Contents lists available at ScienceDirect

Ecological Indicators

Original Articles

Assessing biological and environmental effects of a total solar eclipse with passive multimodal technologies

Emma M. Brinley Buckley[a,*], Andrew J. Caven[b], Benjamin L. Gottesman[c,d], Mary J. Harner[a,e], Bryan C. Pijanowski[c,d], Michael L. Forsberg[f,g]

[a] Department of Communication, University of Nebraska at Kearney, Kearney, NE 68849, USA
[b] The Crane Trust, Wood River, NE 68883, USA
[c] Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA
[d] Center for Global Soundscapes, Purdue University, West Lafayette, IN 47907, USA
[e] Department of Biology, University of Nebraska at Kearney, Kearney, NE 68849, USA
[f] Department of Agricultural Leadership, Education & Communication, University of Nebraska-Lincoln, 68583, USA
[g] Michael Forsberg Photography, Lincoln, NE 68542, USA

ARTICLE INFO

ABSTRACT

On 21 August 2017, a total solar eclipse crossed the continental United States, providing a unique natural experiment to observe how wildlife and plants respond to rapid and drastic changes in photic conditions using a multi-modal suite of tools. We installed passive time-lapse and infrared cameras, sound recorders, and data loggers in the Central Platte River Valley of Nebraska to study this phenomenon. The eclipse lasted about three hours, and complete obscuration of the sun (totality) lasted for about 2 min and 30 sec. Light values, measured with time-lapse camera systems, decreased 67% on average during totality relative to the daily mean light value. Ambient temperatures decreased by 6.7 °C on average (12% of the daily mean) approximately 11–16 min after totality; concurrently, humidity increased by an average of 12% of the daily mean. We found evidence for altered acoustic activity in response to the eclipse, including site and species-specific changes in the call activities of late season breeding birds and insects in the orders orthoptera and hemiptera. In addition, acoustic indices were differentially correlated with changes in photic and thermal conditions. However, we did not observe changes in flowering plants nor detect bat activity at known night roost and foraging areas. Historically, observations during rare occurrences, such as a total solar eclipse, were anecdotal or limited in scope, and thus, how they changed the light, sound, and meteorological conditions on the landscape were difficult to validate and measure. In comparison, anthropogenic disturbances, including impacts from light pollution and climate change, often take place slowly over long periods, and therefore, can be complex and challenging to assess. Documentation of this stochastic occurrence, with an immediate change in environmental conditions, highlights the utility of passive multimedia technologies to increase our capacity to monitor ecosystem dynamics and chronicle the variations of abiotic properties of a landscape and concomitant responses of organisms with varying sensory abilities.

1. Introduction

Sunlight is one of the foremost abiotic mechanisms governing the natural world. As the primary source of energy on Earth, solar radiation dictates atmospheric conditions and structures the biological world (Ramanathan et al., 2001; Wild et al., 2005). Light-dark cycles act as a reliable environmental cue to regulate circadian and circannual rhythms in plants and animals, facilitating synchronization of

physiological and biological responses with temporal niches (Shuboni and Yan, 2010), including dormancy/hibernation, migration, and reproduction (Helm et al., 2013). However, human-caused disturbances, such as light pollution and climate change, have altered environmental conditions and destabilized biological rhythms (Bradshaw and Holzapfel, 2010; Gaston et al., 2013). As these disturbances often occur gradually over an extended period (decades), observing and evaluating biotic and abiotic responses is often challenging due to the temporal

limitations of datasets, the complexity of parsing apart interacting factors over time, and the inconspicuousness of gradual changes.

On 21 August 2017, a total solar eclipse provided a rare natural experiment to investigate the response of organisms and atmospheric conditions to an immediate and concentrated drastic reduction in solar intensity. As the moon aligned between the earth and sun, a 95–115-km wide shadow crossed from the northwestern to southeastern United States, traversing the Great Plains and Central Platte River Valley in south-central Nebraska, where obscuration of the sun reached 100%. Although this periodic phenomenon is relatively frequent, about two to four times a year, the limited spatial scope reduces the observational opportunity to approximately once every hundred years for any given location (NASA, 2017). The last total solar eclipse in the continental United States occurred 26 February 1979, and was visible from only five northwestern states (NASA, 2017). Due to this infrequency, there is sparse information available about the response of flora and fauna concurrent with atmospheric changes during eclipses.

An event rooted in the mythical and spiritual fascination of mankind, there exists an abundance of total solar eclipse guides (Littmann et al. 2008) and narratives, including folklore telling of an eternal bat gnawing at the moon (Deutsch, 2017), humbling personal revelations (Tamarkin, 2017), and even news stories reporting on the abundance of solar eclipse-related media coverage throughout history (Kutner, 2017). However, documented observations of plant and animal responses to an eclipse are limited and often rely on anecdotal accounts rather than systematic observations. A comprehensive report of plant and wildlife sightings reported to newspapers and interspersed with accounts from natural history experts during eclipses from 1544 to 1932 notes birds stopped singing, crickets began chirping, and bees returned to their hive during totality (Wheeler et al., 1935). More recent studies examining the effect of an eclipse on biota have found varied results and often rely on manual observations that can be species-specific or limited in scope. During an eclipse, documented variations in animal behavior include birds ceasing to call (Hughes et al., 2014), diurnal fish seeking shelter (Jennings et al., 1999), spiders destroying their webs (Uetz et al., 1994), and captive animals, such as chimpanzees, hamadryas baboons, and antelope ground squirrels altering their activity (Kavanau and Rischer, 1973; Branch and Gust, 1986; Gil-Burmann and Beltrami, 2003). Bats in Mexico were recorded flying down a ravine during a total solar eclipse, however at the same time and location, monitoring of cave-dwelling bats found no changes in behavior (Sanchez et al., 1999). Albeit, some animals have not responded to changing light conditions during these rare occurrences; dairy cows demonstrated no change in rumination during a total eclipse (Rutter et al., 2002), and European ground squirrels (*Spermophilus citellus*) demonstrated no change in burrowing behavior during a partial eclipse (Spoelstra et al., 2000). Additionally, a limited number of studies have observed various responses of plants to total solar eclipses, including the opening and closing of leaf stomata in grey birch (*Betula populifolia*) (Deen and Bruner, 1933), opening and closing of Helianthemum (*Helianthemum vulgare*) flowers (Kullenberg, 1955), and a change in the photosynthetic activity of crops and marine plankton (Economou et al., 2006). Although informative, many studies assessing biological effects of an eclipse have had a mono-specific focus. Increasingly, emerging technologies are being used to understand multimodal responses to disturbance, assess ecological condition, inform conservation actions, and communicate through novel techniques (Blumstein et al., 2011; Sueur and Farina, 2015; Brinley Buckley et al., 2017; Raynor et al., 2017). Integration of these technologies into a suite of multi-modal tools can support investigations of ecological responses at various spatio-temporal scales, including community-level responses to a unique event (Allan et al., 2018).

The objective of our study was to capture and quantify changes in atmospheric conditions and behavioral responses by a variety of biota to a total solar eclipse that occurred in North America on 21 August 2017. To measure these effects, we installed passive monitoring equipment, including time-lapse camera systems and audio recording devices, in diverse habitats associated with the Platte River in south-central Nebraska, USA. We sought to i) describe how atmospheric conditions and biological activity change before, during, and after the eclipse and ii) demonstrate how different methods, notably photography and soundscape recordings utilizing image processing and acoustic indices, capture atmospheric and biotic responses to abrupt changes in sunlight. Specifically, we first hypothesized that flowering species of vascular plants (Dicotyledoneae) known to bloom periodically under particular light conditions (morning, night, etc.; Raguso et al., 2003; Atamian et al., 2016) or track the movement of the sun, would alter their daily rhythm during the eclipse. Secondly, we monitored two known bat foraging locations with ultrasonic recorders, as well as a known roosting location for insectivorous bats and an active wildlife corridor with two motion-activated cameras, hypothesizing that the eclipse would initiate activity for bats and additional crepuscular wildlife. Lastly, we hypothesized that the eclipse would influence vocalization patterns of birds and calling insects, like crickets, cicadas, and grasshoppers, known to respond to various levels of light and atmospheric conditions (Heller and Von Helversen, 1993; Greenfield, 1997; La, 2012; Bruni et al., 2014).

2. Materials and methods

2.1. Study area

The path of the solar eclipse spanned the northwestern to the southeastern United States on 21 August 2017 (Fig. 1a). Our study was conducted in south-central Nebraska, USA, near the Platte River, a biologically unique and important landscape (Fig. 1b; Schneider et al., 2005). Here the eclipse lasted for 2 hr and 52 min, from 11:34 h to 14:26 h (Central Daylight Time; CDT). The sun was 100% obscured (totality) for approximately 2 min and 34 sec between 12:58 h and 13:01 h CDT at an altitude of 60.0° at 161.8° SSE (NASA, 2017). We deployed monitoring equipment across three locations managed for habitat conservation: Mormon Island of the Crane Trust (2,025 ha; 40.798306°N, −98.416298°W; 581 m elev.), Shoemaker Island of the Crane Trust (40.7902345° N, −98.4675122° W; 595 m elev.), and Audubon's Rowe Sanctuary (980 ha; 40.669323° N, -98.887926° W, 633 m elev.) (Fig. 1c). These locations consisted of relict and restored sub-irrigated prairies and meadows, as well as riparian woodlands adjacent to the Platte River (Currier, 1989, 1982; Nagel and Kolstad, 1987). Across these locations, we studied specific sites and habitats that included a wet meadow (Mormon Island), riparian woodland (Rowe Sanctuary), and a trout pond, beaver lodge, utility garage with a bat roost, and a cottonwood savanna (all on Shoemaker Island).

2.2. Equipment

Time-lapse imagery, sound recordings, and data loggers collected information from 20 August 2017 to 22 August 2017, however the primarily focus to assess changes related to the eclipse was from 10:30 to 15:30 CDT, one hour before the onset of the partial eclipse phase to one hour after the completion of the eclipse, on 21 August 2017 (see Supplementary Material: Passive Monitoring Equipment for further details).

Images were collected from two cameras, one on Mormon Island and one at Rowe Sanctuary, which are part of a network of time-lapse camera systems extending through the Platte River watershed of the Great Plains as part of the Platte Basin Timelapse (PBT) project (www. plattebasintimelapse.org). Each time-lapse camera system included a Nikon D300 (Exposure compensation: -0.3, ISO: 400; aperture-priority: Rowe Sanctuary- f/9, Mormon Island f/8) within water resistant housing and powered by a solar panel. An intervalometer engineered by TRLcam remotely controlled the capture interval via wireless and satellite connections (TRLcam.com, Lincoln, Nebraska). During the day of
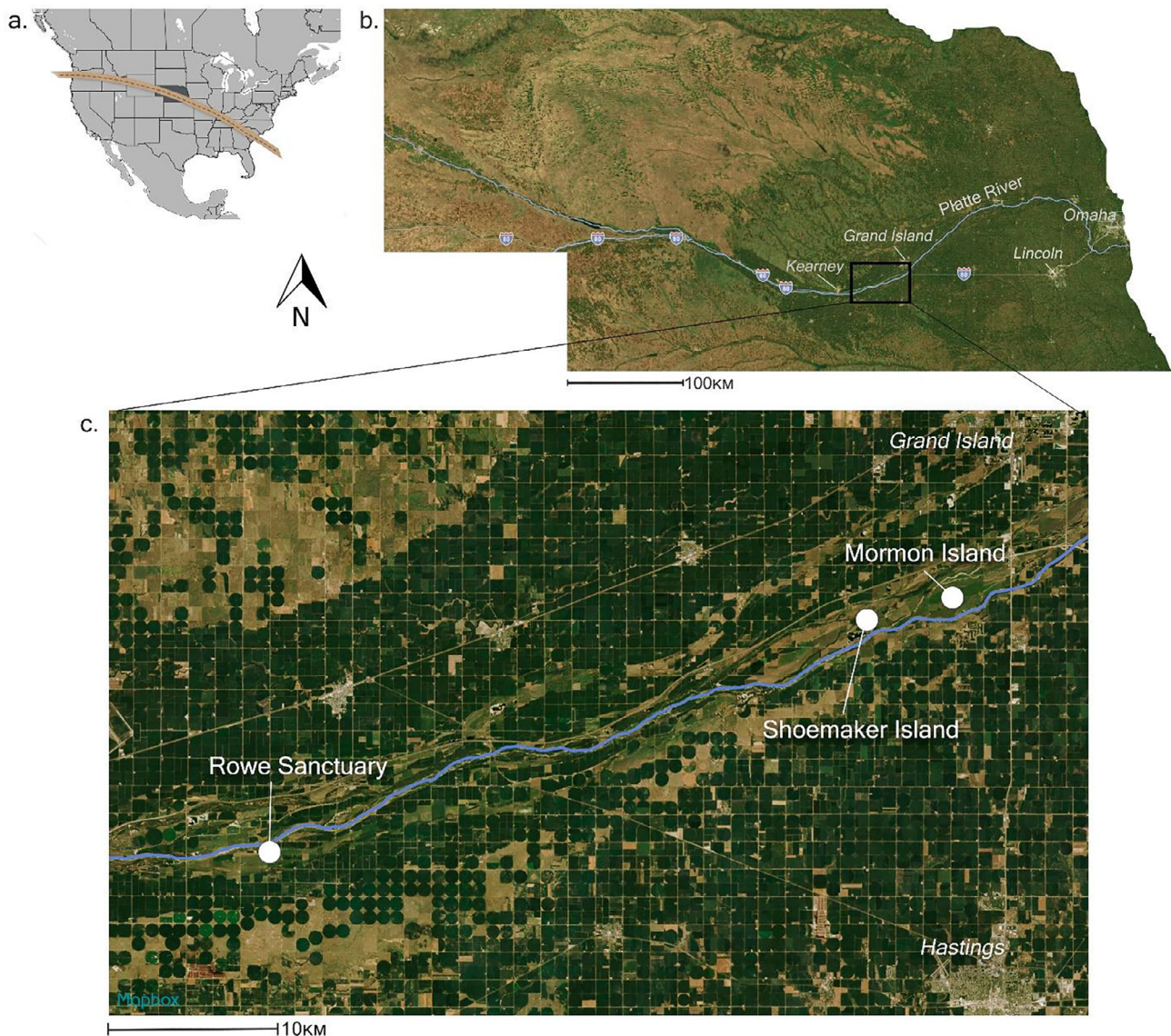
Fig. 1. (a.) Approximate path of totality across the United States of the solar eclipse on 21 August 2017. Map adapted from NASA.gov. (b.) Regional setting of the Central Platte River Valley and study area in Nebraska, USA. (c.) Study locations, Rowe Sanctuary, Shoemaker Island, and Mormon Island, hosting passive monitoring equipment for documenting biological and atmospheric effects of a total solar eclipse.

