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<td>Author(s)</td>
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Spatio-Temporal Dynamics in Collective Frog Choruses Examined by Mathematical Modeling and Field Observations

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This paper reports theoretical and experimental studies on spatio-temporal dynamics in the choruses of male Japanese tree frogs. First, we theoretically model their calling times and positions as a system of coupled mobile oscillators. Numerical simulation of the model as well as calculation of the order parameters show that the spatio-temporal dynamics exhibits bistability between two-cluster antisynchronization and wavy antisynchronization, by assuming that the frogs are attracted to the edge of a simple circular breeding site. Second, we change the shape of the breeding site from the circle to rectangles including a straight line, and evaluate the stability of two-cluster and wavy antisynchronization. Numerical simulation shows that two-cluster antisynchronization is more frequently observed than wavy antisynchronization. Finally, we recorded frog choruses at an actual paddy field using our sound-imaging method. Analysis of the video demonstrated a consistent result with the aforementioned simulation: namely, two-cluster antisynchronization was more frequently realized.
Figure 1 | A schematic diagram describing our mathematical model of equations (5) and (6) that are mentioned in Methods. The calling times and position of the nth frog are modeled by using the calling phase $\theta_n$ and the spatial position $r_n$, respectively. The $n$th and $m$th frogs mutually interact according to the functions $\Gamma_{nm}$, $\Gamma_{mn}$, $F_{nm}$, and $F_{mn}$. The function $G_n$ is used to explain our field observations that male Japanese tree frogs aggregate along the edges of paddy fields. The geometric shape of the field is first assumed to be a circle with the radius $L$ and the origin $0$, for simplicity. This diagram was drawn by I.A.

Results

Numerical simulation of spatio-temporal dynamics in collective frog choruses at a circular field. We model the spatio-temporal dynamics inherent in the calling times and positions of male Japanese tree frogs by using equations (5)–(9) that are mentioned in Methods. Based on this model, we theoretically examine organized structures in their choruses at a paddy field. Note that the geometric shape of a paddy field is first assumed to be a circle in this model, for simplicity (Fig. 1). The parameter values of the model are then fixed on the basis of laboratory experiments and field observations. Laboratory experiments have revealed that an isolated male Japanese tree frog calls about 4 times per second\(^5\), so that the intrinsic angular velocity $\omega_n$ in equation (5) is fixed as $\omega_n = 8\pi \text{ rad/s}$ for all the individual frogs. Furthermore, in our field observations, the perimeter of all the edges of a paddy field was typically more than 100 m, and more than about 20 individual frogs simultaneously called in one paddy field. Therefore, the radius of the paddy field $L$ and the total number of the male frogs $N$ are fixed as $L = 20 \text{ m}$ and $N = 20$, for simplicity. However, since the parameter $K_{nm}$ in equations (7) and (8) is difficult to be estimated from laboratory experiments or field observations, $K_{nm}$ is fixed to be the unit value as $K_{nm} = 1$, for simplicity.

Figures 2 and 3 show the results of numerical simulation, which are obtained by assuming different initial conditions but the same parameter values $\omega_n = 8\pi \text{ rad/s}$, $L = 20 \text{ m}$, $N = 20$, and $K_{nm} = 1$. Frogs are indexed from 1 to $N$ along the edge of the circular field in the counterclockwise direction (Fig. 2A). Our simulation demonstrates that two kinds of spatio-temporal dynamics are bistable depending on the initial conditions (Figs. 2 and 3). The first dynamical structure is shown in Figure 2A and B; whereas the male frogs are positioned along the edge of the field at the same interval (Fig. 2A), each neighboring pair of male frogs synchronize in anti-phase, forming two clusters (Fig. 2B). The second structure is shown in Figure 3A and B; whereas the male frogs are positioned along the edge of the field as well (Fig. 3A), each neighboring pair of male frogs synchronize in almost anti-phase with a spatial phase shift (Fig. 3B); consequently, a wavy state is realized in each cluster, which can be described as $\theta_{n} - \theta_{n+1} = \pi + \frac{2\pi k}{N}$ by using a nonzero integer $k$ describing the wave number of this state. We name the spatio-temporal dynamics in Figure 2 as two-cluster antisynchronization, and that in Figure 3 as wavy antisynchronization.

