Assessing ecological and environmental influences on boreal chorus frog (*Pseudacris maculata*) spring calling phenology using multimodal passive monitoring technologies

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ABSTRACT

Although anuran reproductive behavior follows a phenological pattern, environmental factors may influence the timing of anuran activity. To characterize the spring calling phenology of *Pseudacris maculata* (boreal chorus frog) we installed acoustic recorders during three spring breeding seasons (2015–2017) within wet meadow and forested slough habitats in central Nebraska near the Platte River. The recorders were paired with time-lapse camera systems that were used to measure vegetation change and wet meadow inundation. We examined the relationship between environmental variables, including temperature, precipitation, and hydropattern, and *P. maculata* calling activity using random forest models. Calling activity exhibited diel and seasonal variation with differences observed between habitats. Hourly call activity was highest between 20:00 and 01:00, with diurnal and sometimes near-continuous calling observed at the wet meadow but not at the forested slough. Random forest models explained 73% of calling activity variance at the wet meadow and 45% at the forested slough, suggesting additional factors, such as predation, may be influential at the forested slough, as it exhibited near permanent hydrology. *P. maculata* was predicted to increase chorusing at the 70th day of the year at the wet meadow but not until the 100th at the forested slough. When average air temperatures exceeded 5 °C, calling activity was predicted to increase at both wetlands, and calling declined below this temperature. Hydropattern and weekly precipitation accumulation were important predictors of *P. maculata* calling activity. Our findings highlight the importance of climatic factors such as temperature and precipitation regimes, in addition to habitat conditions such as water-availability, on *P. maculata* calling activity. Furthermore, this study demonstrates the utility of multimodal passive monitoring technologies, including both visual and auditory tools, for understanding the environmental factors that influence biological activity. Multimodal approaches can be especially useful for documenting and measuring vocal-taxa diversity, activity, and drivers of change.

1. Introduction

The relationship between animals and their environment is synchronously intertwined, as biotic and abiotic conditions influence the timing of important animal behaviors (Johansson et al., 2015). In temperate regions, amphibians such as anurans have adapted life history strategies aligned with local climatic and physical conditions (Lofts, 1974; Amburgey et al., 2012). Over the last four decades, anuran populations have declined globally due to compounding factors including changes in land and water use, habitat loss, pathogens, and a changing climate (Sodhi et al., 2008; Grant et al., 2016; Green et al., 2020). In the Great Plains, amphibians are declining by an estimated >3% annually, however, information on anuran phenology and environmental drivers of anuran behavior in the region is sparse (Mushet et al., 2012; Grant et al., 2016). Often anuran research, including trapping, manual listening, and visual encounter surveys, is conducted for short periods at infrequent intervals (Bridges and Dorcas, 2000). For elusive yet vocal animals, such as small and mostly nocturnal anurans, auditory surveys

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have proven beneficial for monitoring, for example the North American Amphibian Monitoring Program (Weir and Mossman, 2005). As their main form of communication, anurans vocalize predominately to attract mates and alert rival males to their presence (Bee et al., 2010). Manual listening surveys of anuran calling frequency, intensity, and number (usually in the form of scaled indices) can be used to model species behavioral patterns, spatial distribution, temporal occurrence, and responses to environmental change (Stevens et al., 2002; Nelson and Graves, 2004; Both et al., 2008). Although these methods can provide important information about long term trends and change, the data is often temporally limited, which can be problematic considering the high variability in anuran calling activity (Bridges and Dorcas, 2000; Todd et al., 2003). Passive acoustic recording, which is increasingly used to monitor and assess changes in soundscapes (Pijanowski et al., 2011), ecosystem state (Sueur and Farina, 2015), and vocalizing taxa including bird communities (Gasc et al., 2017; Abrahams and Geary, 2020) and bat activity (Whitby et al., 2014; Reichert et al., 2018), may offer an alternative with higher temporal resolution at hourly or daily intervals (Digby et al., 2013; Sugai et al., 2019). Moreover, this technology remains comparatively underutilized for anurans considering its potential benefits (Bee et al., 2010; Madalozzo et al., 2017; Brodie et al., 2020).

Anuran calling activity exhibits a phenological pattern, occurring during the breeding season but influenced by biotic and abiotic factors, including habitat, vegetation, hydrology, food availability, and climatic factors (Oseen and Wassersug, 2002; Klaus and Lougheed, 2013; Ospina et al., 2013). Changes in climatic and habitat conditions, such as an altered hydrologic regime or vegetation phenophase, can result in phenological shifts of behavior, such as reproduction, leading to potential resource mismatches (Klaus and Lougheed, 2013). Studies have consistently found that temperature influences the lifecycle and activity of ectothermic anurans, however even similar species have shown differential responses to temperature regimes (Oseen and Wassersug, 2002; Hillman et al., 2009; Steelman and Dorcas, 2010). Many anuran species are dependent upon aquatic-terrestrial ecotones, utilizing terrestrial habitat during their adult phase and aquatic habitat during reproduction and metamorphose, and therefore, water availability generally plays an important role in reproductive behavior (Ryan and Winne, 2001; Amburgey et al., 2012). However, the magnitude and mechanism of influence, such as precipitation or hydropattern (the hydroperiod, hydrologic fluctuation, timing, and flow regime of a system; Matthews et al., 2013; Amburgey, 2014), likely differs between ephemeral and permanent or semi-permanent wetlands, as well as geographic regions, and by species (Werner et al., 2009; Ospina et al., 2013). In addition to the hydropattern of a system, habitat conditions such as vegetation structure may influence calling, as many anurans, including *Pseudacris maculate* (boreal chorus frog), depend on plants for protection from predators, cling to vegetation during chorusing, as well as lay egg masses beneath vegetation (Conant and Collins, 1991; Andersen et al., 1999; Grant et al., 2015).

P. maculata, a small (~3.3 cm) trilling chorus frog, is found in emergent wetlands and grasslands across central parts of the United States and Canada, with statewide distribution in Nebraska (Fogell, 2010). Populations of *P. maculata* are broadly considered stable, however, declines in *Pseudacris* species (*sensu lato*, trilling chorus frogs) have been observed in several regions, including the Great Plains, Midwest, eastern Ontario, western Quebec, as well as possible extirpation from New York and Vermont (Knutson et al., 2000; Seburn et al., 2014). Studies show that *P. maculata* are exposed to a myriad of threats, including human influences, disease, toxins, and climatic factors (Grant et al., 2016), and populations are impacted by drought and flooding (Werner et al., 2009; Grant et al., 2015). In the Great Plains, *P. maculata* chorusing is often one of the earliest vocalizations heard and an iconic sign of spring, with breeding taking place as early as March and continuing as late as May with occasional breeding activity into the summer following large precipitation events (Jones et al., 1981; Fogell, 2010). As *P. maculata* exhibits an early spring phenological pattern,

likely driven by weather and habitat conditions, pairing auditory and visual autonomous technologies can provide documentation of local biotic and environmental changes at various scales, which may help to disentangle complex ecological interactions (Buxton et al., 2018).

In this study, we aimed to assess how *P. maculata* calling activity related to local environmental conditions in central Nebraska during three spring breeding seasons (2015–2017) using multimodal passive monitoring technologies. We used aural surveys, acoustic metrics, and automated classification of sound recordings to examine hourly and daily call activity patterns and characterize variability in *P. maculata* spring calling phenology. Image analysis was used to quantify changes in hydroperiod and vegetation. We assessed the importance of hydropattern (inundation and river streamflow), vegetation, temperature, wind speed, precipitation, and snowfall on *P. maculata* activity using random forest models. We examined the call activity of *P. maculata* within wet meadow habitat compared to a semi-permanent forested wetland. Combining acoustic and visual monitoring technologies, our research attempted to gain insight into the phenological patterns of *P. maculata* spring calling activity and to identify important environmental factors influencing activity.

