

LRH: Igić & Fenberg

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Nectar larceny is common in the trainbearers (*Lesbia*, Trochilidae)

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Abstract

Many hummingbirds engage in floral larceny, a suite of so-called ‘illegitimate’ visits in which birds take nectar without providing pollination services. To the best of our knowledge, we provide the first published report of nectar robbing behavior in trainbearers and analyze the proportion
5 of plant visits categorized by mode of interaction as primary robbing, secondary robbing, theft, and/or pollination. We then augment our original field observations with a trove of data from citizen science databases and literature to find that ca. 40% of recorded nectar foraging visits are ‘illegitimate,’ dominated by nectar robbing. We discuss the significance of the findings in the context of recent developments in study of nectar foraging, larceny, and pollination from both
10 avian and plant perspectives.

Keywords: nectar robbing, floral larceny, pollination, trainbearers, hummingbirds, feeding behavior

There is a growing list of bird species known to rely on so-called ‘illegitimate’ flower visits, or floral larceny, in which nectar is taken without providing pollination services (Irwin et al. 2010). Floral larceny is correspondingly gaining a broader appreciation as an important factor shaping the ecology and evolution of plant-animal interactions. Although species such as flower piercers (*Diglossa*, Passeriformes) are widely appreciated to depend on nectar larceny, there are many reports of illegitimate visits by hummingbirds. Some morphological characteristics of hummingbirds, including bill length and tomial serrations, are thought to be particularly closely associated with nectar larceny (Ornelas 1994).

Nearly all plant species that provide nectar and pollen rewards experience larceny, most often from insects and vertebrates, and many defend against it. The remarkable frequency of illegitimate visits necessitated the development and adoption of a more precise lexicon of larceny (Inouye 1980), which attempts to separate it into canonical modes, partly in service of conceptual clarification useful in pursuit of identifying its ecological and evolutionary causes and consequences. Thus, “primary nectar robbers” mechanically create of a hole in flower tissue through which they remove nectar, bypassing the floral opening. By contrast, “secondary nectar robbers” remove nectar utilizing openings previously fashioned by primary robbers.¹ Nearly as a pollinator might, “nectar thieves” access nectar through the floral opening. Due to a mismatch between flower and thief morphology or behavior, however, pollination does not take place. Finally, some plant species are vulnerable to “base workers,” visitors that can probe along the base of the flower, between the free petals, and obtain nectar while bypassing both the anthers and/or stigma and the requisite damage or robbing. These modes of nectar foraging may be difficult to distinguish from each other and/or legitimate visits—pollination—without careful observations and manipulations. Moreover, they can clearly quantitatively overlap so that, for example, thieving may merely reduce pollination efficiency without eliminating it, or individual birds can engage in a mix of primary and secondary robbing.² While many studies report one or more modes of nectar foraging among hummingbirds, we are unaware of any published assessment of their relative importance.

Here, we present original observations and a larger meta-analysis of nectar foraging by

¹This is stealing without vandalism; the proverbial door was previously broken and now it’s a matter of locating any unstolen goods.

²They could also baroquely combine them, for instance, secondarily robbing flowers they primarily robbed, and which they ordinarily legitimately pollinate.

green- and black-tailed trainbearers (*Lesbia nuna* and *L. victoriae*), and discuss their significance in the context of plant-pollinator co-evolution and bill morphology. The original observations took place in and around Ollantaytambo, Peru, on *Brugmansia sanguinea*, *Fuchsia boliviensis*, and *Pasiflora tripartita*. We document the proportion of pollination, theft, and primary- and secondary-
45 robbing visits to flowers, by leveraging images from citizen-science databases eBird, iNaturalist, and other photographed/reported occurrences in the literature. Our highly preliminary analyses find that floral larceny is surprisingly common, at least ca. 40%, and that secondary robbing may be more common among hummingbirds than is generally appreciated, further complicating the proposed association between tomial serrations and mode of nectar foraging.

