SHORT COMMUNICATION

Biting the hand that feeds you: wedge-billed hummingbird is a nectar robber of a sicklebill-adapted Andean bellflower

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ABSTRACT

I report on nectar robbing behavior of the wedge-billed hummingbird, Schistes geoffroyi (Trochilidae) on the Andean bellflower, Centropogon granulosus (Campanulaceae). Many species of Centropogon are characterized by an abruptly curved corolla tube which is likely specialized for pollination by sicklebill hummingbirds (Eutoxeres), as evident from the matching curvature of flower and bill. Nectar robbing has been documented for some Centropogon spp., but not for sicklebill pollinated C. granulosus. Given recent developments and interest in the Centropogon-sicklebill mutualism, it is pertinent to document any natural history observations that may underlie the ecology and evolution of this pollination system. The establishment of wedge-billed hummingbird as a nectar robber of C. granulosus calls for a new assessment of the ecology and evolution of the highly specialized Centropogon-sicklebill mutualism.

KEYWORDS: nectar robbing, bird pollination, neotropical bellflowers, Schistes geoffroyi, co-evolution

Muerde la mano que le da de comer: Colibrí pico cuña es ladrón de néctar de Centropogon granulosus (Campanulaceae)

RESUMEN

Informo sobre el comportamiento de robo de néctar del colibrí pico cuña, Schistes geoffroyi (Trochilidae) en la flor campanulada neotropical, Centropogon granulosus (Campanulaceae). Muchas especies de Centropogon se caracterizan por tener una flor tubular curvada de distintas formas y probablemente especializadas para ser polinizadas por los colíbiris de pico curvo (Eutoxeres), como es evidente a partir de la curvatura tanto de la flor como del pico. Debido a la exclusividad de este mutualismo, el robo de néctar ha sido ocasionalmente documentado en Centropogon. Aquí amplío el estudio de robo de néctar de Centropogon incluyendo a Schistes geoffroyi. Esta expansión puede ser un indicador de la alta especialización entre el mutualismo de Centropogon y el colibrí de pico curvo, siendo esta más susceptible al robo de néctar de lo que se pensaba previamente. Esto genera preguntas acerca de la evolución de la especialización y parasitismo en este grupo tropical, tanto de las campanuladas como de los colíbiris.

PALABRAS-CLAVE: polinización por aves, campanulada neotropical, Schistes geoffroyi, coevolución

The Andean bellflowers *Centropogon* C. Presl (Campanulaceae) are widespread, but especially conspicuous in the montane rainforests of the eastern Andes, with certain species notable for their hook-shaped corolla, ranging from bright pink to red and orange in colour. While *Centropogon* contains over 200 species (Lagomarsino et al. 2014) occurring from Central America and throughout equatorial South America, it is epitomized by *Centropogon granulosus* C. Presl (Figure 1). *Centropogon granulosus* are readily found in treefall gaps, roadsides, and other forest edges in San Pedro, Peru - the area of interest to this study. *Centropogon granulosus* has long thought to be pollinated by sicklebill hummingbirds (*Eutoxeres* Bourcier, Phaethornithinae Jardine) a genus of two hummingbird species characterized by bills equally dramatic in their curvature (Stein 1992). Although nectar robbing has been occasionally documented in *Centropogon*, the only reports of nectar robbing in a curved-flower *Centropogon* sp. are of *Phaethornis squalidus* Temminck and *Glauis hirsutus* Gmelin (Muruyama et al. 2015) – two hermit hummingbirds (Phaethornithinae) with relatively long and curved bills.

During a pollination study of *Centropogon granulosus*, I recorded nectar robbing by the wedge-billed hummingbird (*Schistes geoffroyi* Bourcier, Trochilinae Jardine). The study site is located in Paucartambo Province, on the eastern slopes of the Peruvian Andes. This site is locally known as ‘San Pedro’ (approximately 13° 3’ 21.0564” S, 71° 32’ 46.9133” W, and 1300 m.a.s.l.) and is about 60 km north-east of the city of Cusco. Eight camera traps were deployed for two months of daily monitoring within 4:00 to 20:00. Camera traps were moved to previously unmonitored *Centropogon granulosus* patches every seven days. *Eutoxeres condamini* Bourcier was the only other vertebrate visitor to *Centropogon granulosus*.

