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# Modeling synchronized calling behavior of Japanese tree frogs

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We experimentally observed synchronized calling behavior of male Japanese tree frogs *Hyla japonica*; namely, while isolated single frogs called nearly periodically, a pair of interacting frogs called synchronously almost in antiphase or inphase. In this study, we propose two types of phase-oscillator models on different degrees of approximations, which can quantitatively explain the phase and frequency properties in the experiment. Moreover, it should be noted that, although the second model is obtained by fitting to the experimental data of the two synchronized states, the model can also explain the transitory dynamics in the interactive calling behavior, namely, the shift from a transient inphase state to a stable antiphase state. We also discuss the biological relevance of the estimated parameter values to calling behavior of Japanese tree frogs and the possible biological meanings of the synchronized calling behavior.

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## I. INTRODUCTION

Synchronization has been observed in many physical oscillators such as Huygens' clocks and superconductive Josephson junctions [1–4]. The possible mechanisms have been studied both mathematically and numerically: Winfree [1] performed the phase description on the oscillatory system; Kuramoto [2] established the general framework for the description on a system of coupled oscillators; and the recent studies include noise-induced synchronization [5], feedback control of coupled oscillator systems [6], and spatiotemporal dynamics of "swarm oscillators" [7].

Moreover, synchronization of biological oscillators, including synchronized behavior of living beings, has been analyzed in various systems [1–4]. In this paper, we study spontaneous calling behavior of male Japanese tree frogs *Hyla japonica* shown in Fig. 1. There have been some experimental studies on synchronization in calling behavior of frogs: Loftus-Hills [8] studied the synchronization in calling behavior of frogs *Pseudacris streckeri*, where tape-recorded calls were used to evoke response of frogs; Lemon and Struger [9] studied acoustic entrainment to randomly generated calls in frogs *Hyla crucifer*.

Japanese tree frogs are distributed widely and ubiquitously in Japan. While the single male frogs call nearly periodically as shown in Fig. 2(a), they can hear sounds through their eardrum [10]. Therefore, the males can interact by producing and hearing sounds, and the situation that many frogs call together is understood as a system of coupled oscillators. We have studied spontaneous calling behavior of male Japanese tree frogs both experimentally and theoretically [11–14].

Especially in calling behavior of two male Japanese tree frogs, we experimentally observed coexistence of inphase synchronization and antiphase synchronization; the time series analysis clarified that while inphase synchronization is just transient, antiphase synchronization is stably observed [see Fig. 2(b)] [14]. In this study, we introduce a general phase-oscillator model and then propose two concrete models with the first- and second-order approximations by fitting the unknown parameters in the models to the average phase and frequency properties during the synchronized calling behavior [14]. Then, we discuss biological relevance of the estimated values of parameters to calling behavior of Japanese tree frogs as well as possible biological meanings of the synchronized calling behavior.

## II. MATHEMATICAL MODELING

### A. Modeling periodic calling of isolated frogs

First, let us consider the situation that two isolated frogs call without interaction. The periodic calling behavior of respective frogs is modeled as the following phase oscillators with the phase variables $\theta_a \in \mathbb{S}^1$ and $\theta_b \in \mathbb{S}^1$ [12,13]:

$$\frac{d\theta_a}{dt} = \omega_a, \tag{1}$$

$$\frac{d\theta_b}{dt} = \omega_b, \tag{2}$$

where $\theta_a$ and $\theta_b$ represent the phases in the calling of frog A and that of frog B, respectively, and $\omega_a$ and $\omega_b$ are the intrinsic frequencies. If we assume that $\theta_a=0$ and $\theta_b=0$ correspond to the timing in the successive calls of respective


FIG. 1. (Color online) Japanese tree frog *Hyla japonica*.

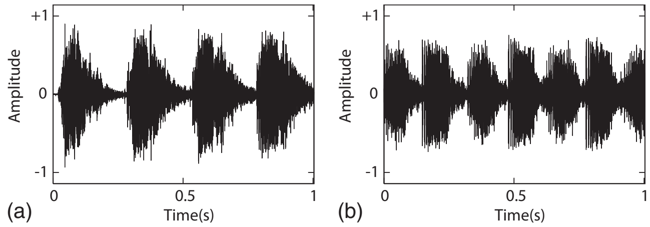


FIG. 2. Time series data in calling behavior of Japanese tree frogs: (a) periodic calling of one frog and (b) alternation calling of two frogs.