2. Methods

2.1. Study area

The study was conducted in the Central Platte River Valley (CPRV) of Nebraska, an important avian stopover location within the Central Flyway migration corridor (Vrtiska and Sullivan, 2009; Pearse et al., 2011; Caven et al., 2019a). The region is used by endangered whooping cranes, hundreds of thousands of sandhill cranes, and millions of other waterbirds as a stopover to rest and refuel by foraging on vegetation, fish, insects, and anurans (Lingle et al., 1991; LaGrange, 2005; Vrtiska and Sullivan, 2009; Geluso et al., 2013; Caven et al., 2019b, 2020). The Platte River extends the reach of tallgrass prairie habitat west into the mixed-grass ecoregion in central Nebraska as a result of subirrigation, and relatively minor elevational changes within this riverine ecosystem provide for a dynamic set of wetland habitats with varying hydroperiods (Currier, 1995; Whiles and Goldowitz, 2005; Kaul et al., 2011). Wet meadows represent more ephemeral wetlands with shorter hydroperiods that usually experience inundation through the early spring, while shallow and deep marsh habitats experience increasing hydroperiods lasting into the summer or even throughout the growing season in some years (Kantrud et al., 1989; Currier, 1995; Whiles and Goldowitz, 2005; Tiner, 2016). These wetlands are connected to the hydrology of the Platte River, which experiences high flows in the spring from snowmelt with declining streamflow into the summer (Williams, 1978; Eschner et al., 1983; Currier and Henszey, 1996). Historically, the Platte River was a wide braided river that sustained a large number of riparian wetlands within a grassland mosaic (Smith, 1971; Williams, 1978; Currier and Henszey, 1996). However, over the last century, extensive land and water use changes have altered the landscape, negatively impacting river hydrogeomorphology, wetland hydrologic connectivity, and wildlife (Sidle et al., 1989; Eschner et al., 1983; Horn et al., 2012; Alexander et al., 2020). Conversion of grassland and wetland habitats to agriculture and diversions for irrigation has removed or retimed the majority of streamflow in the Platte River and erased over 70% of wet meadows and other wetlands from the CPRV (Williams, 1978; Eschner et al., 1983; Sidle et al., 1989; Currier and Henszey, 1996). Understanding how hydrologic and environmental fluctuations influence boreal chorus frog activity in the remaining high-quality wetlands should further inform habitat conservation and restoration efforts focused on preserving this species.

2.2. Environmental variables

Weather data was acquired from the National Oceanic and

Atmospheric Administration, National Centers for Environmental Information, Global Historical Climatology Network–Daily database (Menne et al., 2012). We obtained data from Kearney, NE (station USC00254335) for the forested slough and Grand Island, NE (station USW00014935) for the wet meadow. Daily variables included average wind speed, total precipitation, mean, maximum, and minimum air temperature, snow accumulation and snow depth. Average wind speed was only available at the Grand Island weather station and was therefore used for both study sites. Hydropattern relating to the forested slough was obtained from a USGS stream gage for the Platte River at Kearney, Nebraska (USGS 06770200).

We derived vegetation phenology and water inundation data from analysis of time-lapse images from Mormon Island and Rowe Sanctuary Tower cameras of the Platte Basin Timelapse project, a long-term monitoring and science communication project documenting the Platte Basin (www.plattebasintimelapse.com). The time-lapse camera systems, consisting of a Nikon D300 DSLR with a 12.3 megapixel crop sensor and Nikkor 18–70 mm 1:3.5–4.5 lens set at F/8 and powered by a solar panel, took one image every hour of sunlight. Images were processed by selecting daily images taken between 10:00 and 14:00 to standardize for sun exposure and shadows. We then visually inspected the imagery collections, and images with obstructed views or inconsistencies, such as fog or spider webs, were removed from the analysis. Based on the digital number (DN) within the red–greenblue (RGB) colorspace of a pixel, we calculated green chromatic coordinates (GCC), a greenness index of vegetation phenology (Sonnentag et al., 2012). At each site, we selected a region of interest (ROI) that encompassed vegetation and excluded sky and other features within the frame of view. GCC was calculated for each site's ROI using the equation GCC = G/[R + G + B] (Richardson et al., 2018).

For the wet meadow at Mormon Island, we assessed water inundation through image-analysis using a macro script adapted from microscopy in the Java-based open-access program FIJI (Schindelin et al., 2012; Brinley Buckley et al., 2017). A ROI, separate from the ROI used to calculate GCC, was selected that excluded sky, horizon, and additional grassland landscape to reduce variability. The RGB colorspace was transformed to hue-saturation-value (HSV) to overcome potential limitations of the RGB color space for classifying water (Pekel et al., 2014). The ROI was converted to binary (0,1) by automated thresholding (threshold = (average background + average objects)/2). The binary masked results were visually inspected and manually compared to the original image for accuracy, and if a mask was visibly inaccurate, the original image was classified by manually tracing water inundation. A proxy for ponding surface water, the resulting water inundation (WI) values were the percent area classified as water within the region of interest. The final dataset was averaged into daily values and rescaled to a 0 to 1 value.

2.3. Acoustic analyses

We installed two digital autonomous acoustic recorders paired with time-lapse camera systems within the CPRV from 1 March 2015 to 1 June 2017. Recorders were deployed next to the cameras approximately 1.5 m above the ground. The first paired monitoring system was within Mormon Island, a wet meadow habitat between two channels of the Platte River in southcentral Nebraska (40.799, −98.417). The site is generally devoid of trees and dominated by sedges (*Carex* spp.), common threesquare (*Schoenoplectus pungens*), and slimstem reedgrass (*Calamagrostis stricta*). The site is managed using patch-burn-grazing to simulate natural disturbances (See Fuhlendorf et al., 2009) by the Crane Trust for the benefit of sandhill cranes, whooping cranes, other migratory birds, and overall biological diversity. The second site was a wetland slough, which is a linear swale supporting wetland habitat (Meyer and Whiles, 2008), in this case predominantly deep marsh, at Audubon's Rowe Sanctuary in Gibbon, Nebraska (40.667, −98.892). The slough exists within a former channel of the Platte River in a

complex of accumulated sediment and deposited organic material, resulting from reduced flows over the last century, and one bank includes an erosion control structure built before 1938 as indicated by aerial photographs. The site is dominated by cattails (*Typha* spp.) and is immediately surrounded by trees including green ash (*Fraxinus pennsylvanica*), plains cottonwood (*Populus deltoides*) and woody shrubs including false indigo bush (*Amorpha fruticosa*). This forested slough site sits 22 m south of the Platte River's main (south) channel and retains standing water nearly year-round, while the wet meadow site rarely contains standing water beyond May (Brinley Buckley et al., *In Review*).