To detect occurrences of two-cluster and wavy antisynchronization, we introduce the following order parameters $R_{\text{cluster}}$ and $R_{\text{wavy}}$ as the extensions of the order parameter for in-phase synchronization, i.e., $R_n = \frac{\sum_{n=1}^{N} \exp(i\theta_n)}{N}$:

$$R_{\text{cluster}} = \frac{1}{N} \sum_{n=1}^{N} \exp(i2\theta_n),$$

$$R_{\text{wavy}} = \frac{1}{N} \sum_{n=1}^{N} \exp\left[i2\left(\theta_n + \frac{2nk\pi}{N}\right)\right].$$

Figures 2C and 3C show the time series data of $R_{\text{cluster}}$, $R_{\text{wavy}}$, and $R_n$. When two-cluster antisynchronization is realized as shown in

Figure 2 | Two-cluster antisynchronization obtained from our numerical simulation on the assumption of $\omega_n = 8\pi \text{ rad/s}$, $L = 20 \text{ m}$, $N = 20$, and $K_{nm} = 1$ in equations (5)–(9). (A) Spatial structure in a frog chorus. Frogs are positioned along the edge of the circular field at the same interval. An index $n$ is attached to each frog along the edge of the field in the counterclockwise direction. (B) Two-cluster antisynchronization in a frog chorus. The horizontal axis represents the frog index $n$, and the vertical axis represents $\theta_n$ at $t = 5000$. Each pair of neighboring frogs synchronize in anti-phase $\pi$, and then two-cluster antisynchronization is realized. (C) Time series data of the order parameters $R_{\text{cluster}}$ and $R_{\text{wavy}}$, defined in equations (1) and (2), and $R_n = \frac{\sum_{n=1}^{N} \exp(i\theta_n)}{N}$. Red, blue, green, and black lines represent the time series data of $R_{\text{cluster}}$, $R_{\text{wavy}}$, for $k = 1$ and $k = -1$, and $R_n$ respectively. When two-cluster antisynchronization is realized as shown in Figure 2B, only $R_{\text{cluster}}$ takes a high value around 1.
Figure 2B, only $R_{\text{cluster}}$ takes a high value around 1 (Fig. 2C). In contrast, when wavy antisynchronization is realized as shown in Figure 3B, only $R_{\text{wavy}}$ for $k = 1$ reaches a high value around 1 (Fig. 3C). Thus, the order parameters $R_{\text{cluster}}$ and $R_{\text{wavy}}$ can be used to discriminate between two-cluster antisynchronization and wavy antisynchronization. In addition, we perform linear stability analysis by assuming circular distribution of the calling frogs, and show that both two-cluster antisynchronization and wavy antisynchronization are asymptotically stable (see Supplementary information). Note that the same parameter values are assumed for the linear stability analysis, i.e., $\omega_n = 8\pi$ rad/s, $L = 20$ m, $N = 20$, and $K_{\text{sum}} = 1$.

**Numerical simulation of the stability of two-cluster antisynchronization and wavy antisynchronization at a rectangular field.** The usual geometric shape of a paddy field is not a circle but a rectangle in Japan. In this section, the stability of two-cluster antisynchronization and wavy antisynchronization is analyzed by replicating the shape of an actual paddy field in our model.

