

Photometric decision making during the dawn choruses of cicadasRakesh Khanna A.,^{1,*} Raymond E. Goldstein^{2,†} Adriana I. Pesci^{2,‡} and Nir S. Gov^{3,4,§}¹*Network Centric Systems, Bharat Electronics Limited, Ghaziabad, India*²*Department of Applied Mathematics and Theoretical Physics, Centre for Mathematical Sciences, University of Cambridge, Wilberforce Road, Cambridge CB3 0WA, England, United Kingdom*³*Department of Chemical and Biological Physics, Weizmann Institute of Science, Rehovot 7610001, Israel*⁴*Department of Physiology, Development and Neuroscience, University of Cambridge, Cambridge CB2 3DY, England, United Kingdom*

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We report a quantitative study of the onset of dawn choruses of cicadas in several natural habitats. A time-frequency analysis of the acoustical signals is used to define an order parameter for the development of collective singing. The ensemble of recordings reveals that the chorus onset times accurately track the changing sunrise times over the course of many weeks, occurring at a solar elevation of $-3.8^\circ \pm 0.2^\circ$. Despite day-to-day variations in the amplitude of fully developed choruses, the order parameter data collapse to a common sigmoidal curve when scaled by those amplitudes and shifted by the onset time, revealing a characteristic rise time of ≈ 60 s for a chorus to reach saturation amplitude. The results are used to obtain the cumulative distribution function of singing as a function of ground illumination, from which is obtained a generalized susceptibility which exhibits a narrow peak with a half width of $\approx 12\%$. The variance of the order parameter exhibits a similar peak, suggesting that a generalized fluctuation-dissipation theorem holds for this system. A model of decision making under ramps of a control parameter is developed and can achieve a quantitative match to the data. It suggests that sharpness of the susceptibility peak reflects cooperative decision making arising from acoustic communication.

DOI: [10.1103/4y4d-p32q](https://doi.org/10.1103/4y4d-p32q)**I. INTRODUCTION**

Among the most familiar collective behaviors in the animal world are the choruses of birds and insects at dawn and dusk. In the case of birds, there is a long history of quantitative observational studies dating back well over a century [1] noting how dawn choruses track the seasonally changing sunrise times [2] and the physiology of birds [3–6], and, more recently, quantifying spatiotemporal aspects of multispecies choruses [7]. Many hypotheses have been advanced to explain *why* birds engage in choruses, with explanations ranging from diurnal variations in individual physiology to ones based on social functions of the choruses [8,9]. In addition, mechanisms that underlie the observed synchrony of singing have been investigated both for birds and insects [10–15].

Twilight bird choruses are but one example of collective behavior in response to a changing external cue. A spectacular entomological example on longer timescales is the vast swarms of periodical cicadas that emerge after a (prime) number of years spent developing in underground burrows as the soil warms in springtime [16]. Seminal work [17] showed that

emergence is associated with the soil temperature—and cicada body temperature—passing through a fairly well-defined threshold value, as evidenced by the staggered emergence over several weeks of subpopulations in markedly different microclimates (sunny south-facing hilltops, shaded valleys).

On closer inspection [18] the problem of decision making under such ramps in an external stimulus is complicated by the significant local variations in soil temperature experienced by underground cicada nymphs even within a particular microclimate due to different burrowing depths and local insolation. It was suggested [18] that communication between underground nymphs, most likely by acoustic signaling, could overcome this environmental noise and lead to larger, more coherent swarms than those that would be produced by individuals responding only to their perceived thermal environment.

Such considerations suggest that these kinds of collective decision-making problems conform to a conceptual picture advanced in the context of human decision making [19,20]. There, each individual is aware of “public information” that is known to all, perhaps with additive noise, and is coupled to a set of near neighbors who are also in the process of decision making. An individual’s decision that a threshold in the public information has been crossed is thus affected by its neighbors’ opinions. These ideas naturally lead to theories based on the random-field Ising model in which a uniform external field is slowly changed in time. Examples of processes described by this approach range from coordinated applause at a concert to the mass selling of stocks.

In light of these developments, avian and insectile choruses can serve as paradigms with which to understand decision making by populations subjected to slowly changing cues.

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TABLE I. Recordings locations and dates.

