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What is the password? Female bark beetles (Scolytinae) grant males access to their galleries based on courtship song

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ABSTRACT

Acoustic signals are commonly used by insects in the context of mating, and signals can vary depending on the stage of interaction between a male and female. While calling songs have been studied extensively, particularly in the Orthoptera, much less is known about courtship songs. One outstanding question is how potential mates are differentiated by their courtship signal characteristics. We examined acoustic courtship signals in a new system, bark beetles (Scolytinae). In the red turpentine beetle (*Dendroctonus valens*) males produce chirp trains upon approaching the entrance of a female's gallery. We tested the hypotheses that acoustic signals are honest indicators of male condition and that females choose males based on signal characteristics. Males generated two distinct chirp types (simple and interrupted), and variability in their prevalence correlated with an indicator of male quality, body size, with larger males producing significantly more interrupted chirps. Females showed a significant preference for males who produced interrupted chirps, suggesting that females distinguish between males on the basis of their chirp performances. We suggest that interrupted chirps during courtship advertise a male's size and/or motor skills, and function as the proverbial 'passwords' that allow him entry to a female's gallery.

1. Introduction

Close-range courtship signals may be the most influential type of acoustic signal in mating decisions in insects (Fitzpatrick and Gray, 2001; Rebar et al., 2009). Whereas calling songs precede courtship songs and operate in far-range attraction of mates, courtship songs occur once males and females are in close proximity, and they exhibit variability that infers they are condition-dependent and can convey information on mate quality (Alexander, 1961; Fitzpatrick and Gray, 2001; Zuk et al., 2008). Courtship songs have been found to be important in prompting females to mate across a broad range of taxa, including in Orthoptera (such as in field crickets, e.g. Burk, 1983; Balakrishnan and Pollack, 1996; Nelson and Nolen, 1997), Diptera (such as in *Drosophila* species, e.g. Liimatainen et al., 1992), and Coleoptera (such as for bark beetles, e.g. Wilkinson et al., 1967; Barr, 1969; Ryker and Rudinsky, 1976b). In many *Drosophila* species, where courtship signals have been extensively studied, male courtship song has been found to be an important target for sexual selection (Ritchie et al., 1998). However, it has yet to be firmly established whether signals can be used by females as a basis for distinguishing between males in other insect groups. This is at least partly owing to the many difficulties in observing courtship songs in either natural or artificial conditions (Sueur and Aubin, 2004; Tregenza et al., 2006). Bark beetles (Scolytinae) provide a unique avenue to study the role of courtship songs in mating decisions because it is easy to elicit the production of courtship songs in captivity, and rejected mates are forcibly denied access to mating galleries.

The function of acoustic courtship signals in bark beetles has been the subject of debate (see Fleming et al., 2013). Muting experiments in several species have provided strong evidence that these signals are integral to mating, as muted individuals have a significantly reduced chance of successful mating (e.g. Wilkinson et al., 1967; Barr, 1969; Ryker and Rudinsky, 1976b); however the specific functions of courtship signals are not understood. It has been variously hypothesized that they function to announce the arrival of the stridulating sex (Barr, 1969), in aggression towards the female (Ryker and Rudinsky, 1976b), in "premating recognition" (Ryker and Rudinsky, 1976b), or in species recognition (e.g. Yandell, 1984; Raffa and Dahlsten, 1995). There is presently no experimental evidence to accept or discard any one particular hypothesis. Using the red turpentine beetle (*Dendroctonus valens*), this study is the first formal test of the function of these courtship signals in bark beetles.

Dendroctonus valens are members of the most destructive genus of bark beetles (Hopkins, 1909; Wood, 1963), and in recent years have become significant economic pests in China (Yan et al., 2005).

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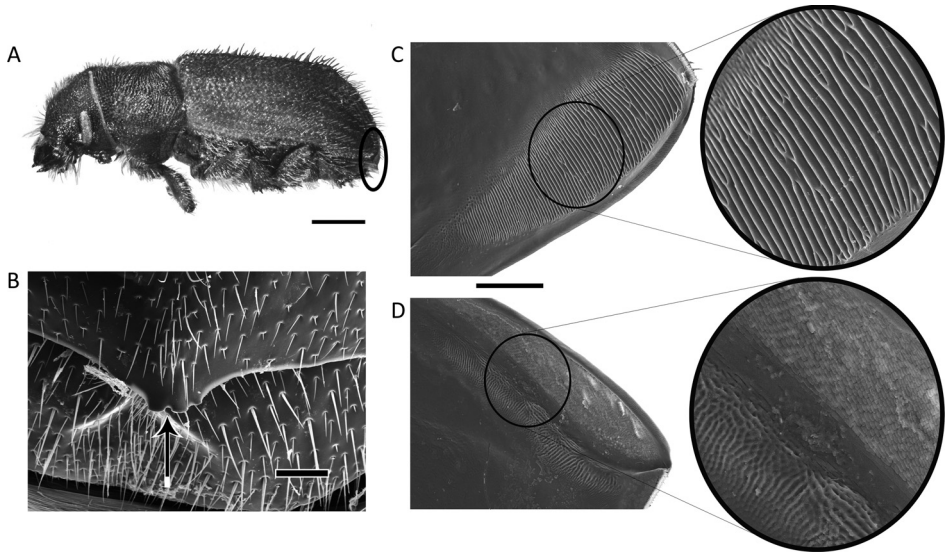

