Mechanisms of call recognition in three sympatric species of N*eoconocephalus* (Orthoptera: Tettigoniidae): Asymmetrical interactions and evolutionary implications.

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Abstract

Scientists have debated the hypothesis of reinforcement. Nevertheless, recent empirical and theoretical work have dispelled doubts about its existence. Reinforcement is most often studied by establishing one of its predicted outcomes: reproductive character displacement. Empirical studies of reproductive character displacement often report that the interactions between species are asymmetrical, such that one species shows the expected pattern of displacement while the other does not. This may be a result of focusing on a limited set of isolation mechanisms.

Graphical presentation of character displacement often depicts a symmetrical displacement occurring along a single axis. Implied is the assumption that both species achieve reproductive isolation using similar mechanisms. However, this is not entirely accurate. Reproductive isolation may be achieved by any number of mechanisms, several of which may presumably act in any given species. Furthermore, the same mechanisms need not be responsible for isolation between interacting species. To address the question of how reproductive isolation occurs among close relatives, I studied three sympatric species of the acoustically communicating genus *Neoconocephalus*. I considered all call parameters (temporal and spectral) that may be important for call recognition, and identified and characterized the mechanisms of female call recognition using a walking compensator.

Female *N. robustus* responded to a continuous unmodulated 7 kHz sine wave. They also responded to pulsatile calls as long as the intervals were short or absent. Female responses were limited to a narrow frequency range around the center frequency of the conspecific call (7 kHz). The addition of higher frequencies resulted in strong inhibition of phonotaxis, which should help females avoid the calls of congeners using slightly higher (10 kHz) carrier frequencies. Female *N. nebrascensis* also responded to sinusoids in which the intervals were short or absent. In addition, females of this species required a higher order temporal pattern (verse structure). Female responses were limited to a narrow frequency range around the center frequency of the conspecific call (10 kHz). The addition of higher frequencies resulted in a weak but significant inhibition. Female *N. bivocatus* required a distinct pulsatile structure for call recognition, responding only when the pulse rate was approximately 87 Hz. Using the duration of the merged double-pulse corresponding to the conspecific pattern, pulse rates from 80-95 Hz elicited significant responses, while pulse rates of 74 and 105 Hz failed to elicit significant responses. Female responses were limited to a narrow frequency range around the center frequency of the conspecific call (10 kHz). The addition of higher frequencies resulted in little if any inhibition.

Strikingly different mechanisms are responsible for reproductive isolation of the three species. In *N. bivocatus* and *N. nebrascensis*, call recognition is based on derived temporal characteristics. In contrast, call recognition in *N. robustus* relies on several less effective cues, both temporal and spectral. This pattern indicates that *N. robustus*, through a reinforcement-like process, was pushed by the other two species to use a suboptimal carrier frequency and to sharpen its temporal recognition mechanisms. The evolutionary processes leading to the qualitatively new call traits and recognition mechanisms in *N. nebrascensis* and *N. bivocatus* are unknown.