the eclipse, cameras were programmed to take one image every 30 s.

To obtain an approximation of changing scene illumination from the time-lapse images, we used light value (Lv) from the exchangeable image file format ("Exif") metadata extracted with the open-source software program ExifTool (Harvey, 2013). Lv is a standardization of exposure value at ISO100. It is calculated with the equation:

$$Lv = \left(log^2 \left(\frac{N^2}{t} \right) \right) + log^2 (ISO/100)$$

where N is aperture (or f-number), t is shutter speed/exposure time, and ISO is the film speed. The resulting value is a proxy for the absolute measurement of light averaged across the entire scene at a given time (Allen and Triantaphillidou, 2009; Hiscocks, 2018; Harvey, 2013; Imatest, 2017).

To observe potential responses of vegetation and wildlife, eight remote cameras (combination of Reconyx PC800 HyperFire Professional Semi-Covert Camera Trap and XR6 UltraFire Covert Camera) were installed at key locations on Crane Trust properties. Two motion-triggered trail cameras capable of both visible and infrared imagery were placed to document wildlife. One of these cameras was

mounted in the rafters of a utility garage to document a night roost of bats frequented by big brown bats (*Eptesicus fuscus*) (Johnson and Geluso, 2017). The second camera was placed on a wildlife trail that runs from the river channel to a restored wetland hosting a beaver lodge with previous observations of otter, beaver, deer, and other animals with known crepuscular activity. The remaining six cameras captured an image at one-minute intervals, as well as time-lapse video for 30 s of each one-minute interval, and were installed on three different species of plants. The first was placed in front of a group of approximately twenty prairie sunflowers (*Helianthus petiolaris*) on a sandy ridge 5 m from the river on Mormon Island. A second camera was focused on a singular common sunflower (*Helianthus annuus*) and a third camera on a cultivated tall morning glory (*Ipomoea purpurea*), both on Shoemaker Island. The final three cameras were installed to examine the behavior of three different moon flower plants (*Datura stramonium*) during the eclipse, with the frames capturing a total of six moon flowers on Mormon Island. We selected these species because they are known to respond to sunlight. Sunflowers, specifically immature sunflowers, use heliotropism to enhance growth and thus track the sun from east to west during daylight and reorient eastward at night (Atamian et al.,

2016), while *Datura* spp. have night-blooming flowers and are highly dependent on light, or the disappearance thereof, as a biological cue (Benvenuti et al., 1994; Raguso et al., 2003).

Four acoustic recorders (Song Meter SM2+; Wildlife Acoustics, Maynard, Massachusetts, USA) recorded daily from 10:30 to 15:30 at four types of habitat. One was placed near an excavated 0.8 ha trout pond (approximately 8-m deep) on Shoemaker Island, immediately south of multiple buildings on the north boundary of a grassland dominated by switchgrass (*Panicum virgatum*) and tall fescue (*Festuca arundinacea*). Surrounding the trout pond were a few large (1-m diameter at breast height) silver maples (*Acer saccharinum*). A second recorder was installed near a beaver lodge in a restored wetland dominated by cattails (*Typha* spp.) and giant burr-reed (*Sparganium eurycarpum*) adjacent to the Platte River also on Shoemaker Island. A third recorder was placed at Mormon Island, a wet meadow complex dominated by switchgrass, common threesquare (*Schoenoplectus pungens*), and other hydrophytes. Lastly, the fourth recorder was located at Rowe Sanctuary within the riparian woodland dominated by cottonwood (*Populus deltoides*), sandbar willow (*Salix exigua*), and eastern red cedar (*Juniperus virginiana*) adjacent to the south channel of the Platte River. Recordings were in ".wav" file format with a sampling rate of 16 kHz, a bit depth of 16 bits, and a gain of 36 dB. Thus, only sounds up to 8 kHz were recorded, which excluded avian species with high-frequency calls, such as grasshopper sparrow (Raynor et al., 2017). At both the Mormon Island and Rowe Sanctuary sites, sound recorders were paired with time-lapse cameras, as well as with environmental data loggers. Data loggers consisted of environmental sensors, a real-time clock, Secure Digital (SD) card, and micro-controller (TRLcam.com, Lincoln, Nebraska) to measure temperature and humidity at continuous one-minute intervals. To detect potential bat activity, two additional ultrasonic Song Meter SM4BAT FS units (Wildlife Acoustics, Maynard, Massachusetts, USA) were set to a continuous triggered recording with a sampling rate of 384 kHz, 12 dB gain, and 16 k high-pass filter. One was placed above an open water slough adjacent to a riparian forest and restored cottonwood savannah, and the second was installed next to a utility garage where bats are known to roost at night (Johnson and Geluso, 2017); both sites were located on Shoemaker Island.

2.3. Acoustic analysis

Acoustic changes were assessed using three techniques; i) visual evaluation of spectrograms created with Raven Lite software (Bioacoustics Research Program, Lab of Ornithology, Cornell, New York), ii) manual counts of avian vocalization activity derived from listening to recordings, and iii) calculation of automated soundscape metrics.

To measure avian vocalization activity, we identified 2.5-minute phase intervals, equal to the duration of totality, before, during, and after the eclipse (see Table 1). Within each of these phases, we listened to the sound recording, identified the species of all audible vocalizations (songs and calls), and totaled the number of vocalizations per species to approximate an avian point count survey (Brandes, 2008; Raynor et al., 2017). All surveys were completed twice for accuracy and were conducted by a single observer proficient in bird call identification who had regularly conducted avian-point counts in the region. The sampling area (truncation distance) was determined by the recording equipment's sensitivity and assumed constant across sites and time (Brandes, 2008).

Numerous acoustic indices have been developed to characterize soundscapes and animal communities (Sueur et al., 2014; Towsey et al., 2014; Fuller et al., 2015; Bobryk et al., 2016). Increasingly, these automated measurements are being applied to understand how environmental disturbances impact wildlife (Coquereau et al., 2017; Deichmann et al., 2017; Lee et al., 2017; Raynor et al., 2017). Three acoustic indices were selected for this study: the Root Mean Squared amplitude (RMS), the Acoustic Complexity Index (ACI), and the Average Signal Amplitude (ASA). RMS—the square root of the mean of the squared sound pressure values—was calculated across the full spectrum of the recordings (0–8 kHz) in order to characterize broad changes across the entire soundscape. To measure changes in biological sounds, ACI and ASA were calculated on sounds between 2 and 8 kHz. ACI—the sum of the spectral difference between successive frames in a spectrogram—has been shown to correlate strongly with the number of bird vocalizations in a recording, as well as other types of biological sounds with amplitudes and frequencies that change rapidly (Pieretti et al., 2011; Depraetere et al. 2012). ASA was selected to characterize changes in avian and insect acoustic activity. Prior to calculating ASA, sounds below 2 kHz were filtered out by applying a 3rd order Butterworth high-pass filter to each recording (Stoddard, 1998). Subsequently, ASA was calculated as the mean amplitude of the wave envelope, based on methods provided in Towsey et al. (2014). To calculate these acoustic indices, stereo recordings were inspected manually; the channel with less high frequency sensitivity loss was selected (Rowe Sanctuary: left track, Trout Pond: right track, Mormon Island: left track, Beaver Lodge: right track). The continuous audio recordings from 10:33:30–15:15:26 were segmented into 117, 2.5-minute files. Acoustic indices were calculated on each of these 2.5-minute files, and resulting values were investigated by listening to the recordings while simultaneously viewing their spectrograms in order to identify drivers of acoustic index patterns.

To statistically measure avian vocalization activity and changes in the soundscape, eclipse phases were binned into two categories (see Table 1): Non-eclipse (Pre-eclipse and Post-eclipse) and Eclipse (95%a, Totality, and 95%b). Generalized linear regression was used to assess the effect of the eclipse on cumulative species richness across all sites. We assessed the influence of the eclipse on individual avian species' vocalization activity using generalized linear mixed-effects regression with a Poisson distribution, and for acoustic indices using linear mixed-effects regression, including location as a random effect for both analyses (GLMER and LMER functions, lme4 package, and LMEtest package). To examine potential proximate drivers of soundscape changes, we compared the strength of the relationships between environmental variables and acoustic indices by calculating Pearson

Table 1
Description of phases of the eclipse and associated time intervals in which avian vocalizations and soundscape metrics were analyzed.

Period	Phase	Avian Vocalization[1]		Soundscape Metrics[2]	
		Definition	Time Interval	Definition	Time Interval
Non-eclipse	Pre-eclipse	30 min before eclipse began	11:01:30–11:04:00	1 hr–30 min before eclipse began	10:33:30–11:03:30
Eclipse	95%a	Start of > 95% eclipsed	12:51:00–12:53:30	> 95% eclipsed prior to totality	12:51:00–12:58:30
Eclipse	Totality	100% obscuration	12:58:30–13:01:00	100% obscuration	12:58:30–13:01:00
Eclipse	95%b	End of > 95% eclipsed	13:06:00–13:08:30	> 95% eclipsed following totality	13:01:00–13:08:30
Non-eclipse	Post-eclipse	30 min after eclipse ended	14:56:00–14:58:30	30 min–1 hr after eclipse ended	14:56:00–15:26:00

[1] For avian vocalizations, 2.5-minute sound recordings equal to the duration of totality were assessed from each of five designated eclipse periods.

