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Multimodal signal compensation: do field crickets shift sexual signal modality after the loss of acoustic communication?

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Several hypotheses could explain the evolution of multimodal signals. One possibility is that such signals allow for communication even when one signalling modality is temporarily unavailable. However, little is known about the consequences of the permanent evolutionary loss of a signal modality. We used the field cricket *Teleogryllus oceanicus* to test the hypothesis that the loss of one mode of signalling can be accommodated by flexibly switching to another pre-existing modality. Field crickets use cues that carry social information in the form of both long-range acoustic signals and short-range cuticular hydrocarbons (CHCs), but males in some *T. oceanicus* populations have permanently lost the ability to sing because of a morphological mutation erasing sound-producing structures on their wings. In assays testing responsiveness to substrate-borne CHCs, *T. oceanicus* females responded to the presence of male, but not female, CHCs, which is consistent with known sexual dimorphism in field cricket chemical cues. However, we found no evidence for signal compensation in male crickets that have experienced an evolutionary loss of acoustic signals: females did not differentially respond to the CHCs of constitutively silent males compared to those of normal males. The ability of organisms to shift adaptively from one signalling modality to another following the evolutionary loss of a signal is likely to be constrained by both the degree to which signal production and receiving is flexible and the existence of suitably preadapted alternative modalities.

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In recent years, several nonexclusive hypotheses have been developed to explain the evolution of complex signals comprising multimodal or multicomponent signals (Candolin, 2003; Hebets & Papaj, 2005; Partan & Marler, 1999, 2005). For example, the 'multiple messages hypothesis' maintains that a complex signal may comprise several units that each convey different information about a sender, while the 'redundant signal hypothesis' posits that different signals each convey the same information and exist to safeguard against imperfect signal coding (Hebets & Papaj, 2005).

The redundant signal hypothesis posits that signallers do not convey all of the information relevant to a receiver when producing a signal in one modality. In contrast, the 'efficacy backup hypothesis' maintains that varying environmental conditions can hinder the transmission and reception of even a perfect signal (one that contains all relevant information about a signaller), so signallers may use multiple signal modalities to increase the likelihood of successful communication (Hebets & Papaj, 2005). That is, multiple modalities may allow the propagation and reception of a signal even if one or more modalities are blocked (Candolin, 2003; Partan, 2004) As such, the efficacy backup hypothesis predicts that organisms compensate for the loss of one signal modality by switching to another, pre-existing modality (Table 1). Support for this hypothesis comes from several empirical avenues. Male satin bowerbirds, *Ptilonorhynchus violaceus*, actively enhance their bowers by adding sticks and reducing the latency to paint their bowers when bower decorations are experimentally removed (Bravery & Goldizen, 2007). Organisms living in temporally, spatially or otherwise heterogeneous environments also demonstrate compensatory mechanisms. For example, male alpine newts, *Mesotriton alpestris*, use relatively more olfactory cues when courting in the dark and more visual cues when courting in brighter conditions (Denoël & Doellen, 2010). Male wolf spiders, *Schizocosa ocreata*, which normally produce substrate-borne courtship signals, perform more visual courtship signals when on surfaces that preclude the transmission of substrate-borne vibrations (Gordon & Uetz, 2011). Males of this species even compensate for the loss of one or both forelegs by performing a particular courtship display at

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Table 1
Selected hypotheses for the existence of complex signals and whether each hypothesis predicts signal compensation

Hypothesis	Brief description	Predicts compensation
Multiple messages	Each signal conveys different information about the signaller	No
Redundant signal	Different signals convey the same information to different receivers, or increase receiver response accuracy	No
Efficacy backup	Different signals convey roughly the same information and serve as a backup to one another when the environment is variable	Yes

Table adapted from Hebets and Papaj (2005).

a higher rate than males with both forelegs (Taylor, Roberts, & Uetz, 2006).

The individual signalling components of complex signals might be used to provide signalling ‘insurance’, enabling organisms to flexibly match signal or cue modality to the prevailing environmental conditions. However, few studies have examined how organisms respond to the permanent evolutionary loss of a sexual signal, rather than the loss of signal or cue production or transmission under varying environmental conditions (though see Taylor et al., 2006). Given that varying environmental conditions may induce organisms to shift investment between two or more sexually selected traits (Basolo, 1998), we hypothesized that signalling individuals compensate for the evolutionary loss of a sexual signal by increasing the use of other, pre-existing cues. To test this, we capitalized on a field cricket system in which a primary signalling modality has been evolutionarily lost on a contemporary timescale.