Site	Coordinates	Acquisition dates
I	13°9'18.82"N, 77°28'18.04"E	24 April–1 May 2023
II	13°9'28.63"N, 77°29'48.99"E	15–20 May 2023

While the vast body of prior work on such choruses mentioned above has almost exclusively focused on defining only the apparent *start* of collective behavior, in reality the choruses grow in amplitude over a finite timescale on the order of minutes. In this paper, in contrast, we focus on the detailed temporal development of the dawn choruses of adult annual cicadas which are well known to produce deafening choruses [11,12] and are sensitive to sound through specialized organs known as tympana [14]. With the goal of quantifying how the synchronous singing develops in response to changing light levels, we extract from the acoustic signals an order parameter for the amplitude of the choruses. We find first that the dawn choruses on clear days commence at a sharply defined value of the predawn solar elevation, which corresponds to a critical ground illumination level I , and that, in fact, on cloudy days the onset is delayed. Secondly, the daily chorus amplitudes are found to grow sigmoidally as a function of light intensity and are self-similar. Third, we extract from the chorus amplitudes a generalized susceptibility $\chi(I)$ of singing to light and show that $\chi(I)$ is sharply peaked around a critical intensity I_c . The fluctuations around the average C are also found to peak at I_c , suggesting the existence of a generalized fluctuation-dissipation theorem (GFDT) at work. Finally, we develop a mathematical model for decision making that suggests that this sharpness arises from collective effects.

II. RESULTS

Recordings of the choruses produced by the species *Platypleura capitata* [21] were obtained at two distinct sites near Bangalore, India on multiple days in April and May of 2023, as indicated in Table I. Site I is a shrubland with scattered grasses and site II is a bamboo forest. Figure 1 displays photographs of the terrain and a typical example of *P. capitata*.

Stereo recordings were obtained at a sampling rate of 24 kHz using an off-the-shelf recorder the Nyquist frequency

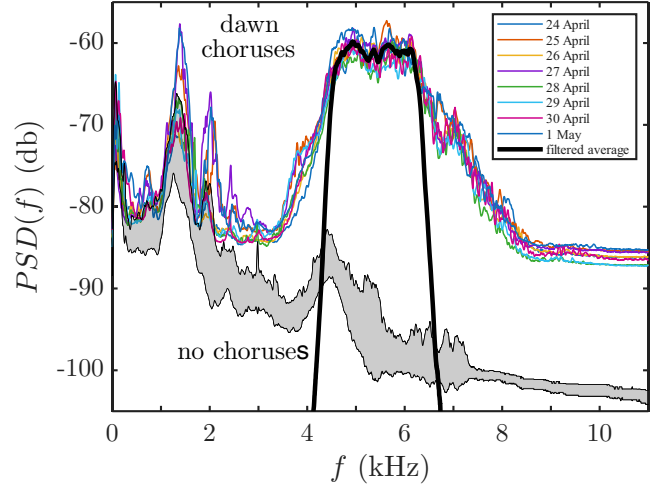


FIG. 2. Power spectra of dawn choruses at location I. Colored thin lines are raw power spectral densities of the eight data sets, while the heavy black line is the average of the eight bandpass-filtered signals. The shaded gray region shows the mean \pm standard deviation for eight quiet periods after the choruses.

of 12 kHz of which is approximately twice the dominant frequencies found in the choruses (see below), assuring that they are accurately captured. The recorder was mounted ≈ 1 m above the ground on a tree branch and remained in a single place for eight continuous days of recording at each site, broken up into consecutive time-stamped 4-h recordings that were spliced together for analysis. Cicadas are spatially distributed over a broad area, and the microphone can detect their acoustic signals at distances ranging from 100 to 150 m, depending on ambient noise conditions. Signals were analyzed with built-in and bespoke signal processing algorithms in MATLAB. The recorded signals $S(t)$ are composed of the episodic cicada choruses superimposed on background noise arising from wind, other insects, and distant environmental sounds. A spectral analysis of the eight dawn choruses at location I, shown in Fig. 2, reveals structure at frequencies below ≈ 4 kHz the amplitude of which varies considerably from day to day, and a highly reproducible peak above that frequency, with a clear flat maximum extending from a lower frequency of $f_l = 4.3$ kHz to an upper frequency $f_u = 6.3$ kHz, the latter

