

## SHORT COMMUNICATION

# Bark beetles use a spring-loaded mechanism to produce variable song patterns

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## ABSTRACT

Many insects vary their song patterns to communicate different messages, but the underlying biomechanisms are often poorly understood. Here, we report on the mechanics of sound production and variation in an elytro-tergal stridulator, male *Dendroctonus valens* bark beetles. Using ablation experiments coupled with high-speed video and audio recordings, we show that: (1) chirps are produced using a stridulatory file on the left elytron (forewing) and a protrusion (plectrum) on the seventh abdominal segment; (2) chirps are produced by 'spring stridulation', a catch-and-release mechanism whereby the plectrum catches on a file tooth and, upon release, springs forward along the file; and (3) variability in chirp types is caused by introducing multiple catch-and-release events along the file to create regular interruptions. These results provide experimental evidence for the mechanics of elytro-tergal stridulation, and provide insight into how an insect can incorporate variability into its acoustic repertoire using a spring-loaded mechanism.

**KEY WORDS:** Sound, Stridulation, Insect, Acoustic, Communication, *Dendroctonus valens*

## INTRODUCTION

Variation in the acoustic repertoires of insects is widespread. The functional significance of signal variability has been well documented; different signals can convey a variety of messages, or enhance the efficacy of transmission in different environments (Balakrishnan, 2016; Gerhardt and Huber, 2002; Greenfield, 2002). Comparatively little is understood about the underlying neural and mechanical control – the proximate mechanisms – required to produce different signal types (Podos and Patek, 2014). Yet, such mechanisms are the basis upon which selection acts and are therefore important for understanding the evolution of communication (Podos and Patek, 2014). This study focused on the mechanisms of sound production and variation by an elytro-tergal stridulator.

Elytro-tergal stridulation is the most common means of sound production in Curculionidae beetles (Lyal and King, 1996), one of the largest animal families. Some species that use this mechanism are reported to produce complex repertoires of up to five different signal types (e.g. Ryker, 1988). However, little is known about the mechanical events leading to signal production. This is partly owing to the location of the sound-producing mechanism, which purportedly comprises a file on the underside of one or both elytra, and a plectrum on the abdominal tergite(s) beneath the elytra. In this study, we tested hypotheses on elytro-tergal chirp

production mechanics using the bark beetle *Dendroctonus valens* as a model.

Bark beetles (Scolytinae) are of great importance on a global scale owing to the pest status of many species, such as those belonging to the tree-killing genus *Dendroctonus* (Six and Bracewell, 2015). Male *Dendroctonus* produce sound using an elytro-tergal stridulatory mechanism (Barr, 1969; Lyal and King, 1996), and their signalling repertoire varies between and within species (Ryker, 1988). In *D. valens*, two distinct chirp types are recognized: simple and interrupted (Fig. 1; Lindeman and Yack, 2015). Simple chirps comprising short pulse trains are prominent during disturbance (Lindeman, 2015; Ryker and Rudinsky, 1976); interrupted chirps containing longer pulse trains with distinct interruptions are prominent during courtship and rivalry (Fig. 1; Lindeman and Yack, 2015; Ryker and Rudinsky, 1976). The mechanisms for chirp production (simple and interrupted) are not well understood: it is not known whether one or both elytra contribute to sound production, whether sound pulses result from one-to-one interactions between the plectrum and file teeth, and how the plectrum engages with the file to produce chirps.

The main goals of this study were: (1) to identify the anatomical structures responsible for chirp production; (2) to test the assumption that each sound pulse corresponds to one tooth strike; and (3) to test hypotheses regarding the mechanics of chirp production. Two hypotheses could explain the mechanism of chirp production: (i) a coupled mechanism, where the movement of the plectrum is coupled to that of the abdomen, as seen in crickets and some katydids, tegmino-tegmina stridulators, in which the plectrum movement is coupled to the movement of the tegmen it is attached to, in an action that has been likened to a clock escapement mechanism (Elliot and Koch, 1985; Koch et al., 1988; Montealegre-Z and Mason, 2005; Prestwich and O'Sullivan, 2005); or (ii) an uncoupled mechanism, which we refer to as 'spring stridulation', whereby the plectrum moves independently from the abdomen, as proposed for some ultrasonic katydids (Montealegre-Z et al., 2006; Morris and Pipher, 1972), in a catch-and-release mechanism where the distal tip of the plectrum catches on a file tooth and elasticity in the plectrum causes it to deform and then spring back upon release. Interrupted chirps could be produced by: (i) rapid repetition of the sound production cycle, as seen in field crickets that produce multiple sound pulses (syllables) per chirp by repeating the wing closing cycle; or (ii) the plectrum pausing as it passes down the file, creating interruptions, as is proposed for some katydids (Montealegre-Z et al., 2006).