The field cricket *Teleogryllus oceanicus* is widely distributed from northern and western Australia to Hawaii and throughout the Pacific (Otte, 1994; Otte & Alexander, 1983). Males of this species use at least two signal modalities in mate attraction: a long-range acoustic signal, calling song (Balakrishnan & Pollack, 1996; Rebar, Bailey, & Zuk, 2009; Zuk & Simmons, 1997), and a sexually dimorphic contact (short-range) chemosensory cue in the form of cuticular hydrocarbons (hereafter CHCs; Thomas & Simmons, 2008a; Tregenza & Wedell, 1997). Cuticular hydrocarbons are found on insect exoskeletons and are thought to have evolved to resist desiccation, but they have also evolved into a chemical form of communication in many insects (Blomquist, Tillman, Mpuru, & Seybold, 1998). Males and females both produce CHCs, but unlike some other insect species that produce airborne or otherwise volatile cues, chemical communication appear to be limited to contact chemoreception in crickets, including *T. oceanicus* (Thomas & Simmons, 2008b).

In two Hawaiian populations of *T. oceanicus*, some males have lost the ability to produce song. A recent wing mutation, ‘flatwing’, renders males on the Hawaiian Islands of Kauai and, more recently, Oahu, obligately silent (Tinghitella, 2008; Zuk, Rotenberry, & Tinghitella, 2006). Flatwing males represent more than 90% of the males on Kauai, and approximately 50% of all males on Oahu (Zuk, n.d.).

In *T. oceanicus*, cuticular hydrocarbon expression is heritable (Thomas & Simmons, 2008b) and subject to sexual selection (Thomas & Simmons, 2009a, 2010). However, CHC expression in this species is also highly plastic. Male normal-winged crickets reared in silent environments, such as one that would be experienced in a low-density population or in a population consisting mainly of flatwing males, increased the relative expression of CHCs that females find attractive (Thomas, Gray, & Simmons, 2011). Moreover, subordinate males of this species increase the relative expression of the same attractive CHCs (Thomas & Simmons, 2009b), and hydrocarbon profiles can change within short time spans (Thomas & Simmons, 2011). In addition to being deposited on other crickets during mating and other interactions (Thomas & Simmons, 2009c), CHCs can be deposited on the substrate (Bailey, 2011; Kortet & Hedrick, 2005). These CHCs remain detectable for long periods, having been successfully identified from museum specimens (Brenner, Carlson, Roth, & Patterson, 1993). As such, substrate-borne CHCs represent a stable source of information that conspecific crickets may utilize during everyday interactions to inform behavioural decision-making processes (Bailey, 2011).

Given existing phenotypic plasticity and the known role of CHCs in mediating mate choice (Kortet & Hedrick, 2005; Thomas & Simmons, 2010), we hypothesized that CHCs might function as an ‘efficacy backup’ to the loss of song. Specifically, we predicted that flatwing males compensate for their inability to produce an acoustic sexual signal by upregulating the production of attractive chemical cues. To test this, we measured how much time female *T. oceanicus* spent in association with substrate-borne CHCs from males of each morph. We also measured female response to CHCs from other females to control for a generalized response to any chemosensory cues. In this study, we used crickets from Oahu because both male morphs are represented in roughly equal numbers (Zuk, n.d.), so females are likely to encounter both morphs under natural conditions.

We predicted that, if CHCs can function as an efficacy backup to acoustic sexual signals, female crickets would spend more time in association with CHCs from normal-winged males than expected by chance, but not spend more time in association with CHCs from conspecific females than expected by chance. Furthermore, we predicted that flatwing males compensate for a lack of sound production by producing more attractive or a greater quantity of CHCs, in which case females would spend more time attending to substrate-borne CHCs from flatwing males than they would those from normal-winged conspecifics.

METHODS

We used a female response assay to determine how CHCs from different crickets function in the absence of acoustic signals. Females were allowed to interact with substrate-borne CHCs from conspecific females, flatwing males or normal-winged males and could choose to spend time on substrates with these CHCs or on substrates free of CHCs. Two distinct groups of crickets were reared. One group, consisting solely of females, was reared for use in female-response assays (‘focal females’). The other group, consisting of females, flatwing males and normal-winged males, provided crickets for CHC deposition in the testing arenas (‘CHC donor crickets’). Crickets in this latter group were reared individually. Review by an Institutional Animal Care and Use Committee was not required for this research. All trials were performed in accordance with local and federal laws and regulations regarding the use of animals in experiments.

General Rearing

Crickets were taken from a large outbred population originating from Oahu, Hawaii in the early 1990s and supplemented with the offspring of 12–25 field-caught females approximately once annually. Crickets were selected as late-instar juveniles as soon as sex differences were apparent. Females for behavioural trials were removed to female-only 1.8-litre containers with cardboard egg

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