Why are calling songs of cicadas complex?: From behavioral and evolutionary ecological aspects

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Doctoral thesis

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Abstract

Cicadas (Hemiptera: Cicadidae) are insects in which only males produce prominent songs. Most cicada species produce loud calling songs, which attract females for mating and other males to form the chorus. The calling songs of cicadas show various patterns by species and sometimes show complex acoustic structures. However, there are only a few evolutionary and behavioral ecological studies on calling songs of cicadas. In this Ph.D. thesis, I show the results of evolutionary and behavioral ecological research on two Japanese cicada species.

First, I examined the relationship between the phylogeography and acoustic traits of *Planopleura miyakona*. This species is a terrestrial cicada species native to the Miyako Islands, Okinawa Prefecture. This species shows different emergence periods of the adults depending on the habitats within the island. Such local differences in emergence times may result in temporal reproductive isolation, hindering genetic exchange between localities. This process could potentially result in the accumulation of specific alleles to each habitat, resulting in local differences in characteristics. Additionally, given that this species inhabits each island in the Miyako Islands, it is possible that the sea becomes the dispersal barrier, hindering the genetic exchange among the populations on each island. However, the details of the genetic variation of this species across the entire Miyako Islands remain unknown.

I collected adult *P. miyakona* individuals across the Miyako Islands and analyzed their mitochondrial COI and nuclear 18S rRNA gene sequences to investigate the phylogenetic relationships among the local populations. Phylogenetic trees constructed using the maximum likelihood method revealed six distinct clades: (A) Miyako Island clade (excluding Gusukube-Bora), (B) Kurima Island clade, (C) Irabu-Shimoji Islands clade, (D) Tarama Island clade, (E) Ogami Island clade, and (F) Ikema Island and Gusukube (Miyako Island) clade. A significant correlation between genetic and spatial distances. Furthermore, substantial genetic divergence was detected between clades E, F and the other four clades.

I also recorded the calling songs of wild males from different habitats and quantified three acoustic parameters: phrase duration, peak frequency after modulation (AM), and peak frequency before modulation (BM). Statistical analyses revealed significant effects of recording sites (i.e., local populations) on all the three parameters, while temperature also significantly influenced peak frequency BM. On the other hand, the tendency that the acoustic traits were more similar between the phylogenetically closer populations was not found.

Next, I investigated the effects of complex calling song structures in *Meimuna opalifera* on male conspecific responses. The calling song of this species is highly complex, comprising two distinct parts (former and latter), which are unique characteristics in this species. Furthermore, *M. opalifera* males are known to produce short response calls (RCs) near calling conspecific males, known as “Ainote” or “Aizuchi”, demonstrating male-male communication. Such complex communication systems may enable more sophisticated information transmission compared to simpler calls in different species.

I conducted playback experiments using modified calling songs of *M. opalifera* to evaluate male responses. Playback stimuli included the intact song (IS), the former part only (FPS), the

latter part only (LPS), and two control sounds, no sound (NS) and white noise (WN). Males responded with RCs only to IS, FPS, and LPS, but not to the control sounds. The response frequency to LPS was significantly lower than that to IS or FPS. To investigate the effects of the order of the parts, I conducted additional experiments using normal-order song (N), reversed-order song (R), and normal- or reversed-order song with the elongated latter part (NE and RE, respectively). Frequencies of RCs were significantly lower for reversed-order songs (R and RE) than for normal-order songs (N and NE). These findings suggest that the sequential structures of the calling song components play a critical role in male-male communications.