frogs, this model exhibits that the isolated frogs call periodically with their own intrinsic frequencies. From the experimental data [14], $\omega_a$ and $\omega_b$ are estimated as follows:

$$\frac{\omega_a}{2\pi} = 3.87 \text{ Hz}, \tag{3}$$

$$\frac{\omega_b}{2\pi} = 4.33 \text{ Hz}. \tag{4}$$

### B. Modeling antiphase synchronization in the interactive calling behavior

Second, we model interactive calling behavior of two frogs with a system of coupled phase oscillators as follows [2]:

$$\frac{d\theta_a}{dt} = \omega_a + g_{ab}(\theta_a - \theta_b), \tag{5}$$

$$\frac{d\theta_b}{dt} = \omega_b + g_{ba}(\theta_b - \theta_a), \tag{6}$$

where $g_{ab}$ and $g_{ba}$ are $2\pi$-periodic functions that represent the mutual interaction of frogs. To examine whether oscillators $a$ and $b$ synchronize or not, we define the phase difference $\phi \equiv \theta_a - \theta_b \in \mathbb{S}^1$ and analyze the dynamics. Subtracting Eq. (6) from Eq. (5) yields

$$\frac{d\phi}{dt} = (\omega_a - \omega_b) + g_{ab}(\phi) - g_{ba}(-\phi). \tag{7}$$

If $\omega_a = \omega_b$ and $g_{ab}(\phi) \equiv -g_{ba}(-\phi) = \sin\phi$, the stable equilibrium point $\phi^* = \pi$ is obtained and the perfect antiphase synchronization, which is similar to the experimental observation in Fig. 2(b), can be represented by the model. Then, for simplicity, we assume that $g_{ab}$ and $g_{ba}$ are given by the first-order components in Fourier expansions as $g_{ab}(\phi) \equiv -K_0 \sin(-\phi + \alpha)$ and $g_{ba}(-\phi) \equiv -K_0 \sin(\phi + \alpha)$, where $K_0$ is a coupling coefficient and $\alpha$ is a phase-shift parameter. Therefore, Eqs. (5)–(7) yield

$$\frac{d\theta_a}{dt} = \omega_a - K_0 \sin(\theta_b - \theta_a + \alpha), \tag{8}$$

$$\frac{d\theta_b}{dt} = \omega_b - K_0 \sin(\theta_a - \theta_b + \alpha), \tag{9}$$

$$\frac{d\phi}{dt} = (\omega_a - \omega_b) + 2K_0 \cos\alpha \sin\phi. \tag{10}$$

If $|\omega_a - \omega_b| \leq |2K_0 \cos\alpha|$, the following equilibrium points $\phi^*$ exist:

$$\phi^* = \arcsin\left(\frac{\omega_b - \omega_a}{2K_0 \cos\alpha}\right). \tag{11}$$

Substituting $\phi^*$ into Eqs. (8) and (9) gives the synchronized frequency as follows:

$$\left.\frac{d\theta_a}{dt}\right|_{\phi^*} = \omega_a - K_0 \sin(-\phi^* + \alpha), \tag{12}$$

$$\left.\frac{d\theta_b}{dt}\right|_{\phi^*} = \omega_b - K_0 \sin(\phi^* + \alpha), \tag{13}$$

where $\frac{d\theta_a}{dt}|_{\phi^*} = \frac{d\theta_b}{dt}|_{\phi^*}$.

On the other hand, the time series analysis clarified the phase and frequency properties during the call alternation corresponding to the antiphase synchronization as follows [14]:

$$\phi^*_{anti} = 1.05\pi, \tag{14}$$

$$\left.\frac{d\theta_a}{dt}\right|_{\phi^*_{anti}} /2\pi = \left.\frac{d\theta_b}{dt}\right|_{\phi^*_{anti}} /2\pi = 3.01 \text{ Hz}, \tag{15}$$

where $\phi^*_{anti}$ is the average phase difference between the call of frog A and the successive call of frog B, and $\frac{d\theta_a}{dt}|_{\phi^*_{anti}}/2\pi = \frac{d\theta_b}{dt}|_{\phi^*_{anti}}/2\pi$ is the synchronized frequency. Note that the phase difference $\phi^*_{anti}$ is close to $\pi$ and the synchronized frequency $\frac{d\theta_i}{dt}|_{\phi^*_{anti}}$ ($i = a$ and $b$) is smaller than the intrinsic frequencies $\omega_a$ and $\omega_b$. Moreover, it should be noted that the phase-shift parameter, $\alpha$, is necessary for explaining the experimentally observed change in the frequencies of Eqs. (3), (4), and (15) between calling alone and call alternation: if $\alpha = 0$, the synchronized frequency is simply given by the mean of the intrinsic frequencies, $(\omega_a + \omega_b)/2$, which contradicts the experimental observation.