The two autonomous acoustic recorders (Song Meter SM2+; Wildlife Acoustics) recorded for one minute out of every twenty minutes, starting on the hour, for a total of three recordings per hour. The sampling rate was 44.1 kHz, the gain was 36 dB, and the bit depth was 16 bits. Each recorder had two omnidirectional microphones with a flat frequency response from 20 Hz to 20 kHz. All incomplete recording days, defined as a day with less than the expected 72 one-minute recordings per 24-hour period, were removed prior to analysis. Recordings were then down-sampled to 8 kHz to accelerate computation time, as *P. Maculata* vocalizations average between 2.7 and 4.2 kHz throughout their range (Bee et al., 2010). Next, stereo tracks were converted to mono. In some cases, the sensitivity of one of the two microphones degraded over the course of deployment, possibly due to rain or other environmental factors. In these cases, we selected the channel of the intact microphone. If there were no microphone performance issues, the channel was randomly selected. We quantified the acoustic activity of chorus frogs by detecting their calls with spectral cross-correlation. This method measures the pixel-by-pixel similarity between the spectrogram of a template call and the spectrogram of windowed selections of a recording (Hafner and Katz, 2018). This method is particularly effective for species with stereotypical calls, such as the characteristic call of *P. maculata,* a rising trill that sounds like fingers running across a comb. However, its call frequency, structure, and rate vary depending on environmental factors like temperature as well as physical characteristics (Bee et al., 2010). *P. maculata* also form choruses, where the calls of different individuals overlap. To accommodate this variation, we created 12 templates for the analysis consisting of a range of observed vocalizations (e. g. different fundamental frequency, call lengths, chorus densities; Table 1). To help quantify the diversity of call templates, we measured their center frequencies and inter-pulse distances in Raven 1.6.1 using spectrograms that had a window length of 256 and a Hann window (Raven Pro: Interactive Sound Analysis Software, 2019). Center frequency refers to the frequency that divides a template recording into two frequency intervals containing equal energy. Inter-pulse distance refers to the interval between consecutive pulses within a call, from the offset of one pulse to the onset of the next; it was manually measured only for non-chorus templates by taking the mean of three inter-pulse intervals per clip. We used the R package "monitoR" (Hafner and Katz, 2018) to perform the spectral cross-correlation, utilizing a window length of 256 and a temporal overlap of 75%. Correlation peaks above a cutoff threshold of 0.4 were counted as detections. As we utilized 12 call templates, there was potential that different templates would detect the same chorus frog call, inflating the total count. To avoid duplicating detections, we divided each recording into 240, 0.25-second windows and counted a detection if the 0.25-second window contained one or more detections. To assess the accuracy of detection algorithms, we assessed their true positive rates by generating 1000 random files from February-May and manually identifying if *P. maculata* was detected via listening and visual inspection of spectrograms.

As detections did not indicate or attempt to approximate a count or true abundance of *P. maculata*, vocalization detections were scaled to create a calling activity index from 0 to 1, where 0 indicates no vocalizations and 1 indicates the highest calling activity of *P. maculata* chorusing during the study. This represents a logical rescaling of count data to a ratio scale, which may help improve interpretation of our abundance index, which is both a reflection of local density as well as

Table 1

Bioacoustic information for the 12 *Pseudacris maculata* call templates used in "monitoR", including call type, lower and upper frequency bounds (of the template, not the call itself), center frequency, duration (of the template, not the call itself), and inter-pulse distance. Center frequency and inter-pulse distance were calculated using Raven 1.6.

Template	Type	Low frequency (kHz)	High Frequency (kHz)	Center Frequency (kHz)	Duration(s)	Inter-Pulse Distance (s)
Frog 1	Chorus	2.5	4.0	3.2	0.30	NA
Frog 2	Chorus	2.7	3.6	3.1	0.30	NA
Frog 3	Chorus	2.6	4.0	3.3	0.31	NA
Frog 4	Chorus	2.6	4.2	3.3	0.30	NA
Frog 5	Chorus	2.6	4.0	3.2	0.30	NA
Frog 6	Individual	2.8	4.5	3.6	0.30	0.05
Frog 7	Individual	3.0	3.9	3.4	0.30	0.06
Frog 5	Individual	2.7	3.6	3.1	0.25	0.04
Frog 9	Individual	2.8	4.0	3.2	0.30	0.06
Frog 10	Individual	2.6	3.6	3.1	0.15	0.01
Frog 11	Individual	2.7	3.6	3.1	0.15	0.02
Frog 12	Individual	2.9	3.6	3.2	0.16	0.03

activity level (Schneider, 2009; Pijanowski et al., 2011).

2.4. Statistical analysis

All analyses characterizing the hourly and daily call activity of *P. maculata* were conducted within R (R Development Core Team, 2020). To assess diel activity we calculated how many recordings had at least one *P. maculata* vocalization identified out of 72 recording intervals per day, or the calling activity frequency. We set a threshold of 0.8 to represent a high frequency of calling, indicative of near 24-hour continuous call activity, and calculated monthly averages. We calculated summary statistics for all variables, in addition to calculating Spearman's Rank Correlation Coefficients to assess daily calling activity in association with environmental variables.

We used random forest regression to determine factors of importance for *P. maculata* calling activity using the "randomForest" package (Liaw and Wiener, 2002). Random forest (RF) is a machine learning technique based on averaging a large collection of decision trees. Each tree is trained on a random bootstrap sample, while each split within a tree is sampled from a subset of candidate variables, making RF less susceptible to overfitting, more robust to correlations, and reducing variance compared to a single decision tree (Breiman, 2001). RF models are non-parametric, non-linear, and can handle numerous continuous and categorical predictor variables. In addition, they can handle complex data with relatively limited observations (Cutler et al., 2012), a common issue with ecological data. RF provides a permutation-based measure of variable importance (VIMP), using mean squared error (MSE) for regression, which denotes the decrease in model accuracy given a variable is removed from the model. We built site-specific RF models with all candidate predictor variables including wind (WND; average wind speed; mph), precipitation (PRCP; daily accumulation; cm), 7-day precipitation (PRCP7; weekly accumulation; cm), 1-day lag precipitation (PRCP1; day prior daily accumulation; cm), daily mean, maximum, and minimum air temperature (TAVG, TMAX, TMIN; °C), day of year (DOY), green chromatic coordinates (GCC), snow (SNW; daily accumulation; cm), and snow depth (SNWD; cm), and included year to account for annual variability. Hydropattern was also included in the models, with water inundation (WI) included for the wet meadow and Platte River streamflow (CMS; m^3/s) at the forested wetland. The number of variables selected as candidates at each split was set to three, and the model was tested and pruned to 500 trees to reduce overfitting. Variables were ranked by variable importance score, and variables with negative MSE scores, indicating they negatively influenced prediction accuracy, were removed from the model. Relationships between environmental variables and *P. maculata* activity were examined using partial dependence plots, which predicts the response of *P. maculata* to a given variable holding all other variables in the model at their mean.

3. Results

From 2015 to 2017 we totaled 472 recording days (227 at wet meadow/Mormon and 245 at forested slough/Rowe) during the spring breeding season (March–June). During the three years of our study, data were missing for 49 days at the wet meadow (18%) and 31 days at the forested slough (11%) due to equipment malfunction or removal of days with incomplete recording intervals. Assessment of detection algorithms resulted in an overall true positive (TP) rate of 97.8% (n = 1000). At Mormon Island, the TP rate was 98.4% (n = 853), and at the forested slough, the TP rate was 94.6% (n = 147). For the sampling duration, mean daily average temperature was approximately 8 °C, ranging from approximately −15 to 24 °C (Table 2). Mean daily precipitation accumulation was approximately 0.2 cm and ranged from 0 to 5.23 cm at Mormon and 0 to 10.16 cm at Rowe, with highest mean and median precipitation in 2016 (Fig. 1). Mean streamflow for the Platte River was 85 m^3/s, with the highest mean and median streamflow occurring in 2016 (107 m^3/s; Fig. 1). Mean streamflow was highest in May followed by March, with the highest variability in May 2015. Contrastingly, wet meadow inundation had the highest mean in March of 2016 and 2017 and was relatively similar across months in 2015, while inundation had the greatest range in April of all years (Fig. 1). The wet meadow had the highest mean inundation in 2016 (0.51), in addition to the highest peak extent of inundation (Table 2).

