



Acoustic niche partitioning in two cryptic sibling species of *Chrysoperla* green lacewings that must duet before mating

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Cryptic species may seem identical to us, but not to each other. The *Chrysoperla carnea* group of green lacewings has species-specific substrate-borne duetting songs that maintain reproductive isolation among its cryptic species. We propose that sympatric species of the group will partition acoustic niche space so as to minimize mating mistakes. Sibling species pairs could therefore occupy abutting regions of acoustic space without hybridizing in nature. One species pair, *Chrysoperla plorabunda* and *C. adamsi*, are not only closest relatives, but are also the most acoustically similar among sympatric congeners. Using F₁ hybrids as a surrogate taxon occupying acoustic space between the parents, we tested the hypothesis that this space cannot support an additional species. Focusing on a critical song feature, volley period, we confirm firstly that the hybrid song occupies unfilled signal space between the parents. Secondly, we show that song discrimination is strong between parents, but weaker between parents and hybrids. Thirdly, each parent has the ability to respond to the other's signal in a narrow region of overlap. Finally, preference functions for hybrids broadly overlap those of parents. These acoustic tests confirm that a species of this intermediate song phenotype could not persist.

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Sexual selection is a powerful evolutionary force in nature. Historically, it has been implicated in changes within species, producing sexually dimorphic ornamentation, armaments and behavioural repertoires through the dual mechanisms of intra-sexual competition and intersexual mate choice. More recently a role for sexual selection in speciation has been postulated, supported by both theoretical and empirical studies (Lande 1981; West-Eberhard 1983; Seehausen 2000; van Doorn et al. 2004; Boake 2005; Genner & Turner 2005; Rodriguez et al. 2006; Ritchie 2007; Guerra & Ron 2008; Elmer et al. 2009; Funk et al. 2009; Ribeiro & Caticha 2009; Sauer & Hausdorf 2009; Cocroft et al. 2010). An important component of speciation by sexual selection on courtship signals is the existence of a genetic correlation between a sexual signalling trait in one sex and a preference for it in the other (Shaw & Lesnick 2009). This covariance between the sexes is necessary for 'runaway' or 'chase-away' divergence of mating signals, which drives the rapid acquisition of reproductive isolation between populations (Fisher 1958; Gavrillets et al. 2001).

It follows that sexual selection, initially measurable within species, may continue to be measurable between species after the completion of speciation (West-Eberhard 1984; Ryan & Rand 1993; Boake et al. 1997; Ptacek 2000).

Assuming that mate preference and species recognition can be located along an evolutionary continuum (but see Arbuthnott 2009 for a review of counterexamples), there should exist a threshold beyond which mating signals will be too different to elicit consistent, positive responses from other members of the species. Individuals having such critically modified mating signals will mate principally with individuals like themselves, cutting off gene flow between subgroups and facilitating or causing speciation. However, confirming the existence of such behavioural thresholds is rarely possible. One way to do so is by studying mating signal and preference differences between two sibling species that diverged recently, preferably by sexual selection, in order to characterize the 'courtship niche space' that separates them. Two such recently diverged sister taxa are *Chrysoperla plorabunda* (Fitch) and *C. adamsi* Henry et al., belonging to the North American clade of the large, cosmopolitan *carnea* group of cryptic green lacewing species (Henry 2006). Neutral divergence (and hence time since speciation) amongst members of this clade is very low, averaging 0.03–0.06 for genetic distances determined from allozymes (Wells 1994) and less than 0.018 for uncorrected sequence divergences calculated from

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mtDNA (Henry et al. 1999b). Furthermore, explosive speciation in the *carnea* group is probably due to sexual selection (Henry et al. 2002; Henry & Wells 2004).

Mating in the *carnea* group is preceded by the obligatory exchange between heterosexual partners of low-frequency, substrate-borne vibrational signals in a precise duetting format (Wells & Henry 1992b). Males and females within each species share very similar songs (e.g. Fig. 1a, e), and either partner is equally likely to terminate an incipient interaction if the signals do not match each other closely enough. Lack of an accurate and persistent response during duets effectively isolates the different species in the complex (Wells 1993; Wells & Henry 1998). Once established, a heterosexual duet guarantees copulation. Consequently, the coordinated duetting response of an individual is the ideal assay for the sexual acceptability of a partner or signal.

In the present study, we investigated the behavioural distance that isolates *C. plorabunda* and *C. adamsi* from each other by examining differences in their acoustic niches or signal space (sensu Duellman & Pyles 1983; Pfennig & Pfennig 2009). These two reproductively isolated but broadly sympatric, locally syntopic,

ecologically indistinguishable and morphologically identical species have been shown to be each other's closest relatives and have duetting songs that differ only in tempo (Henry et al. 1993, 1999b). In addition, they can be coerced to hybridize in the laboratory, producing offspring with an intermediate song phenotype. Thus, the F₁ hybrid can be used in behavioural experiments as a surrogate for a hypothetical third species occupying the signal space between *C. plorabunda* and *C. adamsi*.

