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OBSERVATIONS ON THE VERVAIN HUMMINGBIRD'S (*MELLISUGA MINIMA*) DISPLAY DIVE AND TERRITORIAL BEHAVIOR

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Resumen. – **Observaciones en el vuelo de despliege y comportamientos territoriales del Zumbadorcito (*Mellisuga minima*)**. – A diferencia del vuelo de despliege de algunos picaflores abeja, se ha reportado que en el Zumbadorcito tanto la hembra como el macho realizan una serie de vuelos ascendentes verticales. Realizando trabajo de campo durante 2005, descubrí a un macho que mantenía su territorio en una ladera escarpada. Esto me permitió realizar observaciones y grabaciones sobre su comportamiento territorial. La filmacion de dos machos en cortejo realizando el vuelo de atracción me lleva a interpretar este comportamiento como competitivo. Describo este tipo de vuelo por primera vez, presentando adicionalmente evidencia acústica de que el ruido producido por esta especie es de origen vocal.

Abstract. – Unlike the display dives of other bee hummingbirds, the Vervain Hummingbird (*Mellisuga minima*) mating display has been reported as a series of vertical ascents performed by both male and female. The discovery of a male holding a territory on a steep hillside allowed me to make observations and recordings of his territorial behavior. My video-recordings of two males engaging in the vertical ascent behavior leads me to interpret the behavior as competitive. Furthermore I describe for the first time the species' display dive and present acoustic evidence that the dive-noise made by this species is vocal. *Accepted 20 March 2006*.

Key words: Vervain Hummingbird, *Mellisuga minima*, display dive, natural history.

INTRODUCTION

Many hummingbirds perform elaborate displays, such as the display dives performed by bee hummingbirds (a monophyletic clade including the genera *Archilochus*, *Calypte*, *Mellisuga, Selasphorus, Stellula,* and several others; Bleiweiss 1998, Altshuler *et al.* 2004, McGuire pers. com.). In these dives, the male ascends 10 to 40 m, and then drops headfirst towards the object of the display, which is often another hummingbird. While these dives have been well characterized in the genera *Calypte*, *Archilochus* and *Selasphorus* (Pitelka 1942, Stiles 1982, Johnsgard 1983, Tamm *et al.* 1989, Sibley 2000, Hurly *et al.* 2001), these behaviors in bee hummingbirds from the Caribbean and Latin America are poorly known.

The Vervain Hummingbird (*Mellisuga minima*) is a bee hummingbird endemic to the islands of Jamaica and Hispaniola. Breeding males sing from an open perch, usually at the top of a tree 5 to 30 m tall, in open canopy (Downer & Sutton 1990). Published accounts of its display describe a behavior unlike a typical dive, in which male and female fly straight up 20 m or more together, and then glide down on outspread wings (Smith 1967, Downer 1976, Tyrrell & Tyrrell 1985, Downer & Sutton 1990). From these

accounts it seemed this behavior represented the Vervain Hummingbird's dive. The purpose of this paper is to present more detailed observations of this display behavior, which I term the "vertical ascent display" after Altshuler (2006). I also describe the species' display dive, including the dive sounds produced.

METHODS

During fieldwork near Hardwar gap, Jamaica (18°05.31'N, 078°41.92'W), between 15 June and 13 July 2005, I found the territories of six male Vervain Hummingbirds. I was unable to effectively observe the behavior of five birds due to obscuring trees. Accordingly my observations are limited to the sixth bird owning a territory on a hillside. The terrain allowed me observation posts from which all of the bird's song perches were visible. The steep slope made estimating heights difficult, so all heights refer to how high the bird was above my observation post at the top of the hill, rather than the ground directly below him. I was 5 to 10 m below the height of his tallest perch, but I was level with or above the remaining perches. Many of the observations, including those of the vertical ascent display, were made in good light, approximately 15 m away from the birds, using 10 x 43 binoculars.