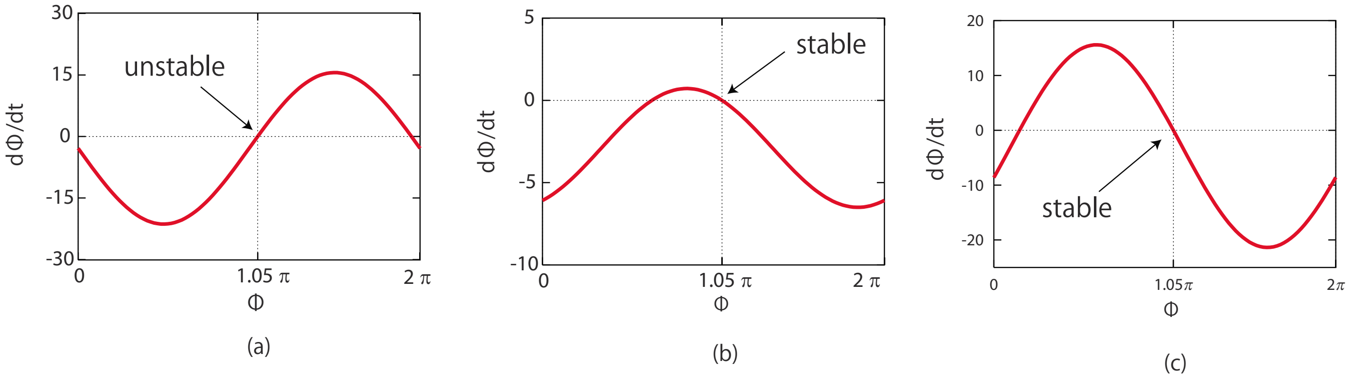
Substituting Eqs. (3), (4), (14), and (15) into Eqs. (12) and (13) provides the values of unknown parameters as follows [15]:

$$K_0 = -11.551, \tag{16}$$

$$\alpha = 0.204\,96\pi. \tag{17}$$

The set of the parameter values given by Eqs. (3), (4), (16), and (17) satisfies the condition for existence of equilibrium points, $|\omega_a - \omega_b| \leq |2K_0 \cos\alpha|$. However, the set cannot explain the experimental result unfortunately because, under these conditions, the equilibrium point representing the phase property $\phi^* = 1.05\pi$ in the alternation calling is unstable as shown in Fig. 3(a); since $\omega_b > \omega_a$, if $\phi^*$ is nearly equal to $\pi$ with $\phi^* < \pi$ then it can be stable as understood by Eq. (10), but $\phi^* > \pi$ in fact.

Then, we extend the model of Eqs. (8) and (9) to reproduce the stable antiphase synchronization experimentally ob-



(a)

(b)

(c)

FIG. 3. (Color online) Stability of the phase property in the call alternation, which is estimated from the experimental data [14]. (a) The curve shows $(\omega_a-\omega_b)+2K_0\cos\alpha\sin\phi$ under the conditions of Eqs. (3), (4), (16), and (17), and it is confirmed that the equilibrium point of the antiphase synchronization $(\phi^*_{anti},\frac{d\theta}{dt}|_{\phi^*_{anti}}/2\pi)=(1.05\pi,3.01)$ is unstable. (b) The curve shows $(\omega_a-\omega_b)+2K\cos(\frac{\alpha_a+\alpha_b}{2})\sin(\phi-\frac{\alpha_a-\alpha_b}{2})$ under the conditions of Eqs. (3), (4), and (27), and the equilibrium point of the antiphase synchronization becomes stable. (c)The curve shows $(\omega_a-\omega_b)+2K\cos(\frac{\alpha_a+\alpha_b}{2})\sin(\phi-\frac{\alpha_a-\alpha_b}{2})$ under the conditions of Eqs. (3), (4), and (28), and the equilibrium point of the antiphase synchronization is stable.

served as Fig. 2(b) by considering the effect in asymmetry of the phase-shift parameter $\alpha$: we assume that $g_{ab}$ and $g_{ba}$ are given as $g_{ab}(\phi)\equiv -K\sin(-\phi+\alpha_a)$ and $g_{ba}(-\phi)\equiv -K\sin(\phi+\alpha_b)$, where $\alpha_a\neq\alpha_b$. Therefore, Eqs. (5)–(7) are given as follows:

$$\frac{d\theta_a}{dt}=\omega_a-K\sin(\theta_b-\theta_a+\alpha_a), \tag{18}$$

$$\frac{d\theta_b}{dt}=\omega_b-K\sin(\theta_a-\theta_b+\alpha_b), \tag{19}$$

$$\frac{d\phi}{dt}=(\omega_a-\omega_b)+2K\cos\left(\frac{\alpha_a+\alpha_b}{2}\right)\sin\left(\phi-\frac{\alpha_a-\alpha_b}{2}\right). \tag{20}$$