We describe the shape of a rectangular paddy field by using two parameters $L_x$ and $L_y$, which represent the length and width of the field, respectively (Fig. 4A). In addition, the summation of $L_x$ and $L_y$ is constrained as $L_x + L_y = 60$ m, for consistency with the perimeter of the circular field shown in Figures 2A and 3A. Then, $G_n(r_n)$ in equation (6) is defined as follows:

$$G_n(r_n) = r_n^* - r_n,$$

where $r_n^*$ represents the vector from the origin 0 to the point on the edges that is nearest to the position of the $n$th frog $r_n$, as shown in Figure 4A. We use the term $G_n(r_n)$ in equation (3), which changes its sign across the boundary condition $r_n = r_n^*$, to explain the attraction of the male frogs towards the edges of the field.

Figure 4B shows the results of numerical simulation based on the assumption of $\omega_n = 8\pi$ rad/s, $N = 20$, $K_{\text{sum}} = 1$, and $L_x + L_y = 60$ m in the present mathematical model of equations (3) and (5)–(8). In this simulation, the parameters $L_x$ and $L_y$ are varied with an interval of 2 m in the ranges $30 \leq L_x \leq 60$ and $0 \leq L_y \leq 30$ under the constraint $L_x + L_y = 60$. For each parameter set of $L_x$ and $L_y$, occurrences of two-cluster antisynchronization and wavy antisynchronization are calculated for 500 runs of the simulation with different initial conditions: namely, if only $R_{\text{cluster}}$ is
more than 0.9 at \( t = 30000 \), the dynamics is considered as two-cluster antisynchronization; if only \( R_{\text{wavy}} \) is more than 0.9 for one of \( k = -4, -3, -2, -1, 1, 2, 3, \) and 4 at \( t = 30000 \), the dynamics is considered as wavy antisynchronization. As shown in Figure 4B, two-cluster antisynchronization is more frequently observed than wavy antisynchronization, except for the cases of \((L_x, L_y) = (52, 8), (54, 6), \) and \((56, 4)\).

When \((L_x, L_y) = (52, 8), (54, 6), \) and \((56, 4)\), both two-cluster antisynchronization and wavy antisynchronization are not or very rarely detected (Fig. 4B). Why does such instability occur at these parameter values? Figure 5A and B represents an example of the spatio-temporal dynamics at \((L_x, L_y) = (56, 4)\). As shown in Figure 5A, almost equilaterally triangular patterns are realized in many frog trios because of the narrow and long geometric shape of the rectangular field characterized by \((L_x, L_y) = (56, 4)\). Since the coupling strength of \( \Gamma_n = \theta_n - \theta_m, r_n - r_m \) in equation (7) depends on the distance between frogs, such equilateral-triangle structures cause the frog trios to interact with almost the same strength. Moreover, \( \Gamma_n = \theta_n - \theta_m, r_n - r_m \) in equation (7) is assumed to be a sinusoidal function. It has been theoretically shown that almost the same coupling strength with the sinusoidal function, e.g.,

\[
\frac{d\theta_n}{dt} = \omega_n - \sum_{m=1,m \neq n}^{3} K_{nm} \sin (\theta_m - \theta_n) \quad \text{with} \quad n = 1, 2, 3, \quad \omega_n = \alpha_n \quad \text{and} \quad K_{12} = K_{13} \approx K_{23}, \quad \text{can strongly frustrate the calling behavior of three frogs}. \]

We speculate that such frustration is the source of the instability of two-cluster and wavy antisynchronization at \((L_x, L_y) = (52, 8), (54, 6), \) and \((56, 4)\). In fact, a snapshot of the phases at \( t = 20000 \) does not show any organized structure such as the two-cluster and wavy antisynchronization (Fig. 5B), and all the order parameters \( R_{\text{cluster}}, R_{\text{wavy}}, \) and \( R_{\text{in}} \) take considerably less values than 1 (Fig. 5C).

Thus, our numerical simulation of the present mathematical model suggests that the two-cluster antisynchronization of the male frogs can be more frequently observed than wavy antisynchronization at a rectangular paddy field.

Field research on collective choruses of male Japanese tree frogs.

