

Research



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Animal behaviour

Aeroecology of a solar eclipse

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Light cues elicit strong responses from nearly all forms of life, perhaps most notably as circadian rhythms entrained by periods of daylight and darkness. Atypical periods of darkness, like solar eclipses, provide rare opportunities to study biological responses to light cues. By using a continental scale radar network, we investigated responses of flying animals to the total solar eclipse of 21 August 2017. We quantified the number of biological targets in the atmosphere at 143 weather radar stations across the continental United States to investigate whether the decrease in light and temperature at an atypical time would initiate a response like that observed at sunset, when activity in the atmosphere usually increases. Overall, biological activity decreased in the period leading to totality, followed by a short low-altitude spike of biological activity during totality in some radars. This pattern suggests that cues associated with the eclipse were insufficient to initiate nocturnal activity comparable to that occurring at sunset but sufficient to suppress diurnal activity.

1. Introduction

Light is a powerful stimulus for a great diversity of organisms, e.g. [1,2]. The regularity of this stimulus, resulting from the rotation of the planet and its path around the sun, makes light periodicity a critical component of biological cycles. Experimental manipulation of light cues at large scales is all but impossible, but on rare occasions, disruptions to this predictable daily and annual periodicity occur, such as during unusual celestial events.

One such celestial event was the total solar eclipse of 21 August 2017. The path of totality, in which the sun was completely obscured by the moon, spanned the continental USA from the Pacific to the Atlantic coast (figure 1). This eclipse was the first on the USA mainland since 1979.

The uniqueness and short duration of total solar eclipses, as well as the challenge of studying biological responses at large spatial scales, have severely constrained behavioural studies of animals during eclipses. Published accounts of small-scale responses include initiation of a variety of nocturnal behaviours, including diurnal birds returning to nocturnal roosts [3,4], nocturnal insects taking flight [4,5], crickets chirping [4], diurnal fishes ceasing to feed and nocturnal fishes emerging [6], and spiders deconstructing webs [7]. Such stereotypically nocturnal behaviours during diurnal periods suggest that an eclipse may mimic cues relevant to schedules of daily routines. In addition to fluctuations in light intensity, corresponding temperature decreases can alter behaviours during a solar eclipse, but the magnitude of temperature shifts vary with local conditions such as the time of day of the eclipse, type of ground cover and proximity to coast [8], and may lag behind the immediate changes in light intensity [9]. Furthermore, wind speeds may also decrease, as the atmosphere becomes less turbulent [10].

The August 2017 eclipse (figure 1) provided a unique opportunity to investigate migrants and other flying organisms' reactions to changes in light at a