[2] For soundscape indices, metrics were calculated by creating 2.5-minute bins within the five designated eclipse periods.
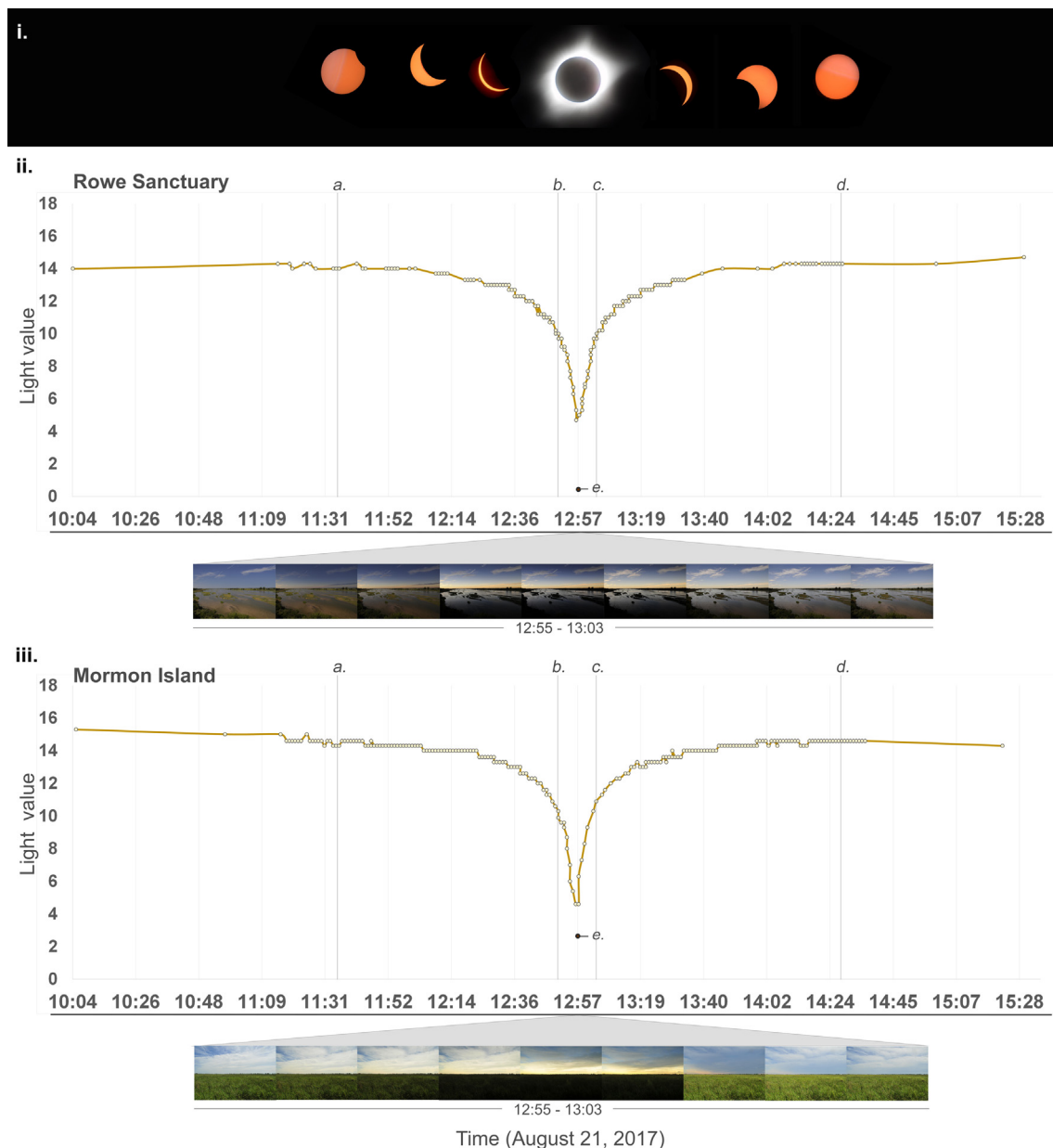
Fig. 2. Composite image of the total solar eclipse (i.). The seven individual images were captured from the same point of view on Mormon Island, near the Platte River in Nebraska, USA. The first image was shot at approximately 11:35 and the last at 14:30 CDT on 21 August 2017. *Images copyright: Emma Brinley Buckley*. Light values at Rowe Sanctuary (ii), a riparian woodland adjacent to the Platte River, and Mormon Island (iii), a wet meadow complex, derived from time-lapse imagery from 10:04 (pre-eclipse) to 15:28 (post-eclipse) CDT on 21 August 2017. The eclipse began at 11:24 (a.), was 95% eclipsed by 12:51 (b.), totality occurred from 12:58 to 13:01, the period of > 95% eclipsed ended at 13:08 (c.), and the eclipse ended at 14:26 (d.). Light values at sunrise (e.) are included for reference. Time-lapse camera systems took an image every 30 s as part of the Platte Basin Timelapse project. Corresponding time-lapse images, below the graphs, illustrate the change in light on the landscape from 12:55 to 13:03 at approximately 1-min intervals. *Images copyright: Michael Forsberg*.

product-moment correlation coefficients (ρ) for each acoustic index with light value and with temperature. For this analysis, datasets were truncated to the onset of partial phase at 11:34 and the end of the partial phase at 14:26 to reduce variability unrelated to the eclipse. All statistical analysis and graphics were completed in R (v. 1.0.153, R Core Team, 2017).

3. Results

3.1. Light value

As the moon moved into alignment between the sun and earth, the round disc sun gradually narrowed until the thin sliver of sunlight was

replaced with a solar corona, a faded outline of light encompassing a black sphere (Fig. 2i). The solar illumination across the landscape faded with the moon's shadow, mimicking a sunset but never reaching complete darkness, even during totality. Light value (Lv) began to decline half an hour after the onset of the eclipse at both locations, changing from full sunlight to muted illumination (Fig. 2). At Rowe Sanctuary, Lv declined steeply in a convex shape during totality, with a rapid decrease beginning ten minutes before totality and then a slightly more gradual increase in illumination immediately after. Conversely, Lv at Mormon Island declined more gradually when approaching totality and then increased at a steeper slope following the reemergence of the sun. The Lv comparison in light illumination before and after totality also was visually evident in the images. The Mormon Island imagery had an
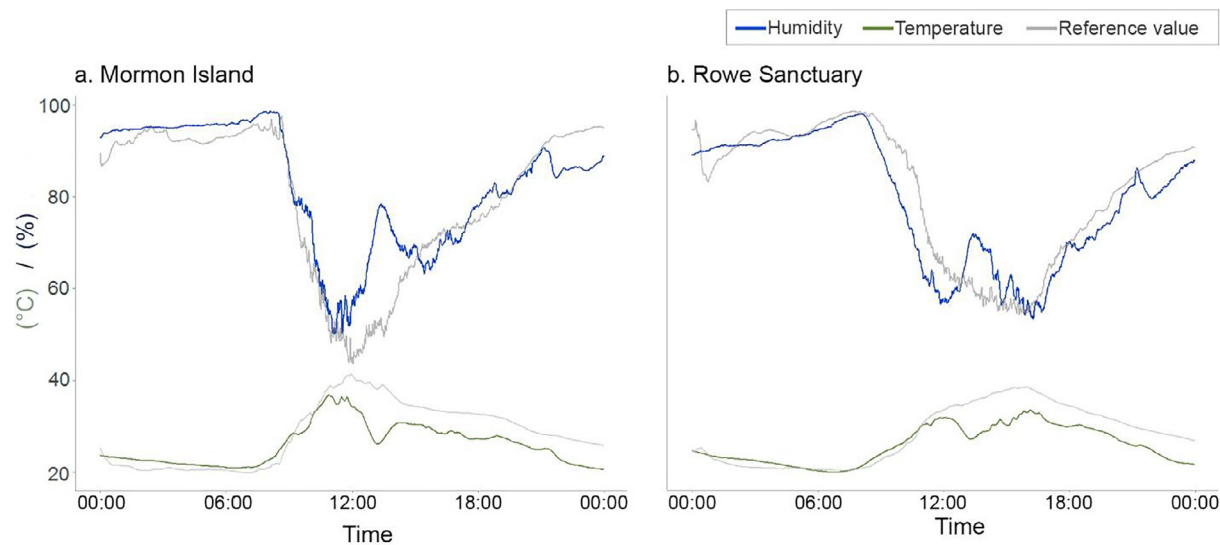
Fig. 3. Humidity (top blue line) and temperature (bottom green line) measured at one-minute intervals from 00:00 to 23:59 on 21 August 2017 at Mormon Island (left) and Rowe Sanctuary (right). Underlying gray lines denote measurements of humidity and temperature from the previous day, 20 August 2017, and are provided for reference.
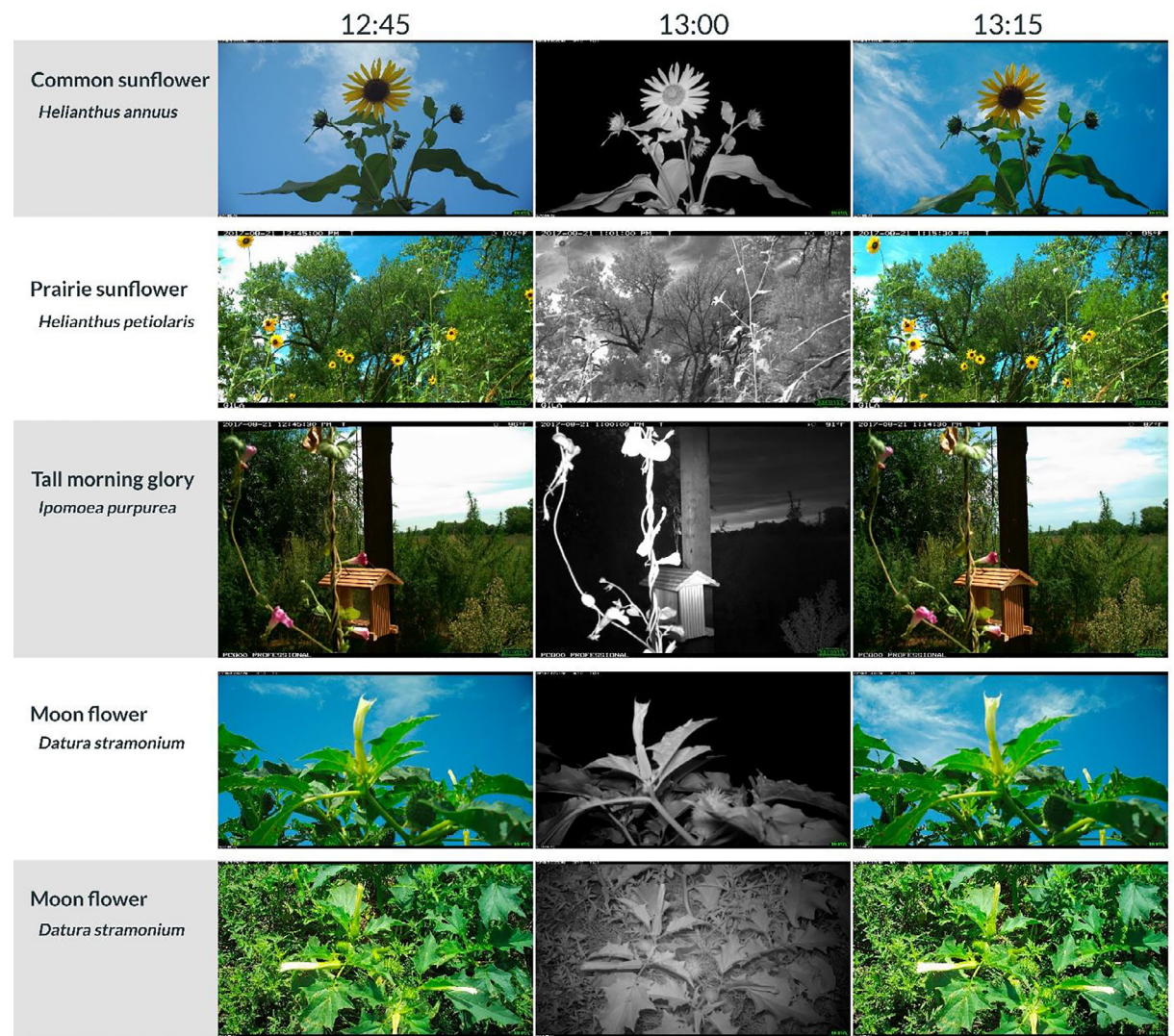

Fig. 4. Images from trail cameras showing the frame of view for five vascular plants at 14 min before totality, at totality, and 14 min after totality ended. No changes were observed.

overall higher light value for the day (Mormon Island Lv_{mean} = 13.65, SD = 1.62; Rowe Sanctuary Lv_{mean} = 11.66, SD = 2.52), but during totality at both sites overall scene illumination decreased to approximately the same value: 4.7 at Rowe Sanctuary, a deviation of 65% from the daily mean, and 4.6 at Mormon Island, a 68% decrease from the daily mean (Fig. 2). Comparatively, approximately 35 min prior to sunrise at 06:14, Lv at Mormon Island was 2.4 and 0.4 at Rowe Sanctuary, while approximately 20 min after sunset at 20:45, Lv at Mormon Island was 2.7 and at Rowe Sanctuary Lv was 1.4. These times correspond to the first and last set of images taken on 21 August 2017, before the time-lapse camera systems were remotely programmed to turn off for the night.

3.2. Atmospheric conditions

Generally, air temperature decreased while humidity increased surrounding the eclipse, an observation that differed in pattern from the same time period the previous day (Fig. 3). In addition, the magnitude and timing of fluctuations varied between Mormon Island and Rowe Sanctuary. At Mormon Island, temperature increased the morning of 21 August 2017 to a high of 34.3 °C at 11:51 CDT, about 15 m after the initial phase of the eclipse began and approximately 1 h 7 min prior to totality (Fig. 3a). Temperature began to decrease afterwards, declining by 8.1 °C or 17% of the daily mean temperature, to reach a low of 26.2 °C at 13:12, about 11 min after totality ended. Temperature remained below 27 °C from 13:00 to 13:26, then increased to approximately 30 °C by 13:50 and did not return to pre-eclipse levels. Humidity, declining since morning, reached a low of 50.7% at 11:09 before the eclipse began and then gradually increased until 12:33 when it abruptly increased from 60% at 12:33 to 78.5% at 13:21, 20 min after totality. Humidity remained above 77% for 22 min, before declining again.

