Male competition and aggregative behaviour are mediated by acoustic cues within a temporally unstructured aggregation

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Summary
We investigated the dynamics of temporally unstructured acoustic signalling aggregations, where direct interactions among males appear to be absent. The short-winged meadow katydid, \textit{Conocephalus brevipennis} Scudder (Orthoptera: Tettigoniidae), is a species whose males form dense, aphasisic singing aggregations. By studying both phonotactic responses and male calling behaviour towards conspecific, heterospecific, and aggregate signals (combined songs of many individuals), we examined how males might respond to acoustic signals within such aggregations, and whether such apparently unstructured groups do in fact possess spatial or temporal structure. Phonotactic bioassays demonstrate that males and females are attracted to conspecific and aggregate, but not heterospecific song. When given a choice between individual conspecific and aggregate song, females prefer conspecific song, whereas males preferred aggregate song, but only if it was presented at a lower relative intensity than the individual song. Response to aggregate song also depended on male size --- the largest males approached the broadcast speaker more closely than smaller males. Experiments examining male calling behaviour show that they respond differently to playback of conspecific song, as compared to heterospecific and aggregate signals. For heterospecific and aggregate song, males decrease their singing rate, but recover after playback ceases. Playback of conspecific song resulted in a decrease in singing that persisted after the end of playback when males were initially weak singers, but little effect for males that were initially strong singers. Males also varied the number of species-specific ‘tick’ elements they included in songs. Weaker singers reduced

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the number of ticks per song in response to playback. Stronger singers increased tick rates for conspecific and heterospecific playback, but decreased during aggregate song playback. Our results demonstrate that calling song, in addition to attracting females, may be used by males to facilitate aggregation and mediate the segregation of large and small signallers. Males also compete acoustically with one another by varying their overall singing rate and the frequency of tick elements relative to competing signallers.

Keywords: Orthoptera, Tettigoniidae, phonotaxis, competitive signalling, chorus, aggregation.

Introduction

Males from diverse taxa (e.g., insects, birds, anurans) produce acoustic advertisement signals — calling songs — to attract sexually receptive females for mating (Gerhardt & Huber, 2002; Greenfield, 2002). Although mate attraction is competitive, calling males often form aggregations that increase their attractiveness to females through collective signalling (Alexander, 1975; Höglund & Alatalo, 1995). Within an aggregation, however, males incur a cost of associating with other calling males — the risk of losing attracted females to nearby rivals — that must be balanced by benefits of aggregation. Previous studies on the dynamics of signalling aggregations in acoustic insects have largely focused on species where males form temporally structured choruses in which the attractiveness of males to approaching females varies with the relative timing of their call in the chorus (e.g., Alexander, 1975; Ryan et al., 1981; Greenfield & Shaw, 1982; Greenfield, 1994; Greenfield et al., 1997; Greenfield & Snedden, 2003). In comparison, little work has investigated the signalling dynamics of temporally unstructured aggregations, in which males signal together, yet do not appear to be acoustically interacting with one another (e.g., Morris & Fullard, 1983; Walker, 1983; Greenfield & Shaw, 1982). Although the songs of individual males in these aggregations possess species-specific temporal structure, male singing is aphasic in that there is no consistent temporal relationship between the calls of different individuals. It is not currently clear how aggregated males compete acoustically, how they mediate the costs of aggregative behaviour, or how males can advertise their status to females within a temporally unstructured aggregation, given the inevitable temporal distortion due to overlapping calls (Schwartz et al., 2001, 2002; Wollerman & Wiley, 2002).

In this paper we examine the possible role of calling song in the dynamics and spatial structure of temporally unstructured signalling aggregations of a diurnal meadow katydid (*Conocephalus brevipennis* Scudder