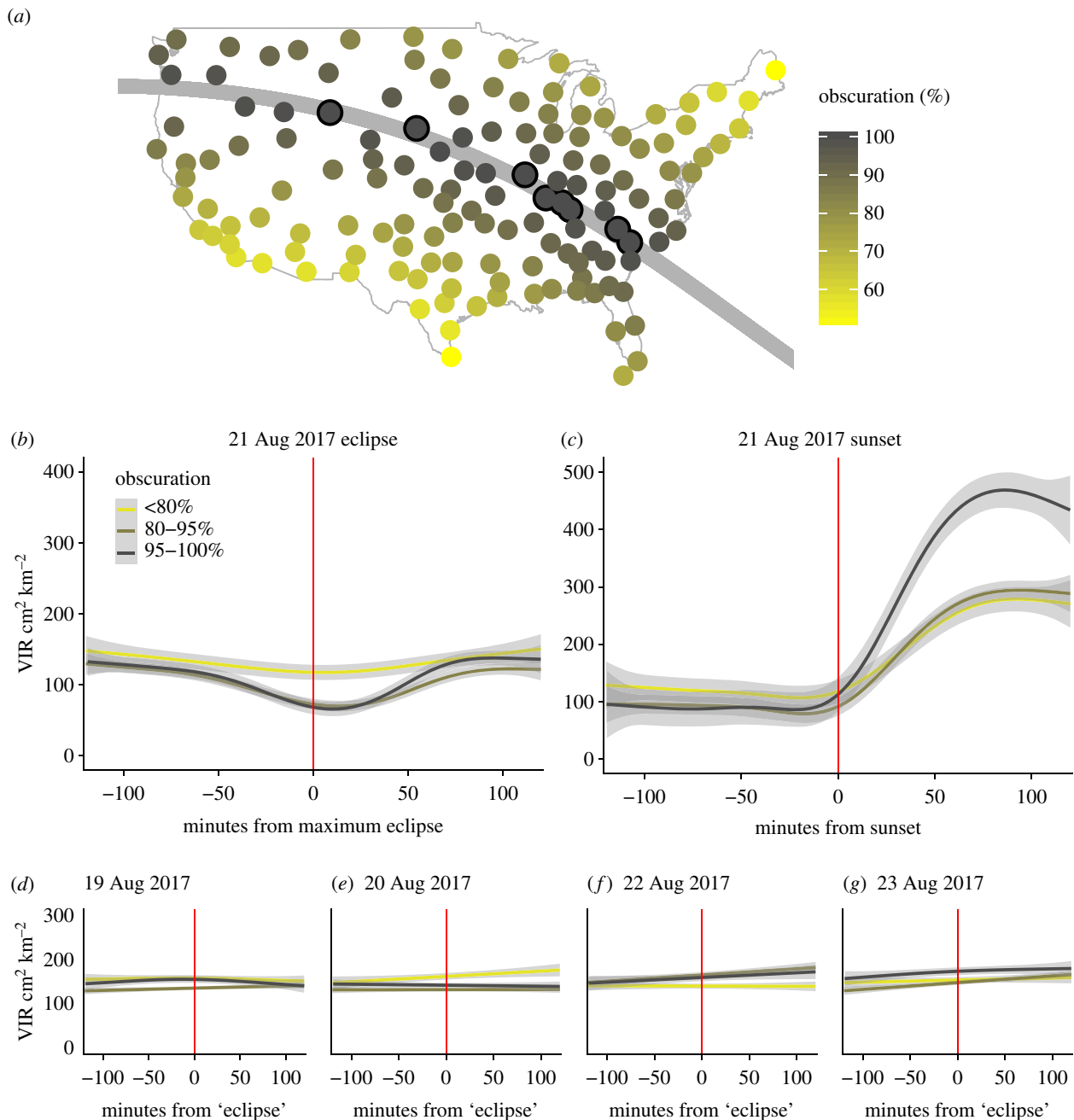


Figure 1. (a) The path of eclipse totality through the network of weather surveillance radars in the continental USA, 21 August 2017. All 143 sites included in this study, coloured by the maximum amount of obscuration. The path of totality, where obscuration is 100%, is shown in grey, and the eight sites located within the path of totality are outlined in black. (b–g) Patterns of biological activity in the atmosphere as sampled by NEXRAD. The smoothed mean (generalized additive model) amount of vertically integrated reflectivity (VIR) at all sites, grouped after amount of maximal obscuration: (b) during the eclipse (less than 80: $n = 54$, 80–95: $n = 58$, 95–100: $n = 26$), (c) at sunset the day of the eclipse (less than 80: $n = 52$, 80–95: $n = 59$, 95–100: $n = 26$); and at the time of day of the eclipse on: (d) 19 August (less than 80: $n = 54$, 80–95: $n = 58$, 95–100: $n = 27$), (e) 20 August (less than 80: $n = 54$, 80–95: $n = 59$, 95–100: $n = 27$), (f) 22 August (less than 80: $n = 55$, 80–95: $n = 59$, 95–100: $n = 27$), and (g) 23 August (less than 80: $n = 55$, 80–95: $n = 60$, 95–100: $n = 27$). Note different scale on y-axis in (c).

large geographical scale. August is the onset of autumn migration for many North American birds and insects, and bats are also active and present across the continent during this month. The nocturnal migration of birds and insects is closely associated with celestial cues at sunset, as is foraging and migratory behaviour for most bats, and these animals typically initiate nocturnal movements shortly after local sunset, e.g. [11,12]. By contrast, diurnally active birds and insects that occupy the airspace usually settle down for night roosts around sunset [13]. Since the darkness of an eclipse makes direct observations of flight behaviours of birds and insects inherently difficult, we chose a remote sensing approach. We leverage the power of an existing network

of sensors (i.e. 143 weather surveillance radars, NEXRAD; figure 1) to monitor the airspace usage of birds and insects during this celestial event. We used radar data to investigate whether the changes in light level during the eclipse lead to an increase in the number of biological targets in the air (similar to what occurs at sunset), or if it mainly suppressed diurnal activity, decreasing the number of biological targets in the air.

