



RESEARCH NOTE

Long corolla flowers in Tropical Andes favour nectar robbing by the Black Metaltail hummingbird: A study using citizen science and field observations

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Abstract

Understanding what drives the evolution of nectar-robbing strategies is key for gaining insight into the functioning of pollination networks. However, nectar robbing is often an anecdotal behaviour, difficult to quantify and record through field observations, especially in hummingbirds, limiting our understanding of how ecological networks change across communities. Here, we report new records of nectar robbing by Peru's endemic Black Metaltail (*Metallura phoebe*) in a high-elevation forest at ca. 4000 m a.s.l. and how this species uses either legitimate pollination feeding or nectar robbing in relation to corolla lengths. Furthermore, by analysing 452 citizen science records of photographic observations, we found that 36% of the photographs depicting a foraging event in this species were actually nectar-robbing events. After identifying the plant species in all photographs involving foraging events, we describe how nectar robbing conducted by this hummingbird species is strongly associated with flowers that have longer corollas. We propose that the hummingbird-flower interactions in harsh high-altitude environments, where resources and competition vary markedly across seasons, can offer insight into the ecological drivers of nectar-robbing behaviour in hummingbirds.

KEYWORDS

Black Metaltail, eBird, foraging flexibility, iNaturalist, nectar robbing, pollination networks, *Polylepis*, *Salpichroa*

INTRODUCTION

Food-rewarding plants that have coevolved in mutualistic interactions with pollinators are vulnerable to exploitation by floral thieves and robbers (Inouye, 1980). Nectar robbing exemplifies this phenomenon, where certain insects, birds, and mammals obtain nectar by piercing flowers (primary robbers) or utilizing existing holes created by other individuals (secondary robbers) (Anselmo et al., 2023; Inouye, 1980). Hence, nectar robbers bypass the anthers and stigma to gain direct access to the nectary, avoiding pollination. Nectar robbing mainly modifies the flower morphology, which might result in deterring legitimate pollinators (Varma et al., 2020), and increasing self-pollination (Hou et al., 2021). The effects

of nectar robbers on plant fitness, coupled with indirect impacts on other organisms, give rise to significant ecological and evolutionary implications within ecological networks (Cuta-Pineda et al., 2021; Irwin et al., 2010; Varma et al., 2020). As a result, nectar robbing remains a subject of substantial scientific interest, with a growing number of documented records across taxa (Deng et al., 2004; Igić, Nguyen & Fenberg, 2020; Marks et al., 2023; Raju, Kumar, et al., 2022; Raju, Raju, et al., 2022; Telleria et al., 2023; Walsh et al., 2022).

Among birds, hummingbirds are known for their ability to switch between legitimate pollination and nectar robbing opportunistically (Irwin et al., 2010). Specifically, among hummingbirds, engaging in nectar robbing is often associated with having shorter bills (Colwell et al., 2023). Short-billed species typically have longer feet, particularly the hallux, which aids in their ability to cling to surfaces compared to their long-billed counterparts. This adaptation might favour both nectar-robbing behaviour and legitimate visits (Colwell et al., 2023). Additionally, short-billed hummingbirds tend to exhibit specialized bill shapes, including serrated edges, hooks, and exceptionally sharp tips, potentially facilitating their ability to pierce flowers (Ornelas, 1994). These morphological traits likely evolved as adaptations or exaptations for nectar robbing, driven by the challenge of accessing nectar from flowers with long corollas (Colwell et al., 2023).

There is evidence indicating that corolla length and flower abundance influence nectar robbing in tropical plant communities (Rojas-Nossa, 2007, 2013), and that flowers with longer corolla lengths might favour nectar robbing in at least some hummingbird species (Lara & Ornelas, 2001). However, there remains an overall scarcity of data on the prevalence of nectar robbing in hummingbirds (Marks et al., 2023). Understanding how nectar robbing relates to plant and flower characteristics is crucial for determining the factors driving ecological interactions between plants and animals.

