

**Gape-feeding, Primary, and Secondary Nectar Robbing Behavior in
Yanacocha Reserve, Ecuador**

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Observations on Primary and Secondary Nectar Robbing in Yanacocha Reserve, Ecuador

ABSTRACT

Hummingbird-pollinated flowers often have their nectar extracted by nectar robbers who do not act as pollinators. I studied the nectar robbing community in a cloud forest in Yanacocha Reserve, Ecuador, with the objectives of determining which species of flowers were being robbed by primary and secondary nectar robbers, the frequency of nectar-robbing, and recording any aggressive interactions between robbers and other robbers or legitimate pollinators. Feeding behavior and flower visitation data were collected during walking transects and stationary observation periods in front of *Siphocampylus giganteus* and *Fuchsia sp.* Hole counts and corolla measurements were collected to analyse the frequency of robbing and the characteristics of robbed flowers. A high incidence of nectar robbing was found. *Diglossa humeralis* (Black Flowerpiercer) and *Diglossa Lafresnayii* (Glossy Flowerpiercer) are primary nectar robbers, and three species of hummingbirds, *Metallura tyrianthina*, *Coeligena lutetiae*, and *Eriocnemis luciani*, act as secondary nectar robbers on five plant species. Aggressive interactions were observed, *M. tyrianthina* in particular was a frequent target of aggression by larger hummingbird species. The role of primary nectar robbers affects other avian flower visitor by allowing secondary nectar robbing and increasing competition for legitimate pollinators. I hypothesize that the most important effect of nectar robbing on the flowers of Yanacocha is the cost of nectar production and the indirect effect of a reduced appeal to legitimate pollinators.

Colibríes son polinizadores normales para muchas flores, pero también hay ladrones de néctar que extraen el néctar de estas flores sin actuando como polinizadores. Estudié la comunidad de ladrones de néctar en un bosque nublado en la Reserva de Yanacocha, Ecuador. Mis objetivos principales fueron a determinar cuales especies de flores los ladrones robaron, y estudié la cantidad del robo y las interacciones entre los ladrones y otros ladrones o polinizadores normales. Para hacer mis observaciones sobre el comportamiento de las pincha-flores y colibríes, caminaba por los senderos y sentía frente arbustos de *Siphocampylus giganteus* y *Fuchsia sp.* Conté los huecos en las flores y medí la longitud de las corolas para analizar la cantidad del robo que ocurrió y las características de las flores robadas. Hay mucho robo de néctar en la comunidad. *Diglossa humeralis* (Black Flowerpiercer) and *Diglossa Lafresnayii* (Glossy Flowerpiercer) actúan como ladrones primarios y tres especies de colibrí, *Metallura tyrianthina*, *Coeligena lutetiae*, and *Eriocnemis luciani* son ladrones secundarios de cinco especies de plantas. Observé interacciones agresivas, *M. tyrianthina* frecuentemente era víctima de especies más grandes de colibríes. El papel de los ladrones de néctar primarios permite el robo secundario y aumenta la competición para los polinizadores legítimos. Supongo que el coste de la producción de néctar y el efecto indirecto de un atractivo reducido a los polinizadores sean el efecto más importante del robo de néctar en Yanacocha.

INTRODUCTION

Flowers with long, tubular corollas, normally pollinated by hummingbirds, frequently lose their nectar to avian nectar robbers. Species of short-billed

hummingbirds and *Diglossa* flowerpiercers are known exploiters of these flowers, frequently visiting the same species as legitimately pollinating hummingbirds and extracting the nectar through holes made in the corolla by the flowerpiercers. Primary nectar robbing has been described (Inouye 1980, Vogt 2006) as the act of piercing the corolla wall and using the hole to gain access to a flower's nectar resources without coming into contact with the plant's reproductive organs or acting as a pollinator. Secondary nectar robbing is the use of an existing corolla hole made by a primary nectar robber by a species unable to pierce the corolla wall, allowing the bird to reach the nectar without acting as a pollinator (Inouye 1980).