2. Methods

Weather surveillance radar networks register not only meteorological, but also biological targets (e.g. birds, bats, and insects [14]).

Table 1. Generalized additive model of the amount of VIR at 138 sites during the four hours surrounding the eclipse using a Gamma distribution with a log link function. (Included variables were: maximum amount of obscuration at each site, minutes from eclipse maximum, the interaction between maximum obscuration and minutes to eclipse maximum, proximity to midday of the occurrence of the eclipse at the site, and site identity (as a random effect). Test performed in R (v. 3.4.1 [17]) with function 'gam' in package mgcv [18].)

	estimated d.f.	F	p-value	s.d. (95% CI)
smooth terms				
maximum obscuration	1.52	0.47	0.679	
time from eclipse maximum	8.39	207.83	<0.001	
maximum obscuration $\times$ time from eclipse maximum	12.56	12.72	<0.001	
time from midday	2.80	9.57	<0.001	
random effects				
site identity			<0.001	1.12 (1.00–1.27)
residual error				0.40 (0.39–0.41)

Since such networks have continental-scale coverage and operate continuously, they are ideal for investigating rare, large-scale events and their effects on aerial biological targets. We gathered data from 143 NEXRAD weather radar stations across the continental USA during the total eclipse of 21 August 2017 and sunset of the same day. We also investigated the two previous and the two following days (19, 20, 22 and 23 August 2017) as controls lacking the eclipse stimulus. Owing to radar malfunction or maintenance, a few sites are missing from some of the sampling periods. See figure 1 for number of sites used during each period.

We obtained NEXRAD weather radar data from the open National Oceanic and Atmospheric Administration archive at Amazon Web Services [15] and extracted biological targets using the vol2bird algorithm in bioRad [14,16]. We integrated the amount of reflectivity from biological targets over altitudes from 0 to 5000 m above ground level and investigated changes in this vertically integrated reflectivity (VIR, $\text{cm}^2 \text{km}^{-2}$, see [16]) during the four hours surrounding the eclipse maximum (figure 1). We collected data every 5–10 min. We tested VIR during these four hours against the maximum amount of obscuration and the absolute time from the maximum eclipse using a generalized additive model with a Gamma distribution and a log link function (see table 1 for included variables and details). We also calculated VIR in the four hours surrounding sunset on the same day, as well as during the same time of day as the eclipse on the two previous and two following days (figure 1). Information on the amount of obscuration at each weather radar site location was obtained from: <http://aa.usno.navy.mil/data/docs/api.php#soleclipse>.

3. Results

Of the 138 sites with available data during the eclipse, the sun reached 95–100% obscuration at 26 sites, and eight of these experienced totality with the sun 100% obscured between 1.2 and 2.7 min (figure 1). Fifty-eight sites had a maximum obscuration of 80–95%, and 54 sites had a maximum of less than 80% obscuration. It took between 71 and 92 min from the start of the eclipse until maximum obscuration was reached at the different sites, during which the solar radiation gradually decreased. The overall amount of VIR was higher the closer to midday the eclipse occurred, and sites differed significantly in the amount of VIR (table 1). VIR decreased with proximity to the eclipse (figure 1*b* and table 1), and more so at sites with more obscuration (figure 1*b* and table 1). The decrease in activity started

around 50 min before maximum obscuration (figure 1*b*). At this point the mean obscuration was approximately 30% at sites that reached less than 80% obscuration, 35% in the 80–95% group and 40% in the greater than 95% group. We did not observe a similar decrease in activity on any of the two preceding or two following days (figure 1*e–g*). Biological activity during the eclipse was markedly different than activity at local sunset (figure 1*c*, note *y*-axis scales).