Here, we present novel observations of nectar robbing by the Black Metaltail hummingbird (*Metallura phoebe*) in a high-elevation forest (3800–4300 m a.s.l.) in the Peruvian Tropical Andes. We used this opportunity to gain insights into the prevalence of nectar-robbing behaviour in the short-billed Andean Black Metaltail and explore whether this behaviour is affected by the length of the flower corollas. For that, we analysed photographic records from citizen science databases, identifying all the plant species to examine how foraging strategies are associated with flower species and corolla length. Specifically, we predict that longer corolla flowers may promote nectar-robbing behaviour because short-billed hummingbirds cannot efficiently extract nectar through legitimate visits (Lara & Ornelas, 2001; Maruyama et al., 2015).

METHODS

Field observations of foraging strategies in the Black Metaltail

The Black Metaltail is a hummingbird species endemic to Peru in the tribe *Lesbiini*, within the subfamily *Lesbiinae* (Høgsås et al., 2002). It inhabits the western slope of the Andes, with an elevation range between 1500 and 4500 m a.s.l., predominantly above 2700 m a.s.l. (Heindl et al., 2021). Whilst its usual distribution area overlaps with other hummingbird species, specifically, during our data collection it was found in sympatry with the Giant Hummingbird *Patagona gigas* sensu lato and the Black-breasted Hillstar

Oreotrochilus melanogaster (Heindl et al., 2021; Medrano et al., 2022). However, this last species was only observed once and not during a feeding event. On the contrary, the Black Metaltail and the Giant Hummingbird were repeatedly observed feeding on the same plant species.

We observed the foraging behaviour of the Black Metaltail in a high-altitude forest (3800–4300 m a.s.l.) of *Polylepis pilosissima* (family Rosaceae), in the district of Laraos, within the Yauyos province of Peru (Sinchimarka Forest; -12.396750° , -75.816910°). The forest experiences seasonal variation in precipitation regimes, with rainfall usually concentrated between December and April (peaks in February and March), and annual precipitation varying from 500 to 1000 mm (INRENA, 2006). Our observations occurred at the end of the dry season. After the first anecdotal nectar robbing event, one observer, equipped with binoculars, sat in front of one of the three *Polylepis* trees with the most abundant *Salpichroa glandulosa* flowers in our study area, where the two hummingbird species had previously been observed feeding. He recorded all the foraging events occurring both in *S. glandulosa* and adjacent flowers, consisting of mistle-toes species of the genus *Tristerix*. The observation times were chosen at random throughout the day between 08:00 and 17:00 hours. Observations started on 29-10-2022 and stopped on 4-11-2022, with a total effort of 840 minutes along these dates.

Feeding behaviour in the Black Metaltail hummingbird on citizen science platforms

To understand the prevalence of nectar-robbing behaviour in the Black Metaltail, we reviewed citizen science platforms looking for all the Black Metaltail pictures uploaded until 4th October 2023 from [eBird.org](https://ebird.org) and iNaturalist.org searching for photographs by the scientific name of the species under pictures explorer. We ensured the correct identification of the species and considered a record as independent when the picture was made by a different observer at different locations or taken at different dates and times. Additionally, we cross-checked pictures from both platforms to avoid counting the same record twice due to users who upload pictures to both platforms. We distinguished pictures in which individuals were depicted foraging: clinging next to a flower, flying close to a flower in feeding behaviour, head within a flower or accessing the flowers from the side (nectar robbing), from those exhibiting other behaviours (just perched or flying). From the pictures classified as foraging, we analysed whether the foraging event on flowers could be classified as 'nectar robbing', 'not nectar robbing', or 'ambiguous foraging'. A clear nectar robbing event was considered if the bird was portrayed introducing the beak at the base of the corolla and not through the front of the flower.

To assess whether average corolla length influenced the foraging strategy (nectar robbing vs legitimate feeding) of the Black Metaltail, we first identified plant species and extracted corolla length measurement from specialized literature (Table 1). We subsequently conducted a one-sided t-test on the mean corolla length ranges of all identified species (Table 1), including our on-site observations for *Salpichroa glandulosa* (family Solanaceae). However, we excluded the *Tristerix* species on which legitimate feeding events were observed from the t-test because we were uncertain whether the flowers involved were *Tristerix chodatianus* or *T. longebracteatus*, as they were too high in the tree to collect for identification. In total, we identified 5 plant species for nectar robbing (four from citizen science platforms and one from our own observation) and 12 plant species for legitimate feeding (all from citizen science platforms).