Figure 7A shows the time series data of the light pattern of sound-imaging devices\(^4\) deployed at an actual paddy field (see Methods and Fig. 6), capturing the chorus structures of male Japanese tree frogs. The colored plots represent the light intensity of each device, which has been calculated by subtracting the average light intensity of each device that can slightly vary depending on its tuning\(^4\); an index is attached to each device from one end of the edge, which is closer to the camera, to the other end (Fig. 6C). The device nearest to each calling frog was estimated every 15 sec, by analyzing the summation of the light intensity of the deployed devices: namely, if the summation at one device exhibited a local peak and exceeded a threshold, the device was determined to be nearest to one calling frog. Through this analysis, the threshold was set as \( 3 \times 29.97 \text{ fps} \) (frames per second) \( \times 15 \) sec. To estimate the calling times of each frog, the light pattern of the device nearest to each calling frog was then analyzed: namely, when the light pattern of the device exceeded a threshold, the corresponding times were detected as the calling times of the frog (see supplemental materials of the reference 6).
this analysis, 50% of the maximum light intensity of respective devices was used as a threshold value.

Figure 7B shows the calling times of 6 frogs obtained from the light pattern shown in Figure 7A. We observed that some pairs called synchronously. For instance, the 2nd and 3rd frogs stably synchronized in almost anti-phase $\pi$ (see the two red arrows). The calling times and positions of male Japanese tree frogs. Each black dot represents the calling times and positions of the 6 frogs. We observed that some pairs of these frogs called synchronously. For instance, the 2nd and 3rd frogs stably synchronized in almost anti-phase $\pi$ (see the two red arrows).

(B) Calling times and positions of male Japanese tree frogs. Each black dot represents the calling times and positions of the 6 frogs. We observed that some pairs of these frogs called synchronously. For instance, the 2nd and 3rd frogs stably synchronized in almost anti-phase $\pi$ (see the two red arrows). C) Time series data of the order parameters, $R_{\text{cluster}}$, $R_{\text{wavy}}$, and $R_{\text{in}}$, which were calculated from the calling times of the 6 male Japanese tree frogs. Red, blue, green, and black lines represent the time series data of $R_{\text{cluster}}$, $R_{\text{wavy}}$, for $k = 1$ and $k = -1$, and $R_{\text{in}}$, respectively. $R_{\text{cluster}}$, stably took considerably larger values than $R_{\text{wavy}}$ and $R_{\text{in}}$, which meant that two-cluster antisynchronization was realized in this chorus.

Discussion

This paper presents theoretical and experimental studies on spatio-temporal dynamics in collective frog choruses. First, a mathematical model is proposed to describe the nonlinear dynamics inherent in the calling times and positions of male Japanese tree frogs. The numerical simulation shows that organized spatio-temporal dynamics, i.e., two-cluster antisynchronization and wavy antisynchronization, are realized in the mathematical model (Figs. 2 and 3). Second, the stability of two-cluster and wavy antisynchronization is analyzed by numerically varying the length parameters of a rectangular paddy field. It is demonstrated that two-cluster antisynchronization is more frequently observed than wavy antisynchronization (Fig. 4B). Finally, field research was performed on actual choruses of male Japanese tree frogs at a paddy field by using our sound-imaging method. Analysis of the recorded video showed that two-cluster antisynchronization was more frequently detected in choruses of male Japanese tree frogs (Fig. 7 and Table 1). Thus, the present mathematical model qualitatively explains the result of the field research, i.e., the existence of two-cluster antisynchronization in the choruses of male Japanese tree frogs.

As for the spatial structures in frog choruses, our field research revealed that calling frogs were sparsely positioned along an edge of a paddy field at an interval ranging from 0.8 to 3.2 m (Fig. 7B), using the spatial resolution by the devices deployed at intervals of 40 cm. In general, most frog species can be classified as either explosive or prolonged breeders. Experimental studies have shown that, whereas explosive breeders exhibit considerably denser distribution in their breeding site, prolonged breeders exhibit sparser distribution. Since Japanese tree frogs are classified as prolonged breeders, their sparse spatial distribution revealed by our field research can be well understood on the basis of their breeding type. Moreover, as shown in Figures 2A, 3A, and 5A, our mathematical model qualitatively explains the sparse distribution of male Japanese tree frogs according to the competitive interaction terms described by equations (7) and (8).

