictates the impact of climate change on geographic distributions of six co-**  
30 **occurring North American grasshoppers**

32 Running title: Phenology determines range expansion

## **Abstract**

34 Throughout the last century, climate change has altered the geographic distributions of many  
species. Insects, in particular, vary in their ability to track changing climates, and it is likely  
36 that phenology is an important determinant of how well expands can either expand or shift  
their geographic distributions in response to climate change. Grasshoppers are an ideal group  
38 to test this hypothesis, given that co-occurring confamilial, and even congeneric, species can  
differ in phenology. Here, I tested the hypothesis that early- and late-season species should  
40 possess different range expansion potentials, as estimated by habitat suitability from ecologi-  
cal niche models. I used nine different modeling techniques to estimate habitat suitability of  
42 six grasshopper species of varying phenology under two climate scenarios for the year 2050.  
My results support the hypothesis that phenology is an important determinant of range expan-  
44 sion potential. Early-season species might shift northward during the spring, while the mod-  
eled geographic distributions of late-season species were generally constant under climate  
46 change, likely because they were pre-adapted to hot and dry conditions. Phenology might  
therefore be a good predictor of how insect distributions might change in the future, and con-  
48 servation efforts might focus most heavily on early-season species that are most impacted by  
climate change.

## **50 Key words**

species distribution model; ecological niche model; orthoptera; climate change; extrapolation;  
52 phenology; grasshoppers

## Introduction

54 Throughout the last century, climate change has altered the geographic distributions of many  
species. Insects, in particular, are rapidly expanding poleward as warming enables them to  
56 colonize previously inhospitable areas (Chen *et al.*, 2011). Such range shifts are best docu-  
mented in lepidopterans, having been recorded in Europe (Parmesan *et al.*, 1999), Korea  
58 (Adhikari *et al.*, 2020), southeast Asia (Au & Bonebrake, 2019), and North America (Wilson *et al.*  
*et al.*, 2021), making butterflies and moths the characteristic example of poleward mobility. How-  
60 ever, poleward shifts of other insect species are relatively sparse, documented for a handful  
of dragonflies, lacewings, spiders, and grasshoppers (Hickling *et al.*, 2006; Chen *et al.*, 2011),  
62 or for a few economically important agricultural pests, such as the Colorado potato beetle  
(Wang *et al.*, 2017) or mountain pine beetle (de la Giroday *et al.*, 2012). The data that do exist  
64 for suggest that latitudinal shifts are quite variable among species (Chen *et al.*, 2011; Beck-  
mann *et al.*, 2015). There is, as yet, no consistent pattern that explains which insect species  
66 exhibit range shifts and which do not.

68 Life history strategy is often invoked as a determinant of potential for range shifts (Estrada *et al.*  
*et al.*, 2015), but there are few phylogenetically controlled studies that contrast different life his-  
70 tory strategies within a single clade. Orthopterans (grasshoppers, crickets, and katydids) pro-  
vide an opportunity to compare sensitivity to climate change among life history strategies,  
72 given that co-occurring grasshopper species possess a remarkable functional diversity (Deraison  
*et al.*, 2015a,b; McClenaghan *et al.*, 2015). In the United Kingdom, for example, warm-  
74 adapted, generalist grasshoppers with high dispersal ability are the only species to have un-  
dergone range expansion (Beckmann *et al.*, 2015). In the Great Plains of North America,  
76 grasshoppers can be broadly partitioned into two life history groups. Early emerging species,  
such as *Arphia conspersa*, *Eritettix simplex*, and *Xanthippus corallipes*, overwinter as nymphs

78 and emerge as adults in the spring (Capinera & Sechrist, 1982). These three species reach  
peak abundance in April or May, several months before most other grasshopper species  
80 (Buckley *et al.*, 2021). Late emerging species, such as *Arphia pseudonietana*, *Opeia obscura*,  
and *Phoetaliotes nebrascensis* overwinter as eggs, hatch in early summer, and reach the  
82 adult stage by mid-to-late summer in July or August (Capinera & Sechrist, 1982; Branson,  
2016). Given their different climatological niches, *i.e.* cold wet spring vs. dry hot summer,  
84 these species groups provide a phylogenetically controlled experiment for how life history  
might impact how species respond to climate change.

86

It is possible to compare how species of different life history strategies might respond to cli-  
88 mate change using ecological niche models (ENMs). ENMs correlate occurrence records with  
climate and are often used to predict range expansions. For example, ENMs can identify ar-  
90 eas at risk of invasion under future climates (Kistner-Thomas, 2019; Gong *et al.*, 2020) or  
identify high-priority conservation targets (Garzon *et al.*, 2021), which is critically important as  
92 the ranges of many threatened species might collapse in the near future (Lemoine, 2015).  
One shortcoming is that ENMs rarely account for phenology (Ingenloff & Peterson, 2021);  
94 many simply use mean annual temperature or precipitation (Booth *et al.*, 2014; Title & Bem-  
mels, 2018). In seasonal environments, however, mean temperature and precipitation can dif-  
96 fer markedly from the environment experienced by an organism. The shortgrass steppe of  
Colorado, on average, is 8.7 °C and receives 395 mm of rainfall per year. Yet early-season  
98 grasshoppers that emerge in May experience an environment that is 22 °C and receives 61  
mm of rain. Late-season grasshoppers, in contrast, emerge into an arid environment of 29 °C  
100 and 40 mm of rainfall. Thus, accurate predictions in ENMs require that climatological data  
match life history data as closely as possible (Ingenloff & Peterson, 2021). Using mean an-

102 nual temperature or precipitation might over or underestimate the sensitivity of species to cli-  
mate change by mis-characterizing their environmental niches.