At Rowe Sanctuary, temperature reached a high of 32.4 °C at 12:14, 28 min after the eclipse began and 44 min before totality (Fig. 3b). Beginning at 12:15, temperature declined by 5.3 °C to a low of 27.1 °C at 13:17, a 6% deviation from the daily mean temperature. It remained below 28 °C from 13:03 to 13:36, and then began increasing at 13:37 and reached above 31 °C by 14:43. Beginning in the morning, humidity began decreasing until 12:09, when it started increasing from 59% to reach a high of 71.9% at 13:24, 23 min after totality. Afterwards, it declined gradually and remained stable around 68% until 14:14, when it began to decline again.

3.3. Plant and wildlife behavior from trail cameras

We observed no changes in the images or videos of the sunflowers, domesticated morning glory, or moon flowers (Fig. 4). Images of the morning glory showed the day-blooming flowers beginning to close at approximately 11:30, and nearly wilted immediately after the eclipse. Contrary to our hypothesis, this timing was consistent with the timing of the previous and following day. Similarly, there was no wildlife movement recorded with the motion-triggered camera on the game trail or in the night roost of bats of the utility garage.

3.4. Acoustics

During the eclipse, there were changes in the soundscape from anthropogenic, atmospheric, and biological sources (Fig. 5). At the onset of totality, distant sounds of howling, cheering and yelling, ranging from 5 to 15 sec, were recorded at all four sites from people who had congregated in the path of totality. Sounds of wind through dry, late-summer vegetation, which appeared on spectrograms as broadband vertical streaks and energy from 0 to 1 kHz, generally decreased about an hour before, quieted during, and restarted about an hour after totality (Fig. 5). Biological responses, notably by insects and birds, were mixed, species-specific, and sometimes site-specific (Table 2). Animals

responded in three ways, by changing their 1) call frequency (mean frequency or frequency bandwidth), 2) call activity (number of calls per unit time), or 3) overall call intensity (mean or peak call amplitude).

We detected various changes in the sound production patterns of calling insects during the eclipse, including declines in call frequencies and differences in calling activity (Table 2). For example, orthoptera calls with center frequencies at approximately 4.2 kHz and 7.5 kHz declined to approximately 3.5 kHz and 7 kHz, respectively, about twenty minutes before totality (Fig. 5). These calls gradually increased in frequency to pre-eclipse levels about 30 min after totality. For calling activity, insect taxa between 4.5 and 6 kHz, likely attributed to field crickets (Gryllidae: Gryllinae), increased calling around the period of 95% obscuration. The same trend was found for tree crickets (Gryllidae: Oecanthinae) at sites with significant nearby tree cover (Trout Pond, Rowe Sanctuary). Albeit, at Trout Pond, presence of an aerial drone (periodically within 100 m of the recorder) made interpreting fine-scale changes in insect calls difficult at this site. However, aerial drone sounds were below 1 kHz and low in amplitude, and thus, likely did not have an impact on the acoustic indices. We generally detected calls of cicada (Cicadidae) before and after the eclipse, with call amplitude perceptibly higher at the beginning of the eclipse, declining up to and ceasing before the period of 95% eclipse coverage, and increasing again after light returned. Cicada calls were most prominent at Rowe Sanctuary. On sites with a nearby prairie landscape (Mormon Island, Trout Pond, Beaver Lodge), we recorded ground cricket (Gryllidae: Nemobiinae) calls. At Mormon Island, ground cricket calls continued throughout the eclipse, declining in amplitude near totality. Similarly, at the Beaver Lodge site, ground cricket calls ceased during the period of 95% eclipse coverage.

Differential changes in avian vocalization during the eclipse were species-dependent (Table 2). Several species were heard only during totality and/or the phases where obscuration was > 95%, while others either increased or decreased call activity during totality compared to other phases (Fig. 6). During the eclipse, increased vocalization activity was found for sedge wren ($\beta_{eclipse}$ = 3.455, p-value < 0.001), American goldfinch ($\beta_{eclipse}$ = 0.624, p-value < 0.001), and song sparrow ($\beta_{eclipse}$ = 0.667, p-value = 0.036). Contrastingly, vocalization activity for western meadowlark declined during the eclipse ($\beta_{eclipse}$ = −1.26, p-value < 0.001). Cumulative avian species richness across all sites was higher during the eclipse period ($\beta_{eclipse}$ = 1.958, p-value = 0.0263), with the highest species richness across all sites found during the 2.5-min interval following totality (Fig. 7).

Results from the acoustic indices showed evidence of changing soundscapes during the eclipse compared to the non-eclipse period, and various biological and environmental drivers contributed to this variation (see Supplementary Materials for further explanation on drivers of acoustic indices). ACI values increased during the eclipse period ($\beta_{eclipse}$ = 2.932, p-value < 0.001) at three of the four recording sites (Beaver Lodge, Rowe Sanctuary, Trout Pond; Fig. 8), suggesting an increase in biotic sounds with rapidly changing frequencies or amplitudes (i.e. bird song and some insect calls) during this time (Pieretti et al., 2011). These three sites also exhibited large increases in ACI approximately 20 min after totality, coinciding with an increase in avian acoustic activity, as indicated by the ACI time-series plots in Fig. 8. Our results show RMS amplitude values were reduced by approximately 10 dB during the eclipse period ($\beta_{eclipse}$ = −10.407, p-value < 0.001; Fig. 9). RMS values began to decline approximately one hour before totality, reached the lowest values during totality, and then gradually increased to higher than pre-eclipse levels, indicating a decrease in broadband sound levels during and near obscuration. Decreases in RMS values were more pronounced in the three grassland habitats during the eclipse (Beaver Lodge, Mormon Island, Trout Pond; mean $RMS_{eclipse}$ = −12.62 ± 2.87 dB) than at the riparian woodland habitat at Rowe Sanctuary ($RMS_{eclipse}$ = −4.15 dB). ASA values sharply declined at all sites during totality (Fig. 10). On average, ASA at totality was 3.70 ± 2.58 dB lower than the rest of the > 95% period.
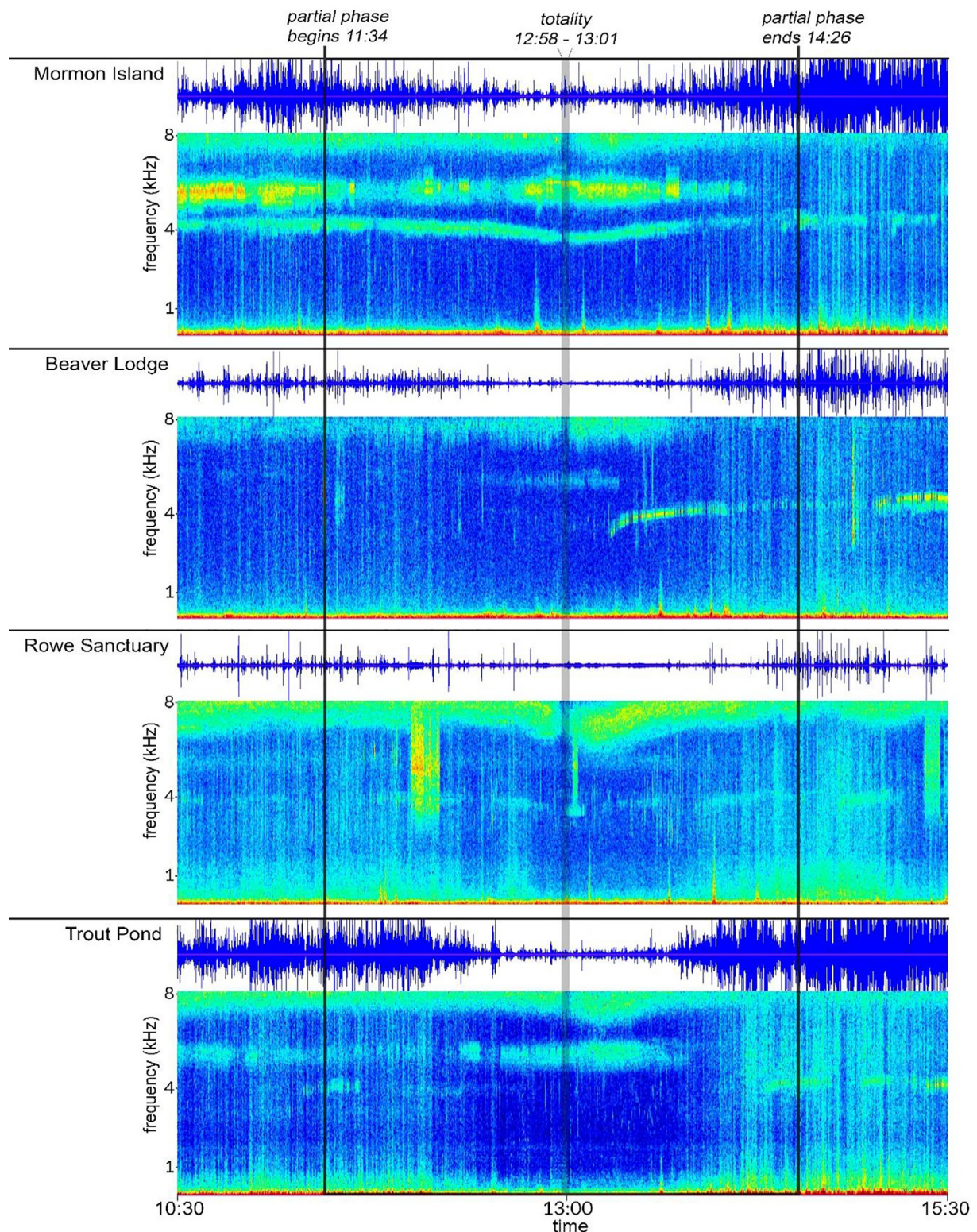
Fig. 5. Waveforms and spectrograms of sound recordings from 10:30 to 15:30 at Mormon Island, Beaver Lodge, Rowe Sanctuary, and Trout Pond study sites. Black vertical lines indicate the onset and end of partial eclipse. Gray line denotes totality.

However, ASA during the entire > 95% obscuration was not significantly different from the non-eclipse period ($\beta_{eclipse} = -0.005$, p-value = 0.688).

3.4.1. Comparisons between acoustic indices and environmental variables

During the eclipse, there was a strong association between temperature at Mormon Island and temperature at Rowe Sanctuary ($\rho = 0.93$, p-value < 0.01), as well as between Lv at both sites ($\rho = 0.99$, p-value < 0.01). Lv and temperature at Rowe Sanctuary were slightly correlated ($\rho = 0.35$, p-value < 0.01), while Lv and temperature at Mormon Island were moderately correlated ($\rho = 0.51$, p-value < 0.01).

Table 2

Acoustic responses to the total solar eclipse discerned from sound recordings and attributed to specific sources, with the direction of the response, time period, and site of occurrence noted.

Response	Source	Direction of change	Time period	Sites
Sound intensity	Wind	Decreased	About an hour before to an hour after totality	All sites
Call frequency	Orthoptera @ 4.2 kHz	Declined to 3.5 kHz	About 20 min before totality until 30 min after totality	Beaver Lodge, Mormon Island, Rowe Sanctuary
	Orthoptera @ 7.5 kHz	Declined to 7 kHz	About 20 min before totality until 30 min after totality	Beaver Lodge, Trout Pond, Rowe Sanctuary
Call activity	Field crickets	Increased	Around the period of 95% obscuration	Mormon Island, Beaver Lodge, Trout Pond
	Tree crickets	Increased	Around the period of 95% obscuration	Trout Pond, Rowe Sanctuary
	Ground crickets	Reduced or ceased	During the period of 95% eclipse coverage	Mormon Island, Beaver Lodge, Trout Pond
	Cicadae	Reduced or ceased	During the period of 95% eclipse coverage	Most prominently Rowe Sanctuary
	Sedge Wren	Increased	Around the period of 95% obscuration	Trout Pond, Mormon Island, Beaver Lodge
	American Goldfinch	Increased	Around the period of 95% obscuration	Trout Pond, Beaver Lodge
	Song Sparrow	Increased	Around the period of 95% obscuration	Beaver Lodge
	Western Meadowlark	Decreased	Around the period of 95% obscuration	Mormon Island
Species richness	Aves	Increased	Around the period of 95% obscuration	All sites

As changes in environmental conditions at both Rowe Sanctuary and Mormon Island (sites with data loggers and time-lapse cameras) were highly correlated, acoustic index values at Beaver Lodge and Trout Pond were compared to Lv and temperature values at Mormon Island, the site in closest proximity (approximately 2.4–3.2 km). Correlations between RMS and Lv, as well as RMS and temperature, were significant at all four sites (Table 3). There was a slightly stronger association between RMS and Lv at all sites, except at Rowe Sanctuary, where temperature was slightly more correlated to RMS (Table 3). Correlations between ASA and temperature were significant and negatively correlated at Mormon Island and Trout Pond (Table 3). Concurrently, ASA and Lv were negatively correlated at Mormon Island ($\rho = -0.52$, p-value < 0.01), yet positively correlated at Rowe Sanctuary ($\rho = 0.27$, p-value = 0.03) and Beaver Lodge ($\rho = 0.42$, p-value < 0.01). ACI and environmental changes were negatively correlated at Trout Pond, where ACI had a stronger association with temperature ($\rho = -0.74$, p-value < 0.01) than Lv ($\rho = -0.24$, p-value = 0.05).