TABLE 1 List of pictures reporting Black Metaltails' nectar robbing and legitimate feeding events in citizen science platforms with associated corolla lengths and the references used to extract length measurements.

Plant species	Corolla length (mm)	Platform	Observation & picture ID	References
Nectar robbing				
<i>Cantua buxifolia</i>	55–80	eBird	1. https://macaulaylibrary.org/asset/365628001 2. https://macaulaylibrary.org/asset/365617981 ; https://macaulaylibrary.org/asset/365617941 3. https://macaulaylibrary.org/asset/85153421 4. https://macaulaylibrary.org/asset/79585151	Gibson (1967)
		iNaturalist	5. https://www.inaturalist.org/observations/130793285	
<i>Cantua candelilla</i>	50–80	eBird	6. https://macaulaylibrary.org/asset/569575301	Gibson (1967)
<i>Passiflora trifoliata</i>	55–75 ^a	eBird & iNaturalist	7. https://macaulaylibrary.org/asset/468198491 ; https://www.inaturalist.org/observations/126888945	Killip (1938)
		eBird	8. https://macaulaylibrary.org/asset/258647901	
<i>Salvia dombeyi</i>	60–90	eBird	9. https://macaulaylibrary.org/asset/503125831	Macbride (1960)
Legitimate feeding				
<i>Barnadesia dombeyana</i>	12–21	eBird	1. https://macaulaylibrary.org/asset/478007541 ; https://macaulaylibrary.org/asset/478007441 2. https://macaulaylibrary.org/asset/448073501	Ferreyra (1964)
<i>Bomarea rosea</i>	25–30	eBird	3. https://macaulaylibrary.org/asset/145563631	Hofreiter and Rodríguez (2006)
<i>Chuquiraga rotundifolia</i>	19–22	eBird	4. https://macaulaylibrary.org/asset/93076051	Tovar (1952)
<i>Dunalia spinosa</i>	25–40	eBird	5. https://macaulaylibrary.org/asset/469917651 6. https://macaulaylibrary.org/asset/414557281 ; https://macaulaylibrary.org/asset/414557291 7. https://macaulaylibrary.org/asset/206173481	Macbride (1962)
<i>Echeveria excelsa</i>	16–20	eBird	8. https://macaulaylibrary.org/asset/366067401 ; https://macaulaylibrary.org/asset/366067391 ; https://macaulaylibrary.org/asset/366067341	Macbride (1938)
<i>Kniphofia uvaria</i>	28–40 ^b	eBird	9. https://macaulaylibrary.org/asset/66625901	<i>Kniphofia uvaria</i> – JSTOR
<i>Mutisia acuminata</i>	20–30	eBird	10. https://macaulaylibrary.org/asset/365627241	Ferreyra (1995)
<i>Nasa ranunculifolia</i> subsp. <i>ranunculifolia</i>	20–40	eBird	11. https://macaulaylibrary.org/asset/57344941	Henning et al. (2011)
<i>Salpichroa weberbaueri</i>	22–34	eBird	12. https://macaulaylibrary.org/asset/214983331	González (2019)
<i>Tecoma stans</i> var. <i>sambucifolia</i>	35–55	eBird	13. https://macaulaylibrary.org/asset/188042221	Wood (2008)
		iNaturalist	14. https://www.inaturalist.org/observations/169701142	
<i>Tristerix</i> cf. <i>chodatianus</i>	30–40	eBird	15. https://macaulaylibrary.org/asset/214983301	Macbride (1931)
<i>Tropaeolum tuberosum</i>	22–28	eBird	16. https://macaulaylibrary.org/asset/259130091	Macbride (1949)

^aThe measurement corresponds to the tube formed in the flower by the hypanthium and the corolla.

^bMeasurements extracted from the JSTOR Global Plants database (plants.jstor.org).