For the eight sites in the path of totality, responses varied. High altitude activity decreased at most sites during the entire duration of the eclipse (figure 2), especially at KCAE, KGSP and KLNK. At four (KHPX, KLSX, KPAH and KOHX) out of five sites where a radar scan was recorded overlapping with totality there were brief increases in activity during the moment of totality with sudden peaks in the numbers of biological targets at low altitudes (figure 2; electronic supplementary material, movie S1, animating the lowest elevation scans of radars in the path of totality). These short peaks of activity appeared only during totality, and were too short and small to affect the overall mean decrease of activity seen at the 26 sites with 95% obscuration or more (figure 1). At one site in the path of totality (KRIW), we saw no clear response. Even at the sites with an increase in activity, the response was still minor relative to the increase of activity at sunset the same day (electronic supplementary material, figure S1).

4. Discussion

With our remote sensing approach, we determined that the darkness of a total solar eclipse was insufficient to trigger biological activity in the air with the same magnitude as that typically observed at sunset during migration season. Furthermore, biological activity decreased leading up to and after the maximum eclipse, indicating that diurnally active birds and insects were landing. This is consistent with radar observations of decreasing reflectivity in the air at one site during a partial eclipse in Oklahoma [9]. It is also consistent with anecdotal observations of wildlife exhibiting behaviours such as roosting, ceasing vocalizations, and increasing stationarity during an eclipse [3,4]. Many observers also reported birds descending and exhibiting roost-like behaviours during the eclipse [19]. The decrease of biological activity