For the duration of the study, *P. maculata* vocalizations on average were highest between 20:00 and 01:00 (8:00 pm to 1:00am) at both sites, and activity decreased between 01:00 and 02:00 markedly (Fig. 2). Calling activity increased moderately between 08:00 and 15:00 in the wet meadow, however this trend was not observed at the forested wetland. Monthly averaged calling frequency, with a threshold of 0.8, also differed between habitats. At the wet meadow, *P. maculata* called near continuously 18% of days in March, 30% of days in April, and 37% of days in May. Comparatively, at the forested slough, *P. maculata* called continuously 0% of days in March, 9% of days in April, and 6% of days in May (Fig. 3). In addition, calling frequency differed by year, with nearly continuous calling occurring at the wet meadow>40% of the time in April and May of 2016 and 2017 (Figs. 1 and 3).

At both sites, *P. maculata* calling activity was highest during April of all years, with the exception of the forested slough in 2017, where vocalizations were greater in May (Fig. 3). Generally, calling activity was sustained from March to May, with vocalizations beginning on average the first week of March (mean DOY 60), peaking from early to mid-April depending on site (mean DOY 92 at Mormon, mean DOY 111 at Rowe), with a second peak occurring the first week of May (mean DOY 124).

Snow and snow depth negatively contributed to the predictive accuracy of the random forest models at both sites and therefore were removed from the final models. Once the models were adjusted, the RF model explained 73% of the variance in *P. maculata* calling activity at the wet meadow (MSE = 0.02), while for the forested slough, the RF

Table 2

Summary statistics (min = minimum, max = maximum, mean, and sd = standard deviation) for *Pseudacris maculata* calling activity (Count), average wind speed (WND), daily precipitation accumulation (PRCP), average air temperature (TAVG), and green chromatic coordinates (GCC). Hydropattern also was included as water inundation (WI) at the wet meadow (Mormon Island) and streamflow (CMS) at the forested slough (Rowe Sanctuary).

Wet meadow							
		Count	WND	PRCP	TAVG	GCC	WI
2015	min	0	2.1	0	−15.3	0.33	0.04
	max	0.16	11.2	2.18	22.9	0.52	0.85
	mean	0.01	5.16	0.14	7.3	0.38	0.45
	sd	0.03	1.71	0.38	8.98	0.06	0.2
2016	min	0	0	0	−8.7	0.33	0
	max	0.98	15.2	5.23	21.7	0.48	1
	mean	0.29	5.75	0.3	9.19	0.37	0.51
	sd	0.32	2.12	0.89	6.98	0.04	0.29
2017	min	0	2	0	−8.2	0.33	0
	max	1	12.5	4.34	24	0.4	0.97
	mean	0.23	5.47	0.19	8.61	0.35	0.44
	sd	0.31	1.82	0.65	7.31	0.02	0.2
All years	min	0	1.8	0	−15.3	0.33	0
	max	1	15.2	5.23	24	0.52	1
	mean	0.19	5.46	0.21	8.37	0.37	0.47
	sd	0.29	1.9	0.68	7.82	0.04	0.23
Forested slough							
		Count	WND	PRCP	TAVG	GCC	CMS
2015	min	0	2.1	0	−15.85	0.33	18.15
	max	0.56	11.2	2.08	22.25	0.44	353.96
	mean	0.08	5.16	0.14	6.87	0.36	85.52
	sd	0.11	1.71	0.37	8.82	0.04	78.85
2016	min	0	1.8	0	−7.75	0.33	28.6
	max	1	15.2	10.16	22.2	0.43	246.64
	mean	0.05	5.75	0.24	8.4	0.36	107.26
	sd	0.14	2.12	1.08	6.68	0.04	50.13
2017	min	0	2	0	−8.85	0.33	8.72
	max	0.63	12.5	4.06	22.5	0.42	124.03
	mean	0.06	5.47	0.21	8.38	0.35	62.67
	sd	0.14	1.82	0.62	7.19	0.02	21.92
All years	min	0	1.8	0	−15.85	0.33	8.72
	max	1	15.2	10.16	22.5	0.44	353.96
	mean	0.06	5.46	0.19	7.88	0.36	85.21
	sd	0.13	1.9	0.75	7.63	0.03	58.18

model explained 45.3% (MSE = 0.01) (Table 3). Year, day of year, hydropattern, green chromatic coordinates, average temperature, and 7-day total precipitation were the highest ranked variables of importance at both sites, indicating removal of these variables from the models would decrease predictive accuracy substantially. *P. maculata* calling activity was predicted to begin increasing at DOY 60 and then substantially at DOY 70 at the wet meadow and to increase more gradually at DOY 60 followed by a substantial increase at DOY 90 at the forested slough (Fig. 4). Similarly, at both sites activity was predicted to begin increasing at temperatures above 5 °C, and in response to GCC, peak at 0.35. Activity increased at seven-day precipitation accumulation levels of approximately 0.25 cm at the wet meadow and at approximately 3 cm at the forested slough. Hydropattern was an important variable at both sites, with *P. maculata* activity predicted to increase with inundation levels above 0.2 at the wet meadow and predicted activity peaking at streamflow of approximately 50 m³/s, declining with increases thereafter. There was also an observed difference in activity based on year, with activity highest in 2016 and 2017 at the wet meadow, and 2015 and 2017 at the forested slough.

4. Discussion

In the Great Plains, the life cycle and behavioral activity of *Pseudacris maculata* is closely tied to the grasslands and interspersed wetlands. However, these habitats face increasing pressure from human development, agriculture, water-use changes, and a globally changing climate (Sidle, 1989; LaGrange, 2005; Matthews et al., 2013). Multimodal

monitoring—the pairing of autonomous sound recorders, time-lapse cameras, and additional sensors—collects data streams capable of reflecting changes in environmental and habitat conditions, as well as vocal-taxa communities. Using multimodal monitoring, we identified the spring calling phenology of *P. maculata* in central Nebraska and found that vocalization activity was highly influenced by weather and habitat conditions.

P. maculata vocalization activity occurs predominantly in the spring across the species' wide geographic extent, with precise timing of breeding activity dependent on latitude and elevation in addition to environmental conditions (Dodd, 2013). Near the northern extent of *P. maculata*'s range in Quebec, Canada, and at higher elevations such as the Rocky Mountains, calling often begins in May and is associated with snowpack melt (Ouellet et al., 2009; Corn et al., 2000; Muths et al., 2016). In the southern extent of their range in New Mexico, breeding occurs from February to August (Degenhardt et al., 2005), and similar *Pseudacris* spp. have been reported to call as early as January and into March in Texas (Saenz et al., 2006). Prior studies utilizing trapping techniques in the Central Platte River Valley of Nebraska found *P. maculata* activity was highest in mid-April (Jones et al., 1981; Goldowitz and Whiles, 1999), with calling observed as early as 18 March (Geluso and Harner, 2013a). Although beneficial for specific questions, manual survey methods can have limitation for understanding phenological timing and associated drivers, and many surveys often did not begin until April (Jones et al., 1981; Goldowitz and Whiles, 1999; Geluso and Harner, 2013a). Furthermore, trapping surveys are likely more reflective of movement than calling though both behaviors may be associated with reproduction (Spencer, 1964; Kramer, 1973). We observed *P. maculata* vocalization beginning in early March, often continuing into late May, and peaking in April. Differential activity patterns were observed between the wet meadow and forested slough, with *P. maculata* chorusing increasing at approximately day of year 70 (10 March) at the wet meadow and at day of year 100 (9 April) at the forested slough. This spring phenological pattern of *P. maculata* overlaps with the migratory timing of endangered whooping cranes in the CPRV, which on average occurs from late March through mid-April, with a mean initial Julian day of 92 (+/- 1; 2 April; Silcock and Jorgensen, 2020). As whooping cranes stop to refuel and forage in sloughs and wet meadows along the Platte River, the overlapping phenology in conjunction with prior literature (Archibald and Meine, 1996; Bergeson et al., 2001; Geluso and Harner, 2013b; Dinets, 2016) suggests that *P. maculata* and similar anuran species may be an available food resource for whooping cranes during their migration (Jones et al., 1981; Bergeson et al., 2001; Johnsgard, 1983; Geluso et al., 2013). However, more research is needed, as little is known regarding whooping crane diet throughout most of the Great Plains (Caven et al., 2019b).