104

Here, I tested the hypothesis that phenological differences among co-occurring species would  
106 lead to different range expansion potentials, as estimated by habitat suitability from ENMs.  
Specifically, early-occurring species that emerge as adults in April/May favor cool, wetter tem-  
108 peratures. Thus, both the southern and northern boundaries of suitable habitat conditions  
should move northward (*i.e.* total range shift) and could also occur earlier in the year, which  
110 would predict an advancing phenology. Late-occurring species that emerge as adults in July  
and August should also have suitable habitat expand northward while maintaining the current  
112 southern boundary (*i.e.* range expansion), and suitable habitat should extend later into the  
year. Contrasting phenological responses, advanced for spring species and delayed for fall  
114 species, have already been observed in flowering plants (Sherry *et al.*, 2007). To test this hy-  
pothesis, I constructed ENMs using nine separate machine learning classification techniques  
116 and predicted suitable habitat into the future for two different climate scenarios, with four gen-  
eral circulation models for each climate scenario used to produce an ensemble prediction.

118

## Methods

### 120 *Environmental Data*

To construct climatic niches, I downloaded WorldClim2 climate data (Fick & Hijmans, 2017),  
122 which is an interpolated climate dataset covering the years 1970 - 2000. As I was specifically  
examining phenological patterns, I used monthly data at a 5 arc-minute resolution. The use of  
124 monthly data restricted the environmental variables to average monthly precipitation, average  
monthly temperature, minimum monthly temperature, and maximum monthly temperature, as  
126 other WorldClim2 variables are either seasonal aggregates or unavailable at monthly time

steps. Given the extremely high correlation among temperature variables ( $r > 0.90$  for all temperature combinations, Table S1), I used only mean monthly precipitation (mPPT) and mean minimum monthly temperature ( $mT_{\min}$ ) for all subsequent analyses.

130

### *Species Occurrence Records*

132 I constructed ENMs for six grasshopper species: *A. conspersa*, *A. pseudonietana*, *E. simplex*,  
*O. obscura*, *P. nebrascensis*, and *X. corallipes*. These species are all common throughout  
134 North American grasslands and cluster into Early (*A. conspersa*, *E. simplex*, *X. corallipes*) and  
Late (*A. pseudoneitana*, *O. obscura*, *P. nebrascensis*) phenological life histories (Capinera &  
136 Sechrist, 1982). Further, these six species possessed suitable numbers of occurrence  
records; records for most other North American grasshopper species were too limited to accurately  
138 construct ENMs. I downloaded species occurrence records from GBIF in April, 2018. In  
total, there were 9,091 georeferenced locations (*A. conspersa*: 2,117; *A. pseudonietana*: 788;  
140 *E. simplex*: 2,441; *O. obscura*: 659; *P. nebrascensis*: 634; *X. corallipes*: 2,452). Date ranges  
for the six species are: *A. conspersa*: 1899 – 2013; *A. pseudonietana*: 1885 – 2013; *E. simplex*:  
142 *1912 – 2017*; *O. obscura*: 1905 – 2012; *P. nebrascensis*: 1889 – 2013; *X. corallipes*:  
1903 – 2017. Accession data are available on figshare (10.6084/m9.figshare.14411048), and  
144 distribution maps of the raw data are available in Fig. S1.

### 146 *Data Cleaning, Filtering, and Pseudoabsences*

I cleaned GBIF records following a standard pipeline (Feng *et al.*, 2019; Zurell *et al.*, 2020).  
148 First, I dropped any records with null values for latitude, longitude, month, or year. Next, I removed  
records with a '0' for latitude or longitude. I then dropped any observations that had  
150 coordinates identical to those of a US state capital city to within 0.01 decimal degrees, and  
also dropped any duplicate geographic coordinates except for those observations in different

152 months and years. Once this pre-screening was complete, I visually checked distribution  
maps and removed any erroneous observations. During visual checks, I removed two obser-  
154 vations of *E. simplex* in the southeastern US, as well as any observations falling below 20°N,  
which were outside the range of environmental layers. These data cleaning steps reduced the  
156 number of records to *A. conspersa*: 1,255, *A. pseudonietana* 309, *E. simplex*: 1,830, *O. ob-*  
*scura*: 315, *P. nebrascensis*: 372, and *X. corallipes*: 1,746.