Fig. 1. Light, and scanning electron microscope (SEM) images of male *Dendroctonus valens*. (A) Light microscope image of a male, with circled area indicating location of stridulatory organ; Scale bar = 1000 μm. (B) SEM of the 7th and 8th abdominal tergites, showing the plectrum (arrow); Scale bar = 100 μm. (C) SEM of the file (pars stridens) located at the posterior tip of the underside of the left elytron. (D) SEM of the posterior tip of the underside of the right elytron. (C and D) Scale bar = 100 μm.

This species employs a mating strategy prevalent among bark beetles – serial monogamy – where galleries are established and guarded by individual females and a male partner will arrive later and join her (Kirkendall, 1983). To ensure the arrival of potential mates, bark beetles do not use acoustic calling songs but rather rely on chemical communication. During gallery construction, females release attractant pheromones as a form of long-range communication with males (Zhang and Sun, 2006). Upon arrival, males produce signals called chirps which function in close-range communication during courtship (Ryker and Rudinsky, 1976a). Bark beetles produce sound in general through stridulation, where the teeth on a file, the pars stridens, are excited by a plectrum (Barr, 1969). In *D. valens* there exists an elytra-abdominal stridulatory structure (Fig. 1). Their chirps have been distinguished into two types: simple and interrupted. Simple chirps have been defined subjectively as comprising one series of regularly spaced tooth strikes while interrupted chirps have two or more components interrupted by brief periods of silence (Ryker and Rudinsky, 1976b). In previous literature, *D. valens* chirp types were assigned meaning based on the behaviour they were associated with: simple chirps were observed during disturbance and courtship and so speculated to function in those contexts, while interrupted chirps were observed during intrasexual interactions and were speculated to have a rivalry function (Ryker and Rudinsky, 1976a). However, interrupted chirps were also observed during intersexual interactions but were not considered to play a role in that context. The meaning of signals in various contexts was never empirically tested.

The purpose of this study was to test hypotheses on the function of male courtship signals. The first hypothesis is that signals are honest indicators of signaller quality. We predicted that individual variability would exist in chirp characteristics, and that this variability would be related to male quality. We chose body size as our indicator of quality because, in bark beetles, size is correlated with various measures of fitness (e.g. McGhehey, 1971; Botterweg, 1982; Anderbrant, 1989; Reid and Roitberg, 1995; Evenden et al., 2014). The existence of honest indicators of mate quality is an important consideration for determining whether or not mate choice is significant in a given system (Andersson, 1994; Maynard Smith and Harper, 2003). Therefore, we also hypothesized that acoustic signals are involved in female choice. Earlier studies involving silenced individuals have shown that acoustic signals in general play an important role in successful mating (e.g. Wilkinson et al., 1967; Barr, 1969; Ryker and Rudinsky, 1976b). In our study we moved beyond presence or absence of signals to examine whether variability between males' acoustic performances would provide a basis for a female to choose one male over another. Bark beetle life history typically enables a high mate encounter rate (Vité et al., 1972) and a cost to mating (e.g. serial monogamy can reduce future mating opportunities, Anderbrant, 1989), thus promoting a sexual selection strategy rather than random mating (Kokko and Monaghan, 2001). Additionally, it was previously shown in another *Dendroctonus* species that females prefer to mate with larger males, demonstrating the presence of female choice in this system (Reid and Baruch, 2010). Thus, we predicted female *D. valens* would be choosy over mates, and that their choice would be based on some aspect of the acoustic signal related to body size.

2. Methods

2.1. Animals

Adult *D. valens* (Curculionidae: Scolytinae) were collected from May to September of 2011–2013 at several locations near Ottawa, Ontario, Canada (Limerick Forest, Spencerville, 44.876248, −75.636419; the arboretum at the Ottawa Central Experimental Farm, 45.391021, −75.70489; Carleton Lands, Manotick, 45.183882, −75.604673; and outside Petawawa, 45.853530, −77.536156). Collection was done using Lindgren funnel traps baited with *D. valens* lure (Contech, British Columbia, Canada). Animals were kept at Carleton University, and stored in vials at 5–10 °C until use. Bolts of red pine (*Pinus resinosa*) were obtained by cutting fresh trees taken from Carleton lands into bolts (~60 cm long, ~15 cm diameter) and sealing the ends with wax to prevent desiccation and mould infestation. These bolts were then used for female gallery construction and male–female interactions. Only one trial was performed per bolt. Voucher specimens are held at Carleton University.

2.2. Scanning electron microscopy

Scanning electron micrographs were taken of the stridulatory organs (elytra-abdominal) of nine males, by dissecting elytra and