Flowerpiercers are well documented primary nectar robbers (Lyon & Chadek 1971, Colwell et al. 1974, Arizmendi et al. 1996, Navarro 1999, Arizmendi 2001), they use the hook on the tip of their upper mandible to grasp and secure a flower while piercing the corolla wall with their lower mandible. The tongue, a specially adapted feature with a brush-like tip, is inserted into the corolla with the lower mandible and used to extract nectar. Short-billed hummingbirds, *Metallura tyrianthina* (Tyrian Metaltail) for example, have also been documented as both primary and secondary nectar robbers, summarized in Vogt (2006).

While a high incidence of nectar robbing has been documented (Colwell et al. 1974, Arizmendi 1996, Navarro 1999, Lara & Ornelas 2001) for many floral communities, the effects of this behavior on the flowers involved are variable and controversial. Nectar robbing has been found to have a negative effect on fruit set levels of flowers (Navarro 1999), a net zero effect on fruit set levels (Arizmendi 2001), and a positive effect when the robber appeared to pollinate *Tristerix* mistletoe while robbing its flowers (Graves 1982). The complicated interactions between a flower, its pollinators, and its robbers are governed by a multitude of factors, such as the cost of replacing nectar for the plant.

This study was conducted with the purpose of investigating the nectar robbing community in Yanacocha Reserve, Ecuador. The principal objectives were (1) to determine which species of flowers were being robbed by the primary nectar robbing *Diglossa* flowerpiercers, (2) to learn which secondary nectar robbers were present and which plant species they were exploiting, (3) to look at the amount of nectar robbing occurring through hole count and flower visitation data, and (4) to observe any interactions between nectar robbers and other robbers or legitimate pollinators.

METHODS

SITE—Hummingbird and flowerpiercer behavior was observed, and plant data collected in Yanacocha Reserve, located on the Western slope of Pichincha volcano, 12 km west of Quito, Ecuador. This 1,030 ha reserve stretches from 2,800-4,000 m in elevation and encompasses páramo, *Polylepis* forest, and cloud forest vegetation (Sornoza 2007). This study was conducted from the main trail system located at 3,300 m altitude amidst the cloud forest; observations on nectar robbing were also collected on *Cavendishia* sp., and *Aetanthus* cf. *nodosus* in the higher *Polylepis* forest.

Data was collected from 7 April- 28 April 2007, during the wet season at Yanacocha. Plant identification was done at the University of San Francisco, Quito, with assistance from Professor and herbarium curator Vlastimil Zak.

OBSERVATIONS.^{3/4} Observations were collected on hummingbird and flowerpiercer behavior and plant use during walking transects and stationary observation periods. Walking transects took place on the main trail system (Trocha Inca, Trocha Masked

Trogon, and Trocha Oso de Antojos) between 07:00 h and 11:00 h and lasted from 2-4 h during which hummingbird and flowerpiercer feeding behavior was noted as well as any interactions between the birds. Any new behavior seen at any time was recorded.

Stationary observational periods lasted from 1-3 h and took place between 07:00 h and 10:00 h (23h total) and 11:00 h and 18:30 h (13h total). These observations were made from a distance of 4-6 m and were focused on an individual plant or group of plants. Two species, *Siphocampylus giganteus* and *Fuchsia sp.* were each observed at four different sites for a total of 18 h observation. These species were both nectar-robbled, abundant, and in bloom during the study period.

Data was recorded on each avian visitor, including the time spent per flower, the number of flowers visited, and the method of feeding (nectar robbing or legitimate feeding). Nectar robbing was defined as any time a flowerpiercer grabbed the base of a flower corolla with its bill, or any time a hummingbird inserted its bill into a hole in the base of the corolla. Legitimate feeding was defined as any time a hummingbird put its bill into the corolla through the normal opening.

FLOWER MEASUREMENTS AND HOLE COUNTS.^{3/4}Data was collected on flowers with tubular corollas accessible from the trail system on the total length of the flower, measured from the base of the bract to the farthest corolla point, and on the effective corolla length (Stiles 1992), measured as the shortest distance between the corolla opening and the nectary. Twenty-five individual flowers were measured when possible, and when this number of fully open flowers was unavailable, the maximum number that could be reached were measured.

Hole counts were taken to determine the presence or absence of nectar robbing and the frequency of robbing when present. Individual flowers were examined and the number of holes per flower and the number of open flowers with holes per plant were recorded.