RESULTS

Field observations of primary and secondary nectar robbing

We observed 18 foraging events of the Black Metaltail, 5 nectar-robbing events and 13 legitimate pollination events. All the nectar-robbing behaviours were observed on the tubular yellow flowers of *S. glandulosa* (Figure 1). Specifically, all the foraging events by Black Metaltails on *S. glandulosa*



FIGURE 1 (a) *Salpichroa glandulosa* flower measuring in average $71 \text{ mm} \pm 1.68 \text{ SE}$ (range = 55–85 mm) and (b) *Salpichroa glandulosa* growing on *Polylepis pilosissima*. © Albert Cruz-Gispert.

corresponded to nectar-robbing events and we never witnessed legitimate feeding involving these two species. The mean size of on-site samples of 20 *S. glandulosa* corollas was $71 \text{ mm} \pm 1.68 \text{ SE}$ (range = 55–85 mm). During three independent observations, an individual landed on flowers that had already been nectar robbed and inserted the beak in the visible open perforation at the base of the flower to access nectar (secondary nectar robbing). In two events, individuals landed on *S. glandulosa* flowers that had not been nectar robbed before, and actively perforated the floral tissues to steal nectar (primary nectar robbing). Unlike the Black Metaltail, Giant Hummingbirds were observed feeding on *S. glandulosa* flowers as legitimate pollinators. Aggressive interactions such as chasing and vocalizing were only observed between conspecific Black Metaltails, while no interspecific aggression was observed with the Giant Hummingbirds, even when both were feeding on flowers of the same *S. glandulosa* plant.

All legitimate feeding events by Black Metaltails were observed on the opened short-corolla flowers of mistletoes (*Tristerix* sp., family *Loranthaceae*; 13 observations). When feeding legitimately on *Tristerix* sp. flowers, we observed Black Metaltails foraging by hovering vertically, but also clinging with their toes. There are two sympatric *Tristerix* species recorded in the region, *Tristerix chodatianus* and *T. longebracteatus* (Laraos district; Beltrán, 2018). These two species have relatively long corolla lengths when the flowers are closed (*T. chodatianus*: 40–50 mm, *T. longebracteatus*: 35–60 mm; Macbride, 1931), but during anthesis, the distal part of the petals bend backward, reducing the tube length to 20–35 and 30–40 mm, respectively (measurements extracted from the JSTOR Global Plants database (plants.jstor.org)).

Feeding behaviour of the Black Metaltail hummingbird on citizen science platforms

We found 452 pictures of the Black Metaltail in the citizen science databases, eBird and iNaturalist, uploaded until 4th October 2023. Pictures represent a time span of 20 years (2003 is the older picture, and 2023 is the newest one). From those 452 pictures, we identified 25 independent records of photographs, excluding duplicates within and between platforms, depicting foraging behaviours on flowers, 16 (64%) of which involved foraging through the front part of the flower (legitimate feeding) and 9 (36%) depicting nectar robbing (Table 1). It was not possible to distinguish between primary and secondary nectar robbing in the pictures, but overall they provided insights into the morphology of flowers where the Black Metaltail exhibited this foraging behaviour.

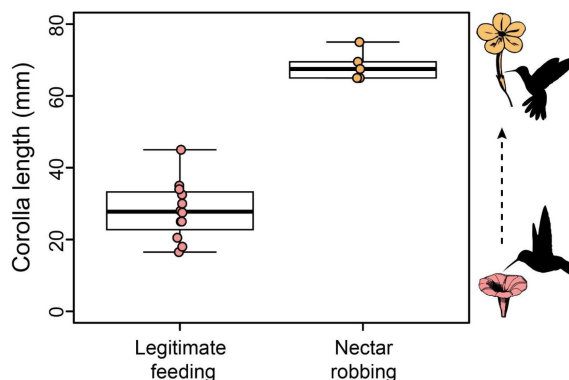


FIGURE 2 Mean corolla lengths of flowers from which Black Metaltails consume nectar, either through legitimate feeding ($n = 12$ plant species) or nectar robbing ($n = 5$ plant species). The boxes depict the median and the 25th and 75th percentiles (i.e., interquartile range, IQR). Analysis based on average corolla lengths from Table 1 including our own average observation for *S. glandulosa* (see Figure 1 caption).