As for the spatio-temporal dynamics in frog choruses, our field research revealed that calling frog croaks were sparsely positioned along one edge of a paddy field.
Table 1 | Stability analyses of synchronization states on the basis of the 5 field observations. In this table, Data (1)–(5) correspond to the 1.5 min video data recorded on 12th, 14th, 15th, 16th, and 17th June in 2011, respectively. Note that we did not use the data recorded on 11th June in 2011, since the data were too complicated to precisely estimate the positions of calling frogs because of the presence of a very large number of calling frogs at the paddy field (Fig. S7 in Supplementary information). (A) The averaged order parameters of two-cluster antisynchronization, in-phase synchronization, and wavy antisynchronization. The total duration of choruses including more than 3 frogs was 11.5 min, 1.7 min, 5.2 min, 0.9 min, and 12.34 min, respectively. By using these data sets of the choruses, we estimated the mean values of the order parameters as \( R_{\text{cluster}}, R_{\text{in}}, \) and \( R_{\text{wavy}} \). It was shown that \( R_{\text{cluster}} \) was larger than \( R_{\text{wavy}} \) for \( k = 1 \) and \( -1 \), and \( R_{\text{in}} \) in all the field observations. (B) Ratios of two-cluster antisynchronization, in-phase synchronization, and wavy antisynchronization. In this analysis, we summed up the times when each order parameter exceeded a threshold value of 0.8, and then divided the duration of each state by the total chorus duration of more than 3 frogs. The ratio of two-cluster antisynchronization was considerably larger than those of in-phase synchronization and wavy antisynchronization.

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<tr>
<th>A</th>
<th>( R_{\text{cluster}} )</th>
<th>( R_{\text{in}} )</th>
<th>( R_{\text{wavy}} ) for ( k = 1 )</th>
<th>( R_{\text{wavy}} ) for ( k = -1 )</th>
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<td>0.336</td>
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<td>Data (3)</td>
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<td>0.350</td>
<td>0.345</td>
</tr>
<tr>
<td>Data (4)</td>
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<td>0.336</td>
<td>0.356</td>
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<td>Data (5)</td>
<td>0.484</td>
<td>0.368</td>
<td>0.305</td>
<td>0.312</td>
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<table>
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<tr>
<th>B</th>
<th>Two-cluster antisync</th>
<th>Insync</th>
<th>Wavy antisync for ( k = 1 )</th>
<th>Wavy antisync for ( k = -1 )</th>
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<td>Data (1)</td>
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<td>2.90%</td>
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This result suggests that male Japanese tree frogs dynamically change their calling times even in the same chorus beyond the expectation of the present mathematical model. Further studies are required to derive a mathematical model explaining such complex dynamics observed in an actual field. For the modification of the present mathematical model, it is useful to estimate three functions, \( \Gamma_{\text{nn}}(\theta_n - \theta_m, r_n - r_m) \), \( \Gamma_{\text{mm}}(\theta_m - \theta_n, r_m - r_n) \), and \( G_n(r_n) \), on the basis of laboratory experiments and field research. The functions \( \Gamma_{\text{nn}}(\theta_n - \theta_m, r_n - r_m) \) and \( \Gamma_{\text{mm}}(\theta_m - \theta_n, r_m - r_n) \) may be estimated by laboratory experiments. For instance, recording of two calling frogs that hop around a room can be used to represent fundamental data to study the interactions between two individuals. Subsequently, \( \Gamma_{\text{nn}}(\theta_n - \theta_m, r_n - r_m) \) may be estimated according to the method provided in the reference 16 that makes it possible to calculate the interaction terms in the phase oscillator model from the desynchronized time series data of two interacting elements. However, it seems to be difficult to experimentally determine \( G_n(r_n) \), because male Japanese tree frogs move to a paddy field without emitting calls according to our field observations. A sound-imaging method cannot be applied to such silent frogs, and other tracking methods need to be developed.