Using playback experiments measuring responsiveness of *C. plorabunda*, *C. adamsi*, and their F₁ hybrids to synthetically modified mating signals, we tested the hypothesis that the acoustic differences in the vibrational songs of these two species are sufficiently small that a third species with an intermediate signal phenotype could not coexist with them. Because signal timing rather than carrier frequency mediates lacing duetting decisions (Wells & Henry 1992a), we focused on a single critical temporal feature of the songs, volley period, VP (Fig. 1), measuring response variation to playback signals in which VPs had been modified. We predicted that recently diverged sister species such as *C. plorabunda* and *C. adamsi* would show song phenotypes

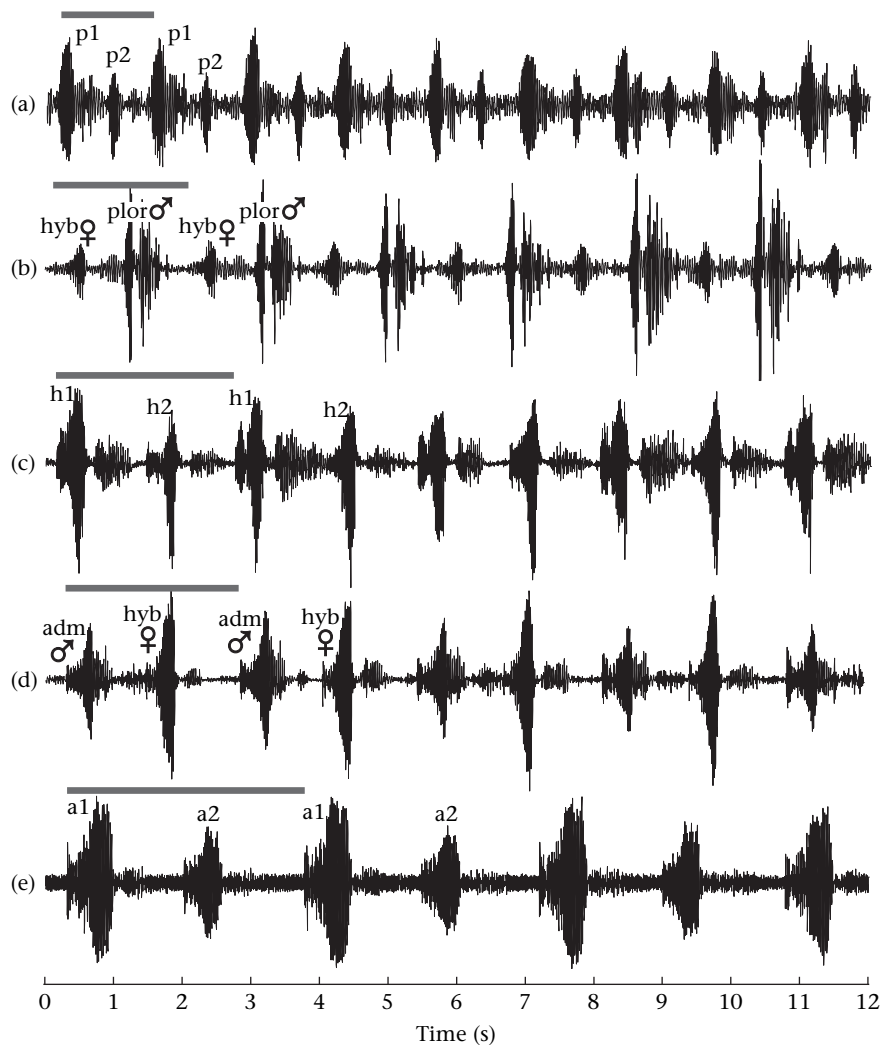


Figure 1. Duetting behaviour in *C. plorabunda*, *C. adamsi* and their F₁ hybrids. Oscillograms of song duets between male and female lacewings, showing 12 s of interaction. In each oscillogram, the first two reciprocal exchanges of song volleys between duetting individuals are marked, and the volley period (VP) for the starting individual is delineated by the shaded horizontal bar. (a) *C. plorabunda* conspecific duet between a male (p1) and a female (p2); (b) F₁ hybrid (female) duetting with *C. plorabunda* (male); (c) F₁ hybrid-only duet between a male (h1) and a female (h2); (d) F₁ hybrid (female) duetting with *C. adamsi* (male); (e) *C. adamsi* conspecific duet between a male (a1) and a female (a2). Note that hybrids have an intermediate VP (grey bar in (c)), and are capable of duetting with either parental species ((b) and (d)).

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