Consistent with our personal observations, pictures from citizen science platforms indicated that nectar robbing records are more common in plant species with elongated corollas and when the corolla length is longer than the bill of the hummingbird. Average corolla lengths were significantly longer in flowers where Black Metaltails performed nectar robbing (mean = 68.4 ± 1.8 SE mm, $n = 5$ plant species) compared to those legitimate-feeding events (mean = 28.1 ± 2.3 SE mm, $n = 12$ plant species) (one-sided t -test: $t = -10.547$, $df = 15$, $p < 0.0001$; Figure 2). We found that nectar robbing by Black Metaltails occurs predominantly on floral morphotypes characterized by a corolla length approximately four times greater than its average bill length, which varies between 15 and 17 mm.

DISCUSSION

What drives the emergence of the nectar robbing strategy, as well as its frequency on pollination networks, is an open question in ecology. In this study, we report for the first time that the Black Metaltail, a short-billed Andean hummingbird, engages in nectar robbing. Furthermore, our observations reveal a distinct association between nectar-robbing behaviour in the Black Metaltail and its tendency to target flowers with a corolla length nearly four times greater than its bill. Our results, therefore, support the idea that flower corolla length is an important factor favouring the emergence of nectar-robbing behaviour in pollination networks.

Our personal observations of Black Metaltails robbing nectar from *S. glandulosa* in a high-elevation *Polylepis* forest are consistent with data on Black Metaltails' foraging strategies extracted from citizen science platforms. Our findings indicate that this hummingbird species engages in nectar robbing when feeding on flowers with long corollas. Additionally, in nearby areas (Canta, Lachaqui, 3500 m.a.s.l.), Black Metaltails have been observed visiting the congeneric but shorter-corolla *Salpichroa weberbaueri*. During the observations of foraging behaviour over *S. weberbaueri*, Black Metaltails introduced their bills almost completely into the flower corolla in an attempt to access nectar (P. Gonz  les, pers. obs). Their foreheads touched the anthers and the style located in the distal part of the tube, suggesting a potential transfer of pollen. Given the flower size of 22–34 mm in *S. weberbaueri*, these anecdotal feeding observations align

with the pattern of foraging strategies extracted from citizen science data (mean corolla length during legitimate feeding = 28.1 mm).

We propose that high-elevation *Polylepis* forests offer a unique system for studying the ecological drivers of nectar-robbing behaviour. These forests are characterized by relatively low but seasonal alpha diversity in plant-pollinator communities, simple plant-pollinator networks, and strong seasonal variation in resource availability (Jameson & Ramsay, 2007; Requena-Rojas et al., 2020). Our observations provide insights into how different bill morphologies shape ecological networks and food competition, as the Black Metaltail (bill length: 15–17 mm; Heindl et al., 2021) and the Giant Hummingbird (bill length: 31–40 mm; Medrano et al., 2022) were observed feeding in the same plant despite differences in bill size. Future studies focusing on the relationship between seasonality in resource availability, feeding competition, and foraging strategies in Black Metaltails within high-elevation *Polylepis* forests can provide important insights into the evolution of nectar robbing in plant-pollinator networks.

AUTHOR CONTRIBUTIONS

Ettore Camerlenghi: Conceptualization (equal); investigation (equal); methodology (equal); writing – original draft (equal). **G. Giselle Mangini:** Investigation (equal); methodology (equal); writing – original draft (equal). **Rodolfo O. Anderson:** Investigation (equal); writing – original draft (equal). **Albert Cruz-Gispert:** Conceptualization (equal); writing – original draft (equal). **Rikkert Loosveld:** Conceptualization (equal); writing – original draft (equal). **Paúl Gonzáles:** Investigation (equal). **Sergio Nolasco:** Conceptualization (equal); investigation (equal); methodology (equal); writing – original draft (equal).

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CONFLICT OF INTEREST STATEMENT

We declared no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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