ORNITOLOGÍA NEOTROPICAL
(2020) 31: 71–75
ORIGINAL ARTICLE
Sociedad de Ornitología Neotropical

HUMMINGBIRD FRUGIVORY IN A COSTA RICAN CLOUD FOREST

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Abstract · Hummingbirds (Trochilidae) are mainly nectivores and rarely consume fruits. Four species of hummingbirds (Purple-crowned Fairy, *Heliothryx barroti*; Stripe-tailed Hummingbird, *Eupherusa eximia*; White-tailed Emerald, *Elvira chionura*; and White-throated Mountain-gem, *Lampornis castaneoventris*) were observed feeding on the fruits of the tree *Saurauia montana* (Actinidiaceae) in a secondary cloud forest in the Talamanca mountains of Costa Rica, which are small (1 cm) berries with mucilaginous pulp. Feeding occurred via repeated puncture of the epicarp. This is the first record of frugivory in any of these hummingbird species and one of the few records of hummingbird frugivory on plants other than Cactaceae.

Resumen · Frugivoría de colibríes en un bosque de niebla de Costa Rica
Los colibríes (Trochilidae) se alimentan predominantemente de néctar y raramente consumen frutos. Se observaron cuatro especies de colibríes (colibrí hada occidental, *Heliothryx barroti*; colibrí colirrayado, *Eupherusa eximia*; esmeralda de Elvira, *Elvira chionura*; y colibrí ventricastaño, *Lampornis castaneoventris*) alimentándose de los frutos del árbol *Saurauia montana* (Actinidiaceae) en un bosque de niebla secundario en las montañas de Talamanca de Costa Rica, que son bayas pequeñas (1 cm) con pulpa mucilaginosa. La alimentación se produjo luego de la punción repetida del epicarpio. Este es el primer registro de frugivoría en estas especies de colibríes y uno de los pocos registros de frugivoría para colibríeas sobre plantas que no sean Cactaceae.

Key words: *Elvira* · *Eupherusa* · Frugivory · *Heliothryx* · Hummingbird · *Lampornis* · *Saurauia*

INTRODUCTION

Hummingbirds (Trochilidae) are important pollinators for many tropical plants. Some plant-pollinator relationships have evolved to the point of extreme specialization, leading to a suite of floral traits that define pollination syndromes (Rosas-Guerrero et al. 2014). In many cases, these hummingbird-plant associations are mutualistic. Hummingbirds transport pollen on their heads and bills, efficiently delivering it to conspecific flowers. In return, they receive nectar rewards to fuel their high metabolism and energetically costly flight (Welch et al. 2006, Johnson & Nicholson 2008). Nectar availability can be highly variable, which may result in territorial defense of flowering plants by some hummingbird species (Kodric-Brown & Brown 1978, Temeles & Kress 2010).

In contrast to their importance as pollinators and their reliance on plant nectar, frugivory in hummingbirds has been reported only rarely. Palacio (2019) recently reviewed the evidence of frugivory in hummingbirds, reporting observations of frugivory in approximately 15 different species of hummingbirds across the Americas. Cactaceae make up the majority of fruits fed upon, likely because cacti represent a significant source of water for hummingbirds in arid habitats, as has been shown for other bird species (Silvius 1995), though some observations of frugivory on Rosaceae, Muntingiaceae, Ebenaceae, and Passifloraceae were also recorded (Palacio 2019). The goal of this short note is to describe our observations of frugivory in four species of hummingbirds on the fruits of *Saurauia montana* in a regenerating cloud forest in the Talamanca mountains of Costa Rica.

METHODS

We conducted our research at the Cloudbridge Nature Reserve (9° 28’ 18” N, 83° 34’ 41” W), a 283 ha private reserve located at 1650 – 1800 m a.s.l. in the Talamanca mountains of Costa Rica. We worked in a secondary forest that has been regenerating from pasture for approximately 17 years. Our observations were made between 1 May and 5 June 2019, during the early part of the rainy season, between 07:00 – 14:00 hours; for the years 2015 – 2018, the average daily temperature in May was 17–

Receipt 30 July 2019 · First decision 21 August 2019 · Acceptance 28 July 2019 · Online publication
Communicated by Kaspar Delhey & Rafael Rueda-Hernández

Figure 1. The open fruit of *Saurauia montana* showing the seeds and the mucilaginous pulp. Photograph by Charlotte Smith at Cloudbridge Nature Reserve, Pérez Zeledón, Costa Rica.

18 °C and the mean monthly precipitation was 360 mm. No observations were made during the rain.