Acoustic metrics indicated *P. maculata* vocalizations at the wet meadow were much lower in 2015 than in the following two years. Upon examining spectrograms and listening to audio recordings, the chorusing of *P. maculata* was faint and sounded distant during spring of 2015, especially compared to 2016 and 2017, while other sounds, such as red-winged blackbirds (*Agelaius phoeniceus;* call frequencies of 1–5 kHz) and sandhill cranes (*Antigone canadensis;* call frequencies of 0.5 – 8 kHz), had similar sounding proximity and amplitude between years. Therefore, the observed decline seems explicit to *P. maculata*. Specific drivers of this decline are uncertain, albeit, we suggest potential influences were related to events that occurred prior to spring 2015. In spring of 2013 and 2014, controlled burns were set to over 375 and 360 acres on Mormon Island, respectively, which contained much of the locally available wet meadow habitat. Although literature is sparse regarding responses of anurans to prescribed fire (Wilgers and Horne, 2006; Harner and Geluso, 2011), the burns may have had direct impacts on *P. maculata*, including mortality of adults, larva, or egg masses (Pilliod et al., 2003; Bowles and Jones, 2013), or indirect impacts through alteration of habitat components, such as a rapid increase in water temperature, altered hydroperiod, changes in water chemistry,
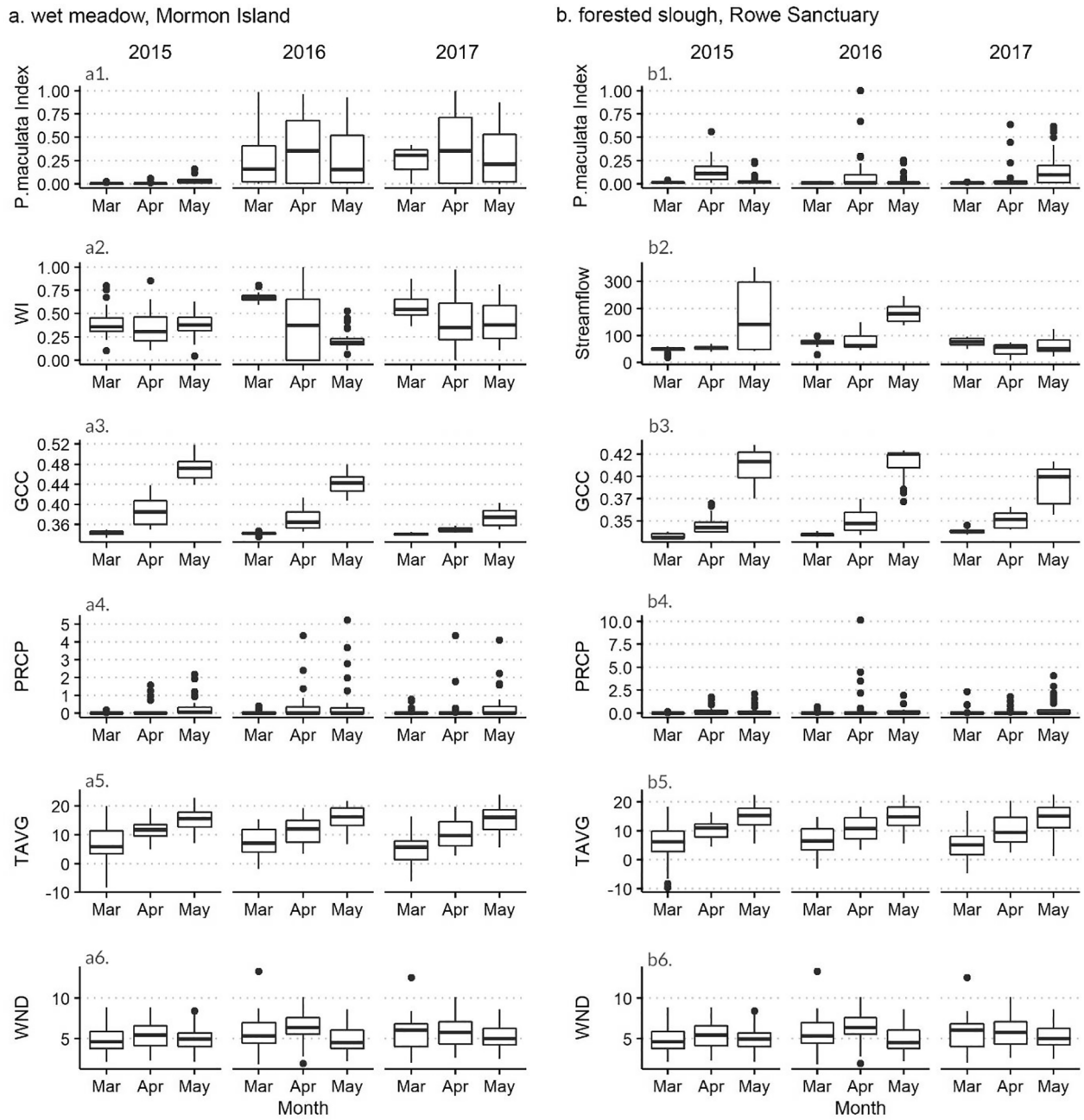
Fig. 1. Monthly boxplots at wet meadow habitat (a.) and forested slough (b.) illustrating the distribution, median, and outliers for *Pseudacris maculata* calling activity index [a1, b1], hydropattern (WI; water inundation [a2], CMS; streamflow CMS[b2]), vegetation (GCC; green chromatic coordinates [a3,b3]), precipitation (PRCP [a4,b4]), temperature (TAVG [a5,b5]), and wind speed (WND [a6,b6]).

interstitial-filling of ash and sediments, or changes in vegetation density (Brown et al., 1990; Pilliod et al., 2003; Caldwell et al., 2013; Westgate et al., 2018). As the area of wet meadow burned contains a high density of ephemeral and intermittent wetlands, and given that dispersal distances of *P. maculata* are limited and usually under 250 m (Spencer, 1964; Werner et al., 2009; Scherer et al., 2012), it is likely that a high density of *P. maculata* were present in this area at the times of the fires. Prior studies report ambiguous findings, including declines in populations following fire (Driscoll and Roberts, 1997), observations of anurans seeking refuge and fleeing from the sound of fire (Grafe et al., 2002), and species-specific responses to various burn regimes (Wilgers and Horne, 2006). However, prescribed fire may have long-term benefits, as it increases habitat heterogeneity, nutrient availability, reduces woody encroachment, and maintains vegetation species richness over

time (Pilliod et al., 2003; Bowles and Jones, 2013; Westgate et al., 2018).