Advertisement calls of male frogs have two roles, i.e., attracting conspecific females and defending their own territories6. In this section, the behavioral meanings of two-cluster antisynchronization are discussed based on these two roles of advertisement calls. As regards the first role of attracting conspecific females, two-cluster antisynchronization of male frogs can strengthen the sound-pressure level of their chorus, because male frogs involved in the same cluster call synchronously almost in-phase. Such a collective chorus with a high sound-pressure level may attract more females far from the chorus site. After the females arrive at the breeding site, the males must compete against each other to mate with one of the females. In this final step, the calling properties of individual male frogs, e.g., sound-pressure level and frequency, can be also important for attracting females, because such calling properties can include information about body sizes and physical conditions of the male frogs. As regards the second role of defending their territories, Figure 7B has demonstrated that neighboring pairs of male frogs, e.g., the pair of the 2nd and 3rd frogs and the pair of the 5th and 6th frogs, tend to call alternately in anti-phase. Such antisynchronization between neighboring males can help them to claim their own territories each other because of a small amount of call overlap5,6,17. If neighboring pairs of male frogs synchronize in anti-phase respectively, two-cluster anti-synchronization is automatically realized. Therefore, antisynchronization of neighboring pairs can be the origin of global two-cluster antisynchronization. However, in-phase synchronization between a neighboring pair was also detected. For example, the pair of the 1st and 2nd frogs synchronized almost in-phase (Fig. 7B). The role of such cooperative behavior is still unknown and needs to be further examined.

The present mathematical model can be applied to theoretical studies on the collective behavior of other species of animals. For instance, several species of insects, such as fireflies, crickets and cicadas, interact with each other by periodically emitting signals involving lights and sounds9. The nonlinear dynamics in the collective behavior of such animals can be examined on the basis of our mathematical model, by varying the interaction terms \( \Gamma_{\text{nn}}(\theta_n - \theta_m, r_n - r_m) \) and \( \Gamma_{\text{mm}}(\theta_m - \theta_n, r_m - r_n) \) and the geometric shape of their habitats. In addition, when the target animals are nocturnal and interact through sounds, our sound-imaging method can be similarly applied to detect their calling times and positions9. However, it should be noted that the present method has several limitations. One of the limitations is that we had to manually tune the gain of each Firefly9, and then the response of each Firefly to the same sound could have been slightly different. Such a difference in the tuning can cause the problem that the position of a single frog is detected twice.
Mathematical modeling of collective frog choruses. To theoretically examine the spatio-temporal structures realized in the choruses of male Japanese tree frogs, we propose a mathematical model describing their behavior in an actual field. Whereas a single male Japanese tree frog calls periodically, a pair of the male frogs interact through sounds\(^2\). In addition, the male frogs hop around fields in natural habitats. We model such dynamics in calling times and positions of the male frogs originating from their acoustic interactions, as follows (Fig. 1):

\[
\frac{d\theta_n}{dt} = \omega_n + \sum_{m=1, m \neq n}^{N} \Gamma_{mn}(\theta_m - \theta_n - \tau_m - \tau_n),
\]

(5)

\[
\frac{dr_n}{dt} = \sum_{m=1, m \neq n}^{N} F_m(\theta_m - \theta_n - \tau_m - \tau_n) + G_n(r_n),
\]

