Courting Bird Sings with Stridulating Wing Feathers

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Since Darwin's time (*1*), the nonvocal, feather-produced sounds of birds have been hypothesized to have evolved by sexual selection (*2*). Here we describe an acoustic signal that is produced by a mechanism unique among vertebrates. High-speed digital video recordings of the courtship displays of male club-winged manakins, *Machaeropterus deliciosus,* show that males produce sustained harmonic tones through interactions among oscillating secondary wing feathers.

The Neotropical manakins (Pipridae) are polygynous, lek-breeding birds in which sonation has evolved multiple times (*2*, *3*). The courtship sonation produced by male *M. deliciosus* sounds like a ringing *Tick–Tick–Ting* (audio S1) (*4*). The sound is as loud as a typical avian vocalization, easily audible from tens of meters away (*4*). The *Tick* notes are sharp tonal clicks, whereas the *Ting* is a sustained, violinlike note ~0.335 s long. Each sound is composed of fundamental frequencies of 1.59 and 1.49 kHz, respectively, with a series of harmonics that are integer multiples of the fundamental (Fig. 1A), a pattern characteristic of resonator-coupled stridulation (*5*, *6*).

The secondary, or inner, feathers have enlarged rachi, or shafts, that form clublike structures. The rachi of the sixth and seventh secondaries are greatly enlarged and hollow. They are twisted nearly 90° along their longitudinal axis so that, at their tips, their dorsal surfaces face medially and the feathers nestle closely together. In contrast, the distal ~12 mm of the rachis of the fifth secondary feather tapers abruptly to a thin, stiff, blade that bends medially to contact the ventral surfaces of the distal tips of the adjacent sixth and seventh secondaries (Fig. 1B). The surface of the sixth secondary has a set of 6 to 8 low, rounded ridges where the stiff tip of the fifth secondary contacts it (Fig. 1C).

Sonations are made while the male is perched (movies S1 and S2). To produce the *Tick* note, the wings are pronated (i.e., rotated forward), rapidly flipping the wing feathers above the bird's back (Fig. 1D). Simultaneously, the male adducts (pulls in medially) the wings, so that the tips of the modified secondary feathers strike together once forcefully across the back. The *Ting* note is produced using these same initial motions. However, after the initial contact of the secondaries over the back, the male shivers the wings, abducting (laterally extending) and adducting (pulling in) the forelimbs in a repeated cycle. This movement causes the flight feathers to oscillate lateromedially above the back (Fig. 1E). Each adduction culminates in a collision between the enlarged seventh secondary feathers above the back, which rebound after ~3 ms, initiating the abduction phase. After the abduction phase, the manus, or hand, is again adducted, redirecting the oscillating secondaries inward. The rate at which the feathers oscillate is 106.06 to 107.10 Hz (n = 3 Tings); thus, a frequency multiplier of 14 is needed to explain the fundamental frequency of 1.49 kHz.

We propose that the rapid pronation and adduction of the wings and the collision between the right and left secondaries produce an impulsive, mechanical excitation that induces the enlarged, hollow sixth and seventh feathers to resonate. The oscillations of the secondary feathers cause the tip of the fifth secondary to rub back and forth against the ribbed surface of the adjacent sixth secondary. The resulting mechanical input and the repeated collisions sustain the resonance of the sixth and seventh secondaries for the duration of the oscillations. The bent shape of the fifth secondary creates relative movement between the plectrum and file as the feathers oscillate, causing the plectrum to rub across the ribbed file twice (once medially and once laterally) for each wing cycle (Fig. 1F).

The derived morphological, mechanistic, and behavioral novelties of *M. deliciosus* are an extreme example of evolutionary modification of a locomotory structure for the production of an acoustic advertisement. The stridulation mechanism used by *M. deliciosus* to produce tonal sounds shows marked convergences with sound production in many insects, including the use of hardened integumentary appendages, extremely rapid limb vibration, and frequency multiplication through pick-and-file stridulation.

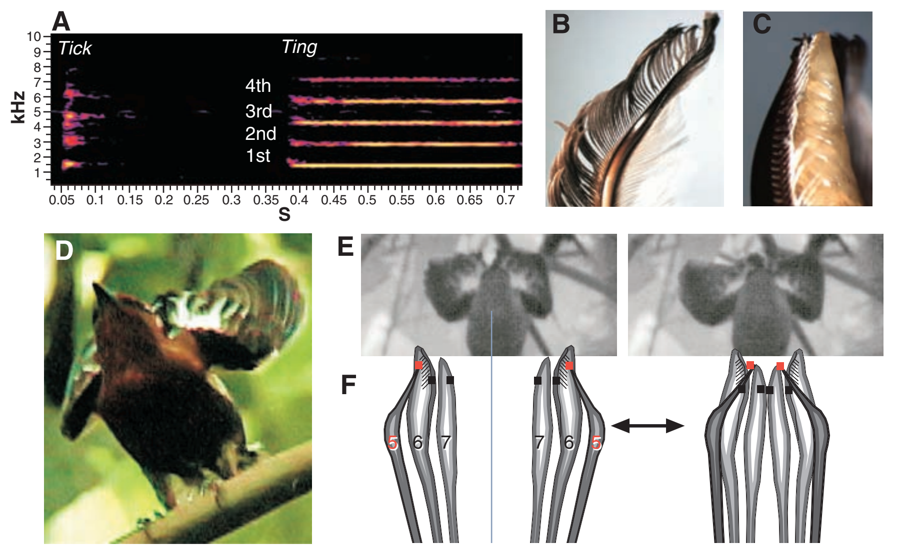

Fig. 1. (**A**) Spectrogram of a *Tick-Ting* sonation of one male *M. deliciosus*, showing signal energy in integer-related harmonic bands (labeled 1 to 4). S, seconds. (**B**) Dorsal surface of the right fifth secondary feather of a male *M. deliciosus*, the distal tip bent medially at 45°. (**C**) The medial surface of the thickened distal end of the right sixth secondary, showing regular, raised ridges. (**D**) Conventional and (**E**) high-speed video of *M. deliciosus* during *Ting* production. (**F**) Graphical depiction of the distal ends of the fifth secondary (the pick) moving across the ribbed surface of the sixth secondary (the file) to create stridulatory impulses that sustain the resonance of the enlarged sixth and likely seventh secondary shafts. Relative motion of the pick and file is indicated by red and black blocks, respectively; the gray line indicates the midline.

References and Notes

1. C. Darwin, *The Descent of Man and Selection in Relation to Sex* (John Murray, London, 1871).
2. R. O. Prum, *Anim. Behav.* **55**, 977 (1998).
3. K. S. Bostwick, R. O. Prum, *J. Exp. Biol.* **206**, 3693 (2003).
4. K. S. Bostwick, *Auk* **117**, 465 (2000).
5. N. H. Fletcher, *Acoustic Systems in Biology* (Oxford Univ. Press, New York, 1992).
6. H. C. Bennet-Clark, in *Cricket Behavior and Neurobiology*, F. Huber, T. E. Moore, W. Loher, Eds. (Cornell Univ. Press, Ithaca, NY, 1989), pp. 227–261.
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Supporting Online Material
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Materials and Methods
Audio S1
Movies S1 and S2

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