Saurauia is a genus of a tropical flowering tree in the family Actinidiaceae. There are three *Saurauia* species at the Cloudbridge Nature Reserve: *S. montana*, *S. pittieri*, and *S. rubiformis*. Flowers in this genus are located on cymes, which yield berry fruits approximately 1 cm in diameter (Soejarto 1969). The fruits contain a mucilaginous pulp with numerous small seeds (Figure 1).

We located fruiting *Saurauia montana* trees by systematically walking the trails around the reserve. We found fruiting trees at nine locations and in two locations there were adjacent fruiting trees; thus, the total number of trees observed was 11. We conducted focal observations of individual trees to watch for hummingbird frugivory. If no birds were seen for 20 min, we moved to the next tree and repeated this process. Frugivory was observed at five of these locations, three with single *S. montana* trees and two with two trees.

The beginning of a feeding visit was defined when a hummingbird was first observed hovering or perched near a fruit, and then subsequent feeding at this or any other fruits before leaving the area. Using binoculars and a stopwatch, we recorded the total duration of each feeding visit, as well as the time spent feeding on some individual fruits. When possible, we recorded the sex of each bird we observed.

RESULTS

We observed four hummingbird species feeding on the fruits of *Saurauia montana* (Figure 2). These included Purple-crowned Fairies (*Heliothryx barroti*; N = 2 observations, both unknown sex), Stripe-tailed Hummingbirds (*Eupherusa eximia*; N = 30 observations, including 3 with an unknown sex, 5 males, and 22 females), White-tailed Emeralds (*Elvira chionura*; N = 13 observations, including 3 with an unknown sex, 7 males, and 3 females), and White-throated Mountain-gems (*Lampornis castaneoventris*; N = 15 observations, all females). The Purple-crowned Fairy was only observed feeding twice within the same observation period, whereas all other species were observed multiple times in different locations. No quantitative observations were made on Purple-crowned Fairies.

When hummingbirds approached the trees, they usually visited multiple fruit clusters before selecting one to feed upon. By either perching or hovering, they pierced the fruit with their bill, sometimes retracting and reinserting their bill multiple times in the same hole (Figure 2). On some occasions, fruit pulp was attached when the birds retracted their bill. This process was often repeated within a single visit to a tree; in some cases, birds perched between feeding events.

The total duration (mean ± SD) of feeding visits, excluding time spent perching, was highly variable: Stripe-tailed Hummingbird (49.73 ± 30.05 s, range = 9 – 108 s, N = 15),

