Temporal Rhythms in the Signals of Insects

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Abstract: The signals generated by acoustic insects exhibit temporal patterns on several time scales. Annual or seasonal rhythms provide information about temporal changes in insect population size. Knowledge of such changes might be useful in ecological monitoring programs. Circadian or daily rhythms commonly seen in insect signaling are generated by endogenous 'clocks' that are reset by environmental cues. Understanding these daily patterns is also important for monitoring insect populations. Within insect populations, the signals of neighbors sometimes show temporal patterns of synchrony or alternation with timing on the order of seconds. The phase relationships among individuals are maintained by acoustic resetting, whereby an individual's temporal rhythm will change depending on the phase that neighboring signals are received. On still smaller time scales, temporal patterns of insect songs are diverse and generally differ among species. These small-scale patterns are often essential components of mating signals and are used in mate recognition and mate choice.

INTRODUCTION

Insects are perhaps one of the most important and successful groups of organisms on the planet. Because of their numbers and their size they serve as predators or as prey for most of the other life forms on earth. Therefore, they often take a central role in the dynamics of an ecosystem. Many, if not all insects, produce signals in a variety of modalities during courtship and mating. The loud, conspicuous acoustic signals generated by signaling insects have intrigued humans for centuries and are some of the best studied groups of acoustic animals. The signals that insects produce are somewhat simple, and are thus easily recorded and analyzed. In addition, the 'robot-like' responses of insects to acoustic playback make them ideal for experiments designed to understand auditory perception. The diversity of the insects and of the sounds they emit makes them an excellent group to study all aspects of acoustic communication.

In this paper I discuss the variation in the temporal parameters of insect acoustic signals at the various time scales. Several aspects of these temporal relationships can be easily quantified so as to provide important information about long-term changes in insect populations. Given their importance in many ecosystems such monitoring may provide useful information regarding changes in habitat quality.

Seasonal Rhythms. Most insects have relatively short life cycles. Many of the loud signals emitted by insects are produced by males advertising for mates. That is, the signals are restricted to adults. Seasonal changes in the outputs of a species can provide information about that species' life history. The most noteworthy examples are the periodical cicadas that have 13 or 17-year life cycles. These cicadas synchronize their emergence. The outbreaks are tremendous and are extremely predictable in their periodicity (1).

Figure 1 shows the seasonal distributions of calling for a katydid (Pterophylla camellifolia) and two crickets (Eunemobius carolinus and Gryllus rubens). I collected these data in northern Mississippi by walking a specified path each week of the year and simply counting the number of males calling within earshot. This simple population census correlates very well with other simultaneous measures of population size (insect traps). Interesting differences in life history are apparent for the three species. The katydid has just one generation per year (univoltine), whereas the two cricket species have two generations per year (bivoltine). There are distinct differences between the bivoltine crickets. Eunemobius carolinus overwinters in the egg stage, hatches in the spring and matures in June and July. The second generation is active from...
September into November. *Gryllus rubens* overwinter as late instar juveniles and become adults in early spring. Adult males call from April to July and the second generation is active from August to October. Changes in insect populations are often the first indicators of changes in habitat. Much could be learned about insect populations using acoustical monitoring and long-term data could detect ecological changes in habitat quality, species distributions, geographical variation and hybridization (2).

**Circadian Rhythms.** The signaling behavior of most insects exhibits daily patterns. Internal (endogenous) clocks generate these circadian rhythms. Individuals removed from external, environmental cues maintain a signaling period slightly longer than a 24 hour. Thus, their patterns shift with respect to natural day length. An external cue or simulated stimulus (typically the sunrise or sunset) can entrain the signaling behavior to begin at about the same time each day. The environmental stimulus acts to reset the insect’s internal clock on a daily basis. Species often differ greatly in their circadian patterns. For instance, individuals of some species of crickets synchronize their activity to a brief period during the day. For other species, an individual may have a specific periodicity that differs from that of other individuals (3). Knowing how circadian rhythms differ among individuals must be known if acoustic monitoring can provide useful information about insect populations.

**Chorusing Rhythms.** Because many insect songs are associated with mating and because males generally sing to attract mates, neighboring males will necessarily compete for the females ‘within earshot’. Selection will favor aspects of songs that improve a male’s competitive ability. Competitive interactions between males result in specialized chorusing, where the songs of neighboring males are emitted with specific phase relationships (4). Synchrony or alternation among males in choruses has been analyzed using the techniques used to investigate coupled oscillators.

**Short-term Rhythms.** The long-range mating songs of insects are generated by a number of mechanisms involving muscle contractions that produce pulsed signals. The temporal patterns of the signals carry information and female insects use this information when choosing a mate. The patterns are almost always species-typical and have often been used successfully to identify cryptic species. In crickets, the song pattern is under the control of a central pattern generator (5). For some species (e.g. *Oecanthus* spp.) the temporal rhythms exhibit very little variation and may be under extreme stabilizing selection from females. Other crickets show greater variation in the rhythms of their songs (Figure 2). The central pattern generator must be complex to produce these variable rhythms. Are the females less discriminating or is more information being transmitted?

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**REFERENCES**