## MATERIALS AND METHODS

### Animals

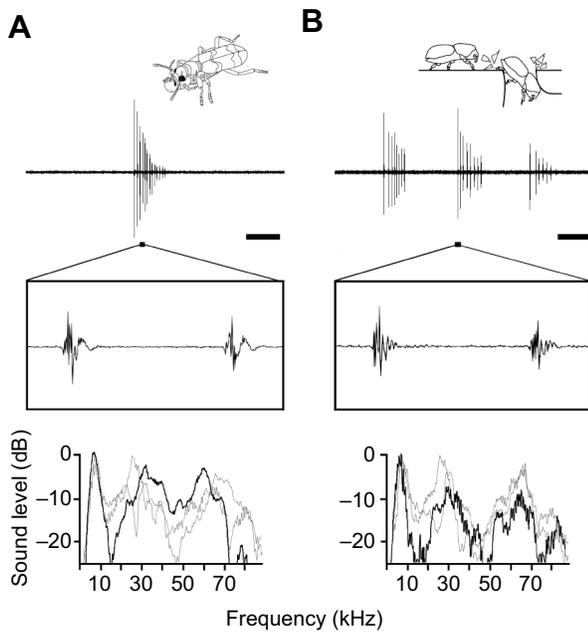
Adult *Dendroctonus valens* LeConte 1860 (Curculionidae: Scolytinae) were collected from May to September of 2013 and 2014 at several locations near Ottawa, ON, Canada (the Central Experimental Farm, 45.391021, -75.70489; Carleton Lands,

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**Fig. 1. Chirp types in male *Dendroctonus valens*.** (A) Top: pulse train of a simple chirp (function linked to anti-predation). Scale bar: 20 ms. Middle: enlargement of two sound pulses from the top trace. Bottom: power spectra from the chirp shown at the top (in black) and from simple chirps of two other individuals (grey). (B) Top: pulse train of an interrupted chirp with three components (function linked to courtship). Scale bar: 20 ms. Middle: enlargement of two sound pulses from the top trace. Bottom: power spectra from the chirp shown at the top (in black) and from interrupted chirps of two other individuals (grey).

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, BC, Canada). Animals were mated and offspring reared on red pine (*Pinus resinosa*). Males were collected as adults upon emergence. Voucher specimens are held at Carleton University.

### Sound recording and analysis of chirp characteristics

To study sound production mechanisms, disturbance chirps were recorded, as this set-up permitted visualization of body movements during sound production. Sounds were evoked by grasping the pronotum and head gently between the thumb and index finger while avoiding the elytra (see Fleming et al., 2013; Ryker and Rudinsky, 1976). Sounds were recorded with a microphone (40 kHz omnidirectional, QTC40, Earthworks, Milford, NH, USA) connected to a data recorder (sampling rate 192 kHz, FR-2, Fostex, Tokyo, Japan). All recordings were performed in a walk-in type acoustic chamber maintained at  $22 \pm 2^\circ\text{C}$ .

Sound characteristics were recorded and analysed for three reasons: first, to confirm that simple and interrupted chirps, as previously distinguished in a study on mating behaviour (Lindeman and Yack, 2015), also occurred during disturbance; second, to assess the proportion of chirp types; and third, to describe the temporal and spectral characteristics of chirp types. Disturbance sounds were evoked for 30 s recordings in 64 males, resulting in 6218 chirps. Of these, 320 chirps were identified by visual inspection as being clearly simple and 56 as being clearly interrupted. These chirps were used to identify a cut-off value to quantitatively distinguish between simple and interrupted types. Of these, 99.7% of the simple chirps had a maximum inter-pulse interval of less than 5 ms, while 100% of interrupted chirps had a