50 **Materials and Methods**

Site description

On January 14th, 2019, we recorded and photographed a male green-tailed trainbearer, *Lesbia nuna* (Lesson, 1832), which nectar-robbed several flowers of *Fuchsia boliviensis* (Onagraceae) in Ollantaytambo, Peru (13°15'44"S, 72°16'14"W), and then followed the same individual on a 50m
55 foraging bout, while it nectar-robbed flowers of *Brugmansia sanguinea* (Solanaceae)—a species with spectacular ca. 30cm-long tubular crimson-to-yellow flowers—and then legitimately visiting *Salvia leucantha* (Lamiaceae). Both rusty and black-throated flowerpiercer (*Diglossa sittoides* and *D. brunneiventris*) occur at relatively high densities in the area (B.I. and P.B.F., unpub. data), are known to pierce both *Fuchsia* and *Brugmansia* species, and may have been responsible for the
60 previously made calyx and petal hole at the base of *B. sanguinea* flower.

Literature searches

We examined the literature and internet resources to accumulate a database of additional instances of nectar collecting visits by *Lesbia* species. First, we used internet and Google Scholar keyword searches of the existing scientific literature (e.g. ‘*Datura*’ or ‘*Brugmansia*’ and ‘*Lesbia*’ or ‘train-
65 bearer’; ‘*Lesbia*’ and ‘diet’). Documentation of any details on foraging ecology of the trainbearers is sparse. We found two references hinting at illegitimate flower visits by trainbearers. Gould (1861, p.15) cited in Ornelas (1994), contains a passing reference to piercing of a *Brugmansia* sp. flower by a *Lesbia* sp., but the visit was inferred as insect predation, not nectar robbing, as later re-framed by Ornelas (1994), and neither the species nor locations were identified. In a paper

documenting secondary robbing behavior in cinereus cone-bills, Vogt (2006) mentions unpublished observations of secondary nectar robbing by a trainbearer species on a species of *Fuschia*. Our literature search and two substantial meta-analyses (Ornelas 1994; Irwin et al. 2010) did not retrieve any other references to illegitimate visits by these species. Additionally, although we could find no papers documenting their foraging ecology in any detail, gut contents of a single individual examined did include arthropods (Remsen et al. 1986). Therefore, as generally holds for hummingbirds, the trainbearers' diet minimally contains arthropods and nectar. The mode of nectar foraging is, however, unclear.

Foraging data collection and scoring procedures

Consequently, we examined all identified species records for the Genus *Lesbia* in two public databases—iNaturalist (iNaturalist 2019) and eBird (Sullivan et al. 2009). For all resulting records, we applied the same methodology. Images without any flowers were discarded, as were those in which birds were simply perched or flying near a flower. We then closely examined the remaining images, in which birds were hovering in close proximity (about a body length) to flowers, and facing them. For that subset, we extracted the location, date, and comment metadata. We scored individual sex ('m', 'f', or unknown), re-visited distinguishing marks and confidence of species identification (scoring specific epithets as 'nuna', 'victoriae', or 'sp.'), estimated the mode of interaction (primary nectar-robbing, secondary nectar-robbing, thieving, pollination, or unknown), as well as our confidence in the estimate of the mode of interaction (Low vs. High). Finally, with the help of several colleagues, we identified the visited plant species.

Often, modes of interaction are unclear and we combined terms for the most accurate characterization of interaction. For example, primary vs. secondary nectar robbing and pollination vs. thieving are generally hard to distinguish, so we simply combined the likely interactions. This enables us to conservatively summarize modes of interactions as approximate ranges, without making unnecessary assumptions. While identification of trainbearers is relatively easy, assignment of the species epithet can be difficult, on account of great amount of geographic variation and possible existence of undescribed species (Weller and Schuchmann 2004). Therefore, while we recorded the species-level data, we often found identifications to be implausible or uncertain, and we jointly present the feeding habits for all *Lesbia*.

Bill morphology

Short-billed hummingbirds and those with serrated tomia are thought to be more likely to nectar-rob, especially flowers with long corolla tubes, co-adapted with long-billed hummingbirds (Lara and Ornelas 2001). We did not find a reference to presence/absence of serrated tomia in trainbearers, so we scored this trait in 13 specimens at the Field Museum of Natural History. We used a dissecting microscope to visualize and score this trait on the available collections (12 males and one female), as well as measure their bill lengths.

All metadata, image locations, and scored data used in our analyses are available online in Supplemental Materials.