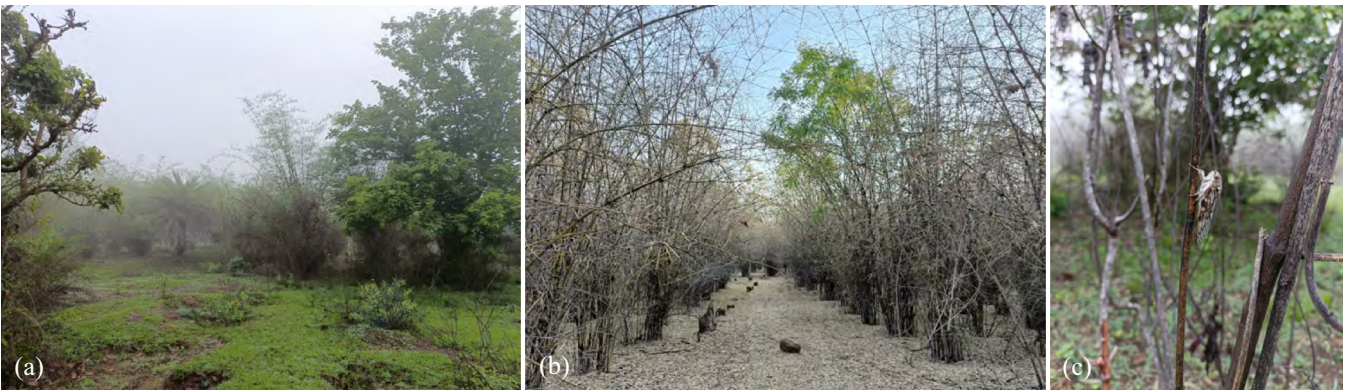


FIG. 1. Field observations. (a), (b) Sites I and II, displaying the range of flora. (c) Exemplar of *P. capitata* on a tree.

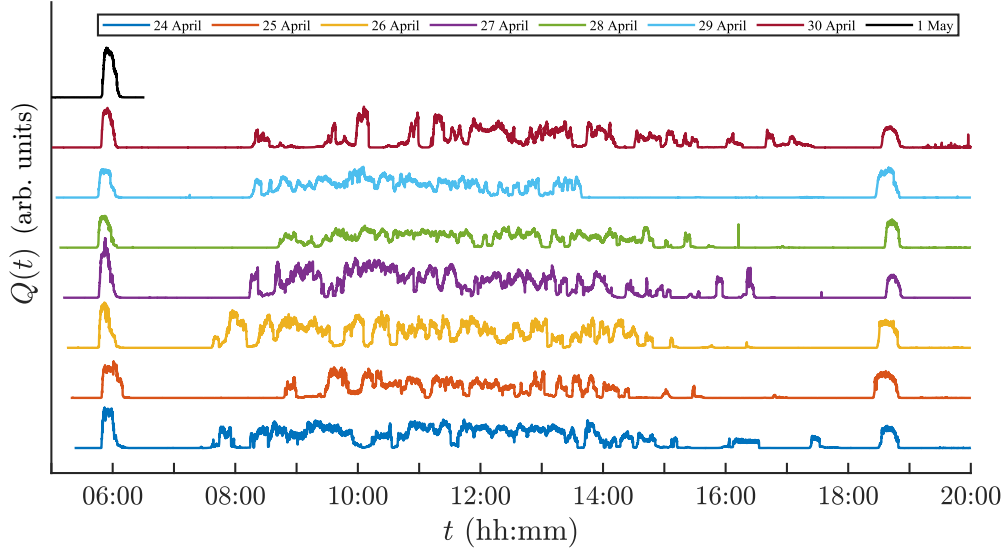


FIG. 3. Timeline of daily cicada choruses at location I. The extended peaks in the time series that occur just prior to 06:00, and just before 19:00, correspond respectively to the dawn and dusk choruses.

being well below the Nyquist frequency. By analyzing segments of the recordings after the end of each dawn chorus we obtained the power spectra in the absence of singing. Figure 2 shows these data as bands of ± 1 standard deviation around the mean. It is clear from this that the background noise is three orders of magnitude below the main signal. Based on this observation, we chose for all subsequent analysis to consider the filtered signal $\tilde{S}(t)$ obtained by passing $S(t)$ through a 20th order Butterworth bandpass filter with lower and upper limits f_l and f_u , yielding the truncated average spectrum shown in Fig. 2.