RESULTS

PRIMARY NECTAR ROBBERS.^{3/4}Three species of flowerpiercers are present in Yanacocha Reserve, two of these were observed acting as primary nectar robbers, the third species *Diglossopsis cyanea* (Masked Flowerpiercer) was more common at the hummingbird feeders than at the sites of observation. *Diglossa lafresnayii* (Glossy Flowerpiercer) is by far the most common of the three species, *D. lafresnayii* was observed robbing *Fuchsia sp.*, *Salvia humboldtiana*, *Passiflora mixta*, *Siphocampylus giganteus*, *Centropogon sp.*, and poking at the base of an *Aetanthus cf. nodulus*. *Diglossa humeralis* (Black Flowerpiercer) was observed robbing *Fuchsia sp.*, and *S. giganteus*.

The two *Diglossa* species robbed flowers by approaching a flower and grabbing onto the base of the corolla with the upper bill while using the lower mandible to pierce the corolla wall and gain access to the nectar. When robbing a *Fuchsia sp.* the flowerpiercer perched on a twig underneath or beside a flower and stretched to reach the base of the corolla with its bill. Often a flower would be dropped the first try, and the bird would reach out again to secure it. *D. lafresnayii* was even seen grasping onto a branch above a *Fuchsia* flower and hanging upside down to reach its target. The time the flowerpiercers spent at each flower was variable, usually they spent 1-2 s, but occasionally a bird would hold onto a flower 3-4 s. Observations of *D. lafresnayii* robbing *Centropogon sp.* and *Salvia humboldtiana* were similar, with the bird finding a

nearby perch or using part of the plant as a base from which to reach the proximal end of these small corollas.

Figure 1. Feeding methods of *Diglossa* flowerpiercers. *Diglossa lafresnayii* grabbing a *Fuchsia sp.* flower in its bill, and inserting lower mandible (right). *D. Lafresnayii* perching on pedicel to reach corolla base of *Siphocampylus giganteus*.

The *Diglossa* robbing technique was different when feeding on the larger *S. giganteus* flowers. Due to the position of the flowers on long, slender pedicels, the flowerpiercers would perch on the pedicels, bending the flower down with their weight, and from this position reach their bills to the corolla base, just beyond the green bract. The *Diglossa sp.* fed from both sides of one flower, frequently twisting their head to rob first from one side and then from a hole on the other side. One *D. humeralis* gripped a flower tightly and moved the whole flower around for 4-5 seconds, perhaps making a new hole; normally 2-3 seconds were spent on each flower.

When robbing *Passiflora mixta*, an individual of *D. lafresnayii* grabbed onto the long corolla base with its feet and from this perch inserted its lower mandible into a hole at the base of the corolla; 2-3 s were spent at this flower.

SECONDARY NECTAR ROBBERS.^{3/4} Three species of hummingbird were observed acting as secondary nectar robbers, *Metallura tyrianthina* (Tyrian Metaltail), *Eriocnemis luciani* (Sapphire-vented Puffleg), and *Coeligena lutetiae* (Buff-winged Starfrontlet).

The short-billed *M. tyrianthina* was the most abundant robber, both in the number of species it robbed and in the number of times it was seen robbing flowers. *M. tyrianthina* inserted its bill into holes in the corolla base of *Fuchsia sp.*, *S. giganteus*, and *Cavendishia sp.* (on which it also fed legitimately), and was observed poking around the base of *Aetanthus cf. nodosus*.

M. tyrianthina accessed corolla holes in *Fuchsia sp.* by gripping onto the corolla stalk with its feet while perching or beating its wings. In Yanacocha, *M. tyrianthina* individuals were observed landing on many *Fuchsia* flowers they did not feed on. Upon perching a *M. tyrianthina* moved its head to both sides of the corolla stalk without inserting its bill, then went to another flower.

Figure 2. *Metallura tyrianthina* inserting its bill into a hole in the base of *Siphocampylus giganteus* while perched on top of the corolla.

The medium-billed *Eriocnemis luciani* was observed inserting its bill into a large hole at the base of a *Cavendishia sp.*, and on 6 occasions was observed acting as a secondary nectar robber of *S. giganteus*. *E. luciani* sat on top of the corolla and poked its bill through holes at the base, one on either side. Both these plant species it also feeds from in a legitimate fashion.