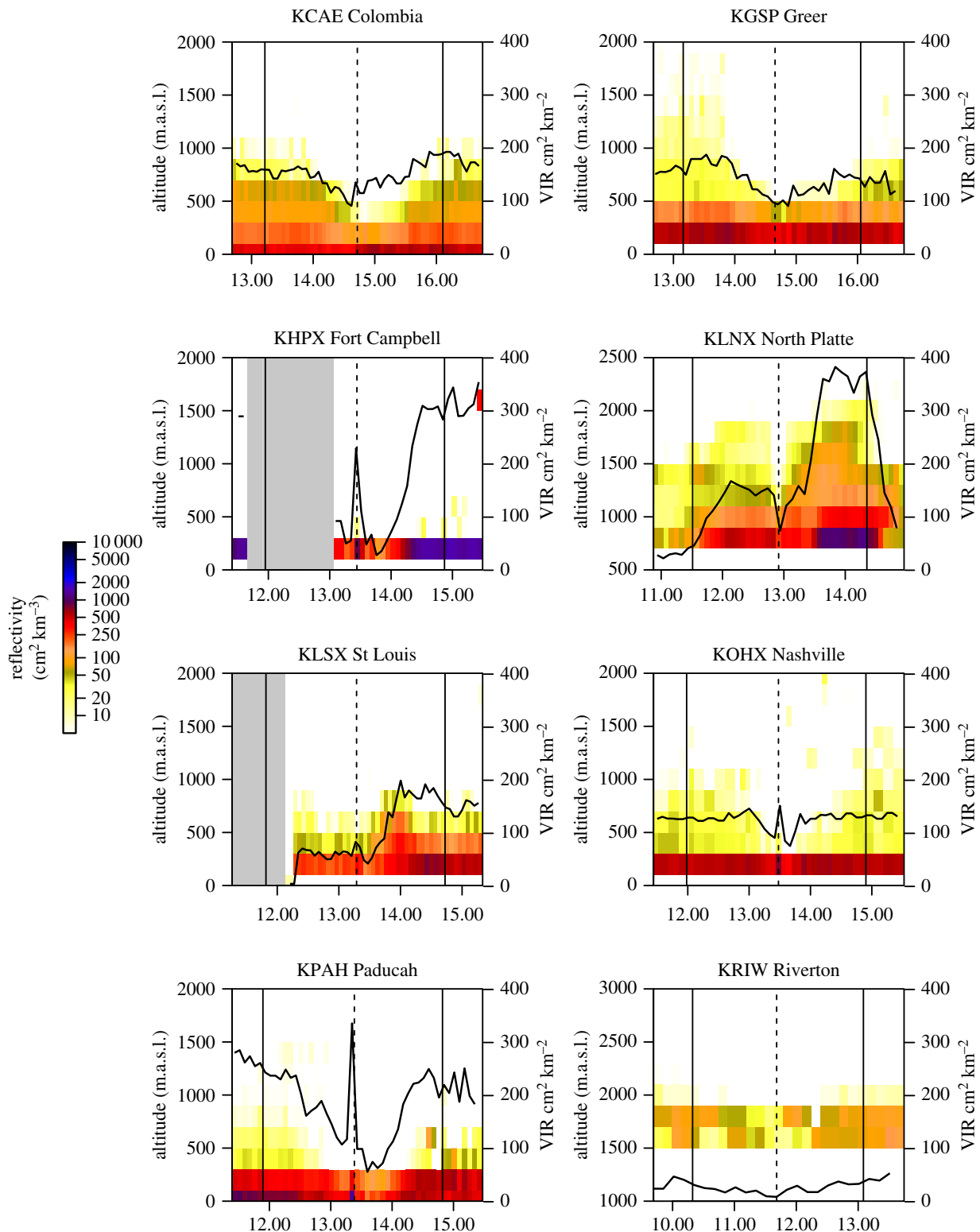


Figure 2. Reflectivity from biological targets for each of the eight sites in the path of totality over time. Heatmap shows the amount of reflectivity at different altitudes (left y-axis), black line shows the sum of reflectivity integrated over altitude (VIR, right y-axis). Altitude is in metres above sea level (m.a.s.l.; data start at ground level) and time is local time at each site. Black vertical lines mark start and end of eclipse, dashed vertical line marks time of maximum sun obscuration (totality). Reflectivity, especially at higher altitudes, decreased during the eclipse. Note that at four sites (KHPX, KLSX, KOHX and KPAH) an increase in reflectivity (darker colour) is seen at low altitudes at the timestamp closest to totality, also seen as peaks in the VIR, and especially visible in animations of the lowest elevation scan (electronic supplementary material, movie S1). Grey areas are data gaps.

started at low levels of obscuration, where humans would not perceive much change in light levels. The closest analogy to the sudden decrease of solar radiation (light and temperature) for flying animals might be rapidly increasing cloud cover, which could lead to a decrease in activity at low levels of obscuration.

At four out of five sites where a radar scan overlapped with totality, there was a short peak of biological activity at low altitudes in the scan during totality only. We could not reliably separate birds from insects in this study: peak movements were short and not concentrated in particular directions, making speed measurements unreliable. At the

sites with a peak in activity, spatial extents appear to be widespread, and not concentrated to specific points in the landscape, as we would expect to see with emerging bats [20]. The site with the largest peak in activity during the eclipse is also the site with the most immediate reaction to sunset, where activity increased as soon as the sun set (electronic supplementary material, figure S1). Both nocturnally migrating insects and birds are expected to initiate migration after sunset, the first birds leaving around an hour after sunset [12], while insects range from immediately after sunset to approximately half an hour after sunset [11]. This could indicate that insects have a more immediate and explicit reaction to darkness, as seen by accounts of crickets starting to sing during an eclipse [4], honeybees returning to hives [4] and nocturnal moths taking flight during an eclipse [5]. This suggests insects, rather than birds, may be more likely to contribute to these peaks in activity.

The next total eclipse in North America will occur on the 8 April 2024. We will then be able to compare reactions of spring migrants to this autumn data. Furthermore, with carefully designed observation schemes and detailed measures of

light levels and cloud cover at different sites, we can gain further insight into how different types of biological targets react to unexpected celestial events. This study highlights the wide scope of the effect of light cues on animal behaviour. Even this relatively short period of darkness was sufficient to affect the behaviour of animals across large scales.

Data accessibility. Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.qp6pt2p> [21].

Authors' contributions. All authors planned the study. A.M.D. processed the weather radar data; C.N. analysed the data and wrote the paper with input from all authors. All authors approved the final version and agree to be held accountable for its content.

Competing interests. We declare we have no competing interests.

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