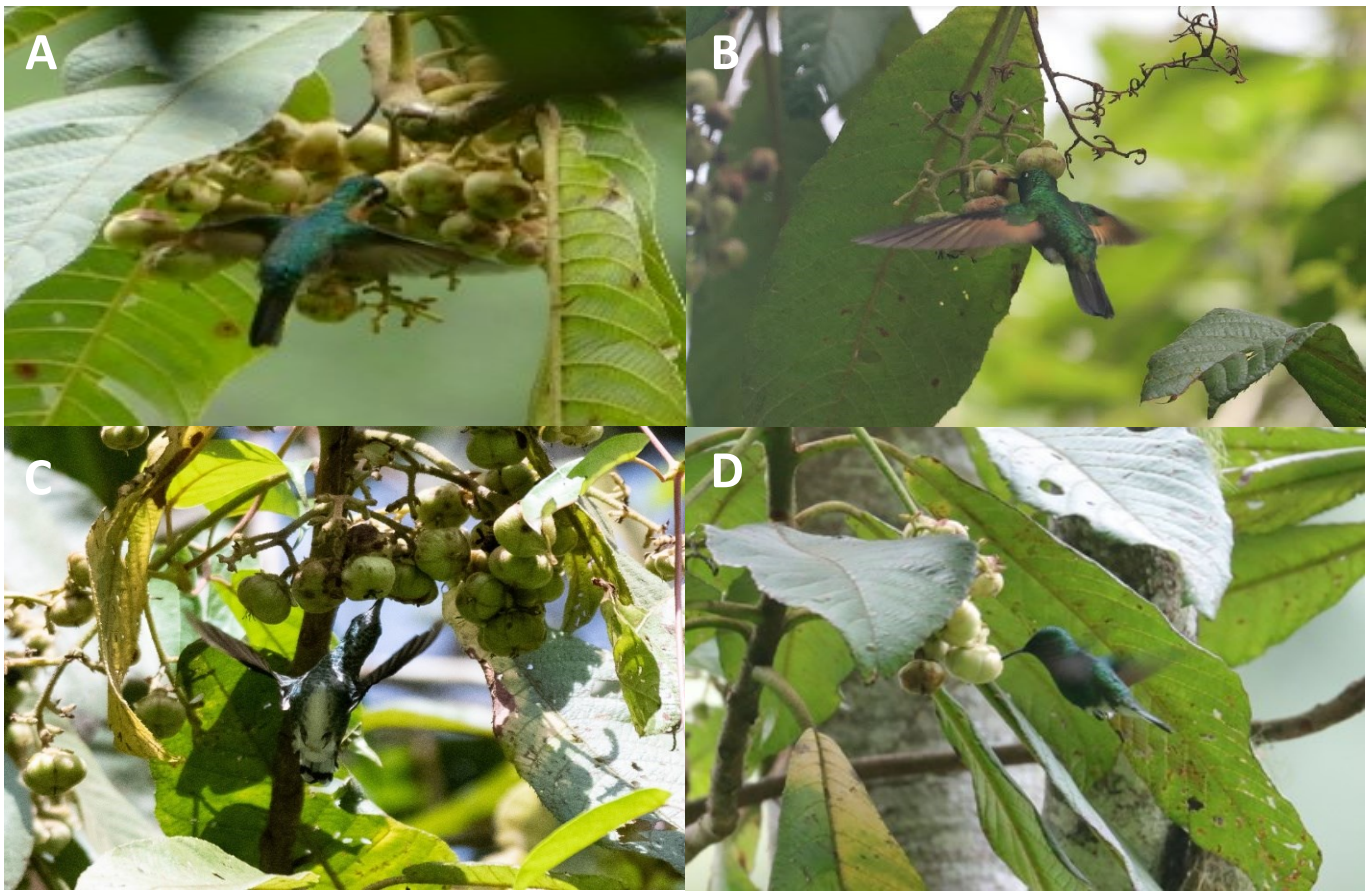

Figure 2. Piercing and consuming of *S. montana* fruit by three hummingbird species in Cloudbridge Nature Reserve, Pérez Zeledón, Costa Rica: (A) White-throated Mountain-gem (*L. castaneoventris),* (B) Stripe-tailed Hummingbird (*E. eximia*), (C) and (D) White-tailed Emerald (*E. chionura*). Photographs by Fabian Kull (A), Jonathan Slifkin (B and D), and Ryan Andrews (C).

White-tailed Emerald (37.50 ± 34.02 s, range = 15 – 88 s, N = 4), and White-throated Mountain-gem (48.50 ± 26.56 s, range 19 – 69 s, N = 3). The mean time spent feeding on individual fruit was: Stripe-tailed Hummingbird (9.83 ± 8.81 s, range = 5 – 20 s, N = 3), White-tailed Emerald (9.0 ± 3.92 s, range = 5 – 13 s, N = 5), and White-throated Mountain-gem (8.81 ± 11.99 s, range = 2 – 36 s, N = 8). These data for time spent feeding on individual fruits may slightly overestimate the lower bound values due to the difficulty in detecting visits shorter than a few seconds.

The Stripe-tailed Hummingbird is a common and widespread hummingbird within the Cloudbridge Nature Reserve. A common source of nectar for Stripe-tailed Hummingbirds is the shrub *Gonzalagunia rosea* (Rubiaceae) (H. Elliott & C. Smith, pers. obs.). At one location in May 2019, *G. rosea* grew alongside two *S. montana* trees, which at the time had abundant fruit. During multiple days of observation, Stripe-tailed Hummingbirds visited and fed on the *S. montana* fruits, but never fed upon *G. rosea.*

During our observations, we also watched five other vertebrates (two mammals and three birds) feeding upon *S. montana* fruits. These were the Common Chlorospingus (*Chlorospingus flavopectus*), the Yellow-thighed Finch (*Pselliophorus tibialis*), the Golden-browed Chlorophonia (*Chlorophonia callophrys*), the White-faced Capuchin (*Cebus imitator*) and the White-nosed Coati (*Nasua narica*). However, these species combined represented only 7.7% of the observed feeding events on *S. montana*. The remaining 92.3% of the frugivory events were by hummingbirds. Scintillant Hummingbirds (*Selasphorus scintilla*) were frequently observed near *S. montana* trees, but showed no apparent interest in their fruits.

DISCUSSION

To our knowledge, there is no prior evidence of frugivory in any of the four hummingbird species reported here. Furthermore, these are some of the few hummingbird species reported to feed on fruits other than Cactaceae (Palacio 2019). In Mexico, four hummingbird species were observed feeding on the nectar of *Saurauia scabrida* (Partida-Lara et al. 2018). The authors reported to us (R. Partida-Lara, pers. comm.) that one of those species, the Green-throated Mountain-gem (*Lampornis viridipallens*, a congener of one of the species we observed), also fed upon *S. scabrida* fruits during the rainy season when fewer plants were flowering, thus suggesting that frugivory may be necessary during times of reduced nectar availability. However, our observations do not support this interpretation, as Stripe-tailed Hummingbirds were observed feeding on *S. montana* fruits even in the presence of flowering *G. rosea*. Scintillant Hummingbirds were often seen as well feeding from the *G. rosea* flowers, confirming that those flowers were providing nectar. Stripe-tailed Hummingbirds are dominant to Scintillant Hummingbirds, which suggests that Stripe-tailed Hummingbirds prefer *S. montana* fruits and were not excluded from the nectar-producing *G. rosea* flowers.