(6)

where \(\theta_n (n = 1, 2, \ldots, N)\) represents the phase of the calling of the \(n\)th frog\(^3\), and the vector \(r_n\) represents the position of the \(n\)th frog in a two-dimensional space. The parameter \(\omega_n\) represents the angular velocity of the calling of the \(n\)th frog. It is then assumed that \(\theta_m = 0 \mod 2\pi\) corresponds to the timing of the calls emitted by the \(m\)th frog, so as to explain the periodic calling behavior of the isolated male frogs\(^4\). The functions \(\Gamma_{mn}(\theta_m - \theta_n - \tau_m - \tau_n)\) and \(F_m(\theta_m - \theta_n - \tau_m - \tau_n)\) \((m, n = 1, 2, \ldots, N, n \neq m)\) represent the effects from the \(m\)th frog to the \(n\)th frog by simply extending the phase oscillator model described by \(d\theta/dt = \omega_n + \sum_{m=1, m \neq n}^{N} \Gamma_{mn}(\theta_m - \theta_n - \tau_m - \tau_n)\). Moreover, the geometric shape of the field is first assumed to include the factor \(1/\tau_m\), and also functions of the relative position between the \(m\)th and \(n\)th frogs, \(\tau_m - \tau_n\). The function \(G_n(r_n)\) is defined to explain our field observations that male Japanese tree frogs aggregate along the edges of paddy fields in natural habitats\(^5\). Moreover, the function \(G_n(r_n)\) is assumed to be a circle, for simplicity; the radius of the field is described by the positive constant \(L\), and the center of the field is set at the origin \(O\) in the two-dimensional space (Fig. 1).

Then, we define the three functions \(F_m(\theta_m - \theta_n - \tau_m - \tau_n)\), \(G_n(r_n)\), and \(G_n(r_n)\) in equations (5) and (6), based on experimental results and field observations of the behavior of male Japanese tree frogs.

Laboratory experiments revealed that two individuals of male Japanese tree frogs, which were placed in small cages respectively, called alternately almost in anti-phase\(^4\). To qualitatively explain this anti-synchronization (or call alternation) unique to male Japanese tree frogs, we used the phase oscillator model with a simple sinusoidal function\(^1\), i.e., \(d\theta/dt = \omega_n - \sum_{m=1, m \neq n}^{N} \frac{K_{mn}}{\tau_m - \tau_n} \sin(\theta_m - \theta_n)\). By extending the model, we define \(\Gamma_{mn}(\theta_m - \theta_n - \tau_m - \tau_n)\) in equation (5) as follows:

\[
\Gamma_{mn}(\theta_m - \theta_n - \tau_m - \tau_n) = -\frac{K_{mn}}{\tau_m - \tau_n} \sin(\theta_m - \theta_n).
\]

Because the male frogs interact through sounds that decay proportionally to the inverse of the square of their distance, \(\Gamma_{mn}(\theta_m - \theta_n - \tau_m - \tau_n)\) is assumed to be a function of \(1/|\tau_m - \tau_n|\). The parameter \(K_{mn}\) represents a positive symmetrical coupling coefficient between the \(m\)th and \(n\)th frogs, i.e., \(K_{mn} = K_{nm}\).

The calling behavior of male Japanese tree frogs studied here is classified as advertisement calls. In general, advertisement calls of male frogs have two roles of attracting conspecific females and also claiming their own territories to other conspecific males\(^6\). The important point is that, during antisynchronization of two individuals, information included in calls of one individual is not masked by calls of the other individual because of a small amount of call overlap\(^7\). These two properties of advertisement calls and call overlap suggest that anti-synchronization is capable of helping each pair of male frogs to mutually interact and then robustly defend their own territories\(^8\). To model this conjecture about anti-synchronization, \(F_m(\theta_m - \theta_n - \tau_m - \tau_n)\) in equation (6) is defined as follows:

\[
F_m(\theta_m - \theta_n - \tau_m - \tau_n) = \frac{K_{mn}}{\tau_m - \tau_n} \left(1 - \cos(\theta_m - \theta_n)\right) \epsilon_m.
\]

(8)