On September 2\textsuperscript{nd}, 2017, at 14:57 PET a *Schistes geoffroyi* individual approached an inflorescence of *Centropogon granulosus* and inserted its bill into the base of the flowers, instead of entering at the opening of the corolla (Figure 1). It then proceeded systematically to visit nearby *Centropogon granulosus* inflorescences, exhibiting the same behavior. Following the bird’s departure, inspection of the flowers revealed fresh punctures at the base of the corollas (Figure 2). It is presumed these punctures were made by *Schistes geoffroyi* because no other nectar robbers were recorded in camera traps, and typical flower-piercing species (e.g. *Diglosa* Wagler) do not occur at this elevation in this region (Jankowski et al. 2013). Nectar concentration was measured from four flowers that had recently undergone anthesis, using an ATC handheld Brix refractometer. The mean nectar sugar concentration was found to be 24.9 ± 1.3% (95% C.I., n=4); this is typical of sugar concentrations found in other bird pollinated plant taxa (Bolten and Feinsinger 1978). Four video recordings of nectar robbery of *Centropogon granulosus* by wedge-billed hummingbird were made over the month of September, and numerous other instances were documented without video. Recordings are available at https://vimeo.com/manfred (contact author for additional footage). Patches of *Centropogon granulosus* with at least one documented visit were very likely to have further visits by wedge-billed hummingbirds, suggesting territory holding behavior. As no birds were marked or had distinguishing individual features, it is unclear whether the observed visits were made by the same or separate individuals.

The diet of *Schistes geoffroyi* is composed of both arthropods (Remsen et al. 1986), and nectar that is primarily obtained from piercing flowers (Walthier and Brieschke 2001; Hilty 2003). Generally, hummingbirds are thought to acquire nectar as legitimate pollinators, however, an increasing number of cases demonstrate the contrary. Fiery-throated hummingbirds (*Panterpe insignis* Cabanis & Heine) have been reported to follow passerine flower piercers in order to drink from the holes made in robbed flowers (Stiles 1983), volcano hummingbirds (*Selasphorus flammula* Salvin) pierce or use holes in *Centropogon* made by slaty flowerpiercers (*Diglosa plumbea* Cabanis) (Henderson 2002), and reddish hermit (*Phaethornis ruber* L.) engages in some form of floral larceny in nearly a third of the plant species it visits (Muruyama et al. 2015). Hilty (2003) describes the wedge-billed hummingbird as a ‘notorious nectar thief’, visiting *Fuchsia* L., *Cavendishia* Lindl., *Palicourea* Aubl., and *Centropogon*, etc.
although species-level descriptions are absent. Additionally, there is evidence that, in general, short-billed hummingbirds are more likely to be nectar robbers of long corolla tubes that have coadapted to long-billed hummingbirds (Feinsinger et al. 1987, Lara and Ornelas, 2001). An analysis of bill measurement data collected from ongoing mist netting efforts in San Pedro reveal Schistes geoffroyi to have the second shortest bill of the 24 hummingbirds found in the region (M. Scholer, unpublished data). Given its tendency to pierce flowers (Walther and Brieschke 2001; Hilty 2003), and serrated upper-bill (Ornelas 1994), wedge-billed hummingbird appears to be a species especially adapted to nectar robbing.

A notable trait of Centropogon and other neotropical Campanulaceae is the secretion of a milky white latex from damaged tissues, including floral tissue, which over an hour turns brown or black as it dries. This latex is irritating to the touch and may be an adaptation to deter herbivory (Mabberley 1975). Whether the latex of all Campanulaceae is an adaptation to deter herbivory remains unknown; nonetheless the above observations suggest that Schistes geoffroyi is not deterred or severely affected by the presence of latex in Centropogon granulosus.

Several Centropogon spp. are widely presumed to be adapted for pollination by sicklebill hummingbirds because the curvature of the bird’s bill appears to fit the hook-shaped flowers like a ‘lock and key’ (Stein 1992). Further evidence supporting hummingbird pollination can be found in the method of pollen dispersal: the floral trichomes of Centropogon granulosus are fused into a scale that covers the anthers. When the scale is pushed back pressurized pollen is released. This trap door mechanism ensures effective placement of the pollen on to the head of a visiting bird (likely Eutoxeres; Stein 1992) and protects the pollen from insects unable to open the scale. Two days following the opening of the flower, the stigma extends past the scale, temporally separating the male and female phase of the flower, and allowing pollen to be deposited from bird to plant.

Despite the compelling, morphological and phenological evidence, it remains that little documentation of sicklebills visiting Centropogon exist, though accounts of nectar robbing in Centropogon have been documented (Table 1). If in fact Centropogon granulosus is pollinated by Eutoxeres, there are potential evolutionary and ecological implications of nectar robbing for both species, including decreased nectar quality

Table 1. Documented or proposed hummingbird visitors to Centropogon.