158

I then filtered data to remove pseudoreplicates in environmental space. Although many stud-  
160 ies advocate spatial filtering, I instead filtered observations on the basis of environmental sim-  
ilarity. Such environmental filtering has shown to be more robust, less biased, and more accu-  
162 rate than spatial filtering (Varela *et al.*, 2014). For the environmental filter, I created 50 evenly  
spaced bins along both mPPT and  $mT_{\min}$ , and dropped any duplicate observations within a  
164 grid cell (Fig. S2). By removing environmental pseudoreplicates, filtering further reduced the  
number of observations to *A. conspersa*: 124, *A. pseudonietana*: 66, *E. simplex*: 85, *O. ob-*  
166 *scura*: 36, *P. nebrascensis*: 41, and *X. corallipes*: 75. The geographic distributions of these  
samples are identical to the raw data, albeit with no duplicates within a given set of coordi-  
168 nates (Fig. S3).

170 Due to the temporal aspect of the hypotheses tested here, I used a phenological approach to  
generating pseudoabsences (Ingenloff & Peterson, 2021). Briefly, for each species, I calcu-  
172 lated the number of observations falling within each month. I then generated the same num-  
ber of pseudoabsences from the mPPT and  $mT_{\min}$  for that month. The end product was the  
174 same number of observations and pseudoabsences for each species within each month. I  
chose to use equal numbers of pseudoabsences because a 1:1 ratio of observations:pseu-  
176 doabsences performs the best for many classification models (Barbet-Massin *et al.*, 2012). I

used a simple random pattern, rather than a gridded or weighted approach, because multiple  
178 studies demonstrated that simple random pseudoabsences perform at least as well as  
weighted or stratified pseudoabsences, especially for some of the classification methods used  
180 here (Barbet-Massin *et al.*, 2012; Hanberry *et al.*, 2012).

## 182 *Ecological Niche Models*

ENMs use correlative approaches to summarize the climatic niche of a species. There is a  
184 large degree of uncertainty in ENMs, including uncertainty in niches due to presence-only  
sampling, spatial biases, and in climate models. Perhaps the largest source of uncertainty,  
186 however, is among modeling techniques (Araújo *et al.*, 2005). Different methods make differ-  
ent assumptions, and these assumptions often result in variable ENM projections (Aguirre-  
188 Gutiérrez *et al.*, 2013). Here, I account for methodological uncertainty by using nine different  
machine learning approaches to construct ENMs:

190

1. *Logistic regression (GLM)*: Logistic regression is a standard technique in many ENM stud-  
192 ies. GLM proceeds by regressing the binary response variable (presence/pseudoabsence)  
against the environmental predictions mPPT and mT<sub>min</sub>. Here, I used an additive model struc-  
194 ture:

$$y \sim \text{logit}^{-1}(z)$$

196

$$z = \beta_0 + \beta_1 \text{mPPT} + \beta_2 \text{mT}_{\min}$$

that did not include an interaction between mPPT and mT<sub>min</sub>.

198

2. *K-Neighbors Classifier (KNC)*: A KNC uses a simple “vote-counting” method to assign a  
200 point to a class. Essentially, an unknown point (test data) is mapped into environmental space  
with training data. The algorithm counts the  $n$  nearest neighbors and assigns the test point to

202 the class with the majority or plurality of neighbors. The output can be converted into a proba-  
bility by counting the fraction of  $n$  points belonging to a given class. For the model here, I  
204 used  $n=5$  equally-weighted neighboring points, and the distances between training points and  
the test points in environmental space were determined via Euclidean distance.

206

3. *Gaussian Process Classifier (GPC)*: Gaussian process models treat data as arriving from a  
208 multivariate distribution, generated by an unknown function:

$$f(x) \sim GP(m(x), K(x,x'))$$

210 where  $f(x)$  is the function describing the variability of  $x$  in space,  $m(x)$  is the mean function,  
and  $K(x,x')$  is the kernel/covariance function. Because the kernels allow for covariance among  
212 observations that varies with the distance of observations, continuous Gaussian process  
models are popular for time series and spatial modeling, where they are known as 'kriging'  
214 (Brahim-Belhouari & Bermak, 2004; Roberts *et al.*, 2013). GPCs extend Gaussian process  
models to a binomial response using latent variables, much like logistic regression:

$$216 \quad f(x) = \text{logit}^{-1}(z(x))$$

$$z(x) \sim GP(m(x), K(x,x'))$$

218 where  $z(x)$  is a latent variable achieved by the logistic transformation of pseudoabsence (0)  
and presence (1) data. In practice, we often assume a constant mean:

$$220 \quad z(x) \sim GP(0, K(x,x'))$$

such that the kernel choice dictates the shape of the function. Researchers have advocated  
222 GPCs for ENMs because they are often more accurate than other classification methods,  
such as boosted regression trees, generalized additive models, and generalized linear mod-  
224 els (Golding & Purse, 2016). Here, I constructed ENMs from GPCs using the radial basis  
function:

$$226 \quad K(x,x') = \sigma^2 \exp(-0.5 l^2 (x-x')^2)$$

where  $\alpha$  is a scaling parameter determining the magnitude of process noise and  $l$  is a length  
228 parameter that determines the smoothness of the function.