Here, \(F_m(\theta_m - \theta_n - \tau_m - \tau_n)\) is assumed to include the factor \(K_{mn} / (\tau_m - \tau_n)\) as in the case of \(\Gamma_{mn}(\theta_m - \theta_n - \tau_m - \tau_n)\), because \(F_m(\theta_m - \theta_n - \tau_m - \tau_n)\) also models the interaction of the male frogs via calling sounds. Moreover, \(F_m(\theta_m - \theta_n - \tau_m - \tau_n)\) is assumed to include the factor \(1/|\tau_m - \tau_n|\), i.e., \(\epsilon_m = \frac{1}{|\tau_m - \tau_n|}\), where \(\epsilon_m\) is a unit vector between \(r_m\) and \(r_n\) i.e., \(\epsilon_m = \frac{r_m - r_n}{|r_m - r_n|}\). In this term, \(1 - \cos(\theta_m - \theta_n)\) takes the maximum positive value at \(\theta_m - \theta_n = \pi\), which means that the \(m\)th and \(n\)th frogs attempt to move towards the opposite directions during anti-synchronization: \(1 - \cos(\theta_m - \theta_n)\) takes the minimum value of 0 at \(\theta_m - \theta_n = 0\), which means that the \(m\)th and \(n\)th frogs do not affect their positions each other during in-phase synchronization. It should be noted that male frogs face difficulties in their acoustic interaction during in-phase synchronization because of a large amount of call overlap.

We previously observed that male Japanese tree frogs aggregated along the edges of paddy fields\(^9\). To explain such local spatial structure aggregated along the edges of paddy fields, \(G_n(r_n)\) is defined as follows:

\[
G_n(r_n) = (L - |r_n|) \epsilon_n,
\]

(9)

where \(\epsilon_n\) represents a unit vector between the position of the \(n\)th frog \(r_n\) and the center of the paddy field \(O\), i.e., \(\epsilon_n = \frac{r_n}{|r_n|}\). Furthermore, \(G_n(r_n)\) is assumed to include the factor \(L - |r_n|\). Here, \(L - |r_n|\) is negative when the \(n\)th frog is positioned outside the circular paddy field, and then the frog is attracted to the edge of the field; on the other hand, \(L - |r_n|\) is positive when the \(n\)th frog is positioned inside the circular paddy field, and the frog is attracted to the edge of the field as well. Equation (3) of \(G_n(r_n) = r_n - r\) is used instead of equation (9) for a rectangular paddy field.

Recording of frog choruses at an actual paddy field. To test the hypothesis of our numerical simulation suggesting that two-cluster antisynchronization can be frequently observed in the choruses of male Japanese tree frogs (Fig. 4B), the positions and calling times of individual frogs must be obtained. For this purpose, we used a sound imaging method\(^10\). The imaging method is based on the device named Firefly, consisting of a microphone and a light emitting diode (LED)\(^11\) (Fig. 6B); the LED of the Firefly unit is illuminated, when capturing nearby sounds. Along one edge of a paddy field where a considerably larger number of male Japanese tree frogs were calling than along the other three edges, 85 or 86 devices were deployed at intervals of 40 cm. The illumination pattern of the devices was recorded by a Sony video camera (HDR- XSR50V, 29.97 fps). Note that the lights of some devices were not detected, when those devices were deployed far from the camera and were not illuminated by frog calls. We carefully checked all the data, and confirmed that the lights of at least 40 devices close to the camera were stably captured even when those devices were not strongly illuminated by frog calls. Hence, we used the light patterns of 40 devices close to the camera for data analysis. An index was attached to each device from one end of the edge, which was closer to the camera, to the other end.

Recordings were carried out between 20:00 h and 24:00 h on 11th, 12th, 14th, 15th, 16th, and 17th June, 2011, in Oki island, Shimane, Japan. The ambient temperature ranged between 15°C and 21.5°C, and the humidity ranged between 49% and 92% (Fig. 7). The first 15 min of the recorded video were then divided into dozens of pictures. All the field observations in this study were performed in accordance with the guidelines approved by the Wako Animal Experiments Committee of RIKEN and the Animal Experimental Committee of Kyoto University.

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**Author contributions**


**Additional information**

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