4. Discussion

4.1. Environmental effects

Time-lapse photography and continuous sound recordings provided digital documentation of a mid-day, late summer total solar eclipse in central Nebraska, allowing us to evaluate environmental and biological responses to reduced solar radiance. As previous observations were often anecdotal, short communications, or limited to a mono-specific focus, the integration of emerging technologies offered a novel and empirical investigation of changes in light and sound to a unique natural phenomenon. Previous studies have shown that wildlife and vegetation vary in their response to a total solar eclipse (Deen and Bruner, 1933; Tramer, 2000; Murdin, 2001; Steppe et al., 2002). Effects are generally attributed to the rapid reduction and reemergence in solar radiance (Jennings et al., 1999; Economou et al., 2006), suggesting that time of year, season, time of day, and latitude influence environmental changes during solar eclipses (Anderson, 1999). Furthermore, as
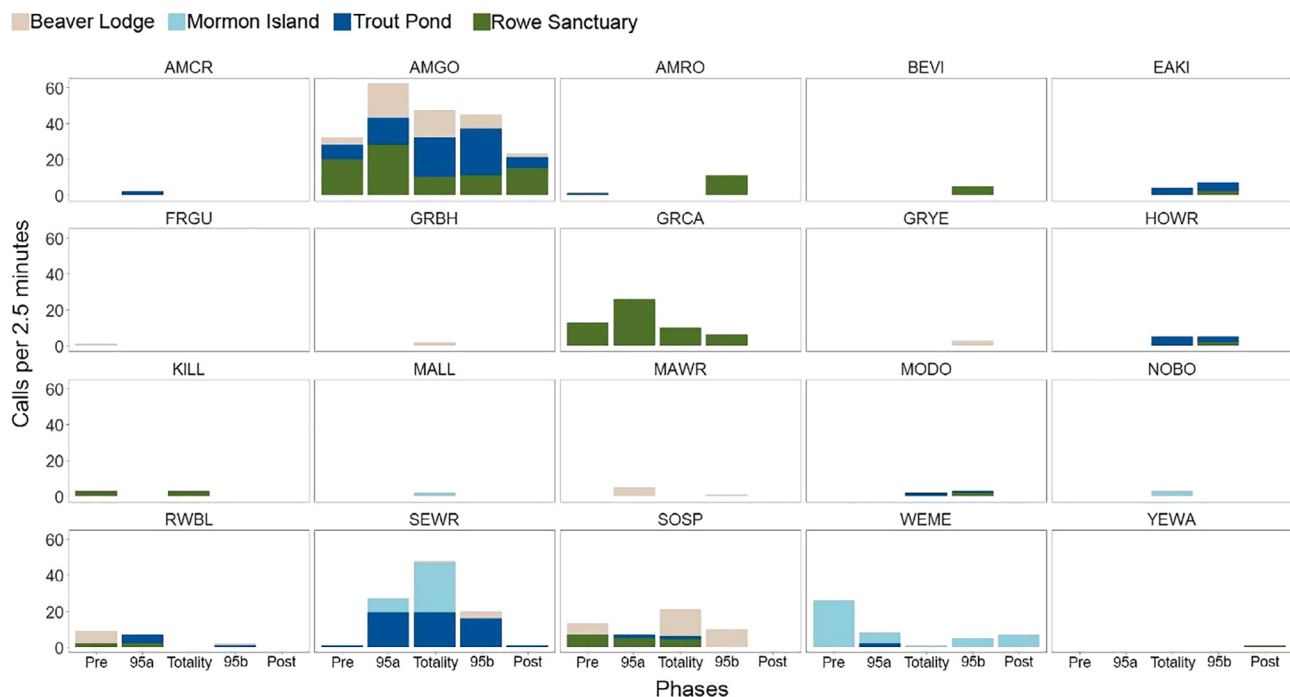

Fig. 6. Species-specific avian vocalization activity recorded as number of calls per 2.5-minute phase (pre-eclipse, 95%a, totality, 95%b, post-eclipse). Study sites are denoted by color. Four-letter alpha codes for standardized common names of birds are as follows: AMCR- American Crow, AMGO- American Goldfinch. AMRO- American Robin, BEVI- Bell's Vireo, EAKI- Eastern Kingbird, FRGU- Franklin's Gull, GRBH- Great Blue Heron, GRCA- Gray Catbird, GRYE- Greater Yellowlegs, HOWR- House Wren, KILL- Killdeer, MALL- Mallard, MAWR- Marsh Wren, MODO- Mourning Dove, NOBO- Northern Bobwhite, RWBL- Red-winged Blackbird, SEWR- Sedge Wren, SOSP- Song Sparrow, WEME- Western Meadowlark, and YEWA- Yellow Warbler. Code names for bird species from Pyle and Desante (2014).
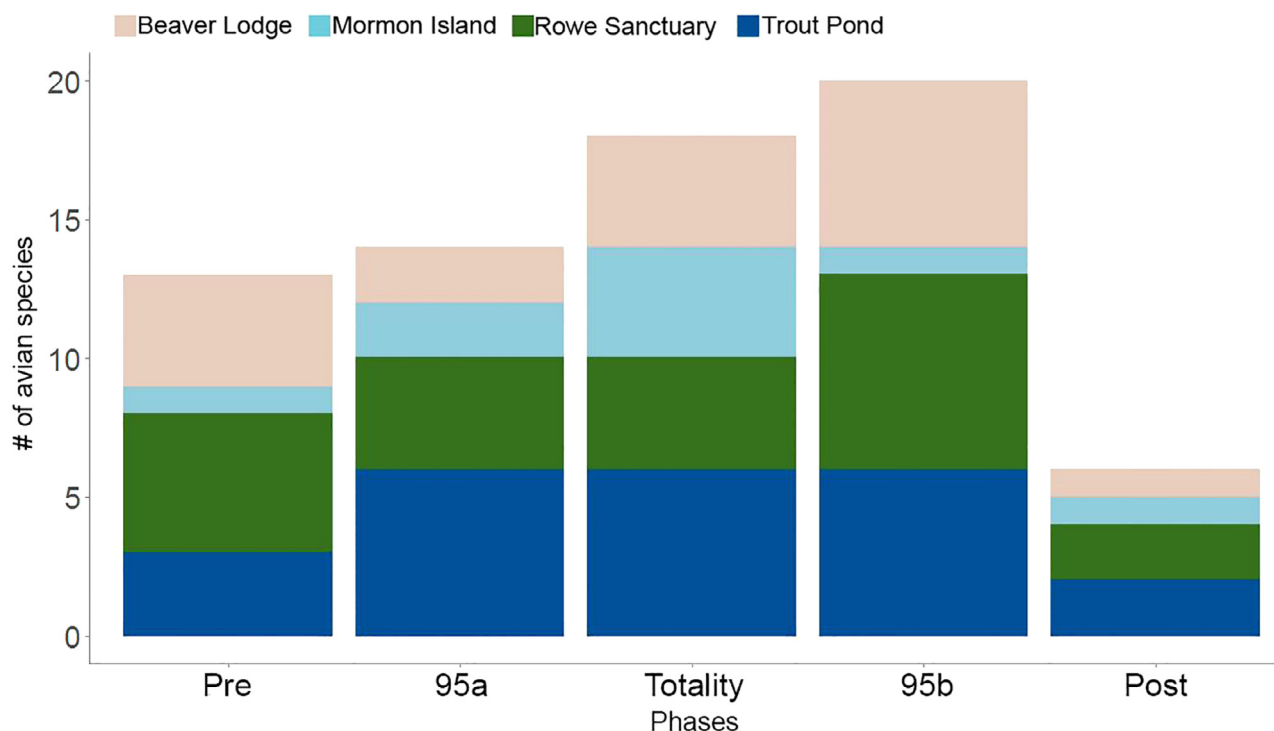
Fig. 7. Avian species richness measured as the number of species heard during each 2.5-minute phase (pre-eclipse, 95%a, totality, 95%b, post-eclipse). Study sites are denoted by color.

anthropogenic changes in the timing and intensity of light have been shown to impact atmospheric conditions and wildlife (Wild et al., 2005; Helm et al., 2013), the total solar eclipse provided a unique opportunity to observe how organisms and atmospheric factors respond to a rapid and drastic decrease in solar illumination.

The average minimum temperature for a total solar eclipse often occurs five to twenty minutes after totality, but the amount of decline depends on a number of factors including location, time of day, and the local environment (Anderson, 1999). Our atmospheric results paralleled these findings, as minimum temperature was reached an average of 13 min following totality and differed by five minutes between the two locations. Anderson et al. (1972) observed a 3 °C decline in temperature immediately following totality in 1972, while comparatively, Bozic (2003) reported that temperature dropped by 5.2 °C during a total solar eclipse in Yugoslavia (1999). Temperature in Nebraska during the eclipse declined an average of 6.7 °C. The observed difference in temperature between sites—Mormon Island reached a lower temperature by 3 °C than Rowe Sanctuary—is likely a result of contrasting landscape-level habitat features. The partial shade of the riparian forest at Rowe Sanctuary likely provided insulation from the full effects of the changing solar radiation. Conversely, the wet meadow prairie at Mormon Island was fully exposed to the sun.

A drastic reduction in illumination with distinctive differences in valley/trough shape was captured by the time-lapse camera systems. Lv values at Rowe Sanctuary exhibited a steep decline into totality, while Lv values at Mormon Island demonstrated a steep incline following totality, a fortuitous result of the orientation of the cameras in different directions. The camera system at Rowe Sanctuary was westward facing and thus, the imagery captured the shadow of the moon coming towards the camera as the path of totality spread from Oregon to South Carolina, USA. Conversely, the eastward facing camera at Mormon Island recorded the eclipse retreating over the landscape. Even during totality, Lv at both locations were higher, and thus brighter, than the scene captured at sunrise or sunset (Fig. 2).

During and near totality, broadband sound pressure levels decreased drastically, consistent with reduced sounds from wind—a

steadfast component of Nebraskan soundscapes. RMS, a measurement of amplitude across the full frequency spectrum (0–8 kHz), declined markedly near totality, reflecting a reduction in wind speed. Declines in RMS were less drastic at the woodland site compared to the prairie sites because the woodland site was less windy in general due to its tree density. For this reason, the woodland site exhibited a weak correlation between RMS and Lv values, while the three prairie sites displayed strong correlations. At all four sites, post-eclipse RMS values were higher than pre-eclipse values, likely caused by increased wind activity after the eclipse. These wind-driven changes in RMS are a characteristic and probable result of an 'eclipse wind'. A commonly observed and theorized topic, an 'eclipse wind', the change in wind direction and wind speed accompanying a total solar eclipse, has most recently been attributed to variations in the boundary layer caused by sudden ground cooling (Dubrovsky et al., 2015; Gray and Harrison, 2016).

4.2. Biological effects

We did not observe changes in the flowering plants documented with trail cameras. As our observations were limited in sample size, both for represented species and number of individual flowering plants, this does not rule out the potential that other unstudied species within this ecosystem reacted to the change of light. In addition, the two minutes of total obscuration and the surrounding relative darkness may not have been sustained enough or a drastic enough change in light conditions to impact plant flowering behavior and metabolic activity, which induces positional shifts. Similarly, we recorded no evidence of bat activity on wildlife cameras or on ultrasonic bat recorders. Although bat activity has been observed and anecdotally recorded during a total solar eclipse (Wheeler et al., 1935; Sanchez et al., 1999), our null findings could be attributed to species-specific or regional differences. Many species of bat commonly found in the Great Plains generally do not become active until about half an hour after sunset (Watkins, 1971; Hayes, 1997), and thus, the two minutes of darkness was likely not enough time for them to fully emerge.