Another possible explanation for the decline in activity was intensive grazing (>300 cow-calf pairs) from mid-April 2014 to early October of the wet meadow, potentially influencing *P. maculata* activity indirectly through defoliation as *Pseudacris* species generally prefer habitats with significant vegetative cover (>75%) of at least moderate height (>30 cm) (Anderson et al., 1999; Mannan, 2008). Alternatively, *P. maculata* activity could have been reduced in 2015 as a result of chytrid fungus (*Batrachochytrium dendrobatidis*). Harner et al., (2011, 2013) first documented the fungal disease in the CPRV at our study site in 2010 in American bullfrogs, then later in Woodhouse's toads and plains leopard frogs. Although chytrid fungus was not documented in boreal chorus frogs in the CPRV at the time, high rates (>80%) of *P. maculata* mortality
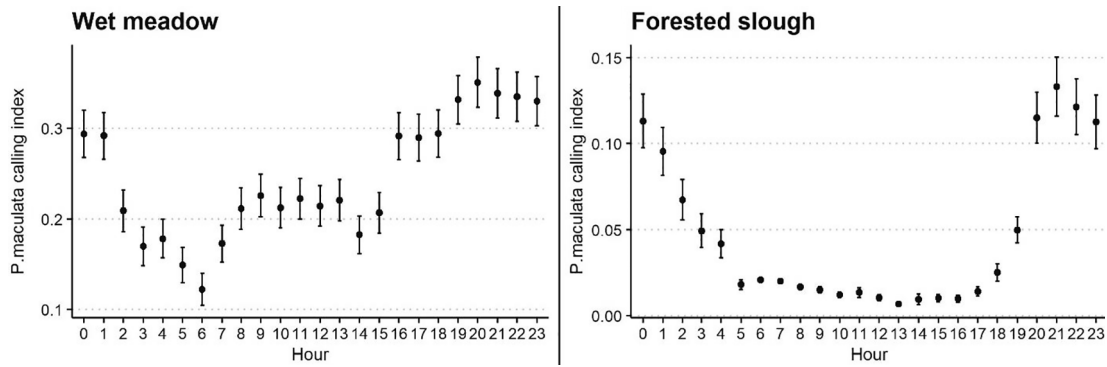
Fig. 2. Mean hourly calling activity for Pseudacris maculata during spring (March–June) of 2015–2017 within wet meadow habitat on Mormon Island and forested slough habitat at Rowe Sanctuary. Of note, y-axis scale differs for wet meadow (0.1–0.3) and forested slough (0–0.15).
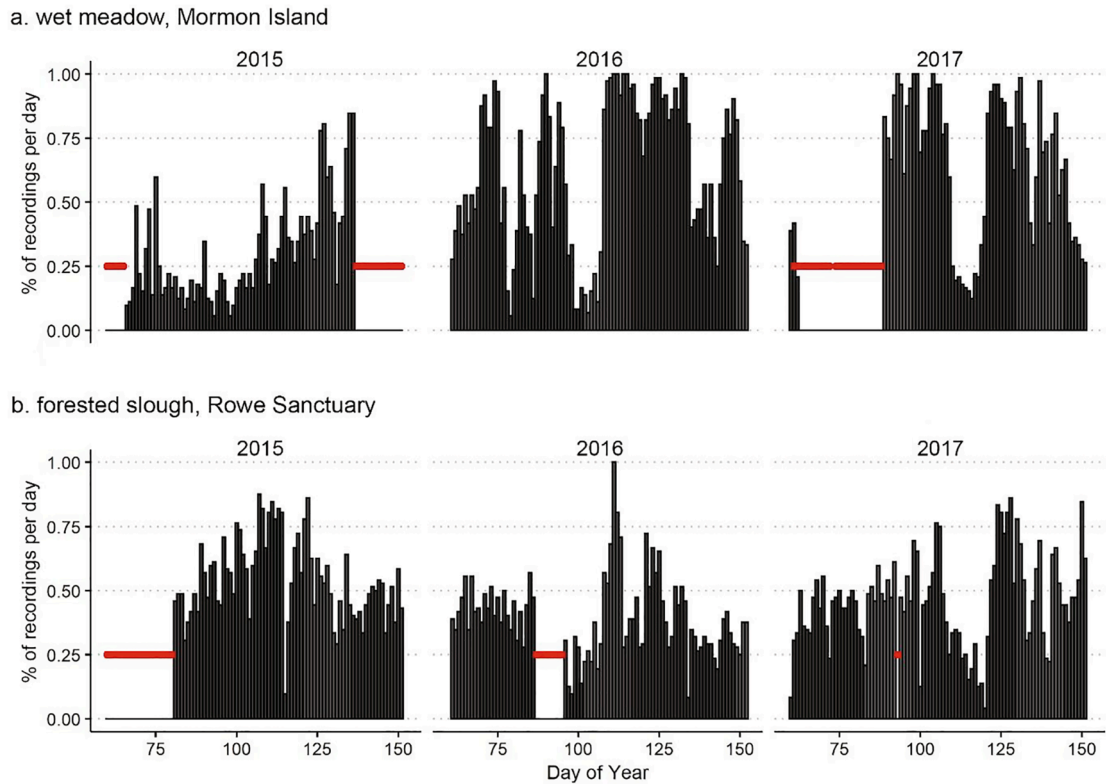

Fig. 3. Percent of recordings with *Pseudacris maculata* detections present per day at a wet meadow (a.) and forested slough (b.) in the Central Platte River Valley of Nebraska. Red lines indicate missing data.

resulting from Chytridiomycosis have been documented elsewhere throughout its range (Hyman, 2012). Mortality generally occurs 20 to 30 days after *B. dendrobatidis* exposure and higher water temperatures decrease infection and mortality rates (Hyman, 2012; Amburgey, 2014). As *P. maculata* reproduction occurs soon after spring emergence, many individuals likely may have had time to lay eggs ahead of potential adult mortality from Chytridiomycosis, and warming waters could have minimized potential impacts on larvae development (Hyman, 2012). Therefore, as *P. maculata* takes 1–2 years to reach sexual maturity, high localized mortality in 2014 could have resulted in low localized calling during the following spring in 2015 (Hyman, 2012; Amburgey, 2014). Our data provides some support for this theory as there was a slight uptick in calling during May compared to March and April of 2015, aligned with the time the first tadpoles hatched in 2014 would reach sexual maturity and potentially become reproductively active (Amburgey, 2014). While the cause is uncertain, the observed decrease in

P. maculata vocalization emphasizes the importance of monitoring and the use of quantifiable measures, such as acoustic metrics, to identify disturbances which may be indicative of longer-term changes, management actions, or an abrupt shift in ecological systems.

