INTRODUCTION

Hummingbirds and their food-plants rely to a large extent on each other for food supply and pollination service, respectively. This mutual relationship has co-evolved for millions of years and across the Americas involving over 330 hummingbird species and an estimated nearly 8000 plant species relying on hummingbirds as their principle pollinators (Feinsinger & Colwell 1978, Schuchmann 1999, Nicolson & Fleming 2003, Dalsgaard et al. 2011). Although birds other than hummingbirds also act as pollinators (Feinsinger & Colwell 1978, Rocca & Sazima 2008, Dalsgaard 2011, Kissling et al. 2011), hummingbird-plant interactions are one of the most striking examples of bird-plant co-evolution, and the associated morphological adaptations have been studied intensively (e.g., Snow...
& Snow 1972, Brown et al. 1978, Feinsinger & Colwell 1978, Stiles 1981, Feinsinger et al. 1982, Arizmendi & Ornelas 1990, Cotton 1998, Buzato et al. 2000, Temeles & Kress 2003, Lara 2006, Dalsgaard et al. 2009, Abrahamczyk & Kessler 2010). These studies have found that plants adapted to hummingbird-pollination typically are odorless, have a long and narrow conspicuous orange-red tubular corolla, and produce extensive dilute nectar - broadly matching the sensory capabilities, morphology and energetic demands of hummingbirds (Temeles & Kress 2003, Dalsgaard et al. 2009). Similarly, hummingbirds show an array of features considered nectar-feeding adaptations, such as the capability to hover, a specialized tongue, highly specialized and variable bill morphologies, as well as a minute body size (Brown et al. 1978).

The smallest of all birds is the Bee Hummingbird (Mellisuga helenae) endemic to the Cuban archipelago, including the main island of Cuba and Isle of Youth (formerly Isle of Pines), in the West Indies (AOU 1998, Garrido & Kirkconnell 2000). Of the 15 hummingbird species endemic to the West Indies (Lack 1973, 1976), the Bee Hummingbird is the only species considered threatened on the IUCN red list (BirdLife International 2011). Although the Bee Hummingbird is the smallest bird in the World, is categorized as Near Threatened and its population size is clearly declining, only very basic information regarding its feeding ecology. For instance, apart from the record of some 15 food plants, nothing is reported about its preferred food plants or the overlap in flower use with the larger-sized Cuban Emerald (Chlorostilbon ricordii) - the only other resident Cuban hummingbird (Martínez et al. 1998, Schuchmann 1999, Garrido & Kirkconnell 2000). We here: 1) identify and describe the floral traits of several food plants the Bee Hummingbird uses; 2) report to what extent the Cuban Emerald uses the same flowers as the Bee Hummingbird; and 3) compare our data on flower use with those previously reported, and discuss how our results could direct future studies beneficial for the conservation of the Bee Hummingbird.

METHODS AND STUDY SITE
Food plants. Our study was conducted near Playa Larga (22°17N, 81°12W) in the outskirts of the Zapata Swamp in Cuba, West Indies - one of the few remaining core areas for the Bee Hummingbird (Garrido & Kirkconnell 2000). We focused our fieldwork on measuring the floral traits (see below) of plants known to be visited by the Bee Hummingbird. All the included food plants were located in the field by OMG and AM (see acknowledgments), both of whom have over 30 years of experience as bird guides locating the Bee Hummingbird and its flowers in the Zapata Swamp, and have studied the Bee Hummingbirds reproduction and use of food plants in the Zapata Swamp (Martínez et al. 1998). We only included plants that OMG and AM knew to be used by the Bee Hummingbird and only at localities they knew well, i.e., we were certain that the individual plants studied had been visited by the Bee Hummingbird (which coincide with Kirkconnell's field data). The plants were later identified by Ramona Oviedo, a botanist from the Institute of Ecology and Systematic, Cuba. Although during the fieldwork period we observed the Bee Hummingbird visiting some of the identified plants (Pavonia paludicola, Lysiloma latissilicium, and Cissus obovata), we did not attempt to estimate how the relative visitation rate varied among plant species. We also report whether the plants were visited by the Cuban Emerald; this information was likewise...
based on the accumulated knowledge by OMG and AM, although during fieldwork we also observed the Cuban Emerald visiting several of the identified plants (Forsteronia corymbosa, Pavonia paludicola, Lysiloma latifoli- um, Turnera ulmifolia, Hamelia patens, and Cissus obovata).