There is a vast separation of timescales between the sub-millisecond period associated with the dominant chorus pitch and the many seconds over which the amplitude of the chorus develops to a quasisteady value. Thus, we can obtain a time-dependent measure of the amplitude of a chorus by dividing up the timeline of the signal into intervals of duration T (in practice, we use $T = 5$ s) and computing within each interval the power $Q(t)$ in the filtered signal $\tilde{S}(t)$ as

$$Q(t) = T^{-1} \int_{t-T/2}^{t+T/2} dt' \tilde{S}(t')^2, \quad (1)$$

which is a simple implementation of a time-frequency analysis [22]. For the pure tone $S(t) = a \sin(2\pi f_0 t)$ with f_0 lying inside the bandpass window, then $Q = a^2/2$, and $Q^{1/2} \propto a$ is a convenient measure of the sound amplitude. We thus define the order parameter as $A(t) = Q^{1/2}(t)$.

Using this procedure, Fig. 3 shows $Q(t)$ of the daily choruses at site I. Viewed on this coarse timescale, both the dawn and dusk choruses exhibit highly reproducible onset times and more varied termination times. The midday choruses are highly variable in detail from day to day, although they are generally most noticeable during the period 08:00–16:00.

In this paper we focus on the dawn choruses. Figure 4(a) gives a magnified view of the power $Q(t)$ as a function of time at location II, illustrating that the start of each chorus exhibits

a similar functional form, albeit with different saturating values $A_{\max}(d)$ on each day d . The same behavior is found in the dawn choruses at site I. Given these features, it is natural to ask if the data can be collapsed under suitable scalings. For data from both sites I and II, Fig. 4(b) illustrates a test using what we term the *chorus order parameter*

$$C(t) = \frac{A(t - t_c(d))}{A_{\max}(d)}, \quad (2)$$

where $t_c(d)$ is a day-dependent shift termed the *chorus onset time*, defined such that $C[t_c(d)] = 1/2$. We see from the figure that the quality of the data collapse is good, encompassing distinct natural locations several weeks apart. A simple parametrization of the sigmoidal shape is $C(t) = [1 + \tanh(t/\tau)]/2$, from which we obtain the estimate $\tau \approx 60$ s for the characteristic rise time of a chorus. This time is well resolved given that it is an order of magnitude larger than the sampling window T . An interesting feature to which we return below is the markedly larger day-to-day fluctuations around the mean near t_c .

We next examine how the chorus onset times $t_c(d)$ relate to the standard predawn periods that are defined by the ranges of (negative) solar elevation angle θ , known as astronomical twilight ($-18^\circ \leq \theta < -12^\circ$), nautical twilight ($-12^\circ \leq \theta < -6^\circ$), and civil twilight ($-6^\circ \leq \theta < 0^\circ$). Data on the beginning and end of each of these periods are readily available [23]. Figure 4(c) shows that $t_c(d)$ tracks the civil twilight and nautical twilight boundary $t_{CT}(d)$. This is reexpressed in Fig. 4(d) as the solar elevation $\theta_c(d)$ at onset, computed (in degrees) as

$$\theta_c(d) = -6 \frac{t_R(d) - t_c(d)}{t_R(d) - t_{CT}(d)}, \quad (3)$$

where $t_R(d)$ is the sunrise time. Examination of historical records on cloud cover [24] shows that the two final days of the data set at site I were significantly cloudy and preceded by heavy rain and thunderstorms, as verified by the audio