Although we are unsure of the specific decrease in *P. maculata* calling observed in 2015, change in vegetation structure from fire or grazing may have influenced the species behavior. *P. maculata* use vegetation for various reasons; they will deposit egg masses beneath partially submerged or emergent vegetation, utilize branching vegetation for breeding displays, and vegetation may provide structural cover and protection from predators (Anderson et al., 1999; Mannan, 2008; Ballinger et al., 2010). *P. maculata* response to green chromatic coordinates, a vegetation index indicative of phenology, was predicted to peak at 0.35, which generally aligns with when vegetation begins to green-up, before declining steadily to minimal calling activity around 0.41, at which time vegetation would likely be dense and in full bloom, offering

Table 3

Results of random forest models predicting *Pseudacris maculata* calling activity at a wet meadow and a forested slough. Variable importance scores ranked from most important (greatest percent increase in mean squared error) to least for all eleven predictor variables. Predictor variables including wind (WND; average wind speed; mph), precipitation (PRCP; daily accumulation; cm), 7-day precipitation (PRCP7; weekly accumulation; cm), 1-day lag precipitation (PRCP1; day prior daily accumulation; cm), daily mean, maximum, and minimum air temperature (TAVG, TMAX, TMIN; °C), day of year (DOY), green chromatic coordinates (GCC), snow (SNW; daily accumulation; cm), snow depth (SNWD; cm), and year (Year).

a. Wet meadow		b. Forested wetland	
Mean of squared residuals: 0.02		*Mean of squared residual: 0.01*	
Variance explained: 72.7%		*Variance explained: 45.3%*	
Variable	% Inc. MSE	Variable	% Inc. MSE
Year	36.5	PRCP7	20.13
DOY	31.9	GCC	13.42
WI	28.5	DOY	12.85
GCC	22.0	CMS	10.56
PRCP7	18.9	Year	8.08
TAVG	17.9	TAVG	7.4
TMIN	15.8	PRCP1	5.08
TMAX	13.6	TMIN	4.46
PRCP1	5.2	TMAX	4.42
PRCP	4.0	WND	4.07
WND	3.1	PRCP	2.64

cover and protection for *P. maculata* post-breeding and natal dispersal into terrestrial environments (Wells 2010; Malzahn et al., In Review). Although random forest utilizes bagging and thus is known to be more robust in handling complex and interacting data (Breiman, 2001), some studies suggest that there is potential for bias in the measures of importance for highly correlated variables (Strobl et al., 2008). Given the high correlation of vegetation and Julian day (r = 0.8), we recognize the limitations of this approach and acknowledge the possibility for inflating the importance of these variables. However, considering the iterations of randomness introduced within random forest models, examination of the partial dependence plots, and the *a priori* importance of both variables, we chose to include both vegetation and Julian day. As a proxy for seasonality, both vegetation and Julian day may offer useful information into the phenological pattern of *P. maculata* activity. Individually, they may provide different insight into potential long-term decoupling from climatic shifts, such as earlier breeding activity (Julian day) or potential resource mismatches (vegetation) (Klaus and Lougheed, 2013; Visser and Gienapp, 2019).

While there is a geographic difference in the timing of call activity based on latitude and elevation, *P. maculata* and similar *Pseudacris* species have been found to occupy a comparable temperature regime across their distribution. Our findings indicate *P. maculata* activity increased when average air temperature exceeded 5 °C, an observation synonymous with prior studies across the geographic range of *P. maculata*. Oullete et al., (2009) found *P. maculata* vocalizations began when temperatures were >5 °C in the Rocky Mountains, while Saenz et al., (2006) found *Pseudacris* species in Texas called at temperatures ranging from 5° C to 22 °C (41°F to 72°F). Clarke, 1958 reported *P. maculata* vocalized between air temperature ranges of approximately 4.5 °C to 32 °C (40°F to 90°F). In addition, we found a decline in calling activity when temperatures dropped below 5 °C, such as in late March of 2016 and mid-April of 2017. Relative to other anuran species, *P. maculata* has been shown to breed earlier and in colder temperatures (Howard, 1980). *Lithobates pipiens* (northern leopard frogs) were observed initiating calling 8–11 days after ice melt on an ephemeral breeding pond (Sommers et al., 2018). From the time-lapse images, we approximated an ice-off date of the wet meadow during our study and found that *P. maculata* on average started calling approximately 5 days after ice-melt. Similar to the snow-melt driven ponds in higher elevations (Corn, 2003), snow and ice melt resulting from warming seasonal temperatures may act as an environmental cue (Corn and Muths 2002).

As *P. maculata* relies on ponded water for critical stages in their life cycle, including breeding, egg laying, and metamorphose, hydropattern is likely a key determinant of activity patterns (Saenz et al., 2006; Ballinger et al., 2010). Prior research shows *P. maculata* is adapted to local hydroperiod and lacks plasticity, suggesting their ability to respond to changes in hydropattern may be limited (Amburgey et al., 2012). Within the Central Platte River Valley, most wetlands are connected to the hydrology of the Platte River (Henszey and Wesche, 1993), however, water and land use changes have greatly altered the remaining wetlands and their hydropattern (Sidle et al., 1989). Our results indicate hydropattern was an important variable at both the wet meadow and forested slough, with slight differences in the response of *P. maculata* calling likely a factor of site-specific hydrological conditions. In mid-April 2016 as well as the end of April and beginning of May 2017, *P. maculata* calling decreased precipitously at both sites, concurrent with a decline in wet meadow inundation and decrease in Platte River streamflow, suggesting the decrease in *P. maculata* vocalization was likely attributed to water availability. Calling activity increased following much higher weekly rain totals at the forested slough (3.0–6.0 cm; Fig. 4) than at the wet meadow (0.2–0.5 cm; Fig. 4), where these large rain events most commonly occurred at the site in April when calling activity peaked (Figs. 2, 3). It is possible that breeding activity also occurred in temporary pools outside of the forested slough following significant precipitation accumulation, explained by the high importance rank of 7-day precipitation at the forested slough but less important at the wet meadow. However, seven-day rainfall accumulation was an important predictor of *P. maculata* calling activity at both sites, indicating precipitation regimes sufficient to inundate temporary and intermittent wetlands likely act as an environmental cue for opportunistic *P. maculata* breeding activity (Saenz et al., 2006; Ballinger et al., 2010).

Hydropattern was an important variable at both sites, albeit, site specific differences in hydrology and resulting characteristics potentially influenced *P. maculata* calling at the wet meadow compared to the forested slough. Although calling activity generally peaked in April at both sites, peak activity was broadly more stochastic and frequent at the wet meadow, often with near-consistent vocalizations from mid-March declining into April followed by another peak into May. As groundwater, a major driver of wetland inundation (Wesche et al., 1994, Davis et al., 2006), is generally highest in March, high levels may have provided suitable inundation for breeding at the wet meadow site, but generally too much water for breeding at the forested slough, which consisted of topographically deeper marsh habitat (Kantrud et al., 1989, Whiles and Goldowitz, 1998, Goldowitz and Whiles, 1999, Dodd et al., 2013). Prior research suggests *P. maculata* prefers intermittent wetlands, likely as an avoidance of potential desiccation from quick-drying shallow wetlands and to avoid predation from fish and other frog species within more permanent bodies of water (Kolozsvary and Swihart, 1999; Dodd, 2013). In the CPRV, *P. maculata* was found to be most abundant in wetlands with water present 60–90% of the time (Goldowitz and Whiles, 1999), while they were not observed in perennial waters (Geluso and Harner, 2013a). *P. maculata* calling activity was predicted to increase when water inundation was above 0.2 at the wet meadow, which remained inundated for most of the spring breeding season. At the forested slough, *P. maculata* activity was predicted to increase when streamflow reached 50 m^3/sec (~1766 ft^3/sec; Fig. 4), and when streamflow exceeded this, *P. maculata* activity was predicted to decline. Our results suggest at the forested slough, streamflow above 50 m^3/sec may increase water depths in the wetland dominated by shallow and deep marsh habitats (Kantrud et al., 1989) above preferred levels for boreal chorus frogs.