230 4. *Decision Tree Classifier (DTC)*: DTCs are nonparametric, supervised machine learning  
techniques that construct decision trees using if/then rules from training data in order to infer  
232 the class of the test points. Essentially, decision trees split the data into groups then conduct  
logistic regressions to classify the training data. The split with the highest predictive ability is  
234 taken as the first decision criteria to generate two new groupings within the next level of the  
tree. The procedure proceeds iteratively within each grouping until a maximum tree depth is  
236 achieved. These models are simple, fast, and nonlinear, but can be prone to overfitting, par-  
ticularly if a tree is too deep. For the model here, I used the Gini criteria to evaluate the quality  
238 of a given split, with a maximum tree depth of 5 levels. I required each group to have a mini-  
mum of two samples.

240

5. *Random Forest Classifier (RFC)*: An RFC is a “meta”-classifier that constructs a number of  
242 DTCs from random subsamples of the training data and averages the outputs. For the RFC  
here, I generated 100 random DTCs using the same criteria as above.

244

6. *Artificial Neural Network (ANN)*: ANNs with multilevel perceptrons approximate the way hu-  
246 man brains process information by allowing computing nodes, called neurons, to process and  
share information to inform an output. Basically, ANNs consist of three layers of nodes: input  
248 nodes, hidden process nodes, and output nodes. The input layer contains nodes for each fea-  
ture (*i.e.* explanatory variable), hidden process nodes combine features with a weighted linear  
250 function, and an output function uses a nonlinear function to transform the process nodes into  
a binary or continuous response. Several authors have advocated using ANNs for ENMs

252 (Maravelias *et al.*, 2003), in particular because they outperform many other methods for con-  
structing ENMs, such as classification trees, generalized linear models, generalized additive  
254 models, and spatial interpolators (Segurado & Araújo, 2004). I trained the linear weights using  
a stochastic gradient optimizer, and the nodes were translated into a real output using the rec-  
256 tified linear unit function  $\max(0,x)$ . The ANN here had one hidden layer with 100 nodes, and a  
regularization parameter  $\alpha = 1$ .

258

7. *Ada Boost Classifier (ABC)*: The ABC is similar to RFC, in that it relies on multiple DTCs.  
260 However, whereas RFCs generate 100 random DTCs and then average the outputs, ABCs  
proceed iteratively, repeatedly fitting the same DTC on the training data but with the weights  
262 of incorrect cases adjusted so the classifier focuses on more difficult cases. I used the  
SAMME.R algorithm, stopping at a maximum of 50 iterations.

264

8. *Naïve Bayesian Classifier (NBC)*: NBCs are simple classifiers based on Bayes' rule. Bayes'  
266 rule can calculate the probability that a given map pixel should belong to a class  $k$  (*i.e.*  
present/absent) as:

268

$$p(k | x) = p(x | k) p(k) / p(x)$$

where  $x$  is the environmental variable,  $p(k | x)$  is the probability that a pixel of a given environ-  
270 ment  $x$  belongs to class  $k$ ,  $p(k)$  is the prior probability of belonging to class  $k$ , and  $p(x)$  is the  
probability of the environmental variable. For example, imagine classifying whether a pixel  
272 should be suitable habitat for a bird ( $k = \text{present}$ ), depending on whether it is forested or not.  
In this case,  $p(x | k)$  is the probability that a pixel is forest given that a bird is present, or the  
274 proportion of times a bird was observed in forests,  $p(k)$  is the proportion of sightings of the  
bird throughout the entire dataset, and  $p(x)$  is the proportion of pixels that are forested. This  
276 example has a discrete predictor, but Gaussian NBCs extend classification to continuous pre-

dictors, such as temperature, by using the Gaussian density distribution to calculate the likelihood of a given temperature given an observation of present or absent:

$$p(x | k) = (1/\sqrt{2 \pi} \sigma_k) e[-0.5(x - \mu_k)^2/\sigma_k^2]$$

In this case, the probability of a bird being present at a given temperature is

$$p(k | x) \propto p(x | k) p(k)$$

This method can be extended to multiple predictors by:

$$p(k | x_1, x_2, \dots, x_n) \propto p(x_1 | k) p(x_2 | k) \dots p(x_n | k) p(k)$$

Gaussian NBCs, along with the other methods here, can be used as a classification algorithm to model species niches (Guo & Liu, 2010). A drawback of this method is that it assumes independence of the features, but it has been shown to be an accurate method for constructing ENMs (Guo & Liu, 2010).