If $|\omega_a-\omega_b|\leq|2K\cos\{(\alpha_a+\alpha_b)/2\}|$, this system has the following equilibrium points $\phi^*$:

$$\phi^*=\arcsin\left[\frac{\omega_b-\omega_a}{2K\cos\{(\alpha_a+\alpha_b)/2\}}\right]+\frac{\alpha_a-\alpha_b}{2}. \tag{21}$$

Substituting $\phi^*$ into Eqs. (18) and (19) gives the synchronized frequency as follows:

$$\left.\frac{d\theta_a}{dt}\right|_{\phi^*}=\omega_a-K\sin(-\phi^*+\alpha_a), \tag{22}$$

$$\left.\frac{d\theta_b}{dt}\right|_{\phi^*}=\omega_b-K\sin(\phi^*+\alpha_b), \tag{23}$$

where $\frac{d\theta_a}{dt}|_{\phi^*}=\frac{d\theta_b}{dt}|_{\phi^*}$.

Then, substituting Eqs. (3), (4), (14), and (15) into Eqs. (22) and (23) provides the conditions for estimating the unknown parameters. However, here, we have five parameters, $\omega_a$, $\omega_b$, $K$, $\alpha_a$, and $\alpha_b$ and four experimental conditions given by Eqs. (3), (4), (14), and (15). Hence, we cannot determine the suitable parameter values. To find plausible solutions by simple modification of the model of Eqs. (8) and (9), we assume that one of the parameters, $K$, $\alpha_a$, or $\alpha_b$, is given by corresponding parameter values estimated as Eqs. (16) and (17); namely, there are three possible choices of $K=K_0$, $\alpha_a=\alpha$, or $\alpha_b=\alpha$. First, we assume that $K$ is given by $K_0$ of Eq. (16) as follows:

$$K=-11.551, \tag{24}$$

and estimate the other parameters, $\alpha_a$ and $\alpha_b$. We have substituted $K=K_0$ and Eqs. (3), (4), (14), and (15) into Eqs. (22) and (23) and found the possible parameter values by using the Newton method as follows:

$$\alpha_a=0.204\,96\pi \quad\text{or}\quad 0.895\,04\pi, \tag{25}$$

$$\alpha_b=0.204\,96\pi \quad\text{or}\quad 0.695\,04\pi. \tag{26}$$

Note that the solutions include $\alpha_a=\alpha$ and $\alpha_b=\alpha$ with $\alpha$ of Eq. (17). On the other hand, if we assume that either $\alpha_a=\alpha$ or $\alpha_b=\alpha$, the coupling coefficient $K$ is given by $K_0$ of Eq. (16) [16]. Hence, the assumption of $K=K_0$ comprehends the other two assumptions of $\alpha_a=\alpha$ and $\alpha_b=\alpha$. Then, we have investigated all the possible parameter sets and confirmed that the following two sets can explain the phase and frequency properties of Eqs. (14) and (15) as stable equilibrium points, as shown in Figs. 3(b) and 3(c):

$$(K,\alpha_a,\alpha_b)=(-11.551,\ 0.895\,04\pi,\ 0.204\,96\pi), \tag{27}$$

$$(K,\alpha_a,\alpha_b)=(-11.551,\ 0.895\,04\pi,\ 0.695\,04\pi). \tag{28}$$

### C. Modeling coexistence of two synchronized modes in the interactive calling behavior

Next, let us further model not only the robustly stable antiphase synchronization but also the transient inphase synchronization in the interactive calling behavior [14] as bistability of two modes. From the experimental data, the phase and frequency properties during the mode of the transient inphase synchronization are estimated as follows:

$$\phi^*_{in}=1.56\pi, \tag{29}$$

$$\left.\frac{d\theta_a}{dt}\right|_{\phi^*_{in}}/2\pi=\left.\frac{d\theta_b}{dt}\right|_{\phi^*_{in}}/2\pi=4.29\ \text{Hz}, \tag{30}$$