In Mexico, Green-throated Mountain-gems defend *S. scabrida* plants against intruders (R. Partida-Lara, pers. comm.). This behavior was also observed in Brazil, with male

Blue-chinned Sapphires (*Chlorestes notata*) defending *Mutingia calabura* fruits against conspecifics (Ruschi 2014). We observed no obvious territories around *S. montana*. The hummingbirds we observed showed behavior consistent with 'traplining,' as they would disappear from view for several minutes before another bird would arrive to feed (Feinsinger & Colwell 1978), but this cannot be confirmed without individually marking birds. We occasionally observed aggressive behaviors, particularly by female White-throated Mountain-gems, when two individuals came to feed at the same time.

Hummingbirds are not likely to be important pollinators of *Saurauia*; their petals are white or rarely pink (Soejarto 1969) and they lack the characteristic ornitholophilous flowers (Partida-Lara et al. 2018). Previous authors have noted that bees, including *Melipona* and *Bombus*, are frequent visitors to *Saurauia* flowers in Costa Rica (Haber & Bawa 1984, Cane 1993). Whether *S. montana* flowers provide nectar for hummingbirds is unknown. During our observations at Cloudbridge, the fruiting *S. montana* trees had no flowers, and no flowers were noted on any other *Saurauia* species.

Notwithstanding our observations, bats are more significant frugivores on *Saurauia* fruits than are hummingbirds. In a similar cloud forest habitat, the Monteverde Cloud Forest Reserve in the Tilarán range of Costa Rica (10° 25' N, 84° 50' W; 1500–-1640 m a.s.l.), Dinerstein (1986) noted seeds from *Saurauia veraguensis* in the feces of the highland Yellow-shouldered Bat, *Sturnina ludovici*. Bats accounted for an estimated 76% of the seed dispersal for *S. yasicae* in pastures near the lowland rain forest in Veracruz, Mexico (Galindo-González et al. 2000). In a review, Castaño et al. (2018) reported that at least nine species of bats (particularly *Carollia* and *Glossophaga* spp.) fed on the fruits of at least eight *Saurauia* species throughout mid and upper elevations in the Neotropics. The fruits of *Saurauia* are usually green, even when ripe (Soejarto 1969; see also Figure 2), which is more consistent with bat-dispersed fruits than bird-dispersed fruits (Dinerstein 1986).

We do not know whether hummingbird frugivory affects the dispersal of *Saurauia montana* seeds. By piercing the fruit and removing the juice and pulp, hummingbirds may decrease the quality of fruit for bats, the more effective dispersers of *Saurauia* seeds; this may be particularly problematic for *Carollia* and *Glossophaga* bats, which rely more heavily on *Saurauia* fruit (Castaño et al. 2018). Given the mucilaginous consistency of the pulp and the relatively small detached seeds, some of them might be ingested or stick to the retracting bill, giving hummingbirds the potential to act as minor seed dispersers. However, further observational and experimental (e.g. effect of gut passage on seed germination) work is necessary to determine their role as seed dispersers. Some *Saurauia* species are indicators of mature or old-growth forests (Muñiz-Castro et al. 2012, Toledo-Aceves et al. 2014) and *Saurauia montana* has been found to be linked to regenerating cloud forests, mostly on old pasture land (Loik & Holl 2001, Holl 2002, Myster 2008). Thus, hummingbird frugivory on this species may play a role in forest recovery, but this cannot be confirmed without further investigation.

It is unclear how much frugivory on *S. montana* contributes to the diet of these species, but it may provide an important supplement during fruiting periods for female hummingbirds in general and, particularly, for Stripe-tailed Hummingbirds. The effect of hummingbird frugivory on *S. montana* or its bat dispersers is also unknown. Our observations, along with those of Partida-Lara et al. (2018) from Mexico, suggest that hummingbird frugivory on *Saurauia* may be widespread in Neotropical cloud forests, though its ecological significance is poorly understood.

ACKNOWLEDGMENTS

We would like to thank Ryan Helcoski and Jennifer Powell for their comments and guidance throughout this study, and Jonathan Slifkin, Ryan Andrews, and Fabian Kull for assistance in the field and for the excellent photographs. We also thank the Herbario Nacional de Costa Rica for their assistance with plant identification, and the Departamento de Hidrología del Instituto Costarricense de Acueductos y Alcantarillados for the weather data.

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