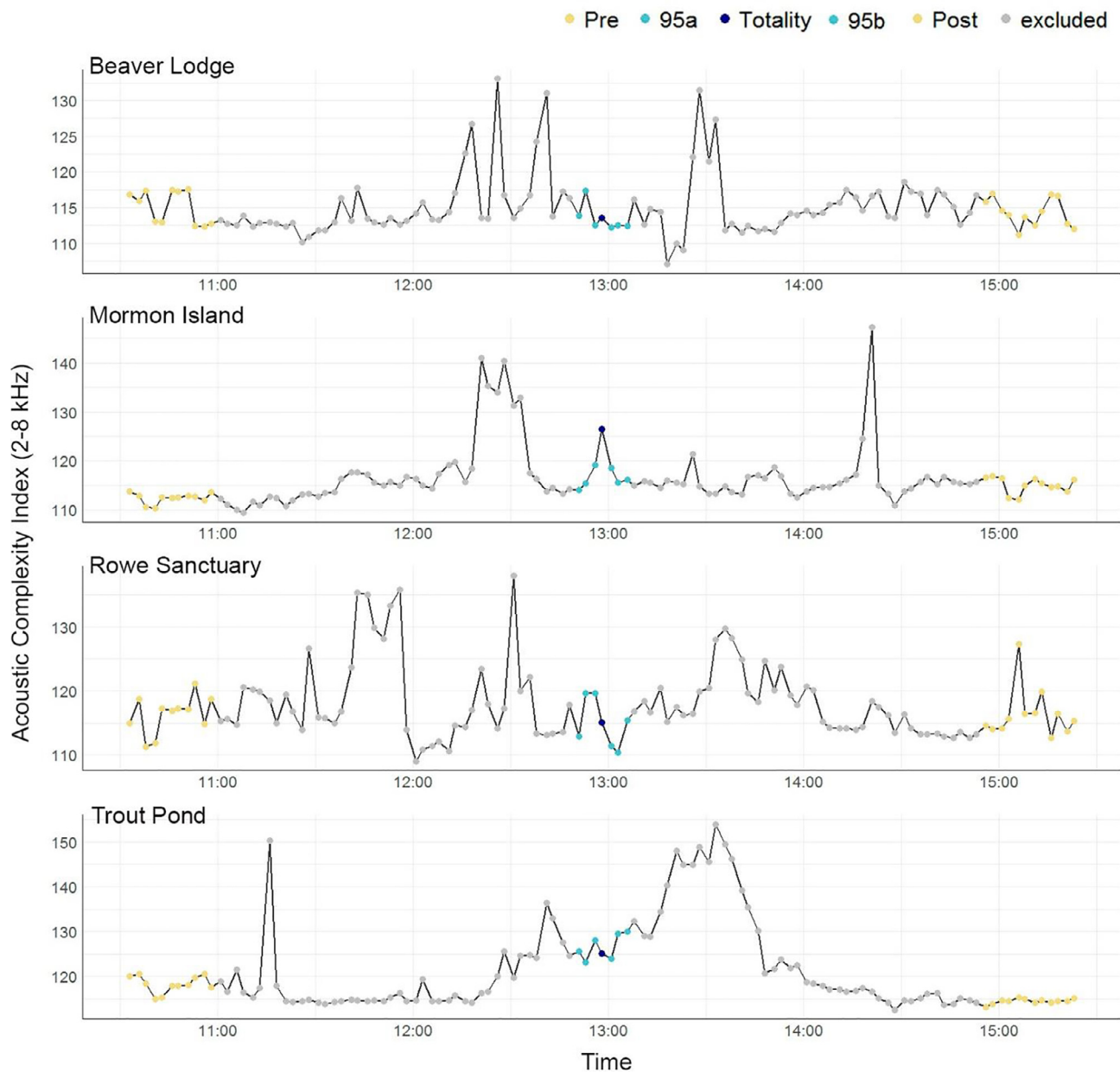Although the first observations date back hundreds of years, records

Fig. 8. Acoustic Complexity Index (ACI) from 10:30 to 15:30 on 21 August 2017. ACI, the sum of the spectral difference between successive frames in a spectrogram, was calculated for 2.5-minute bins in the 2–8 kHz range. Colors designate values within specific phases (pre-eclipse, 95%a, totality, 95%b, post-eclipse) used in other analysis.

of social insects responding to total solar eclipses are sparse. Newport (1837) documented European honey bees (*Apis mellifera*) returning to the hive during a mid-afternoon total solar eclipse in England in May of 1836, only to resume normal activity as the eclipse was ending over 1.5 hrs later. Uetz et al. (1994) found that colonial orb-weaving spiders (*Metepeira incrassata*) reacted to totality by taking down their webs, and upon the sun's reemergence, rebuilding them. Fisher (2001) noted a reduction in calling activity of diurnal Orthoptera during a solar eclipse in Europe. A variety of calling insects including various Orthoptera (Crickets: Gryllidae, Katydids: Tettigoniidae, Grasshoppers: Acrididae) and Hemiptera (Cicadas: Cicadidae) with known diurnal, nocturnal, and crepuscular call activity patterns have been recorded locally in prairie and woodland habitats along the Platte River in central Nebraska, and late summer is an active calling period for these taxa (Racliffe, 1981; Heller and Von Helversen, 1993; Greenfield, 1997; Nemec and Bragg, 2008).

Despite the natural experiment posed by the solar eclipse, it is challenging to discern the driving mechanisms of changes in insect call activity, as the reduced solar illumination resulted in ambient temperature declines, thus introducing likely secondary effects (Fig. 11; Dubrovsky et al., 2015). However, we were able to infer likely abiotic drivers of specific insect responses based on a combination of species natural history traits, inspection of spectrograms, and how behavioral changes tracked environmental stimuli in conjunction with correlation coefficients for acoustic indices with environmental variables. Broadly, manual inspection of audio recordings, spectrograms, and soundscape metrics demonstrated a decline in call frequencies, likey due to changes in temperature and a transition from diurnal to nocturnal insect activity potentially caused by the reduction in Lv around totality, as ground crickets, cicadas, and other insect taxa ceased or reduced their calling near this period. As cicada calls are affected by the their internal body temperature, changes in external temperatures can affect the interpulse
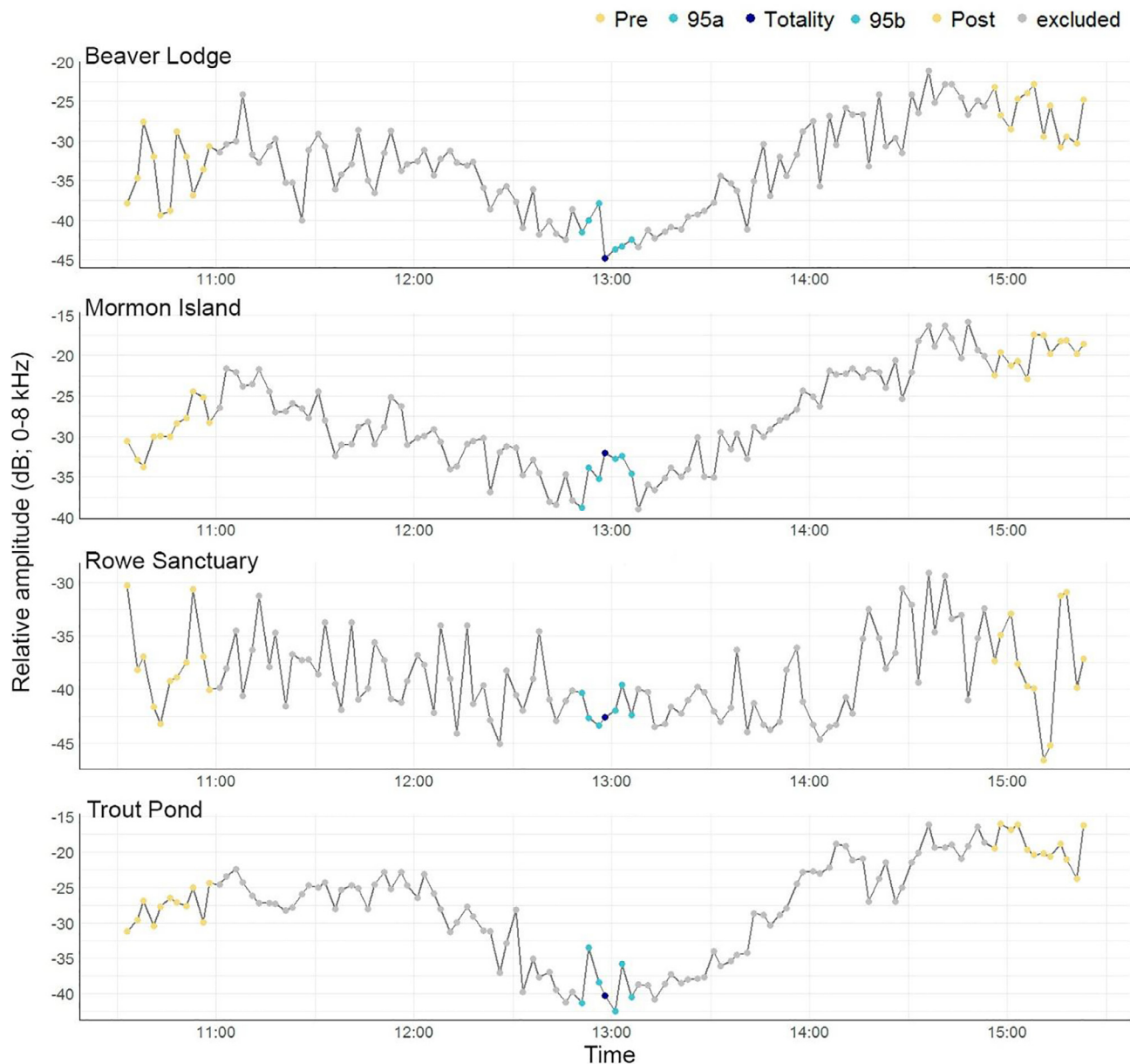
Fig. 9. Root Mean Squared amplitude (RMS) values plotted from 10:30 to 15:30 on 21 August 2017. RMS, the square root of the mean of the squared sound pressure values, was calculated for 2.5-minute bins in the 0–8 kHz range. Colors designate values within eclipse phases (pre-eclipse, 95%a, totality, 95%b, post-eclipse) used in other analysis.

interval (rhythm) and amplitude of their calls (Sueur and Sanborn, 2003); however, their call frequencies remain relatively stable due to their abdominal air sac with particular resonance (Josephson and Young, 1979). By contrast, Orthoptera are highly poikilothermic, as their internal temperatures vary considerably with ambient temperature, which affects the speed of muscular contraction and the character of their calls (Toms, 1992; Toms et al., 1993; Greenfield, 1997).

We found various diurnal Orthoptera species (predominantly Gryllidae: ground crickets) exhibited decreased call frequencies at two different bands, decreasing from 4.2 kHz to 3.5 kHz and 7.5 kHz to 7.0 kHz near the period of totality. These trends generally mirrored the decrease in ambient temperature associated with the total solar eclipse, a response similarly documented in previous studies (Walker, 1975; Pires and Hoy, 1992; Greenfield, 1997). Comparatively, the majority of calls beginning during or near the period of totality were nocturnal or crepuscular calling Orthoptera (field crickets, tree crickets, etc.), and no variation in call frequency was observed for these species. This is

consistent with the findings of Wheeler (1935), who observed crickets beginning to chirp during a total solar eclipse. The oscillations in the peaks and nadirs of ASA values mirrored several trends in the acoustic activity of Orthoptera and Cicadidae. Although the measure was not statistically significant between the eclipse and non-eclipse periods, likely due to high variability near the beginning and end of the eclipse, the overall pattern elucidated the change in diurnal insect activity patterns, specifically the steep decline at totality (Fig. 10).

ASA values were significantly correlated, however differentially, with Lv at three of the four sites, and negatively correlated with temperature at two sites, suggesting changes in insect call activity may be dually related to an altered photic and thermal environment and dependent upon specific habitats and insect communities. It appears that light may be the proximate influence on the initiation and cessation of Orthoptera and Cicadidae calling behavior (see Fischer, 2001), as nocturnal species calls persisted for shorter durations while environmental conditions were coolest and darkest, and diurnal species calls

Fig. 10. Average Signal Amplitude (ASA) values plotted from 10:30 to 15:30 on 21 August 2017. ASA, the mean amplitude of the wave envelope based on methods in Towsey et al. (2014), was calculated for 2.5-minute bins in the 2–8 kHz range. Colors designate values within eclipse phases (pre-eclipse, 95%a, totality, 95%b, post-eclipse) used in other analysis.

Table 3
Pearson correlation coefficients between acoustic index values and environmental variables (light and temperature) at four sites from the start of the initial phase of the eclipse (11:34) to the end (14:26).

Site	Acoustic Index	Light Value	p-value	Temperature	p-value
Mormon Island	RMS	0.525	< 0.01	0.304	0.01
	ASA	−0.523	< 0.01	−0.352	< 0.01
	ACI	−0.002	0.99	0.175	0.15
Rowe Sanctuary	RMS	0.257	0.03	0.364	< 0.01
	ASA	0.269	0.03	−0.002	0.98
	ACI	0.215	0.07	0.087	0.47
Beaver Lodge	RMS	0.641	< 0.01	0.534	< 0.01
	ASA	0.42	< 0.01	-0.129	0.29
	ACI	0.035	0.78	0.048	0.7
Trout Pond	RMS	0.66	< 0.01	0.634	< 0.01
	ASA	−0.07	0.57	−0.572	< 0.01
	ACI	−0.236	0.05	−0.738	< 0.01

declined during totality. Ground cricket (Gryllidae: Nemobiinae) and cicada (Cicadidae), in particular, seemed to be cued to both initiate and cease calling behavior based on changes in light values (Fig. 11).