Floral traits. We measured six quantitative and semi-quantitative floral traits, which have been shown previously to be important in structuring West Indian hummingbird-plant communities into traditional ornithophilous flowers and more generalistic entomophilous syndrome flowers (Dalsgaard et al. 2009). The six floral traits can be divided into: two “restriction” traits (corolla depth, corolla width); two “reward” traits (nectar volume, nectar concentration); and two “attraction” traits (color, odor). Corolla depth was measured as the internal distance from the opening to the base of the flower. When the nectar was not protected by a tubular corolla, we measured the distance from the start of the floral restriction to the base of the flower. Likewise, corolla width was measured as the internal width of the opening of the flower. Both restriction traits were measured with a digital caliper to nearest mm. Nectar volume was measured using 1, 5, and 10 µl micropipettes, while nectar concentration (expressed as % sucrose equivalents) was measured with a refractometer and corrected for temperature. The floral color of each species was assigned as perceived by the human eye. Where the floral bracts/stems were a major part of the color display, as in C. obovata, they were included in the assignment. Finally, the flower of each species was coded according to their odor, with (1) representing no odor; (2): little; (3): moderate; and (4): strong odor. All floral trait estimates were obtained during 15–27 July 2010 (i.e., in the rainy season outside of the Bee Hummingbirds breeding season), and are means of 8–15 flowers measured on un-bagged and fresh flowers sampled within the first hour of sunrise. Hence, nectar volume estimates express standing crop available to hummingbirds and other visitors in the early morning and not nectar production per se (Cotton 1998, Dalsgaard et al. 2009).

RESULTS AND DISCUSSION

Each of the identified ten plant species visited by the Bee Hummingbird belongs to different plant families, of which one species (Antigonon leptopus) was introduced to Cuba. The remaining nine plant species are either native or endemic to Cuba (Table 1). Most of the ten flowers visited by the Bee Hummingbird - of which nine were also visited by the Cuban Emerald, as well as insects, such as bees and butterflies (pers. observ.) - have floral traits that fall outside the traditional ornithophilous syndrome, noticeably most flowers had little nectar and a short, white corolla, although some had more vivid colors (Table 1, Fig. 1). This indicates that the Bee Hummingbird uses plants with generalized pollination systems as has also been reported for plants visited by small hummingbirds on Trinidad, Tobago, and other islands in the West Indies (Feinsinger et al. 1982, Dalsgaard et al. 2008, 2009).

Conclusions. A total of 15 plant species from 15 different genera had previously been reported to be visited by the Bee Hummingbird, but no study had described their floral traits (Martínez et al. 1998, Schuchmann 1999). Of the herein reported ten food plants, only one species (Hamelia patens) occurs in the 15 genera previously listed as being visited by the Bee hummingbird. Many of the previously reported food plants in the Zapata Swamp were observed in March–June during the breeding season of the Bee Hummingbird (Martínez et al. 1998), whereas the food plants we here report bloom in the latter part of July,
TABLE 1. Floral traits of ten plant species visited by the Bee Hummingbird (*Mellisuga helenae*). The Cuban Emerald (*Chlorostilbon ricordii*) visited all species except *Chrysobalanus icaco*. ¹Plant origin: 1 = endemic; 2 = native; 3 = introduced. ²Odor: coded as 1–4: 1 = no odor; 2 = little; 3 = moderate; and 4 = strong odor.