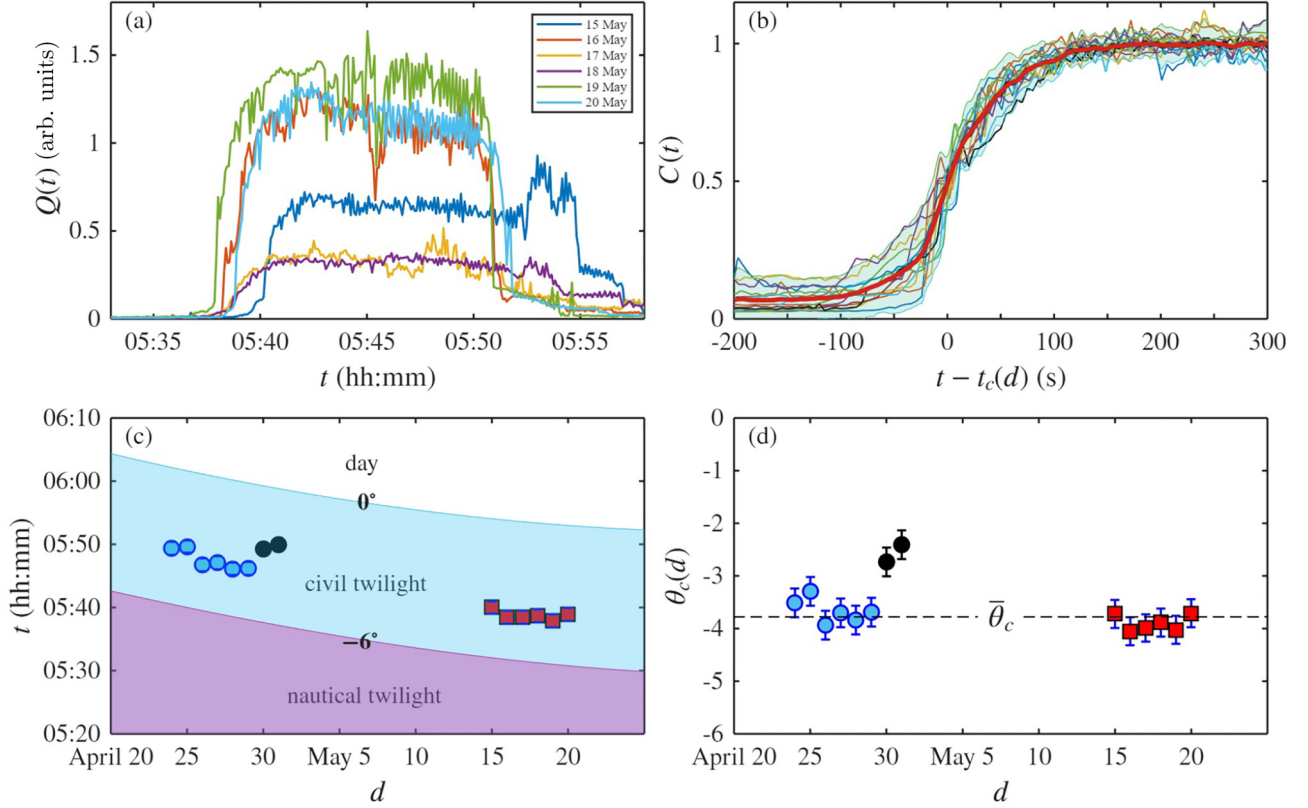


FIG. 4. Dawn choruses. (a) Magnified view of dawn chorus power $Q(t)$ at site II. (b) Chorus order parameter $C(t)$ near onset, for sites I and II, showing data collapse. The heavy red line is the mean, while the shaded area represents 95% confidence intervals. (c) Chorus onset times relative to civil twilight (solar elevation of -6°) and sunrise (0°) for sites I (circles) and II (squares). For site I, light blue circles are for fair weather, and black is for cloudy days. Smooth boundaries between the different periods are cubic interpolants of public data [23]. (d) Solar elevation at chorus onset vs day. Average $\bar{\theta}_c$ excludes two cloudy days.

recordings. This strongly suggests that the delay in the choruses is due to a lower light intensity due to the cloud cover. The records also show several days in which, while the weather was clear in the period leading up to the chorus, rain had occurred many hours earlier, leading to a noticeable increase in humidity and decrease in temperature. Nevertheless, the choruses on those clear days conformed to the general pattern, indicating that temperature and humidity do not play a role in the chorus onset. Excluding the data from site I on those cloudy days, the remaining data cluster very well around the average value $\bar{\theta}_c \simeq -3.8 \pm 0.2^\circ$.

These results indicate the high precision with which the choruses are associated with a particular solar elevation. This precision can be reexpressed in terms of the solar illumination I experienced by the cicadas. Direct measurements of the prevailing illumination with a hand-held light meter showed values of 4–6 lux at the beginning of the choruses, and we may appeal to standard astronomical observations [25] to obtain estimates during the entirety of civil twilight. Figure 5(a) shows that the ground illumination $I(\theta)$ varies over ≈ 2.5 orders of magnitude as the sun moves from -6° to 0° .