maximum inter-pulse interval of greater than 5 ms (due to the large interruptions between chirp components), agreeing with previously published criteria for distinguishing between chirp types (Lindeman and Yack, 2015). This value of 5 ms was then applied to categorize all chirps (see Results). Three hundred and twenty simple chirps (five each from the 64 males) and 56 interrupted chirps (up to five each – or as many as were present, as not all males produced five interrupted chirps – from 17 males) were measured for temporal and spectral analysis. Temporal characteristics – chirp duration, number of pulses and inter-pulse interval – were analysed using Avisoft SAS Lab Pro (Avisoft Bioacoustics, Glienicke Germany). Following characterization, these three temporal properties were used to confirm the distinctiveness of the two chirp categories using a discriminant analysis. Spectral characteristics were analysed using Raven Pro 1.5 (Raven Bioacoustics Research Program, Cornell Laboratory of Ornithology) (Hamming FFT window, 512 samples).

### Mechanism of sound production

#### Morphology

*Dendroctonus valens* males have ridges on the ventral posterior margins of each elytron, with most ridges occurring on the left elytron (Fig. 2A,B,D). It is not understood whether one or both elytra contribute to sound production. Males also have a sclerotized protrusion on their seventh abdominal tergite, hypothesized to function as a stridulatory plectrum (Fig. 2A,C) although this has not been directly tested. These putative sound-producing structures were examined in seven males using light microscopy (Olympus SZX12, Tokyo, Japan) and scanning electron microscopy (SEM; JOEL JSM-6400). In preparation for SEM, elytra were cleaned and placed on aluminium stubs, while abdomens were prepared following the procedure outlined by Rumph and Turner (1998) and placed on separate stubs. Specimens were sputter coated with gold-palladium and examined.

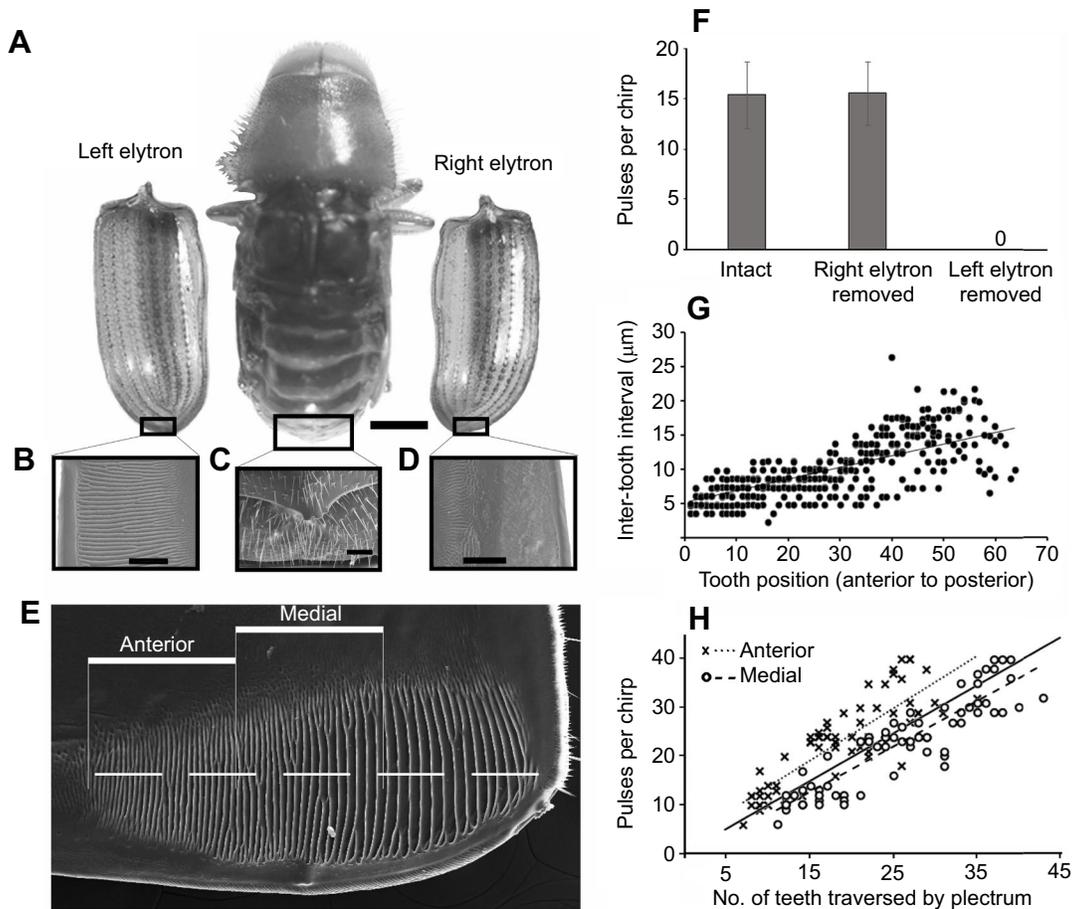
#### Contributions of the file and plectrum to sound production