<table>
<thead>
<tr>
<th>Plant family</th>
<th>Plant species</th>
<th>Plant origin</th>
<th>N</th>
<th>Corolla depth (mm)</th>
<th>Corolla width (mm)</th>
<th>Nectar volume (ml)</th>
<th>Nectar conc. (%)</th>
<th>Color</th>
<th>Odor²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apocynaceae</td>
<td>Forsteronia corymbosa</td>
<td>1</td>
<td>8</td>
<td>2.62 ± 0.44 SD</td>
<td>1.97 ± 0.13 SD</td>
<td>0.48 ± 0.31 SD</td>
<td>40.03 ± 5.21 SD</td>
<td>red</td>
<td>1</td>
</tr>
<tr>
<td>Boraginaceae</td>
<td>Tournefortia hirsutissima</td>
<td>2</td>
<td>15</td>
<td>6.79 ± 0.54 SD</td>
<td>1.09 ± 0.26 SD</td>
<td>0.25 ± 0.10 SD</td>
<td>15.85 ± 2.67 SD</td>
<td>white</td>
<td>3</td>
</tr>
<tr>
<td>Chrysobalanaceae</td>
<td>Chrysobalanus icaco</td>
<td>2</td>
<td>12</td>
<td>4.87 ± 0.44 SD</td>
<td>1.81 ± 0.30 SD</td>
<td>0.82 ± 0.93 SD</td>
<td>27.19 ± 9.41 SD</td>
<td>white</td>
<td>1</td>
</tr>
<tr>
<td>Malvaceae</td>
<td>Pavonia paludosa</td>
<td>2</td>
<td>11</td>
<td>16.83 ± 1.64 SD</td>
<td>6.52 ± 0.90 SD</td>
<td>29.61 ± 24.37 SD</td>
<td>16.64 ± 2.03 SD</td>
<td>yellow-green</td>
<td>2</td>
</tr>
<tr>
<td>Mimosaceae</td>
<td>Lysiloma latissilquum</td>
<td>2</td>
<td>9</td>
<td>1.03 ± 0.34 SD</td>
<td>1.12 ± 0.19 SD</td>
<td>0.51 ± 0.41 SD</td>
<td>35.89 ± 22.14 SD</td>
<td>white</td>
<td>3</td>
</tr>
<tr>
<td>Passifloraceae</td>
<td>Turnera umbrosa</td>
<td>2</td>
<td>11</td>
<td>8.88 ± 0.80 SD</td>
<td>0.84 ± 0.15 SD</td>
<td>1.26 ± 1.14 SD</td>
<td>26.89 ± 2.51 SD</td>
<td>yellow</td>
<td>2</td>
</tr>
<tr>
<td>Polygonaceae</td>
<td>Antigonon leptopus</td>
<td>3</td>
<td>11</td>
<td>3.29 ± 0.38 SD</td>
<td>1.73 ± 0.21 SD</td>
<td>1.25 ± 0.66 SD</td>
<td>16.88 ± 2.65 SD</td>
<td>pink</td>
<td>2</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Hamelia patens</td>
<td>2</td>
<td>8</td>
<td>21.33 ± 1.27 SD</td>
<td>3.47 ± 0.47 SD</td>
<td>5.41 ± 5.30 SD</td>
<td>25.91 ± 0.89 SD</td>
<td>orange-red</td>
<td>1</td>
</tr>
<tr>
<td>Verbenaceae</td>
<td>Clerodendrum acutatum</td>
<td>2</td>
<td>11</td>
<td>18.20 ± 1.97 SD</td>
<td>1.53 ± 0.14 SD</td>
<td>0.37 ± 0.30 SD</td>
<td>22.91 ± 2.88 SD</td>
<td>white</td>
<td>1</td>
</tr>
<tr>
<td>Vitaceae</td>
<td>Cissus obvata</td>
<td>1</td>
<td>9</td>
<td>0.00 ± 0.00 SD</td>
<td>1.48 ± 0.15 SD</td>
<td>0.50 ± 0.34 SD</td>
<td>22.35 ± 5.55 SD</td>
<td>orange-red</td>
<td>1</td>
</tr>
</tbody>
</table>
FIG. 1. The flowers of ten plant species visited by the Bee Hummingbird: a) *Forsteronia corymbosa* (Apocynaceae); B) *Tournefortia hirsutissima* (Boraginaceae); C) *Chrysobalanus icaco* (Chrysobalanaceae); D) *Pavonia paludicola* (Malvaceae); E) *Lysiloma latisiliquum* (Mimosaceae); F) *Turnera ulmifolia* (Passifloraceae); G) *Antigonon leptopus* (Polygonaceae); H) *Hamelia patens* (Rubiaceae); I) *Clerodendrum aculeatum* (Verbenaceae); J) *Cissus obovata* (Vitaceae). Note that the photos of each flower have a different scale. For the actual size of each flower, see Table 1 (photos: Bo Dalsgaard).
outside the breeding season of the Bee Hummingbird. In Cuba, the dry season extends from November to April, whereas the wettest months are from June to October (Garrido & Kirkconnell 2000). Therefore, it seems likely that the flower community largely changes between the dry and the rainy season, roughly coinciding with the termination of the Bee Hummingbirds breeding season.

This study is a first step in identifying the floral niche of the Bee Hummingbird. We recommend that a quantitative field study be undertaken to evaluate the floral overlap in the context of floral use and availability, and behavioral interactions with the Cuban Emerald (Vaurie 1957) and insect-pollinators, such as the potential negative impact of the non-native honeybee (*Apis mellifera*). Comparing the herein reported food plants of the Bee Hummingbird with the plant species reported by Martínez *et al.* (1998), indicates that it would be essential to examine both dry season and rainy season floral overlap and behavior. It would also be interesting to study the effect of introduced plants, forest loss and degradation on the feeding behavior of the Bee Hummingbird (BirdLife International 2011). Finally, we recommend that field studies are also conducted in other areas than the Zapata Swamp, e.g., in the Bee Hummingbirds strongholds in the lowlying Guanahacabibes peninsula in western Cuba and in the eastern mountains of Cuchillas del Toa and Sierra Cristal. This should prove valuable for the conservation of the Bee hummingbird, an endemic and threatened species of the Cuban archipelago, West Indies.

**ACKNOWLEDGMENTS**

Thanks to Ramona Oviedo for identifying the plants, to Angel Martínez and Lazara Reina Rodríguez Gazmury for help in the field, and to Joseph M. Wunderle, André Weller, Gary F. Stiles, and an anonymous reviewer for providing useful comments improving the manuscript. BD was supported by The Carlsberg Foundation, The Danish Research Council | Natural Sciences and Weis-Fogh Fund at Department of Zoology, University of Cambridge, DWC by The Faculty of Science and Technology at Aarhus University, AMMG by the Spanish Ministry of Education, and WJS by Arcadia.

**REFERENCES**


Accepted 14 March 2012.