In view of the relatively short timescale $\tau \approx 60$ s over which cicada choruses develop, it is natural to estimate the changes in I during that period. Earth's rotational frequency ω_E is $360^\circ/24$ h, or conveniently $(1/4)^\circ/\text{min}$. Thus, in the time $\tau \approx 1$ min associated with the onset of the dawn chorus the Earth rotates through an angle $\delta\theta = \omega_E\tau \approx (1/4)^\circ$. As

the rotation is slow compared to the chorus onset time, the relative change $R(\theta)$ in ground illumination during the rise of the chorus can be estimated as

$$R(\theta) = \frac{I(\theta + \delta\theta) - I(\theta)}{I(\theta)} \simeq \omega_E\tau \frac{1}{I(\theta)} \frac{dI(\theta)}{d\theta}. \quad (4)$$

As shown in Fig. 5(a), $R(\theta)$ varies by less than a factor of 2 during civil twilight, with $R(\bar{\theta}_c) \simeq 0.25$. We conclude that under cloudless conditions and in the absence of any obstructing foliage the ground illumination would vary by $\approx 25\%$ during the rise time of the dawn chorus.

A more detailed examination of the photometric response involves viewing the chorus order parameter $C(t)$ not as a function of time, but rather as a function of the (time-dependent) ground illumination I . This is analogous to the way in which the changing time-dependent ground temperature for cicada emergences is the relevant parameter [17, 18]. As it is typical for visual systems to exhibit logarithmic light sensitivity (the Weber-Fechner law [26]), we show in Fig. 5(b) C as a function of

$$z \equiv \log(I/I_c) \quad (5)$$

smoothed by a Savitzky-Golay (SG) filter, where $I_c = I(\bar{\theta}_c)$. To make a thermodynamic analogy, we view $C(z)$ as an order parameter as a function of the variable z and hence there is a

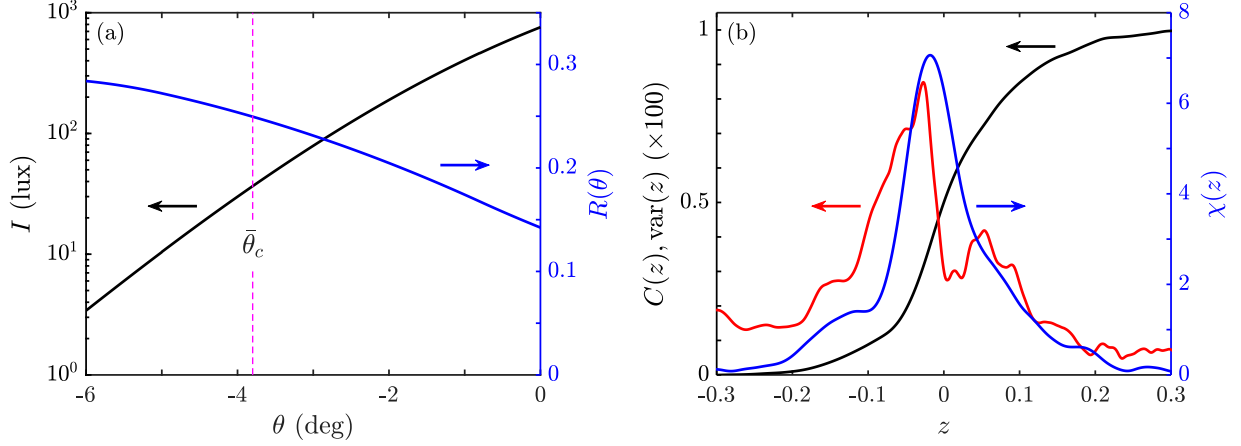


FIG. 5. Illumination and decision making. (a) Ground illumination I as a function of solar elevation θ (black, left axis) during civil twilight, using standard formulas [25]. The right axis (blue) shows relative changes in illumination from (4) during the period, using $\tau = 60$ s. (b) Smoothed values of chorus order parameter $C(z)$ (black), variance $\text{var}(z)$ of the order parameter (red), and generalized susceptibility $\chi(z)$ (blue) as functions of the logarithm of normalized ground illumination (5).

generalized susceptibility $\chi(z)$ defined as

$$\chi(z) = \frac{dC}{dz}. \quad (6)$$

The SG-filtered $\chi(z)$ is shown in blue in Fig. 5(b). The central peak of $\chi(z)$ is reasonably well approximated by a Gaussian, with a standard deviation of 0.06 on a logarithmic scale or 0.14 on a linear scale, reinforcing the conclusion that the singing decision is made with $\approx 25\%$ precision with respect to the changing illumination.