<table>
<thead>
<tr>
<th>Centropogon species</th>
<th>Flower shape</th>
<th>Visitor Type</th>
<th>Visitor</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Centropogon valerii</td>
<td>Long, slightly curved</td>
<td>Pollinator</td>
<td>Colibri thalassinus</td>
<td>Colwell et al. 1974</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Eugenes fulgens</td>
<td>Colwell et al. 1973</td>
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<td></td>
<td></td>
<td></td>
<td>Panterpe insignis</td>
<td>Colwell et al. 1973</td>
</tr>
<tr>
<td>Centropogon granulosus</td>
<td>Medium length, very curved</td>
<td>Pollinator</td>
<td>Eutoxeres spp.</td>
<td>Stein 1992</td>
</tr>
<tr>
<td>Centropogon baeanus</td>
<td>Medium length, very curved</td>
<td>Pollinator</td>
<td>Eutoxeres spp.</td>
<td>Stein 1987</td>
</tr>
<tr>
<td>Centropogon talamancensis</td>
<td>Long, straight</td>
<td>Pollinator</td>
<td>Eugenes fulgens</td>
<td>Wolf et al. 1976</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Panterpe insignis</td>
<td>Colwell et al. 1973</td>
</tr>
<tr>
<td>Centropogon femugineus</td>
<td>Medium length, curved</td>
<td>Pollinator</td>
<td>Lafresnaya lafresnayi</td>
<td>Toloza-Moreno et al. 2015</td>
</tr>
<tr>
<td>Centropogon costanicae</td>
<td>Long, slightly curved</td>
<td>Pollinator</td>
<td>Trochilidae (species not indicated)</td>
<td>Fenster 1991</td>
</tr>
<tr>
<td>Centropogon cornutus</td>
<td>Medium length, very curved</td>
<td>Pollinator</td>
<td>Ramphodon naevius</td>
<td>Buzato et al. 2000</td>
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<td></td>
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<td>Phaethornis eurynome</td>
<td>Buzato et al. 2000</td>
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<td></td>
<td>Phaethornis squalidus</td>
<td>Maruyama et al. 2015</td>
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<tr>
<td></td>
<td></td>
<td>Nectar robber (mode not specified)</td>
<td>Maruyama et al. 2015</td>
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<td></td>
<td></td>
<td></td>
<td>Glaucis hirsutus</td>
<td>Maruyama et al. 2015</td>
</tr>
<tr>
<td>Centropogon NA</td>
<td></td>
<td>Nectar robber (1º)</td>
<td>Schistes geoffroyi</td>
<td>Hilty 2003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nectar robber (1º and 2º)</td>
<td>Panterpe insignis</td>
<td>Henderson 2002</td>
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<tr>
<td></td>
<td></td>
<td>Nectar robber (2º)</td>
<td>Selesaphorus flamula</td>
<td>Henderson 2002</td>
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<td></td>
<td></td>
<td>Not specified</td>
<td>Colibri thalassinus</td>
<td>Henderson 2002</td>
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<td></td>
<td></td>
<td>Pollinator</td>
<td>Lampornis castaneoventris</td>
<td>Not specified</td>
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<td>Pollinator</td>
<td>Phaethornis guy</td>
<td>Snow and Snow 1972</td>
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<td>Pollinator</td>
<td>Glaucis hirsutus</td>
<td>Snow and Snow 1972</td>
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and quantity, lower seed set, and modified pollinator behavior (Colwell et al. 1974; Travest et al. 1998; Kjonaas and Rengifo 2006; Hazlehurst and Karubian 2016). In the latter case, nectar robbing may decrease the per-flower reward for legitimate pollinators, leading to increased flight distance to fulfill their energetic needs, ultimately promoting outcrossing (Hazlehurst and Karubian 2016). While nectar robbing is well studied (reviewed in Irwin et al. 2010), it remains unknown whether plant-bird specializations are the cause or result of cheating (by either birds or invertebrates). An analysis of divergence times indicates that *Eutoxeres* existed for nearly 20 million years before the emergence of the eucentropogonids (*sensu* Lagomarsino et al. 2014), and that curvature is an adaptation that first co-evolved with Heliconia (Abrahamczyk et al. 2017). However, it is unclear whether curvature (and therefore specialization) evolved to ensure pollination in a *Centropogon* sp. experiencing a high degree of nectar thievery (*sensu* Irwin et al. 2010), or whether the evolution of curvature has triggered nectar robbing among those hummingbirds that are now excluded from entering the corolla tube from the opening. In light of this, I posit that nectar robbing in sicklebill-pollinated *Centropogon* could be more widespread than is currently realized, and future studies will benefit from a focus on the effects of nectar robbing on reproductive fitness in *Centropogon*.

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**REFERENCES**


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