288

9. *Quadratic Discriminant Analysis (QDA)*: QDA is an generalization of linear discriminant analysis, and also of NBCs. As with NBCs, QDA uses Bayes' rule to maximize the posterior probability  $p(k | x)$ :

$$p(k | x) = p(x | k) p(k) / p(x)$$

There are two big differences between NBCs and QDAs. The first difference is that NBCs assume the predictors are conditionally independent, while QDA allows for the predictors to be correlated:

$$p(x | k) = \{1 / [(2 \pi)^{d/2} \Sigma^{0.5}]\} e[-0.5(x - \mu)' \Sigma^{-1} (x - \mu)]$$

where  $d$  is the number of features and  $\Sigma$  is the covariance matrix of the features. When the classes are assumed to have the same  $\Sigma$ , and also that  $\Sigma$  is diagonal (*i.e.* features are independent), this formula reduces to an NBC. If the  $k$  classes have the same  $\Sigma$ , but  $\Sigma$  is not diagonal, this formula reduces to linear discriminant analysis, as the above equation. If the classes are allowed to have separate covariances  $\Sigma_k$ :

302 
$$p(x | k) = \{1 / [(2 \pi)^{d/2} \Sigma_k^{0.5}] \} e[ -0.5(x - \mu)' \Sigma^{-1} (x - \mu)]$$

then the formula is QDA. QDA is attractive because discriminant analyses typically perform  
304 well and require no hyperparameters to tune. Parameters are fit to training data, and then the  
resulting model is used to estimate the test data.

306

Prior to analyses, both mPPT and  $mT_{\min}$  were standardized to N(0,1) distributions to improve  
308 model fitting. Data were then split into training and test groups containing 66% and 33% of the  
data, respectively. Data were split in a stratified manner to ensure equal proportions of pres-  
310 ences/pseudoabsences in both the training and test data. Models were fit to the training data,  
and then tested for goodness-of-fit on the test data using the area under ROC curves (AUC-  
312 ROC). AUC-ROC scores for each of the nine models were then averaged to produce an 'en-  
semble AUC-ROC' (Araújo *et al.*, 2005).

314

For every species, I projected the current distribution throughout every month of the year  
316 based on WorldClim2 monthly data for mPPT and  $mT_{\min}$  at 5 arc-minute resolution (Fick & Hij-  
mans, 2017). Model outputs were clipped to North American grasslands based on the US  
318 EPA Ecoregions Level 1 (Ecoregion 9.0 – Great Plains). After clipping, predictions from each  
of the nine modeling techniques were averaged to generate a single ensemble prediction for  
320 each species/month combination (*i.e.* model stacking, stacked generalization) (Araújo *et al.*,  
2005).

322

### 324 *Climate Change Projections*

I accounted for uncertainty in climate projections in two ways. First, I projected ecological  
326 niches into 2050 for intermediate and unconstrained representative concentration pathways

(RCPs). The intermediate scenario was RCP 4.5, which assumes that CO<sub>2</sub> emissions peak in 2040 and then decline, CH<sub>4</sub> emissions stop increasing by 2050, and SO<sub>2</sub> concentrations steadily decline from the present day. As a result, average global temperatures increase by 2.5 °C by 2100. The severe pathway was RCP 8.5, which assumes continuous increases in emissions throughout the 21<sup>st</sup> century, resulting in a 5 °C increase in global average temperatures by 2100. The RCP 8.5 scenario is generally considered unrealistic, as it does not account for either biological or political feedbacks to mitigate emissions (Peters & Hausfather, 2020). However, the RCP 8.5 scenario is still useful as a 'worst-case' baseline.

The final source of uncertainty is in general circulation model (GCM) projections themselves; each GCM uses different forcings and parameters, leading to considerable variability among model outputs. To account for model uncertainty, I projected ENMs into future climates using four different GCMs: BCC-CCSM-1-1, CCSM4, IPSL-CM5A-LR, and MIROC5. For each GCM, I estimated habitat suitability of each species, in every month, for each of the nine modeling techniques. I averaged the outputs from each of the nine modeling techniques to produce a single, ensemble estimate for each species/month/GCM combination. I then averaged the four GCM ensemble projections (*i.e.* four stacked models) into a single ensemble prediction of future habitat suitability in each month for each species. As above, RCP projections were trimmed to North American Grasslands using EPA EcoRegions Level 1 – 9.0 – Great Plains. GCMs are available for download from the Livermore National Lab.

348

## Results

350 Co-occurring grasshopper species possessed different climatological niches, depending on phenology. Early-season species (*A. conspersa*, *E. simplex*, and *X. corallipes*) occurred in

352 wetter, cooler conditions common in March through May, while late-season species (*A.*  
*pseudonietana*, *O. obscura*, and *P. nebrascensis*) occupied warmer, drier climate niches  
354 prevalent in July, August, and September (Fig. 1). When reconstructing these climate niches,  
modeling algorithms varied in their performance, although models performed similarly within a  
356 species (Table 1). That is, models within a species produced similar AUC-ROC scores (SD <  
0.05), with the exception of *O. obscura*, where GPCs, NBCs, and QDAs performed exception-  
358 ally well (Table 1). These models only performed well for *O. obscura*, however, and no model-  
ing technique consistently outperformed or underperformed all others across every species.  
360 For example, despite the excellent fit of NBCs and QDAs for *O. obscura*, these two methods  
provided among the poorest fits for *P. nebrascensis* (Table 1). Model stacking eliminated  
362 much of this variability and resulted in ensemble model fits that were consistent (AUC-ROC  
scores between 0.7 – 0.8) across all species, thereby eliminating the vagaries of any single  
364 classifier.