In addition to numerous casual observations of his behavior, I spent 7 h 12 min of timed observations and recordings of the focal male on 30 June, 11 July, and 12 July. Using a GPS unit (Garmin: Geko 301), I mapped all of his song perches to obtain an estimate of territory size. With a Sony DCR-TRV19 DV camcorder, I video-recorded the vertical ascent display, and I recorded his sounds with a Sennheiser ME-67 directional microphone attached to a Sony TC-D5 Pro II tape deck. The microphone was unamplified, and there was a waterfall in the background.

Tape recordings were digitally sampled at 44,100 Hz using Signal 4.0 and sonograms were created using a 512 sample Hann FFT using Raven 1.2.1. Digital video and sound recordings have been deposited in the Macaulay Library at the Cornell Lab of Ornithology.

RESULTS

Territory. The focal male's territory was approximately 400 m^2. It consisted of 4–5 perches, but he spent the majority of his time singing on one main perch, and often used the other perches when disturbed from his main perch by larger birds. The territory had at least one neighboring male, approximately 100 to 300 m away. I did not take a systematic survey for neighboring territories, because most of my observations came a few days after a hurricane and some males seemed to return to their territories more quickly than others after the bad weather.

I did not see the male feed from flowers on his territory, nor did I see any plants blooming in the immediate vicinity that I know Vervain Hummingbirds to visit. On a separate territory I observed a second male frequently visiting unidentified flowers approximately 10 m from one of his song perches.

Behaviors. Of the 7 h 12 min of timed observations of the focal male in which he was present in the vicinity of his territory, he spent 70% of it in my view. He left his territory 33 times for an average of 3.8 ± 4.1 min (mean ± SD). These values underestimate his true time on territory, for at times I did not see that he had returned from out of sight until he began to sing. I took detailed notes for 18 min 38 s on the length of his songs; he sang for 33% of this time, and individual songs lasted 12.0 s ± 6.4 (mean ± SD; N = 31 songs). As others have noted (Bond 1993), he also frequently sang as he flew towards, away, or over the territory; I did not quantify the amount of time

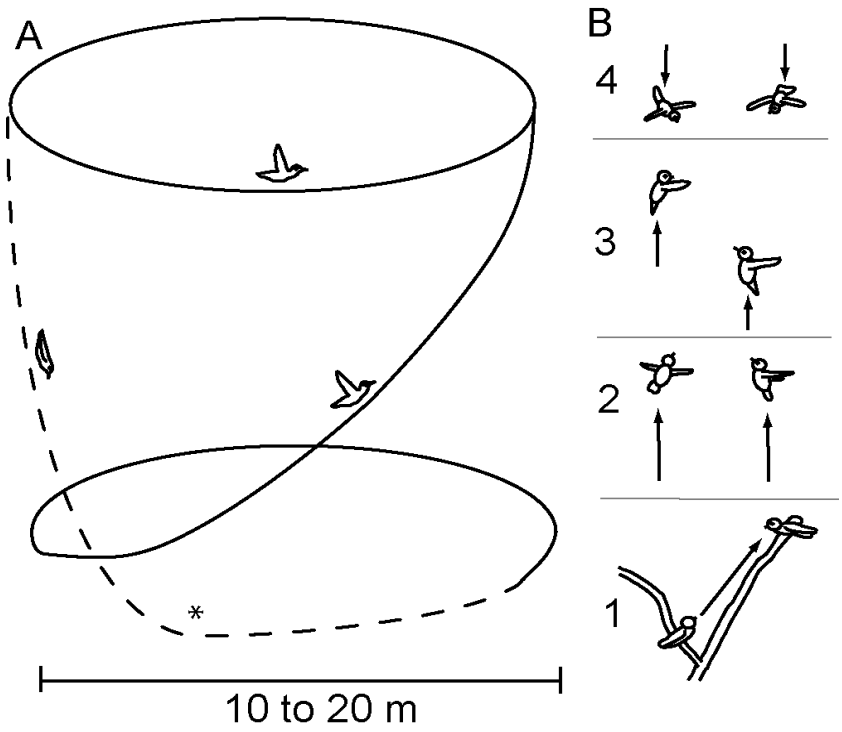

FIG. 1. Left: a stylized drawing of the Vervain Hummingbird's circular flight with display dive; the location of syllable A of the dive-noise is indicated by (*). Right: tracings from video of the vertical ascent display, with arrows indicating the direction of movement; see text for details of the behavior.

he spent singing during flight.