Also shown in Fig. 5(b) is the SG-filtered variance of the order parameter $C(z)$. As can be seen in Fig. 4(b), the scale of the standard deviation is ≈ 0.1 , so the variance is $\approx 1\%$. While small, it shows a somewhat noisy, but clear peak near $z = 0$, and in fact closely parallels the susceptibility $\chi(z)$. While a population of singing cicadas is certainly not in thermodynamic equilibrium, the fact that the variance is proportional to the susceptibility is evidence of a GFDT theorem. There has been significant work in recent years [27–29] on extensions of the fluctuation dissipation theorem to nonequilibrium systems where, rather than being derivable from statistical physics, the proportionality constant between fluctuations and the susceptibility must be viewed as a distinct property of each given system. The case of singing cicadas provides further clues as to the types of dynamical systems for which a GFDT holds.

In developing a model for these observations, we begin by noting that the significant variations in the local illumination based on surrounding vegetation levels and daily cicada positions and orientations are a strong indication that the existence of such a precisely defined transition to the dawn choruses requires a group decision-making process. The notion that groups of organisms can make more accurate decisions when acting collectively [30] has been explored in contexts ranging from animal and insect locomotion [31] to discrimination between possible nesting sites of ants [32], bacterial density determination in the process of quorum sensing [33], and insect clocks [34], often using a statistical physics approach based on spin models [35].

A simple model to describe the onset of singing, motivated by the spin description of animal activity and interactions [36], involves assigning to each insect i a variable n_i , where $n_i = 0(1)$ is the quiet (singing) state. The chorus order parameter is $C = \langle n \rangle$. The collection of variables is governed by an energy E with an external field \tilde{H} and a coupling \tilde{J} :

$$E = -\frac{\tilde{J}}{N} \sum_{i,j} n_i n_j - \tilde{H} \sum_i n_i, \quad (7)$$

where the light intensity, expressed through the variable z in (5), is represented by the external field $\tilde{H} \propto z$. In this way, by itself, a sweep from $\tilde{H} < 0$ to $\tilde{H} > 0$ would result in the variables flipping from 0 to 1. Thus, \tilde{H} corresponds to the public information, and the infinite-range spin-spin coupling $\tilde{J} > 0$ (reflecting acoustic communication as in midge swarms [37]) fosters collective behavior under the assumption that all cicadas behave identically.

In light of the long-ranged coupling between the spins and the fact that $N \gg 1$, the dynamics of transitions between states can be described through a mean field approximation that takes the form

$$\frac{dC}{dt} = (1 - C)R_{0 \rightarrow 1} - CR_{1 \rightarrow 0}, \quad (8)$$

where $R_{0 \rightarrow 1}$ and $R_{1 \rightarrow 0}$ are the relevant transition rates from quiet to singing and from singing to quiet. In the Glauber formalism these rates are

$$R_{0 \rightarrow 1} = \frac{k}{1 + e^{-JC-H}}, \quad R_{1 \rightarrow 0} = \frac{k}{1 + e^{JC+H}}, \quad (9)$$

where k^{-1} is a decision time of a cicada. Here, J and H are dimensionless variables corresponding to \tilde{J} and \tilde{H} scaled by some effective thermal energy. For $J = H = 0$ the two transition rates are both $k/2$. For $J = 0$ the transition to singing is enhanced (and the transition to quiet is diminished) for increasing positive H . Similarly, for $J > 0$, the larger the order parameter C the more the transition to singing increases; this is the collective effect on decision making.