where $\phi^*_{in}$ represents the average phase difference and $\frac{d\theta_a}{dt}|_{\phi^*_{in}}/2\pi=\frac{d\theta_b}{dt}|_{\phi^*_{in}}/2\pi$ the synchronized frequency at the transient inphase synchronization. It should be noted that the phase difference $\phi^*_{in}$ is relatively close to $2\pi$, or zero, and the synchronized frequency takes the value between the intrinsic frequencies $\omega_a$ and $\omega_b$. Here, we assume that the interaction functions in Eqs. (5) and (6), $g_{ab}$ and $g_{ba}$, are given by the first- and second-order components in Fourier expansions as $g_{ab}(\phi)\equiv -K\sin(-\phi+\alpha_a)-\gamma K\sin\{2(-\phi+\alpha_a)\}$ and $g_{ba}(-\phi)\equiv -K\sin(\phi+\alpha_b)-\gamma K\sin\{2(\phi+\alpha_b)\}$ as natural extension of Eqs. (18) and (19), where $\gamma K$ represents the strength in the second-order components. Therefore, Eqs. (5)–(7) yield

$$\frac{d\theta_a}{dt}=\omega_a-K\sin(\theta_b-\theta_a+\alpha_a)-\gamma K\sin\{2(\theta_b-\theta_a+\alpha_a)\}, \tag{31}$$

$$\frac{d\theta_b}{dt}=\omega_b-K\sin(\theta_a-\theta_b+\alpha_b)-\gamma K\sin\{2(\theta_a-\theta_b+\alpha_b)\}, \tag{32}$$

$$\frac{d\phi}{dt}=(\omega_a-\omega_b)+2K\cos\left(\frac{\alpha_a+\alpha_b}{2}\right)\sin\left(\phi-\frac{\alpha_a-\alpha_b}{2}\right)+2\gamma K\cos(\alpha_a+\alpha_b)\sin\{2\phi-(\alpha_a-\alpha_b)\}. \tag{33}$$

At an equilibrium point $\phi^*$, the synchronized frequency is given as follows:

$$\left.\frac{d\theta_a}{dt}\right|_{\phi^*}=\omega_a+K\sin(\phi^*-\alpha_a)+\gamma K\sin\{2(\phi^*-\alpha_a)\}, \tag{34}$$

$$\left.\frac{d\theta_b}{dt}\right|_{\phi^*}=\omega_b-K\sin(\phi^*+\alpha_b)-\gamma K\sin\{2(\phi^*+\alpha_b)\}, \tag{35}$$

where $\frac{d\theta_a}{dt}|_{\phi^*}=\frac{d\theta_b}{dt}|_{\phi^*}$.

Substituting Eqs. (3), (4), (14), (15), (29), and (30) into Eqs. (34) and (35) produces the conditions for estimating the parameter values. Now, we have six unknown parameters, $\omega_a$, $\omega_b$, $K$, $\gamma$, $\alpha_a$, and $\alpha_b$ and six experimental conditions described by Eqs. (3), (4), (14), (15), (29), and (30). Therefore, we can determine some sets of the possible parameters by using the method shown in the Appendix. The following set is one of them:

$$K=-8.0248, \tag{36}$$

$$\gamma=-1.3328, \tag{37}$$

$$\alpha_a=1.2339\pi, \tag{38}$$

$$\alpha_b=0.445\,99\pi. \tag{39}$$

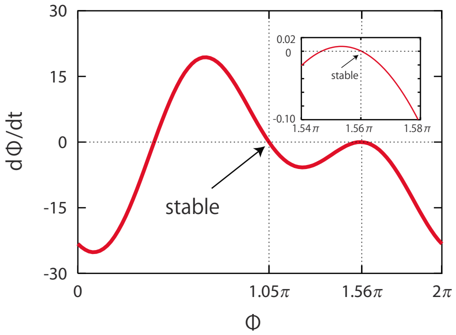


FIG. 4. (Color online) Bistability of inphase and antiphase synchronized states. While the nearly inphase state $(\phi^*_{in},\frac{d\theta}{dt}|_{\phi^*_{in}}/2\pi)=(1.56\pi,4.29)$ is marginally stable as shown in the inset, the antiphase state $(\phi^*_{anti},\frac{d\theta}{dt}|_{\phi^*_{anti}}/2\pi)=(1.05\pi,3.01)$ is robustly stable with a wider basin.

Under the conditions of Eqs. (3), (4), and (36)–(39), the phase and frequency properties both in the inphase synchronization and in the antiphase synchronization are quantitatively explained: the phase differences estimated by Eqs. (14) and (29) are bistable as shown in Fig. 4, and the frequencies at two synchronized states are consistent with the experimental results of Eqs. (15) and (30). Moreover, the state of the nearly inphase synchronization $(\phi^*_{in},\frac{d\theta}{dt}|_{\phi^*_{in}}/2\pi)=(1.56\pi,4.29)$ is marginally stable as shown in Fig. 4 and easy to transit to that of antiphase synchronization $(\phi^*_{anti},\frac{d\theta}{dt}|_{\phi^*_{anti}}/2\pi)=(1.05\pi,3.01)$ as experimentally observed, when some noise is added to this system; this theoretical result qualitatively explains the experimental observation that two frogs transiently synchronized almost inphase and then stably synchronized almost in antiphase [14].