366 The ensemble ENMs successfully replicated the expected patterns of species' phenologies in  
current climate conditions. Early-season grasshoppers were prevalent throughout the south-  
368 ern and eastern Great Plains in March (Figs. 2 – 4), although *X. corallipes* appeared more  
constrained to New Mexico, western Texas, and southeastern Colorado than either *A. con-*  
370 *spersa* or *E. simplex* (Fig. 4). By April, all three species were predicted to occur throughout  
the Great Plains, except for Canada and the eastern portion encompassing Iowa and eastern  
372 Kansas (Figs. 2 – 4). By May, grasslands south of Montana and North Dakota became unsuit-  
able, except for a north-south band along the Rocky Mountains (Figs. 2 – 4). Likewise, pheno-  
374 logical ENMs of late-species grasshoppers also generally followed my hypotheses, but with  
more interspecific variability than demonstrated by early-season species. The red-winged  
376 grasshopper, *A. pseudonietana*, was confined to Montana, Alberta, and Wyoming in July (Fig.

5), whereas suitable habitat for *O. obscura* extended throughout the Great Plains, except for  
378 Kansas, most of Oklahoma, and Iowa (Fig. 6). ENMs predicted that *P. nebrascensis* should  
be found throughout the entire Great Plains in July and August (Fig. 7). By September, *A.*  
380 *conspersa* had extended the southern range limit to New Mexico and the Texas panhandle  
(Fig. 5), the range of *O. obscura* was generally the same as in July and August (Fig. 6), and  
382 the geographic distribution of *P. nebrascensis* excluded Iowa, eastern Nebraska and South  
Dakota, most of North Dakota, and the northern edge of the Great Plains in Alberta (Fig. 7).

384

I expected that climate change would cause suitable habit to expand it's northern range in  
386 March, April, and May for early-season grasshoppers. This is equivalent to both a northern  
range expansion in those months, but also to advanced phenology in those northern locations  
388 that become suitable earlier in the year. As predicted, early-season grasshoppers generally  
showed northern range expansions in the summer months. For *A. conspersa*, the northern  
390 range limit in March moved from Iowa and Nebraska to North Dakota and Montana under  
both RCP 4.5 and RCP 8.5 (Fig. 2). By April and May, however, the range of *A. conspersa*  
392 was generally unaffected by climate change, as this species already extends to the northern  
edge of North American grasslands (Fig. 2). A similar trend was predicted for *X. corallipes*  
394 (Fig. 4), while the range of *E. simplex* was unchanged for either RCP 4.5 or RCP 8.5 (Fig. 3).  
Contrary to my predictions, ENMS did not predict a southern range contraction for any of the  
396 early-season species, meaning that these species might see an expansion of suitable habitat  
area, rather than a range shift, under climate change.

398

In contrast to early-season grasshoppers, the geographic distributions of late-season species  
400 were relatively stable under both RCP 4.5 and RCP 8.5 climate scenarios, refuting my hypoth-  
esis that these species should demonstrate range expansions. For example, the geographic

402 distribution of *A. pseudonietana*, across all months, in both RCP 4.5 and RCP 8.5 was almost  
identical to the distribution of current climates (Fig. 5). Similarly, climate change had little ef-  
404 fect on the modeled distribution of *O. obscura*, except for a slight northward and eastward ex-  
pansion of suitable habitat in July and August (Fig. 6). Only *P. nebrascensis* conformed to my  
406 hypothesis with northward range expansions in all months under climate change (Fig. 7).  
However, as *P. nebrascensis* covers most of the Great Plains under current conditions, the  
408 northward expansion was relatively minor and extended into small regions in central Alberta  
(Fig. 7). Otherwise, suitable habitat for *P. nebrascensis* expanded into the eastern portions of  
410 the Great Plains (Fig. 7).

412 Examining range expansions as an increase in suitable habitat area highlighted the difference  
between early- and late-season grasshopper species. Early-season species, *A. conspersa*, *E.*  
414 *simplex*, and *X. corallipes*, generally showed a 20-80% increase in suitable habitat area dur-  
ing their phenological time period (Fig. 8), much of which was driven by northern range ex-  
416 pansion (Figs. 2 – 4). Late-season species demonstrated a lesser degree of range expan-  
sion; suitable habitat for *O. obscura* and *P. nebrascensis* increased by < 20% for most  
418 months, while *A. pseudonietana* actually showed evidence for range collapse under RCP 4.5  
(Fig. 8). As described above, much of the increase in suitable habitat for *P. nebrascensis* was  
420 a longitudinal expansion, rather than a latitudinal shift (Fig. 7).

422

## Discussion

424 As climate change alters the fundamental abiotic template of most ecosystems, many species  
are tracking favorable climates northward or at higher elevations. Yet species vary in their  
426 ability to follow suitable climates (Chen *et al.*, 2011; Beckmann *et al.*, 2015). While life history

characteristics like dispersal undoubtedly play a role in species range expansion (Beckmann  
428 *et al.*, 2015), I hypothesized that life history phenology might predict which species are most  
likely to shift poleward, as modeled by habitat suitability in future climates. Habitat suitability  
430 for early season species should advance earlier in the year, as well as shifting the entire geo-  
graphic distribution northward. Habitat suitability for late season species should be delayed  
432 longer into the fall, and should expand only the northern borders. In testing these hypotheses,  
I was able to partially confirm my hypotheses. Early-season species exhibited range expan-  
434 sions via a poleward shift of the northern range limit while maintaining southern range limits,  
while late-season species appeared largely unaffected by climate change. Thus, it does ap-  
436 pear that co-occurring species might exhibit different responses to climate change based on  
phenology, and my work highlights the need to account for phenology in species distribution  
438 modeling.