I observed three types of display flights. The first consisted of the bird flying in a horizontal circle approximately 10–20 m in diameter, over the core (*sensu* Stiles 1982) part of his territory (Fig. 1A, solid line). He often sang while performing this flight.

He performed four display dives in my presence, in two sets of two (Fig. 1A, dashed line). Two of the dives were a continuation of the circular flight, and all four dives were from a height of 20–30 m. At the bottom of the dive, he emitted a dive noise and pulled up into horizontal flight. With the momentum he had gained, he flew another horizontal circle 10–20 m in diameter, before ascending again or ending the behavior. I could not determine whether the first pair of dives was directed at another animal, but the second pair appeared to be directed at me, as the bottom of each dive was within 2 m of me and I did not see another likely object of display. I did not manage to film these dives.

The vertical ascent display took place on the morning of 11 July 2005. At 11:45 EST, I heard him sing, indicating he had returned after a 4-day absence caused by hurricane Dennis – I assume it was the same male based on the perches he used. When I arrived on the territory with my equipment at 12:05, two hummingbirds were silently perched on the main song perch, facing each other about 10 cm apart. Both were adult males, based on their forked tails and complete lack of white

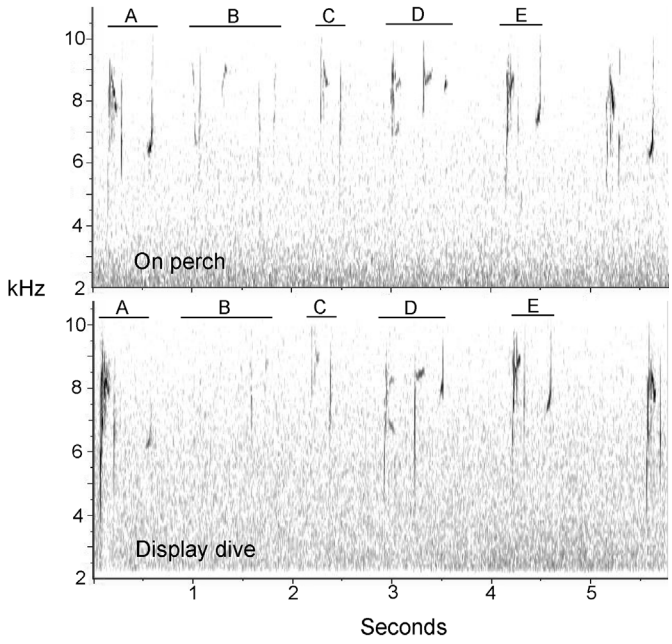

FIG. 2. Sounds produced by the male while singing on a perch (above) and at the bottom of his display dive (below; syllable A roughly corresponds with the bottom of the dive).

on the outer rectrices. Both birds engaged in preening, bill-wiping, and alternated these behaviors with continuous turning from side to side, while perched, in a fashion similar to the "chatter-sway" behavior of the Anna's Hummingbird (pers. observ., Stiles 1982), except that I heard no vocalizations. This swaying continued for 12 min after my arrival, then one bird attacked the other, and locked together and scolding, they both tumbled out of sight. Seconds later they returned to the perch, and began repeatedly performing the vertical ascent display.

One bird would take off from his perch to fly straight at the other (Fig. 1B), and then close together, both would ascend vertically (Fig. 1B-2). Of 19 ascents caught on video, 18 ended when one bird ascended above the other (Fig. 1B-3). Both birds would then glide with spread tail and wings back down to the song perch (Fig. 1B-4). The vertical excursions during this behavior ranged from 1 to 10 m. Sometimes rather than ascending one would collide with the other, and they would drop out of sight clinging together. The behavior ended when one male abruptly flew away from the territory; he was not chased by the other hummingbird.