To assess whether one or both elytra contribute to chirp production, sound recordings were conducted prior to and following ablation of the left ( $n=5$ ) or the right elytron ( $n=6$ ). Ablation was performed by clipping the posterior tip of either elytron, the region of the elytron containing the proposed file ridges, using dissection scissors. Sound recordings (30 s duration) were performed during disturbance trials (set-up as above) both pre- and post-ablation and recordings were analysed for the number of chirps and pulses per chirp.

To view the sound production mechanism, the right elytron was completely removed in seven males and disturbance sounds evoked as described above. Note that the elytron ablation experiment described above confirmed that the right elytron did not contribute to sound production (see Results). Stridulation was filmed at high speed using a GoPro Hero3 camera (frame rate:  $240 \text{ frames s}^{-1}$ , resolution:  $848 \times 480$ , GoPro Inc.) connected to an external microphone (ECM-MS908C, Sony) and mounted on a two-headed observation light microscope (Leica, Wild M3Z). Sounds were simultaneously recorded by an Earthworks microphone on a data recorder as described above. Audio was matched to the high-speed video using Raven Pro 1.5 by aligning several pure tone test sounds made throughout the recording.

#### Mechanism of pulse production

In *Dendroctonus* spp., each sound pulse in a chirp is proposed to result from the plectrum striking one tooth on the file. However, this has not been confirmed for any elytro-tergal stridulator. We tested this using two methods. First, we counted the number of teeth on the file



**Fig. 2. Sound-producing structures of male *D. valens*.** (A) Dorsal view of a beetle with both elytra removed and positioned ventral surface upwards. Scale bar: 1000  $\mu\text{m}$ . (B–D) Scanning electron micrographs (SEMs) of the ridges on the left elytron (B), the seventh abdominal tergite and plectrum (C), and ridges on the right elytron (D). Scale bars: 100  $\mu\text{m}$ . (E) SEM of a file on the left elytron showing 200  $\mu\text{m}$  sampling regions from anterior and medial locations. Dashed line indicates the medial transect along which teeth were counted. (F) Chirps contain the same number of sound pulses when beetles are intact ( $n=11$ ) and following removal of the right elytron ( $n=5$ ); conversely, sound is absent upon removal of the left elytron ( $n=6$ ). (G) Correlation between the location of the tooth on the file and inter-tooth interval. (H) The number of pulses per chirp correlates with the number of teeth traversed by the plectrum. The number of teeth traversed was estimated for two potential starting positions: anterior or medial. For both estimates, the pulse to teeth ratio was close to 1:1 (solid line).

measured along the file midline (see Fig. 2E) using SEMs of 15 males, and compared this with the mean number of sound pulses per chirp. Because there were more teeth than sound pulses (see Results), we then more specifically estimated the number of teeth impacted by the plectrum during chirp production. This was done by examining the location of the plectrum on the left elytron at the first and last pulse of each chirp for 10 simple chirps from the high-speed video footage of each of seven individual males (see above). The distance the plectrum travelled during the chirp was measured from higher resolution images of the stridulatory mechanism taken with a camera (Zeiss AxioCam MRc5, 1.4 megapixels, 1388 $\times$ 1040) mounted on a light microscope (Olympus SZX12) using Zeiss AxioVision digital image processing software. The number of teeth over that distance was then counted using SEMs (see above) of the left files from each male.

#### Mechanics of chirp production and variability

Simple chirps – that consist of continuous pulse production with regular intervals – may be produced by one of two hypothesized mechanisms: (1) an ‘escapement mechanism’ type of action, whereby the plectrum and abdominal movements are tightly coupled as the plectrum passes the file; in this case, we predicted that abdominal movement would be coupled with plectrum movement and sound production; (2) spring stridulation, where

the plectrum temporarily catches on a tooth of the file, is stretched and then released; in this case, we predicted that the plectrum would move independently from the abdomen. To quantify this, we measured the angle between the plectrum (on the seventh abdominal tergite) and the eighth abdominal tergite to establish whether the position of the plectrum against the abdomen was rigid or pliable. From the high-speed video recordings, we analysed each video frame during the production of five simple chirps for each of seven males and then calculated plectrum–abdomen angle measurements for each frame.