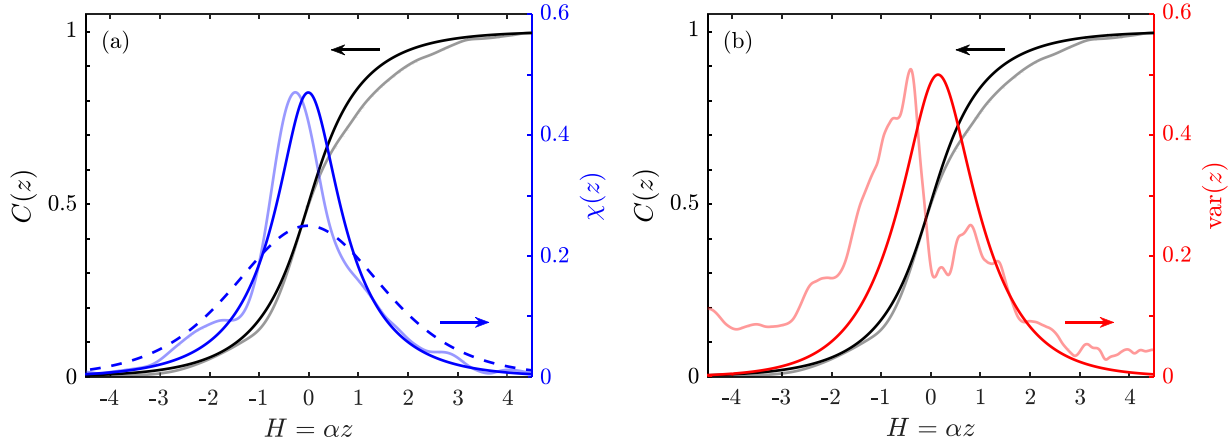


FIG. 6. Test of model for decision making. (a) Chorus order parameter (black) and susceptibility (blue) of the optimum model compared with data from Fig. 5(b) (gray, light blue). The dashed blue line indicates susceptibility for $J = 0$. (b) Comparison between model variance (red) and experimental variance (light red), the latter scaled by a factor of 60 for the purposes of comparison.

When $k\tau \gg 1$ we may use the quasistatic approximation $dC/dt = 0$, giving a self-consistency condition on C like that in the theory of ferromagnetism:

$$C = \frac{1}{2}\{1 + \tanh[(JC + H)/2]\}. \quad (10)$$

When $J = 0$, (10) yields the sigmoidal curve $C = (1/2)[1 + \tanh(H/2)]$; increasing positive J produces a more pronounced sigmoid and larger susceptibility. Within this model, the variance of the order parameter can be expressed in a form similar to the rate equation itself (8), as

$$\text{var}(C) \propto (1 - C)R_{0 \rightarrow 1} + CR_{1 \rightarrow 0}. \quad (11)$$

In testing whether the solutions to (10) are consistent with the data in Fig. 5(b), we must recognize that if $H = \alpha z$ (i.e., proportional rather than strictly equal), then α is to be determined along with J . Numerical comparison between the field data and the model shows that there is an approximately linear locus in the α - J plane along which reasonable fits can be obtained, and that along this locus there is a minimum in the total squared deviation between the data and the model (chi squared) at $\alpha \simeq 15$ and $J \simeq 1.88$. A comparison between the data and the optimum of this model is shown in Fig. 6(a), where we see very good agreement with $C(z)$ and $\chi(z)$. For comparison, the result with $J = 0$ reveals a considerably wider and lower peak in the susceptibility. Note that this value of J is less than the (mean field) critical value $J = 4$ at which the system would display bistability. Figure 6(b) shows that an appropriate scaling of the experimental variance qualitatively matches the theoretical variance. The fact that both H and J of the optimum model are the same order of magnitude provides support for the hypothesis that decision making in the dawn choruses involves a synergy between external cues and collective effects. In particular, the intermediate value of J strikes a balance between on the one hand sharpening the response to changing light levels, giving rise to a rapid chorus development that may be important in such functions as mate

attraction [38,39], and on the other avoiding spontaneous chorus development not strongly correlated with light levels.

III. DISCUSSION

In this paper we have presented a framework for the analysis of data on the collective behavior of decision-making by groups of insects, using the example of dawn choruses of cicadas. Our work highlights the balance that animals need to reach between individual sensory information (light level) and information shared between individuals (acoustic) in order to optimize their decision-making process. This is a process that occurs generally across collective animal behavior. It is natural to ask whether the methods described here can be applied to a wider group of animals responding to various environmental cues. Further tests of the hypothesis that decision making in the dawn choruses involves communication between equivalent insects could involve longer-term field studies in additional natural habitats, and also interventions to compare the behavior of isolated individuals to that of the group.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [40].

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