## III. BIOLOGICAL RELEVANCE OF THE ESTIMATED PARAMETER VALUES TO CALLING BEHAVIOR OF FROGS

As shown in the second section, we estimate the suitable parameter values in two models of Eqs. (18) and (19) and Eqs. (31) and (32), respectively. In this section, let us discuss the biological meanings and suggestions of all the estimated parameters in the models. Let us name, for simplicity, the first-order approximation model of Eqs. (18) and (19) as model 1 and the second-order approximation model of Eqs. (31) and (32) as model 2.

Intrinsic frequencies $\omega_a$ and $\omega_b$ represent the natural calling periods of respective frogs and are estimated from the time series data during periodic calling behavior of the single frogs [14]. In behavioral science of living beings such as frogs and insects, those values are called intercall-intervals and known to vary dominantly dependent on temperature [17]. As shown in Eqs. (3) and (4), in the study, it turns out that $\omega_a$ and $\omega_b$ take close values of 3.87 and 4.33 Hz, which suggests that under isolated situations the two frogs can be described as similar oscillators.

Coupling coefficients $K$ and $\gamma$ represent the strength in vocal communication between the two frogs; $K$ is the strength of the first-order components in the interaction terms, and $\gamma K$ is that of the second-order components, as shown in model 1 and model 2. Substituting the estimated parameter values of Eqs. (27) and (28) into the interaction terms in model 1 and those of Eqs. (36)–(39) into model 2 clarify that the effective coupling coefficients in the two models take close values with each other; namely, the maximum value of the interaction terms in model 1 is estimated as 11.551 and that in model 2 as 16.702 [18]. Note that the distance between frogs dominantly affects the value of $K$ and that of $\gamma$ because frogs interact through sounds, which decay proportionally to the inverse of square of the distance [19]. In addition, since the phase and frequency properties both in the antiphase and inphase synchronization are obtained from the time series data during the same experimental trial, the experimental condition including the distance between the two frogs does not change during the two types of synchronized calling behavior. Therefore, from the biological point of view, it is reasonable that the effective coupling coefficients estimated in the interaction terms in model 1 and those in model 2 take close values because of the decay property of sounds and the stationary condition during the experiment mentioned above.

Phase-shift parameter $\alpha_i$ represents both the effect of the variation from the simplest sinusoidal interaction term of the Kuramoto model [2] and that of the time delay for the oscillator $i$ to respond to signals of the other oscillator [20]. Note that, both in model 1 and model 2, $\alpha_a$ and $\alpha_b$ take distinctly different values with each other except for one example of Eq. (28) in model 1; as shown in the parameter set of Eq. (27) in Model 1 and that of Eqs. (38) and (39) in model 2, the estimated value of $\alpha_a$ is significantly larger than that of $\alpha_b$. Since the frogs in the experiment are the same species, they are expected to behave as similar oscillators. Therefore, the asymmetry in the phase-shift parameters may seem surprising. It should be noted, however, that, especially in frog's vocal communication, leader-follower relationship has been widely recognized [17]: while the leader is the individual that is easy to begin to call first, the follower is the one that tends to be stimulated by leader's call and then starts calling. Therefore, during interactive calling behavior, respective frogs can play different roles, which would be the possible mechanism to generate the asymmetry in phase-shift parameters of the interaction terms, although experimentally examining such relationship in Japanese tree frogs is an important future problem.

## IV. POSSIBLE BIOLOGICAL MEANINGS

Finally, we discuss possible biological meanings in the synchronized calling behavior of male Japanese tree frogs. Antiphase synchronization would be useful both for males and females: males can distinguish the positions of other males easily and keep their own territories; females can also specify the positions of males, smoothly approach one of them, and succeed in mating [11]. On the other hand, inphase synchronization enables males to attract females far from them because the total signal power of the male crowd gets larger in such cooperative behavior, the same as synchronization in flashing of fireflies [1–4]. We guess that the occurrence of these two modes may depend on the proportion in the number of males and that of females in a real field. If there are much more males than females, it is important for males to attract more females to the field; in such a case, inphase synchronization would be useful because of the increase in the total signal power. On the other hand, if there are already a sufficient number of females in the field, males would synchronize in antiphase to keep their own territories and increase the efficiency in mating. Thus, there is a possibility that male Japanese tree frogs change the mode of their synchronized calling behavior depending on their circumstances.

