

BRIEF REPORTS

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 granulatus* (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. granulatus*. 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. granulatus* 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 el ladrón de néctar de *Centropogon granulatus* (Campanulaceae)

RESUMEN

Informo sobre el comportamiento de robo de néctar del colibrí pico cuña (*Schistes geoffroyi* Trochilidae) en la flor campanulada neotropical *Centropogon granulatus* (Campanulaceae). Muchas especies de *Centropogon* se caracterizan por tener una flor tubular curvada de distintas formas y probablemente especializadas para ser polinizadas por los colibríes 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 amplió 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 previamente pensado. Esto genera preguntas acerca la evolución de la especialización y parasitismo en este grupo tropical tanto de las campanuladas como de los colibríes.

PALABRAS-CLAVE: ladrón de néctar, 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 granulatus* C. Presl (Figure 1). *Centropogon granulatus* are readily found in treefall gaps, roadsides, and other forest edges in San Pedro, Peru - the area of interest to this study. *Centropogon granulatus* 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 *Glaucis hirsutus* Gmelin (Muruyama *et al.* 2015) – two hermit hummingbirds (Phaethornithinae) with relatively long and curved bills.

During a pollination study of *Centropogon granulatus*, 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 granulatus* patches every seven days. *Eutoxeres condamini* Bourcier was the only other vertebrate visitor to *Centropogon granulatus*.

On September 2nd, 2017, at 14:57 PET a *Schistes geoffroyi* individual approached an inflorescence of *Centropogon granulatus* 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 granulatus* 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. *Diglossa* 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 $24.9 \pm 1.3\%$ (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 granulatus* 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/mannfred> (contact author for additional footage). Patches of *Centropogon granulatus* 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 (Walther 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 (*Diglossa 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*,



Figure 1. *Schistes geoffroyi* probing the base of the corolla of *Centropogon granulatus*. Taken at San Pedro, outside of the Manú National Park, Peru. This figure is in colour in the electronic version.



Figure 2. Latex exuding from the base of a corolla of *Centropogon granulatus* following a visit from *Schistes geoffroyi*. This figure is in colour in the electronic version.

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 granulatus*.

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 granulatus* 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 granulatus* 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*

<i>Centropogon</i> species	Flower shape	Visitor	Visitor Type	Reference
<i>Centropogon valerii</i>	Long, slightly curved	<i>Colibri thalassinus</i>	Pollinator	Colwell <i>et al.</i> 1974
		<i>Eugenes fulgens</i>	Pollinator	Colwell <i>et al.</i> 1973
		<i>Panterpe insignis</i>	Pollinator	Colwell <i>et al.</i> 1973
<i>Centropogon granulatus</i>	Medium length, very curved	<i>Eutoxeres</i> spp.	Pollinator	Stein 1992
<i>Centropogon baezanus</i>	Medium length, very curved	<i>Eutoxeres</i> spp.	Pollinator	Stein 1987
<i>Centropogon talamancensis</i>	Long, straight	<i>Eugenes fulgens</i>	Pollinator	Wolf <i>et al.</i> 1976
		<i>Panterpe insignis</i>	Nectar robber (1°)	Colwell <i>et al.</i> 1973
<i>Centropogon ferrugineus</i>	Medium length, curved	<i>Lafresnaya lafresnayi</i>	Pollinator	Tolozza-Moreno <i>et al.</i> 2015
<i>Centropogon costaricae</i>	Long, slightly curved	<i>Trochilidae</i> (species not indicated)	Pollinator	Fenster 1991
<i>Centropogon cornutus</i>	Medium length, very curved	<i>Ramphodon naevius</i>	Pollinator	Buzato <i>et al.</i> 2000
		<i>Phaethornis eurynome</i>	Pollinator	Buzato <i>et al.</i> , 2000
		<i>Phaethornis squalidus</i>	Nectar robber (mode not specified)	Maruyama <i>et al.</i> 2015
		<i>Glaucis hirsutus</i>	Nectar robber (mode not specified)	Maruyama <i>et al.</i> 2015
<i>Centropogon</i>	NA	<i>Schistes geoffroyi</i>	Nectar robber (1°)	Hilty 2003
		<i>Panterpe insignis</i>	Nectar robber (1° and 2°)	Henderson 2002
		<i>Selasphorus flammula</i>	Nectar robber (2°)	Henderson 2002
		<i>Colibri thalassinus</i>	Not specified	Henderson 2002
		<i>Lampornis castaneiventris</i>	Not specified	Henderson 2002
		<i>Phaethornis guy</i>	Pollinator	Snow and Snow 1972
		<i>Glaucis hirsutus</i>	Pollinator	Snow and Snow 1972

and quantity, lower seed set, and modified pollinator behavior (Colwell *et al.* 1974; Traveset *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 fulfil 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*.

ACKNOWLEDGEMENTS

I would like to thank Micah N. Scholer, Julian Heavyside, Jeremiah J.C. Kennedy, David Guevara Apaza, Elizabeth Llacta Cuno, Quentin C.B. Cronk, Jill E. Jankowski, and the four anonymous reviewers for their helpful comments in improving this manuscript. This expedition was made possible by funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants to Quentin Cronk (RGPIN-2014-05820) and Jill Jankowski at the University of British Columbia (RGPIN-2012-418294), a Walter H. Lewis Award in Plant Biodiversity from the UBC Herbarium, and the expert advice from the staff of Universidad Nacional Agraria la Molina, Universidad Nacional San Antonio Abad del Cusco, and Perú Verde.

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RECEIVED: 15/11/2017

ACCEPTED: 18/01/2018

ASSOCIATE EDITOR: Sérgio Henrique Borges



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