Results

In addition to our own observations and photographic evidence, we collected and examined a total of 180 individuals' floral visits on 42 flowering plant genera Fig. 1. The mode of interaction for 135 visits could be assigned with some confidence, while the mode of visit interaction for 45 visits is unknown, often because birds were hovering in the vicinity of a flower, immediately before or after nectaring. The most common recorded mode was 'pollination/thieving' (46 visits), a category that we conservatively scored as vague because it was nearly impossible to disentangle those modes in many cases, without functional study (bagging and marking flowers). Our impression, however, is that the majority of these visits plausibly resulted in pollen transfer. The second most common mode was combined 'nectar robbing' (primary and secondary robbing; 41 visits) indicating that an individual fed through a pierced hole in the side of the corolla. It was followed by 'pollination' (36 visits), which indicated a fairly clear legitimate interaction, 'secondary nectar robbing' (10 visits), and thieving (2 visits). Although we could not confidently assign any visits to the 'primary robbing' mode, this is almost certainly only due to the limitations of our approaches.

An examination of 13 specimens of *Lesbia nuna* revealed no evidence of serrations. The imbalance of sex ratio (12 males) is not likely to be important in this instance because serrations are more likely to be present in males (). The mean bill length for males was 16.89 ± 0.47 mm. The female's bill measured 17.38 mm.

Discussion

While short-billed hummingbirds stereotypically rob nectar from long sympetalous tubular flowers, competing with legitimate long-billed legitimate visitors, like sword-billed hummingbirds (*Ensifera ensifera*), observational data presents a slightly more textured picture, with remarkable displays of opportunism. For example, we found a number of documented visits by *Lesbia* sp. to the composite flowers of Asteraceae (daisy family), as well as the remarkable images of apparent nectar robbing of *Brugmansia sanguinea* by sword-bills.

Our findings show that secondary nectar robbing is relatively common, comprising between 7.4% and 37.8% of the visits. If it is true that, on the whole, primary robbing allows access to previously unvisited, relatively nectar-rich flowers, then secondary robbing should generally be disadvantageous (Irwin et al. 2010). In this context, our relatively high observed frequency may appear somewhat paradoxical, and more likely, one or more of our underlying assumptions are flawed. Specifically, we can imagine that, for example, if they are faced with limited supply of resources that are easily legitimately exploited, trainbearers likely respond by robbing or thieving from inferior resources, a situation that may be exacerbated by territoriality.

Both modes of larceny are also likely to cause both plastic and evolutionary responses from flowering plants, including variation in proportion and/or time-dependence of nectar release, and placement of secondary metabolites. Interestingly, a number of plant species visited by trainbearers, including members of the nightshade family (Solanaceae), produce alkaloids broadly toxic to vertebrates. For example, *Brugmansia* species can temporarily incapacitate (much larger) juvenile humans by skin contact alone (Andreola et al. 2008). Perhaps not coincidentally, a great number and quantity of alkaloids are produced by species of *Brugmansia* and *Nicotiana*, and tissues at the base of flowers (calyx) contain some of the highest concentrations of such compounds (Saitoh et al. 1985; Alves et al. 2007).

We hope that our observations and analyses will spur work on systematics and ecology of *Lesbia*, especially the importance of nectar feeding in their energy budgets. Furthermore, we sorely lack observational studies, aimed at determining the relative frequencies of visit modes, and detailed manipulative field study to obtain direct evidence for nectar feeding dynamics across all hummingbirds and other nectar-feeding birds (Irwin et al. 2010). Similarly, a better understanding

155 of plant-side effects and responses, including pollination efficiency, the distribution of visitor interactions (Arizmendi 2001), as well as plant incentives and defenses, may help us better explain the dynamics in the co-evolutionary game between flowers and their visitors.