## V. CONCLUSION

We have proposed two phase-oscillator models obtained by fitting to the experimental data of the synchronized states. Then, we have shown that the second-order approximation model can reproduce not only the average phase and frequency properties during the synchronized states in the experiment but also the transitory dynamics in the interactive calling behavior. Namely, in our model analysis, experimentally observed antiphase and inphase synchronizations were explained as stable equilibrium states with different sizes of the basin of attraction; moreover, since it was shown that the inphase state is marginally stable, but the antiphase state is robustly stable, the experimental observation of the shift from the inphase synchronization to the antiphase synchronization [14] is qualitatively explained, under existence of noise.

In particular, antiphase synchronization between two frogs raises an interesting problem on spatiotemporal behavior of more than two frogs because such a system should be frustrated by the interactions [12,13]. Moreover, it should be noted that frogs can move in the real fields. Calling behavior of many male frogs can be understood as a highly frustrated system of coupled phase oscillators, which can change its spatial structure dynamically [7]. In this study, we have proposed two models, which are derived on the different degrees of approximations: the first-order model (model 1) explains only the dominant mode of antiphase synchronization, and the second-order model (model 2) additionally explains the transient mode of inphase synchronization. From the viewpoint of mathematical modeling, it is an important future problem to investigate the validity of the model analysis by estimating the real phase response curves directly from observed time series data, for example, during desynchronized calling behavior of two frogs [21] and comparing the estimated functions with those in the proposed models.

## ACKNOWLEDGMENTS

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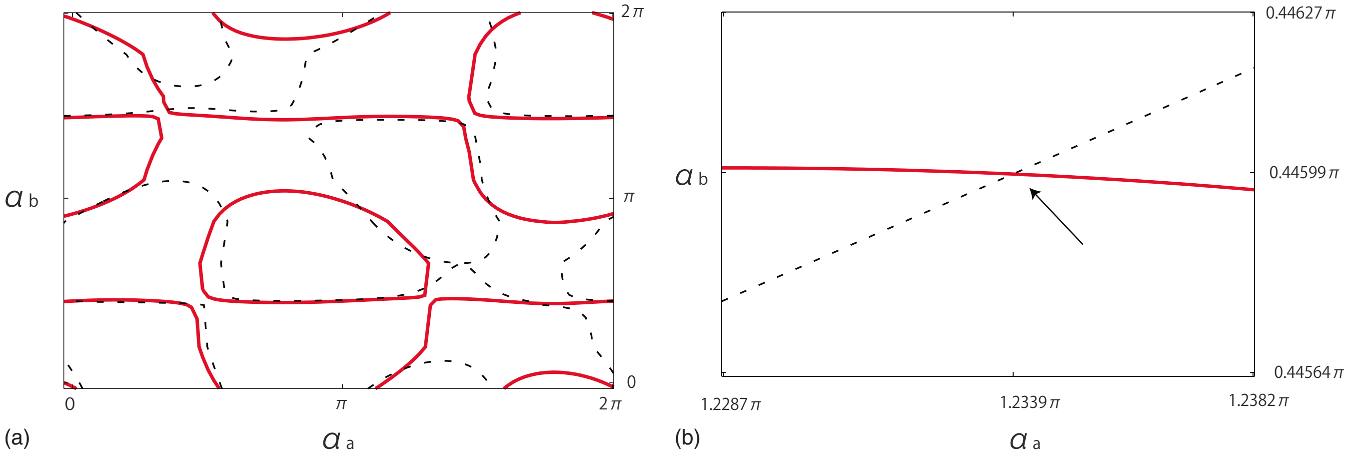

FIG. 5. (Color online) Solutions in Eqs. (A5) and (A6) with respect to $\alpha_a$ and $\alpha_b$ after substituting the experimental values: Fig. 5(a) represents the solutions in the whole parameter region and Fig. 5(b) the enlargement. The solid and dot lines represent the solution of Eq. (A5) and that of Eq. (A6), respectively. The intersection signed with the arrow in Fig. 5(b) gives the parameter values described by Eqs. (38) and (39).