The forested slough has a more permanent hydroperiod and often year-round water availability with close proximity to the Platte River, creating suitable habitat for *Lithobates catesbeianus* (American bullfrog) and posing a potential predation risk to native species through temporary colonization of fish species (Skelly, 1996; Goldowitz and Whiles, 1999; Knapp and Matthews, 2000). Comparatively, the wet meadow
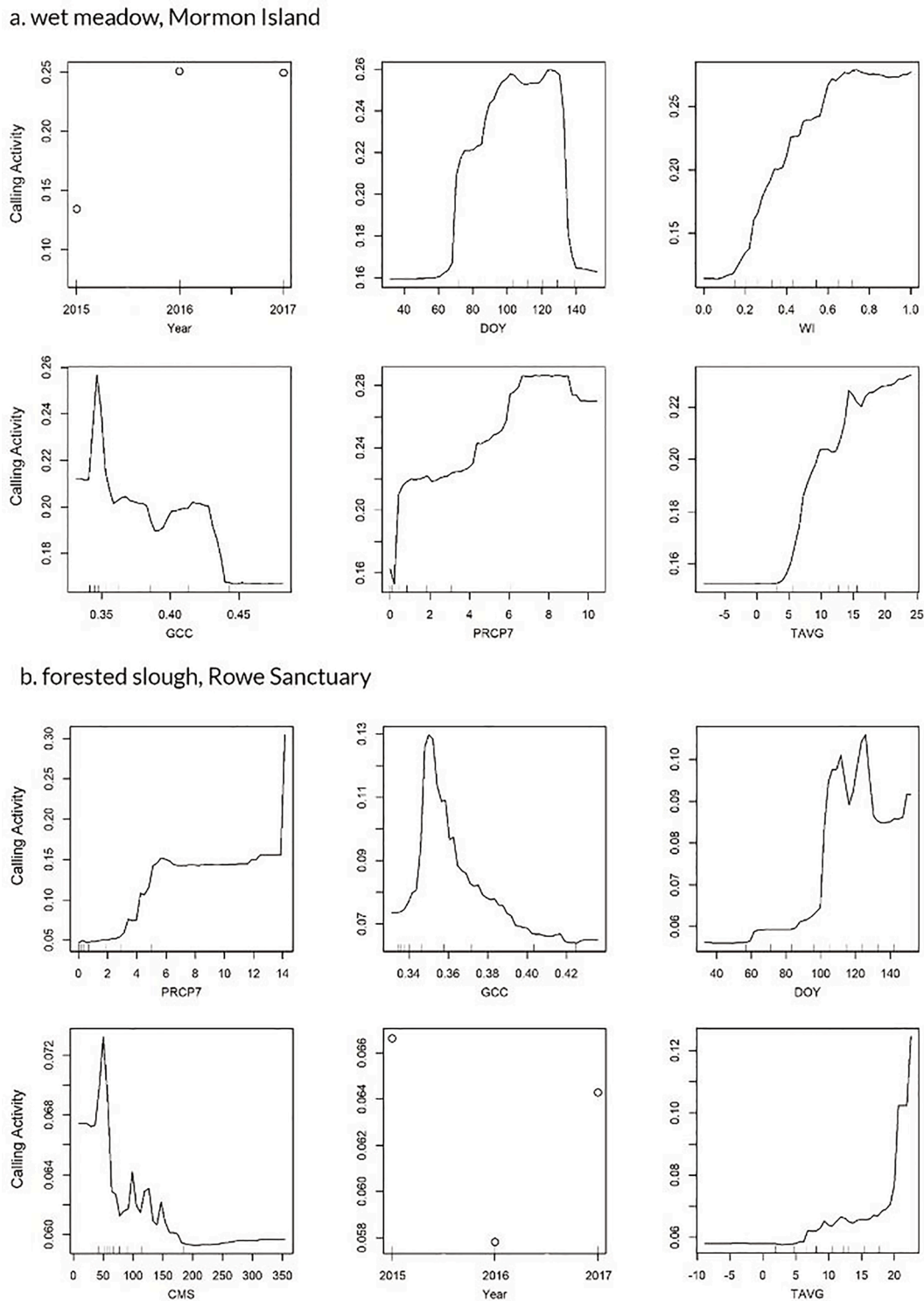
Fig. 4. Partial dependence plots showing predicted response of *Pseudacris maculata* to the six variables with the highest variable importance scores from random forest models at a wet meadow (Mormon) and forested slough (Rowe) in central Nebraska.

exhibits more intermittent hydrology not conducive to bullfrogs. Bullfrog vocalizations were heard semi-regularly in audio recordings at the forested slough, potentially influencing *P. maculata* activity through resource competition, predation, and disease transmission such as the fungal pathogen *B. dendrobatidis* (Pearl et al., 2004; Harner et al., 2013). Introductions of *L. catesbeianus* to aquatic systems have shown that native species of frogs will change their calling behavior in response to overlapping vocalization activity (Medeiros et al., 2016). At the forested

slough, *P. maculata* vocalizations were relatively inactive during the day compared to the wet meadow, where we observed more consistent calling activity within a 24-hour period (Fig. 2). Conversely, woodlands are not preferred habitat for *P. maculata,* which may provide further explanation for lower calling activity at the forested slough (Ballinger et al., 2010; Malzahn et al., In Review).

5. Conclusions

Our findings indicate the spring calling activity of *P. maculata* follows a phenological pattern, initiating on average around day of year 70 and peaking from approximately day of year 100 to 120 in south-central Nebraska, USA. Furthermore, vocalization activity is associated with environmental variables and habitat condition, with predicted calling activity responding to temperatures above 5 °C, weekly accumulated precipitation, and hydropattern. We detected greater vocalizations and near continuous diel calling activity in an intermittent wet meadow habitat compared to a forested slough with semi-permanent hydrology. These findings emphasize the importance of hydroperiod for the life-cycle of *P. maculata*. The small ephemeral wetlands preferred by *P. maculata* may be vulnerable to changes in land and water-use as cropland expands, water demands increase, and precipitation regimes change (Amburgey et al., 2012). As they rely on prairie-wetland eco-tones, *P. maculata* may be a useful bioindicator reflecting environmental conditions across both grassland and aquatic habitats (Knutson et al., 2000). Autonomous sound recorders and acoustic metrics are particularly useful for assessing anurans, as they are often elusive, nocturnal, small, yet vocal (Bee et al., 2010; Ulloa et al., 2019; Sugai et al., 2019). Concurrently, time-lapse cameras offer an approach to examine visual changes in habitat and landscape (Sonnentag et al., 2012; Brinley Buckley et al., 2017). Many challenges still exist with implementing bioacoustics and multimodal monitoring, including processing time, learning curves, accuracy of classification, validation, loss of data due to passive technology malfunctions, integrating datasets, and handling, manipulating, and storing large amounts of data (Digby et al., 2013; Sugai et al., 2019). However, many of these limitations can be addressed with additional approaches such as manual listening and validation techniques. Additionally, multimodal monitoring can offer advantages for studying changing natural systems, including the ability to control frequency intervals and time duration, allowing for high frequency passive data collection over a long duration of time, the ability to have spatial replicates and collect data in remote or difficult to reach areas, minimal up-front human resources, and less time allocation than manual surveys or trapping. Declines in anuran populations have emphasized the need for increased monitoring to establish species-specific and geographically-relevant baseline references to characterize anuran phenology and activity patterns. More research is necessary to establish sound management and conservation practices, such as the effects of restoration activities that create permanent waterbodies in landscapes historically dominated by intermittent wetlands and anuran response to fire regimes and grazing. Integration of auditory and visual technologies into multimodal monitoring is a promising approach for understand species-specific responses to changing climatic and environmental conditions, altered habitat, and management practices (Westgate et al., 2018).

CRediT authorship contribution statement

Emma M. Brinley Buckley: Conceptualization, Methodology, Formal analysis, Data curation, Writing - review & editing, Visualization. **Benjamin L. Gottesman:** Conceptualization, Methodology, Formal analysis, Data curation, Writing - review & editing. **Andrew J. Caven:** Conceptualization, Writing - review & editing. **Mary J. Harner:** Funding acquisition, Project administration, Writing - review & editing. **Bryan C. Pijanowski:** Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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