440 Phenological shifts are common responses to climate change for both plants and insects. In  
plants, warming often advances emergence and flowering dates (Price & Waser, 1998;  
442 Wolkovich *et al.*, 2012). However, not all plant species advance their phenology with warming;  
the phenological response to warming appears to largely depend on plant life history. Spring  
444 species that flower early often advance their phenology, sometimes by several weeks, while  
species that flower in fall can delay their phenology (Sherry *et al.*, 2007). Like plants, insects  
446 also advance their emergence dates (Ellwood *et al.*, 2012), yet no study has tested whether  
life history strategies might affect how insects alter their geographic distributions in response  
448 to climate change. Grasshoppers are an ideal system to test for such possibilities because  
co-occurring species, indeed even co-occurring congeners as in the case of *Arphia*, possess  
450 early and late phenologies (Capinera & Sechrist, 1982), providing the opportunity for phyloge-  
netically controlled tests of range expansion.

My study supports the hypothesis that, as with plants, phenology might be an important predictor of how species respond to climate change. In this study, early season species did not advance their phenology across the board, but only in the northern-most regions of the Great Plains (Figs. 2-4). Viewed spatially, this pattern amounts to a northern range expansion in early spring, and viewed temporally, it amounts to an advance phenology in those northern areas. However, late-season species that share the same geographic distribution as early-season species might be less sensitive to climate change. This is likely because climate change will make much of North America both warmer and drier (Sheffield & Wood, 2008; Greve *et al.*, 2014), an environment to which late-season grasshoppers are already adapted. Importantly, no species here showed a range collapse; all grasshopper species examined here are predicted to maintain, if not expand, their current range size. This matches predictions of many other insects (de la Giroday *et al.*, 2012; Au & Bonebrake, 2019; Wilson *et al.*, 2021), and suggests that climate change might not directly precipitate the decline of insect abundances.

An important caveat is that the ENMs reported here account for only climate and do not include biotic interactions. Though ENMs here predicted range expansions, grasshoppers could experience a large decline in range size in the future with continued disappearance of grasslands, caused by either climate or land-use change. A recent study from Germany found that land-use change and habitat loss were major factors responsible for a decades-long collapse of insect populations (Hallmann *et al.*, 2017). In ENMs, habitat availability can be the strongest determinant of insect distributions in both current and future climates (Lemoine, 2015). Thus, although the ENMs presented here suggest that grasshopper ranges should remain stable, if not increase, in the future, grasshoppers might become geographically restricted

with the continued loss of grasslands. Some grasses, like *A. gerardii*, are predicted to decline  
478 in abundance and extent in the future (Smith *et al.*, 2017), and grasslands are under constant  
threat of development or agricultural use. Though the abiotic environment might remain favor-  
480 able to grasshoppers *per se* in the future, there are a number of other factors that will ulti-  
mately determine the geographic distribution of North American grasslands in the future.

482

Projecting species distributions in future climates remains an important avenue of research.  
484 Doing so can inform us of habitat potentially at risk from species invasions (Kistner-Thomas,  
2019; Gong *et al.*, 2020), identify species at risk of collapse (Lemoine, 2015), and pinpoint re-  
486 gions of high priority for conservation (Garzon *et al.*, 2021). In doing so, researchers must  
carefully account for source of uncertainty. In this study, I accounted for model uncertainty by  
488 using nine different ENM estimation techniques, for projection uncertainty by using four sepa-  
rate GCMs, and for scenario uncertainty by using RCP 4.5 and 8.5 My results illustrate that  
490 phenology can be a good predictor of how insect distributions might change in the future. For  
North American grasshoppers, early-season species from cool environments are likely to ex-  
492 pand the northern range extent, while late-season species that are already adapted to hot and  
dry conditions will likely see only modest changes in geographic distribution. Thus, conserva-  
494 tion efforts might focus most heavily on early-season species that are most impacted by cli-  
mate change.

496

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646 **Data Accessibility**

All data, scripts, and figures available on figshare: [10.6084/m9.figshare.14411048](https://doi.org/10.6084/m9.figshare.14411048)

648 **Table 1.** AUC-ROC estimates for each model type for each of the six species. GLM: logistic  
 regression, KNC: K-nearest neighbors, GPC: Gaussian process classifier, DTC: Decision tree  
 650 classifier, RFC: Random forest classifier, ANN: Artificial neural network, ABC: Ada boost clas-  
 sifier, NBC: Naive Bayesian classifier, QDA: Quadratic discriminant analysis. Ensemble  
 652 shows the average +/- 1 SD of the nine models.