Vocalizations. The Vervain Hummingbird's main territorial song varied in length and was composed of several syllables, including five labeled A B C D and E in Fig. 2. During his songs he frequently sang these five syllables in the order depicted, but he also sang these syllables together in different orders. The sound made during the display dive (Fig. 2) was nearly identical to the song he sang on his perch. The main difference is syllable B, which is nearly imperceptible during the display dive; I attribute this difference to the bird's changing position and orientation rela-

tive to the microphone during the dive, rather than any real difference between the calls.

DISCUSSION

The males fought several times during the entire interaction, suggesting the vertical ascent display is of competitive nature in this context. This does not exclude the possibility of sexual function of the behavior as suggested by the brief, vague descriptions of Smith (1967), Downer (1976), and Downer & Sutton (1990); the competitive and sexual behaviors of many hummingbirds are frequently indistinguishable (Mobbs 1982: 133).

I did not observe any chases between Vervain Hummingbirds, whereas chasing is a large component of the competitive behavior in other species of hummingbirds. Hovering flight is very energetically expensive (Greenewalt 1975), and vertical ascent requires more power than hovering, as metabolic energy is transformed into potential energy, and is therefore one of the most demanding forms of flight (Chai *et al.* 1997, Chai & Millard 1997, Altshuler *et al.* 2004, Altshuler 2006). Because individual bouts of the vertical ascent display ended when one male ascended above the other, I propose that competing male Vervain Hummingbirds may be using the vertical ascent display to assess the flight capabilities of rival males. Other species of hummingbird occasionally engage in vertical ascent when rival birds face off at a feeder (Altshuler 2006) or during a fight (pers. observ.), although these competitive interactions usually also include high-speed chases. The maximal-loading tests of flight performance used by Chai *et al.* (1997), Chai & Millard (1997), Altshuler *et al.* (2004), and Altshuler (2006) are designed to mimic the flight demands of the vertical ascent display, and the observations presented here suggest these flight demands are experienced by wild hummingbirds as well.

Like other bee hummingbirds, the mating system of the Vervain hummingbird appears to be an "exploded lek". Although the territories sometimes contained resources, I never observed the focal male to feed inside his territory, suggesting the territory's function was mate attraction. Anna's Hummingbirds and Calliope Hummingbirds often hold territories that have food on them (Stiles 1973, Armstrong 1987, Powers 1987), but males of these species are also known to hold mating territories with no resources (Stiles 1973, Armstrong 1987, Powers 1987). With the limited observations I report here, I did not detect any differences in the mating system of the Vervain Hummingbird and these relatives.

In contrast, the Vervain's display dive was unique. The bee hummingbirds in North America engage in display dives that typically lie within a single vertical plane, and are therefore approximately two-dimensional (e.g., Sibley 2000). The Vervain Hummingbird's dive appears to be an extension of a horizontal circular flight around its territory, since this flight may be performed immediately prior to and following the dive. Also contrasting with other bee hummingbirds, the dive-noise of the Vervain Hummingbird is unambiguously vocal in origin. The notes emitted at the bottom of the Vervain's dive are identical to notes the male uttered from his song perch (Fig. 2). By contrast, the *Selasphorus* hummingbirds make their dive noise with their tails (Aldrich 1956, Stiles *et al.* 2005, unpubl. data), while the source (non-vocal vs vocal) of the dive noises in the related Anna's Hummingbird and Black-chinned Hummingbird are controversial: Pytte & Ficken (1994) and Baptista & Matsui (1979) disagree with Stiles (1982) and Stiles *et al.* (2005). Clarifying these uncertainties and additional descriptions of display dives will allow phylogenetic reconstruction of dive sound evolution and insights into the function of the

diverse tail morphologies exhibited by bee hummingbirds.

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