## APPENDIX: METHOD OF PARAMETER CALCULATION

We introduce the method for calculating the unknown parameters in Eqs. (31) and (32) (i.e., $\omega_a$, $\omega_b$, $K$, $\gamma$, $\alpha_a$, and $\alpha_b$) from the experimental data given by Eqs. (3), (4), (14), (15), (29), and (30). Substituting two stable solutions $(\phi^*_{anti}, \frac{d\theta}{dt}|_{\phi^*_{anti}})$ and $(\phi^*_{in}, \frac{d\theta}{dt}|_{\phi^*_{in}})$ into Eqs. (34) and (35) yields

$$\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}} = \omega_a + K\sin(\phi^*_{in}-\alpha_a) + \gamma K\sin\{2(\phi^*_{in}-\alpha_a)\}, \tag{A1}$$

$$\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}} = \omega_b - K\sin(\phi^*_{in}+\alpha_b) - \gamma K\sin\{2(\phi^*_{in}+\alpha_b)\}, \tag{A2}$$

$$\left.\frac{d\theta}{dt}\right|_{\phi^*_{anti}} = \omega_a + K\sin(\phi^*_{anti}-\alpha_a) + \gamma K\sin\{2(\phi^*_{anti}-\alpha_a)\}, \tag{A3}$$

$$\left.\frac{d\theta}{dt}\right|_{\phi^*_{anti}} = \omega_b - K\sin(\phi^*_{anti}+\alpha_b) - \gamma K\sin\{2(\phi^*_{anti}+\alpha_b)\}. \tag{A4}$$

Deleting parameters $K$ and $\gamma$ under the assumptions of $K\neq 0$ and $\gamma\neq 0$ gives the following two relations:

$$\begin{aligned}&\left\{-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin(\phi^*_{in}+\alpha_b)-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_b\right)\sin(\phi^*_{in}-\alpha_a)\right\}\left[\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin\{2(\phi^*_{anti}-\alpha_a)\}\right.\\&\quad\left.-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{anti}}-\omega_a\right)\sin\{2(\phi^*_{in}-\alpha_a)\}\right]-\left[\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin\{2(\phi^*_{in}+\alpha_b)\}+\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_b\right)\sin\{2(\phi^*_{in}-\alpha_a)\}\right]\\&\quad\times\left\{-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin(\phi^*_{anti}-\alpha_a)+\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{anti}}-\omega_a\right)\sin(\phi^*_{in}-\alpha_a)\right\}=0.\end{aligned} \tag{A5}$$

$$\begin{aligned}&\left\{-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin(\phi^*_{in}+\alpha_b)-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_b\right)\sin(\phi^*_{in}-\alpha_a)\right\}\left[\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin\{2(\phi^*_{anti}+\alpha_b)\}\right.\\&\quad\left.+\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{anti}}-\omega_b\right)\sin\{2(\phi^*_{in}-\alpha_a)\}\right]-\left[\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin\{2(\phi^*_{in}+\alpha_b)\}+\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_b\right)\sin\{2(\phi^*_{in}-\alpha_a)\}\right]\\&\quad\times\left\{-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{in}}-\omega_a\right)\sin(\phi^*_{anti}+\alpha_b)-\left(\left.\frac{d\theta}{dt}\right|_{\phi^*_{anti}}-\omega_b\right)\sin(\phi^*_{in}-\alpha_a)\right\}=0.\end{aligned} \tag{A6}$$

Substituting the experimental values of Eqs. (3), (4), (14), (15), (29), and (30) into Eqs. (A5) and (A6) yields the two equations with respect to the unknown parameters of $\alpha_a$ and $\alpha_b$; therefore, the number of the obtained conditions is equal to that of the unknown parameters, and the solutions can be calculated. In Fig. 5, the solid and dot lines represent the solution of Eq. (A5) and that of Eq. (A6), respectively. The intersection signed with the arrow in Fig. 5(b) gives $\alpha_a$ and $\alpha_b$ described by Eqs. (38) and (39); we estimated those values with the Newton method. Finally, after substituting the estimated parameter values of Eqs. (38) and (39) and the experimental values of Eqs. (3), (4), (14), (15), (29), and (30) into Eqs. (A1) and (A2), we obtain the values of the rest two parameters of $K$ and $\gamma$ described by Eqs. (36) and (37).

In this analysis, we have two assumptions $K \neq 0$ and $\gamma \neq 0$. Now, let us examine the validity. If $K=0$, there is no interaction between two oscillators and they cannot synchronize. Further, if $\gamma=0$, the effect of the second-order components in Fourier expansions is nothing, and the model of Eqs. (31) and (32) becomes identical with that of Eqs. (18) and (19). Therefore, these two assumptions are consistent with our purpose to explain coexistence of the antiphase and inphase synchronized states as bistability of the two modes.

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[18] In the case of model 1 since $-1 \leq \sin x \leq 1$ $(x \in \mathbf{R})$, the maximum value in the interaction terms is given by the absolute value of the coupling coefficient $|K|$. In the case of model 2, we substitute Eqs. (36)–(39) into the interaction terms, numerically calculate the extrema with respect to $\phi$ by the Newton method, and obtain the maximum value.

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