	<b>Early species</b>			<b>Late species</b>		
	<i>Arphia conspersa</i>	<i>Eritettix simplex</i>	<i>Xanthippus corallipes</i>	<i>Arphia pseudonietana</i>	<i>Opeia obscura</i>	<i>Phoetaliotes nebrascensis</i>
<i>GLM</i>	0.76	0.68	0.62	0.78	0.79	0.74
<i>KNC</i>	0.80	0.81	0.75	0.66	0.86	0.74
<i>GPC</i>	0.83	0.71	0.68	0.81	0.92	0.60
<i>DTC</i>	0.77	0.70	0.62	0.77	0.64	0.74
<i>RFC</i>	0.83	0.77	0.71	0.79	0.81	0.78
<i>ANN</i>	0.85	0.74	0.68	0.84	0.82	0.65
<i>ABC</i>	0.76	0.72	0.66	0.71	0.72	0.65
<i>NBC</i>	0.82	0.71	0.69	0.85	0.97	0.64
<i>QDA</i>	0.82	0.75	0.68	0.85	0.99	0.66
<i>Ensemble</i>	0.81 +/- 0.03	0.73 +/- 0.04	0.68 +/- 0.04	0.78 +/- 0.07	0.84 +/- 0.11	0.69 +/- 0.06

654

656 **List of Figures**

658 1. Early-season grasshopper species were characterized by wetter, cooler conditions than late-season species. This graph shows mPPT and mT<sub>min</sub> for each observation of the cleaned, environmentally filtered data. Each point is a unique observation.

660 2. Predicted, current distribution of the early season species *Arphia conspersa* in March, April, and May throughout the Great Plains of North America under current conditions, RCP 4.5, and RCP 8.5. Predictions are the ensemble/stacked averages from the nine different classifiers. The color palette was chosen so that regions where absence is more likely than presence (probability of occurrence < 0.5) are shaded in blue, while regions where presence is more likely than absence (probability of occurrence > 0.5) are shaded in reds. Regions where presence and absence are equiprobable (probability of occurrence ~ 0.5) are shaded in whites/greys.

668 3. Predicted, current distribution of the early season species *Eriotettix simplex* in March, April, and May throughout the Great Plains of North America under current conditions, RCP 4.5, and RCP 8.5. Predictions are the ensemble/stacked averages from the nine different classifiers. The color palette was chosen so that regions where absence is more likely than presence (probability of occurrence < 0.5) are shaded in blue, while regions where presence is more likely than absence (probability of occurrence > 0.5) are shaded in reds. Regions where presence and absence are equiprobable (probability of occurrence ~ 0.5) are shaded in whites/greys.

676 4. Predicted, current distribution of the early season species *X. corallipes* in March, April, and May throughout the Great Plains of North America under current conditions, RCP 4.5, and RCP 8.5. Predictions are the ensemble/stacked averages from the nine different classifiers. The color palette was chosen so that regions where absence is more likely than presence (probability of occurrence < 0.5) are shaded in blue, while regions where presence is more

likely than absence (probability of occurrence  $> 0.5$ ) are shaded in reds. Regions where presence and absence are equiprobable (probability of occurrence  $\sim 0.5$ ) are shaded in whites/greys.

5. Predicted, current distribution of the late season species *A. pseudonietana* in March, April, and May throughout the Great Plains of North America under current conditions, RCP 4.5, and RCP 8.5. Predictions are the ensemble/stacked averages from the nine different classifiers. The color palette was chosen so that regions where absence is more likely than presence (probability of occurrence  $< 0.5$ ) are shaded in blue, while regions where presence is more likely than absence (probability of occurrence  $> 0.5$ ) are shaded in reds. Regions where presence and absence are equiprobable (probability of occurrence  $\sim 0.5$ ) are shaded in whites/greys.

6. Predicted, current distribution of the late season species *O. obscura* in March, April, and May throughout the Great Plains of North America under current conditions, RCP 4.5, and RCP 8.5. Predictions are the ensemble/stacked averages from the nine different classifiers. The color palette was chosen so that regions where absence is more likely than presence (probability of occurrence  $< 0.5$ ) are shaded in blue, while regions where presence is more likely than absence (probability of occurrence  $> 0.5$ ) are shaded in reds. Regions where presence and absence are equiprobable (probability of occurrence  $\sim 0.5$ ) are shaded in whites/greys.

7. Predicted, current distribution of the late season species *P. nebrascensis* in March, April, and May throughout the Great Plains of North America under current conditions, RCP 4.5, and RCP 8.5. Predictions are the ensemble/stacked averages from the nine different classifiers. The color palette was chosen so that regions where absence is more likely than presence (probability of occurrence  $< 0.5$ ) are shaded in blue, while regions where presence is more likely than absence (probability of occurrence  $> 0.5$ ) are shaded in reds. Regions where

706 presence and absence are equiprobable (probability of occurrence  $\sim 0.5$ ) are shaded in  
whites/greys.

708 8. Percent change in suitable habitat area for each species under two climate scenarios. Suit-  
able habitat area was calculated as the number of grid cells where the probability of occur-  
710 rence was greater than 50%.