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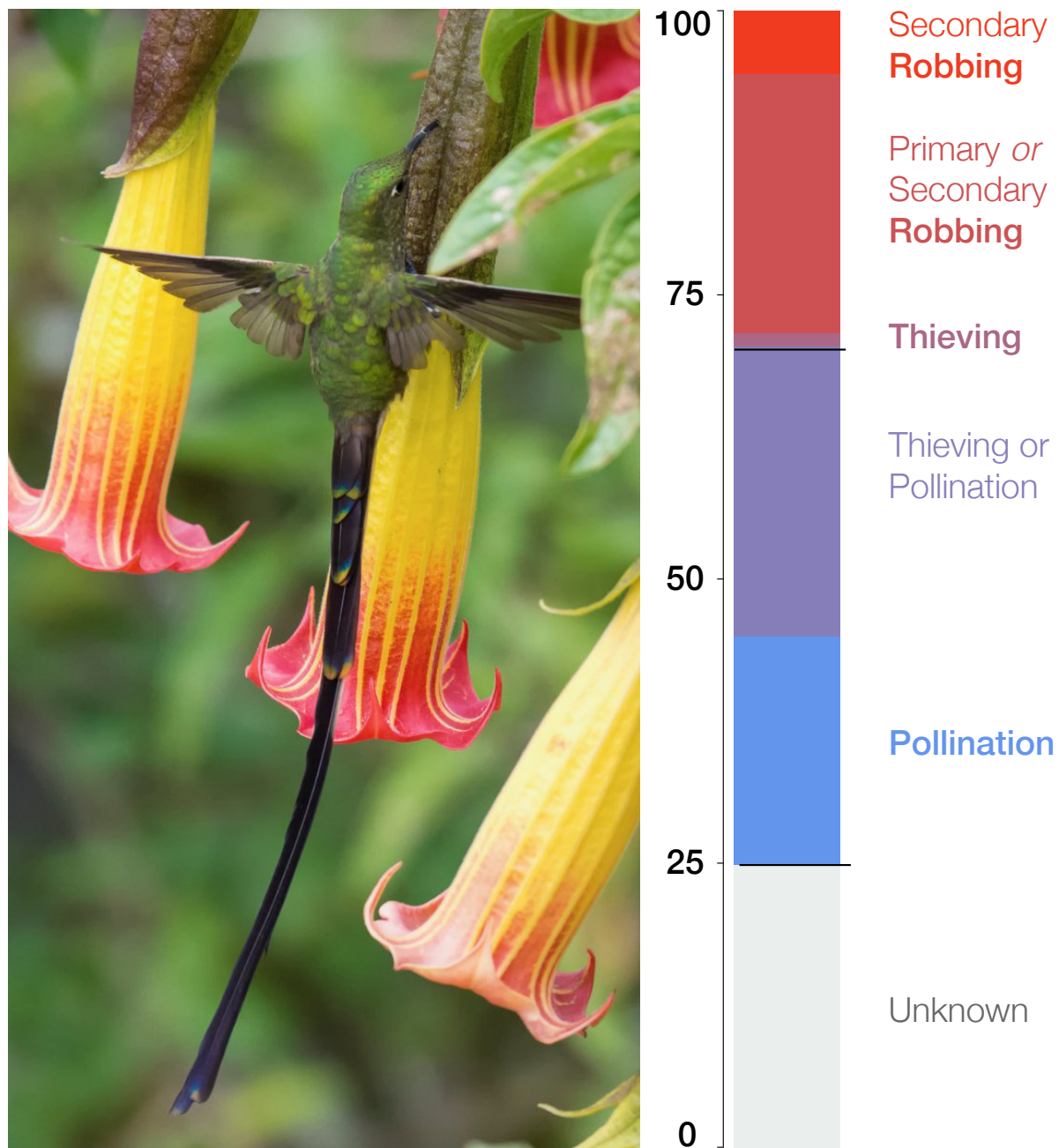


Figure 1: A nectar robbing visit by a black-tailed trainbearer *Lesbia victoriae* on *Brugmansia sanguinea*, whose flower was previously pierced by a species of *Diglossa* (Diego Emerson Torres, pers. comm.). Right panel: A bar plot illustrating the relative visit mode frequencies of *Lesbia* species (n=180).

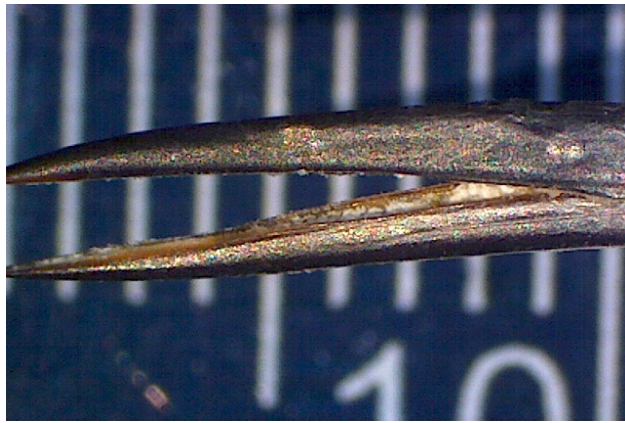


Figure S1: Anterior side of the bill of a male *Lesbia nuna*, FMNH-222250, with no visible serrations on its mandibular (or maxillary) tomia. Background scale is denoted in mm distance units.