Interrupted chirps could result by two hypothesized mechanisms: by rapid repetition of the file–plectrum cycle or by one file–plectrum cycle that is intermittently stopped. Of the seven males with high-speed video trials, one male was observed to produce multiple interrupted chirps. We analysed each video frame during the production of the interrupted chirp and identified the point of contact of the plectrum on the elytral file for each video frame to determine plectrum movement. This was repeated for five interrupted chirps.

#### Statistical analysis

To test the distinctiveness of the two signal types – simple and interrupted – a discriminant analysis test was performed using inter-pulse interval, number of pulses and chirp duration as predictor

variables. To examine the relationship between the number of file teeth and chirp pulses, a linear correlation using Pearson's  $r$  was performed. In all other cases, paired sample  $t$ -tests were done. All probability tests were two tailed with an  $\alpha$  value of 0.05, and were done using SPSS (SPSS Inc., v.19).

## RESULTS AND DISCUSSION

### Simple and interrupted chirp characteristics

Chirps produced during disturbance could be categorized as simple or interrupted based on the absence or presence (respectively) of inter-pulse intervals of 5 ms or greater (Fig. 1). The mean maximum inter-pulse interval for interrupted chirps was 23.7 ms, which corresponded to the large interruptions that occurred between chirp components. Interrupted chirps accounted for roughly 3% of the total number of chirps recorded, and were produced by only 17 of 64 males. Interrupted chirps had more pulses (mean $\pm$ s.e.m.: interrupted 15.8 $\pm$ 3.8, simple 9.1 $\pm$ 1.1) and were longer than simple chirps (mean $\pm$ s.e.m.: interrupted 54 $\pm$ 13.1 ms, simple 13.6 $\pm$ 1.7 ms) ( $n=64$  males producing simple chirps and  $n=17$  males producing interrupted chirps). These variables, and in particular inter-pulse interval, were found to be robust at characterizing simple and interrupted chirp categories (Wilks'  $\lambda=0.128$ ; d.f.=3;  $P<0.001$ ). Additionally, interrupted chirps had lower pulse rates (mean $\pm$ s.e.m.: interrupted 338.3 $\pm$ 82.0 pulses  $s^{-1}$ , simple 695.1 $\pm$ 86.9 pulses  $s^{-1}$ ). However, this difference was due to the interruptions; there was no difference between chirp types when measuring pulse rate within components of interrupted chirps (mean $\pm$ s.e.m. of interrupted chirp component pulse rate: 659.4 $\pm$ 164.8 pulses  $s^{-1}$ ). In the spectral domain, both chirp types were broadband with a bimodal energy distribution (peaks at 6.8 $\pm$ 0.2 and 31.2 $\pm$ 0.5 kHz for simple, and 6.4 $\pm$ 0.4 and 29.2 $\pm$ 1.1 kHz for interrupted) (Fig. 1).

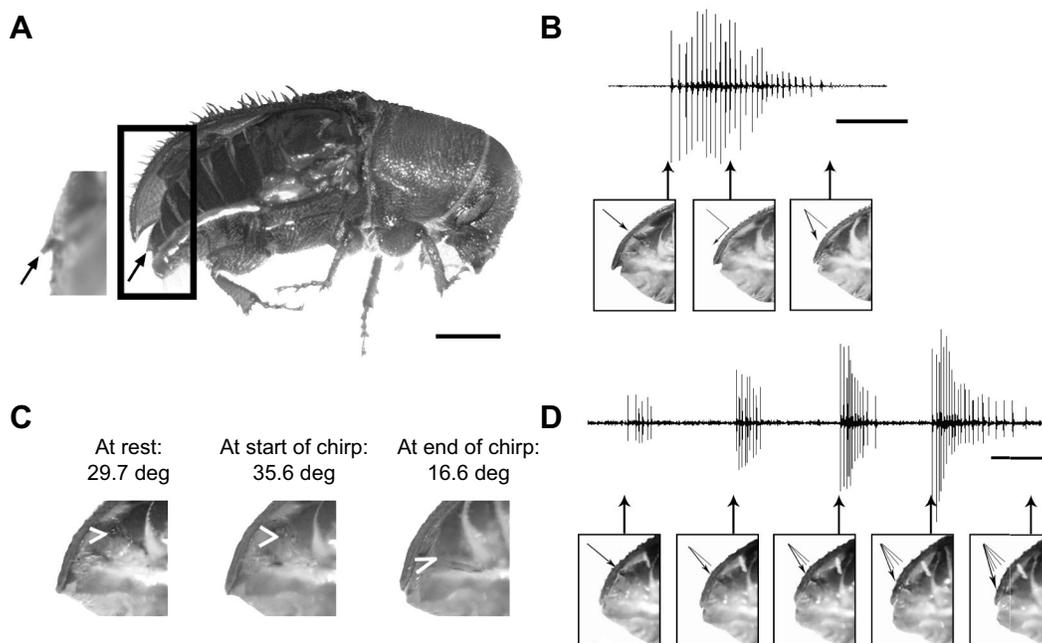
### Structures involved in sound production