Despite the potential impact of temperature on calling insects during a solar eclipse, Fischer (2001) concluded that light intensity was the main factor controlling diurnal grasshopper and katydid calling behavior during a total solar eclipse crossing Germany in 1999. Fischer (2001) noted that the song activity of diurnal grasshoppers and katydids slowly declined during the partial eclipse and ceased during the total eclipse before resuming normal song activity. Our results suggest that both the changes in light conditions and temperature associated with a total solar eclipse can influence insect calling behavior, in this case the calling of Cicadidae and various Orthoptera species. Temperature fluctuations likely resulted in gradual changes to call frequency, while steeper changes in light intensity likely resulted in more sudden changes to calling activity patterns of particular species.

The eclipse that we studied was a late-summer, mid-day event, which is contextually important when considering the impacts of temporary darkness and reduced solar intensity on the vocalizing behavior of wildlife. Late summer is an active time for calling insects in tallgrass prairie systems in central Nebraska including grasshoppers (Acrididae), crickets (Gryllidae), katydids (Tettigoniidae), and cicadas (Cicadidae) (Ratcliffe, 1981; Nemec and Bragg, 2008). Furthermore, taxonomic groups vary in their calling patterns with some orders, families, and genera predominantly singing nocturnally, diurnally, or on a
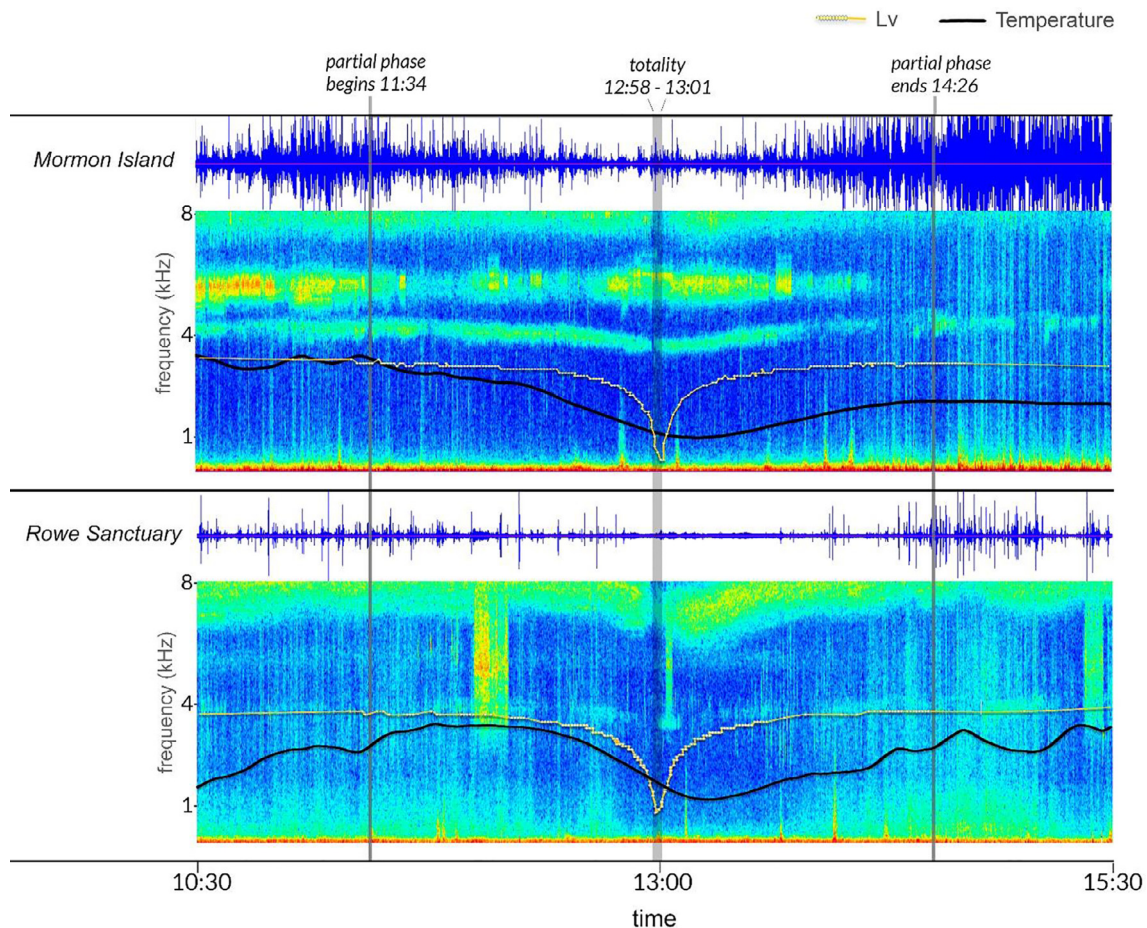
Fig. 11. Spectrograms of sound recordings paired with light value (Lv; yellow line) and temperature (black line) at Mormon Island and Rowe Sanctuary from 10:30 to 15:30 CDT on 21 August 2017.

crepuscular cycle (Heller and Von Helversen, 1993; Greenfield, 1997). By contrast, songbird communities tend to call most frequently in the early morning hours of the spring and early summer during the peak of breeding season in the temperate regions of North America (Cuthill and Macdonald, 1990; Welling et al., 1995; Bruni et al., 2014). However, La (2012) found that nocturnal calling is widespread across North American bird species, including many species classified as diurnal. Furthermore, Bruni et al. (2014) notes that a variety of environmental factors impact the singing start times of different species within the dawn chorus, including the presence of moonlight at dawn, temperature at nautical twilight, cloud cover, precipitation, and Julian date. By the time of the eclipse in mid-August, most songbird species in Nebraska had likely completed their breeding season, the primary phenological period for territorial or mating vocalizations, but remained in the area to rear young or flock, giving way to a less vigorous dawn chorus (Sharpe et al., 2001; Bruni et al., 2014).

We observed a statistically significant change in vocalization activity across all sites for four species of birds associated with the eclipse. Notably, these species are characteristically late season breeders. Three of these species, American goldfinch, western meadowlark, and song sparrow, are resident species (Lingle and Hay, 1982; Sibley, 2016), which tend to have longer breeding seasons, produce a higher number of clutches, and breed later into the season than long distance migrants (Sharpe et al., 2001; Gill, 2007). Furthermore, the American goldfinch is also noted as an exceptionally late breeder, continuing to breed into September in Nebraska (Brown et al., 1996; Sharpe et al., 2001). The fourth species, sedge wren, exhibited the most dramatic change in call activity, with 97% of all vocalizations recorded in the period of > 95% obscuration (Fig. 6), which resulted in an increase in RMS and ACI

values during this period at the Mormon Island site. Sedge wrens are migrants that winter on the southeastern and southcentral coastal plain of the United States (Lingle and Hay, 1982; Sibley, 2016). Albeit, this species is known to have an exceptionally late breeding season in Nebraska (Sharpe et al., 2001). Previous studies suggest that sedge wrens occupy dual breeding ranges, first breeding north and east of Nebraska in South Dakota and Iowa in the early spring before coming to southcentral Nebraska and neighboring parts of Kansas to set up territories, nesting as late as the end of August (Lingle and Bedell, 1989; Bedell, 1996). In addition, sedge wrens have been recorded calling at night, possibly to reduce acoustic competition with other vocalizing songbirds or insects (Walk et al., 2000; La, 2012). The pronounced increase in sedge wren calling during the period surrounding totality may be related to its unique natural history in the region as a late breeder and noted nocturnal singer; calling at night may be an effective way to reduce acoustic competition with diurnal insect noise in wet meadows, which is pronounced in the late summer (Ratcliffe, 1981).

As previous research demonstrates that dawn chorus singing behavior is dependent on fertility (Mace, 1987; Cuthill and Macdonald, 1990), it is possible that the change in illumination and environmental conditions during the eclipse were of greater influence on the species still fertile and nesting during August compared to species that had already concluded their breeding season. In accordance with Tramer (2000) and Murdin (2001), we observed differential and species-specific behavioral responses to the altered conditions of the eclipse. For instance, western meadowlarks ceased vocalization during totality and called at a higher rate before and after the eclipse than during the period of 95% obscuration. All other species with a statistically significant change in vocalization activity demonstrated increased calling

behavior during the period of > 95% coverage. These contrasts are likely the result of individual species' differing natural histories, including the light conditions under which they vocalize and the specifics of their breeding season (Cuthill and Macdonald, 1990; La, 2012; Bruni et al., 2014). Although species demonstrating limited vocalization activity were not analyzed individually to assess their responses to the eclipse, a number of species were found to only vocalize during totality or during the period of > 95% obscuration. This may be partially attributed to more favorable environmental conditions for birds to vocalize during this time, as decreased wind activity increases propagation distance (Richards and Wiley, 1980). The period following totality with > 95% obscuration had the highest species richness (N = 20), suggesting that this reemergence of light stimulated some activity, albeit modest across taxa. Furthermore, ACI values increased at three of the four sites shortly after totality, where these peaks (Beaver Lodge: 13:26:00-13:36:00; Rowe Sanctuary: 13:11:00-14:06:00; Trout Pond: 13:08:30-13:48:30) coincided with increased bird activity following totality (Fig. 8). This is consistent with observations by Murdin (2001) and Hughes et al. (2014) which reported birds quieting during totality and then starting a second dawn chorus when the sun reemerged. We would further hypothesize that the effect of light re-emergence post-totality would be more pronounced, impacting a greater number of species, if the event had taken place during the spring months, the primary breeding season for most songbirds in south-central Nebraska (Sharpe et al., 2001; Bruni et al., 2014).

The countervailing trends in insect and avian calling activity, influenced by a myriad of individual species' natural histories, precipitated a changing yet relatively constant stream of biophony throughout the eclipse recordings. These results suggest that the rapid change in solar radiance, accompanied by altered ambient temperature conditions, influenced the activity of a wide range of biota. The three indices used in this study were effective at characterizing different environmental and biological responses to the eclipse, but only after drivers of these index values were identified by listening to the acoustic recordings and examining the corresponding spectrograms, a method of validation highly recommended for any soundscape study. Moreover, while these indices provided useful system-level information, they could not characterize many species-specific responses that could only be obtained through manual inspection of recordings and knowledge of species life histories.

4.3. Techniques for passive monitoring of ecological events

Where time-lapse imagery sets an ecological stage to witness landscape-level changes, sound recordings convey the biotic and abiotic actors. Combining these two complimentary monitoring approaches allows measurement of both environmental change and corresponding biological responses. The implementation of these synergistic technologies, especially when paired with other passive environmental sensors, provides efficient, affordable, and useful information for managers to address a range of conservation-related questions. We have demonstrated that acoustic and environmental indices, which can be easily obtained from this raw data, can reveal deviations from baseline environmental or biological states. In addition to characterizing the impacts of a solar eclipse, this approach can be used to assess a wide range of natural and human-caused environmental disturbances and also the effects of restoration and specific natural resource management decisions. Unlike traditional monitoring programs that rely on human observation, passive monitoring produces data that are unbiased from human subjectivity and therefore can help to capture ecological baselines and facilitate accurate comparisons between different time periods (Blumstein et al., 2011; Pijanowski et al., 2011; Swaddle et al., 2015). The data from multi-modal technologies enable researchers to preserve a raw record, such as photographs and sound recordings, which can be used for future reference, verified with other methodologies, or re-analyzed later with newer image or soundscape analysis techniques. In addition to their value as ecological indicators, auditory and visual media are excellent tools for conveying science to diverse audiences outside the academic community. They make complex information more accessible, and can inform decision-making processes related to natural resource management.

5. Conclusions

Examination of sound recordings and photographic documentation revealed that the reduction in solar illumination from the total solar eclipse had a perceptible effect on atmospheric conditions and biological organisms, albeit with various responses. As biotic responses were broadly dependent upon site and species, a generalized conclusion summarizing the impacts of the total solar eclipse was challenging. However, a multitude of patterns emerged that depended on the varied natural histories, as well as the entrained circannual and circadian rhythms, of songbirds and calling insects. Audio and visual recordings made with passive monitoring equipment extended our ability to measure and assess biological and atmospheric responses to a rare and widely anticipated stochastic phenomenon. In addition, they documented a short, two-minute slice of time, allowing for an awe-inspiring event to be revisited, and thus, during a time of rapid methodological advancements in technology and statistical analyses, providing flexibility for future analyses and reducing uncertainty. Our research, in conjunction with additional published material, demonstrates that altered photo-regimes can impact atmospheric conditions and biological cycles. In the context of a total solar eclipse, these impacts are the product of geographical location (temperate, tropical), seasonality (spring, winter), time of day, landscape-level habitat features, and the biological health of the ecosystem. These findings highlight the utility of multi-modal passive monitoring technologies to help us understand ecological responses in a fast-changing world.

Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data deposition

Datasets are available via corresponding Data in Brief. Selected audio recordings and time-lapse imagery can be viewed at plattebasintimelapse.com.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the

online version, at https://doi.org/10.1016/j.ecolind.2018.07.017.

References

Allan, B., et al., 2018. Futurecasting ecological research: the rise of technoecology. Ecosphere 9.

Anderson, J., 1999. Meteorological changes during a solar eclipse. Weather 54, 207–215.

Atamian, H.S., et al., 2016. Circadian regulation of sunflower heliotropism, floral orientation, and pollinator visits. Science 353, 587–590.

Bedell, P.A., 1996. Evidence of dual breeding ranges for the Sedge Wren in the central Great Plains. Wilson Bull. 108, 115–122.

Benvenuti, S., et al., 1994. Effects of shade on reproduction and some morphological characteristics oi *Abutilon theophrasti* Medicos, *Datura stramonium* L. and *Sorghum halepense* L Pers. Weed Res. 34, 283–288.

Blumstein, D., et al., 2011. Acoustic monitoring in terrestrial environments using microphone arrays: Applications, technological considerations and prospectus. J. Appl. Ecol. 48, 758–767.

Bobryk, C., et al., 2016. A rapid soundscape analysis to quantify conservation benefits of temperate agroforestry systems using low-cost technology. Agrofor. Syst. 90, 997–1008.

Brandes, T.S., 2008. Automated sound recording and analysis techniques for bird surveys and conservation. Bird Conserv. Int. 18, 163–173.

Brinley Buckley, E., et al., 2017. Capturing change: the duality of time-lapse imagery to acquire data and depict ecological dynamics. Ecol. Soc 22: 30. 10.5751/ES-09268-220330.

Brown, C.R., et al., 1996. Birds of the Cedar Point Biological Station area, Keith and Garden counties, Nebraska: Seasonal occurrence and breeding data. Trans Nebraska Acad. Sci. 23, 91–108.

Bruni, A., et al., 2014. Dawn chorus start time variation in a temperate bird community: relationships with weather, and ambient light. J. Ornithol. 155, 877–890.

Coquereau, L., et al., 2017. Marine soundscape shaped by fishing activity. R Soc. Open Sci. 4.

Currier, P.J., 1989. Plant species composition and groundwater levels in a Platte River wet meadow. Proc. N. Am. Prairie Conf. 31.

Cuthill, I.C., Macdonald, W.A., 1990. Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. Behav. Ecol. Sociobiol. 26, 209–216.

Deen, J.L., Bruner, M.H., 1933. The effect of the 1932 eclipse upon the width of stomatal openings in gray birch. Ecology 14, 76–77.

Deichmann, J.L., et al., 2017. Soundscape analysis and acoustic monitoring document impacts of natural gas exploration on biodiversity in a tropical forest. Ecol. Indic. 74, 39–48.

Depraetere, M., et al., 2012. Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. Ecol. Indic. 13, 46–54.

Deutsch, J. 2017. Swallowing the Sun: Folk Stories about the Solar Eclipse | Smithsonian Folklife - Smithsonian Center for Folklife and Cultural Heritage [accessed 10/11/2017; https://folklife.si.edu/talkstory/swallowing-the-sun-folk-stories-about-the-solar-eclipse].

Dubrovsky, Y. and Tytar, V. 2015. Changes in the dynamics of weather conditions and behavioral activity of animals on the day of the total solar eclipse of August 1, 2008. - GISAP: Earth and Space Sciences 9.

Fischer, F.P., 2001. Total eclipse silences grasshoppers' and bushcrickets' songs. J. Zool. 254, 447–448.

Fuller, S., et al., 2015. Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? Ecol. Indic. 58, 207–215.

Gil-Burmann, C., Beltrami, M., 2003. Effect of solar eclipse on the behavior of a captive group of hamadryas baboons (*Papio hamadryas*). Zoo Biol. 22, 299–303.

Gill, F.B., 2007. Ornithology,. Ornithology. WH Freeman and Company, New York, pp. 758.

Gray, S.L., Harrison, R.G., 2016. Eclipse-induced wind changes over the British Isles on the 20 March 2015. Philos. Transact. A Math. Phys. Eng. Sci. 374.

Greenfield, M.D., 1997. Acoustic communication in orthoptera. In: International, C.A.B. (Ed.), The Bionomics of Grasshoppers, Katydids, and Their Kin. Wallingford, UK, pp. 197–230.

P. Harvey, ExifTool: Read, write and edit meta information. Software package available at http://www. sno. phy. queensu. ca/~ phil/exiftool, 2013.

Hayes, J.P., 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. J. Mammal. 78, 514–524.

Heller, K.-G., von Helversen, D., 1993. Calling behavior in bushcrickets of the genus *Poecilimon* with differing communication systems (Orthoptera: Tettigonioidea, Phaneropteridae). J. Insect Behav. 6, 361–377.

Helm, B., et al., 2013. Annual rhythms that underlie phenology: biological time-keeping meets environmental change. Proc. Biol. Sci. 280.

Hiscocks, P.D, Measuring luminance with a digital camera: case history. [accessed 9/15/17; http://www.ee.ryerson.ca:8080/~phiscock/astronomy/light-pollution/luminance-case-history.pdf].

Hughes, S., et al., 2014. The greatest shadow on Earth. Phys. Educ. 49, 88.

Imatest, 2017. Documentation: Iso Sensitivity and Exposure Index, [accessed 10/9/2017; http://www.imatest.com/docs/sensitivity_ei/].

Johnson, O.J., Geluso, K., 2017. Distributional and reproductive records of bats from south-central Nebraska. Occasional Papers Museum Texas Tech Univ. 347, 1–15.

Josephson, R.K., Young, D., 1979. Body temperaturea and singing in the bladder cicada, *Cystosoma saundersii*. J. Exp. Biol. 80, 69–81.

Kavanau, J.L., Rischer, C.E., 1973. Ground squirrel behaviour during a partial solar eclipse. Ital. J. Zool. 40, 217–221.

Kullenberg, B. 1955. Biological observations during the solar eclipse in southern Sweden (Province of Öland) on 30th June 1954. - Oikos 6: 51–60.

Kutner, M., 2017. Newspapers were just as obsessed with the last great American eclipse as they are with the 2017 event. Newsweek [accessed 9/8/2017; http://www.newsweek.com/great-american-eclipse-1918-media-coverage-652277].

La, V.T., 2012. Diurnal and nocturnal birds vocalize at night: a review. Condor 114, 245–257.

Lee, B.P.Y., et al., 2017. Smoke pollution disrupted biodiversity during the 2015 El Niño fires in Southeast Asia. Environ. Res. Lett. 12.

Lingle, G.R., Hay, M.A., 1982. A checklist of the birds of mormon island crane meadows. Nebraska Bird Rev. 50.

Lingle, G.R., Bedell, P.A., 1989. Nesting ecology of sedge wrens in Hall County, Nebraska. Nebraska Bird Rev. 57.

Littmann, M., et al., 2008. Totality: Eclipses of the Sun. Oxford University Press, Oxford.

Mace, R., 1987. The dawn chorus in the great tit *Paras major* is directly related to female fertility. Nature 330, 745–746.

Murdin, P., 2001. Effects of the 2001 total solar eclipse on African wildlife. Astron. Geophys. 42, 40–42.

Nagel, H.G., Kolstad, O.A., 1987. Comparison of plant species composition of Mormon Island Crane Meadows and Lillian Annette Rowe Sanctuary in central Nebraska. Trans. Nebraska Acad. Sci. 15, 37–48.

NASA 2017. Eclipse 2017 | Total Solar Eclipse 2017. [accessed 09/10/2017 https://eclipse2017.nasa.gov/].

Nemec, K.T., Bragg, T.B., 2008. Plant-feeding hemiptera and orthoptera communities in native and rdestored mesic tallgrass prairies. Restorat. Ecol. 16, 324–335.

Newport, G., 1837. On the temperature of insects, and its connexion with the functions of respiration and circulation in this class of invertebrated animals. Philos. Trans. R. Soc. Lon. 127, 259–338.

Pieretti, N., et al., 2011. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). Ecol. Indic. 11, 868–873.

Pijanowski, B.C., et al., 2011. Soundscape ecology: the science of sound in the landscape. Bioscience 61, 203–216.

Pires, A., Hoy, R.R., 1992. Temperature coupling in cricket acoustic communication. J. Compar. Physiol. A Neuroethol. Sensory Neural Behav. Physiol. 171, 79–92.

Pyle, P., and Desante, D., 2014. List of North American birds and alpha codes according to American Ornithologists' Union taxonomy through the 54th AOU Supplement [Updated 2014-09-29]. - American Ornithologists' Union, Point Reyes Station, CA.

Raguso, R.A., et al., 2003. Trumpet flowers of the sonoran desert: floral biology of peniocereus cacti and sacred datura. Int. J. Plant Sci. 164, 877–892.

Ramanathan, V., et al., 2001. Aerosols, climate, and the hydrological cycle. Science 294, 2119–2124.

Raynor, E.J., et al., 2017. Grassland bird community and acoustic complexity appear unaffected by proximity to a wind energy facility in the Nebraska Sandhills. Condor 119, 484–496.

Richards, D.G., Wiley, R.H., 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. Am. Natural. 115, 381–399.

Schneider, R., et al., 2005. The Nebraska Natural Legacy Project. Nebraska Game and Parks Commission Publications, pp. 1–164.

Sharpe, R.S., et al., 2001. Birds of Nebraska: Their Distribution & Temporal Occurrence. University of Nebraska Press.

Shuboni, D., Yan, L., 2010. Nighttime dim light exposure alters the responses of the circadian system. Neuroscience 170, 1172–1178.

Sibley, D. 2016. Sibley Birds West: Field Guide to Birds of Western North America. - Knopf.

Spoelstra, K., et al., 2000. Ground squirrel activity during the solar eclipse of August 11, 1999. Z. Saugetierkund. 65, 307–308.

Steppe, K., et al., 2002. Sap flow dynamics of a beech tree during the solar eclipse of 11 August 1999. Agric. For. Meteorol. 112, 139–149.

Stoddard, P.K., 1998. Application of filters in bioacoustics. In: Hopp, S.L. (Ed.), Animal Acoustic Communication: Sound Analysis and Research Methods. Springer, Berlin Heidelberg, pp. 105–127.

Sueur, J., Sanborn, A.F., 2003. Ambient temperature and sound power of cicada calling songs (Hemiptera: Cicadidae: Tibicina). Physiol. Entomol. 28, 340–343.

Sueur, J., Farina, A., 2015. Ecoacoustics: the ecological investigation and interpretation of environmental sound. Biosemiotics 8, 493–502.

Sueur, J., et al., 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acustica United Acustica 100, 772–781.

Swaddle, J., et al., 2015. A framework to assess evolutionary responses to anthropogenic light and sound. Trends Ecology Evol. https://doi.org/10.1016/j.tree.2015.06.009.

S. Tamarkin, The total solar eclipse is said to be nature's most spectacular feat - BuzzFeed [accessed 9/15/2017;https 2017 //www.buzzfeed.com/sallytamarkin/astronomers-and-eclipses].

Toms, A.B., 1992. Effects of temperature on chirp rates of tree crickets (orthoptera: oecanthidae): African Zool. 27, 70–73.

Toms, R.B., et al., 1993. Relationship between body temperature and air temperature in stridulating male crickets, *Gryllus bimaculatus* (Orthoptera: Gryllidae). South African J. Zool. 28, 71–73.

Towsey, M., et al., 2014. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. Ecol. Inform. 21, 110–119.

Tramer, E.J., 2000. Bird behavior during a total solar eclipse. Wilson Bull. 112, 431–432.

Uetz, G.W., et al., 1994. Behavior of colonial orb-weaving spiders during a solar eclipse. Ethology 96, 24–32.

Walk, J.W., et al., 2000. Nocturnal singing in grassland birds. Wilson Bull. 112, 289–292.

Walker, T.J., 1975. Effects of temperature on rates in poikilotherm nervous systems: evidence from the calling songs of meadow katydids (Orthoptera: Tettigoniidae:

Orchelimum) and reanalysis of published data. J. Compar. Physiol. Neuroethol. Sensory Neural Behav. Physiol. 101, 57–69.

Watkins, L.C., 1971. A technique for monitoring the nocturnal activity of bats, with comments on the activity patterns of the evening bat, *Nycticeius humeralis*. Trans. Kansas Acad. Sci. 74, 261–268.

Welling, P., et al., 1995. The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. J. Avian Biol. 26, 241–246.

Wild, M., et al., 2005. From dimming to brightening: decadal changes in solar radiation at Earth's surface. Science 308, 847–850 Washington.