Elytro abdominal stridulation has been proposed for several beetle families based on morphological traits (Lyal and King, 1996; Wessel, 2006), but understanding how these traits are involved in sound production requires validation in live stridulating beetles. In male *D. valens*, we show that while file ridges occur on both elytra (Fig. 2A,B,D,E), only the left elytron contributes to chirp production. Ablation of the left elytron eliminated sound, while ablation of the right elytron resulted in no change to chirp characteristics (mean $\pm$ s.e.m. number of pulses per chirp when intact: 13.0 $\pm$ 2.6, with right elytron removed: 13.6 $\pm$ 2.9;  $t_{5,2}=-0.43$ ,  $P=0.68$ ; Fig. 2F). Once confirmed that only the left elytron was involved, it was possible to remove the right elytron and directly observe the sound-producing structures during stridulation; by doing so, we validated that the protrusion on the seventh abdominal tergite functions as the plectrum (Fig. 3).

### Mechanism of simple and interrupted chirp production

#### Production of sound pulses

For bark beetle sound production, the prevailing assumption is that each sound pulse results from one tooth on the file being struck by the plectrum (e.g. Michael and Rudinsky, 1972; Ryker and Rudinsky, 1976). By comparing the number of teeth on the file with the number of pulses in a chirp, we found that there are more teeth than pulses (mean $\pm$ s.e.m. no. of teeth for 15 males: 62.9 $\pm$ 1.8; mean no. of pulses: 9.1 for simple and 13.6 for interrupted chirps). We then confirmed through video analysis ( $n=7$  males) that the plectrum traversed only a portion of the file during chirp production (mean $\pm$ s.e.m. distance: 213.2 $\pm$ 32.7  $\mu$ m; mean $\pm$ s.e.m. file length: 638.2 $\pm$ 33.8  $\mu$ m). Next, we determined how many teeth are traversed by the plectrum per chirp. High-speed video showed



**Fig. 3. High-speed video analysis of sound production.** (A) Lateral view of a beetle with the right elytron removed. The video camera was focused on the abdomen (boxed region). The left image shows the 7th tergite with the plectrum indicated by an arrow. Scale bar: 1000  $\mu$ m. (B) One simple chirp showing image stills of the stridulatory apparatus during sound production. Arrows above stills indicate the time of occurrence. Arrows inside stills illustrate movement of the plectrum. (C) Change in the mean angle ( $N=7$ ) of the plectrum relative to the abdomen between the beginning and end of the chirp (average values). (D) One interrupted chirp with four components, where stills show the stridulatory apparatus at the onset of each component. Arrows above stills indicate the time of occurrence. Arrows within stills point to the plectrum's current position, and lines indicate where the plectrum was located in previous stills. Scale bars for B and C: 20 ms.

that the plectrum's starting location is near the anterior end of the file. Because we could not identify precisely where on the file the plectrum first made contact, estimates for number of teeth were made for two hypothetical start points: anterior and 'medial' (Fig. 2E). This was necessary because inter-tooth intervals on the file increase from anterior to posterior (Fig. 2E,G). Regardless of the starting position of the chirp, there was a strong correlation between the number of teeth estimated and number of pulses recorded (measured anteriorly:  $r=0.89$ ;  $P<0.001$ , slope=0.93; measured medially  $r=0.84$ ;  $P<0.001$ , slope=1.07) (Fig. 2H). We conclude that each pulse is produced by one tooth strike.

### Simple chirps

The hypothesis that simple chirps are generated by spring stridulation was supported. Sound production coincided with movement of the plectrum, which was uncoupled to abdominal movement. As the abdomen moves posteriorly at a constant velocity, the distal tip of the plectrum catches on a file tooth and bends before being released in a spring-back motion (Fig. 3A–C; Movie 1). The plectrum's deflection is quantifiable as an increase over time in the angle between the plectrum and the eighth abdominal tergite (mean±s.e.m. angle: at rest:  $29.7\pm 1.6$  deg; in position on the file just prior to the start of the chirp:  $35.6\pm 2.2$  deg,  $t_{5,1}=-2.5$ ,  $P=0.029$ ) (Fig. 3B,C). After a period of ~8 to 12.5 ms, and coinciding with the start of sound production, the plectrum disengages and travels posteriorly along the file, with a decline in the angle between the plectrum and the eighth abdominal tergite (mean±s.e.m. angle: at the start of sound production:  $35.6\pm 2.2$  deg; at the end of sound production:  $16.6\pm 1.5$  deg). The decline in the angle indicates that the plectrum and abdomen are travelling at different velocities, with the plectrum moving more rapidly. A similar stridulatory mechanism has been reported for some katydids (e.g. Montealegre-Z et al., 2006; Morris and Pipher, 1972), where the plectrum functions like a spring or elastic band; upon being stretched, it builds a store of energy, causing it to snap back when released. In ultrasonic katydids, the elastic potential energy can propel the plectrum at a high enough velocity to produce ultrasonic frequencies. In *D. valens*, the peak frequencies (~7 and 30 kHz) were much higher than the sound pulse rate (695–701 Hz), indicating that the frequency characteristics result from resonance of an associated structure such as the elytron.

### Interrupted chirps

Interrupted chirps could be produced by rapid repetition of the sound production cycle, or by the plectrum intermittently pausing as it travels down the file. Our results support the latter hypothesis. High-speed video showed that the plectrum stopped and started at discrete intervals corresponding to the intervals between chirp components (Fig. 3D; Movie 1). Each component resulted from a spring-stridulation mechanism, as described above for simple chirps. The abdomen's posteriorly directed movement was continuous throughout the chirp, while the plectrum would catch on the file and bend, before being released in a spring-back action, during each chirp component (Fig. 3D; Movie 1). It is not clear what causes the plectrum to stop intermittently. Analysis of the file morphology from SEM images (Fig. 2E) did not reveal any morphological features, such as raised teeth, that would cause the plectrum to pause along the file. We propose that interruptions are under the fine motor control of the plectrum.

### Conclusions

Many beetles use elytro-tergal stridulation to communicate (Wessel, 2006) but the mechanisms underlying song production are poorly

understood. The red turpentine beetle, *D. valens*, uses a spring-loaded mechanism, which we call spring stridulation, to produce different types of chirps. In *D. valens*, different chirps function in two different contexts. Interrupted chirps are more common during courtship and function in female choice decisions. Females may be attracted to interrupted chirps because their increased length is more stimulating or their variable temporal pattern demonstrates skilful movements (Lindeman and Yack, 2015). Simple chirps are more common under distress, and share characteristics with anti-predator signals in other insects (e.g. short duration, simple temporal pattern; Masters, 1980). Divergence of sound characteristics plays a key role in the evolution of communication. This study provides insight into how an insect can employ uncoupled elasticity to enhance its acoustic repertoire, contributing to its signal evolution.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

Conceptualization: A.A.L., J.E.Y.; Methodology: A.A.L., J.E.Y.; Formal analysis: A.A.L.; Investigation: A.A.L.; Resources: J.E.Y.; Data curation: A.A.L.; Writing - original draft: A.A.L., J.E.Y.; Writing - review & editing: A.A.L., J.E.Y.; Supervision: J.E.Y.; Project administration: A.A.L., J.E.Y.; Funding acquisition: J.E.Y.

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### Data availability

Datasets have been deposited in the Dryad Digital Repository (Lindeman and Yack, 2019): [dryad.b97428m](https://doi.org/10.1242/jeb.190660)

### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.190660.supplemental>

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