The long-billed *Coeligena lutetiae* was the third secondary nectar robber. This species feeds legitimately from a wide variety of species, and it was seen inserting its bill into the base of a *Passiflora mixta* corolla while hovering. *P. mixta*, with an average 90 mm length to nectar, is too long for the 33mm bill of *C. lutetiae* to feed on legitimately.

AMOUNT OF NECTAR ROBBING.^{3/4}The amount of nectar robbing occurring in Yanacocha Reserve was assessed through flower hole counts and through stationary observation periods documenting visitors to *S. giganteus* and *Fuchsia sp.*

Table 1. Flower visitation data for *Siphocampylus giganteus*. 18 h of data were recorded at a distance of 4-6 m from the plant. Four sites were used; species, type of feeding behavior, and number of visited flowers were recorded for each avian visitor.

Visitor	Type of Visit	Number of Flowers Visited	Percent of Total Visits
<i>Colibri coruscans</i>	Legitimate	155	13
<i>Lafresnaya lafresnayi</i>	Legitimate	4	0
<i>Aglaeactis cupripennis</i>	Legitimate	62	5
<i>Pterophanes cyanopterus</i>	Legitimate	13	1
<i>Coeligena lutetiae</i>	Legitimate	74	6
<i>Eriocnemis luciani</i>	Legitimate	67	6
<i>Eriocnemis luciani</i>	secondary robber	5	0
<i>Metallura tyrianthina</i>	secondary robber	394	33
<i>Diglossa humeralis</i>	primary robber	237	20
<i>Diglossa lafresnayii</i>	primary robber	197	16
Total		1208	100
Legitimate Feeding		375	31
Nectar Robbing		833	69

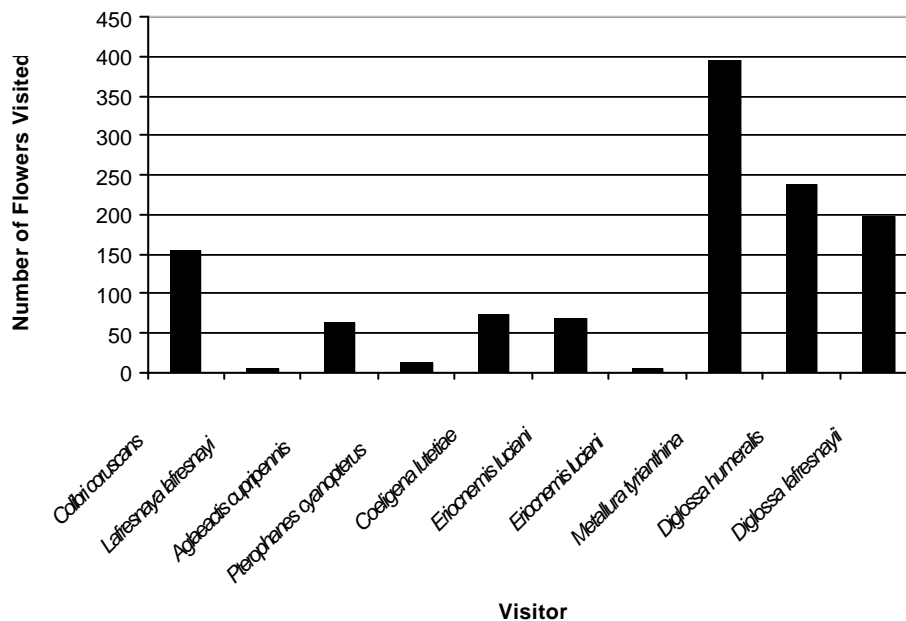


Figure 3. Number of *Siphocampylus giganteus* flowers fed on by avian visitors in 18 hours of observation.

Table 2. Flower visitation data for *Fuchsia sp.* Data was recorded from a distance of 4-6m from the group of plants. Four sites were used, and data was taken on the identity of each avian visitor, the type of feeding behavior, and number of flowers visited.

Visitor	Type of Visit	Number of Flowers Visited	Percent of Total Visits
<i>Coeligena lutetiae</i>	legitimate	131	44
<i>Eriocnemis luciani</i>	legitimate	12	4
<i>Metallura tyrianthina</i>	secondary robber	73	25
<i>Diglossa humeralis</i>	primary robber	15	5
<i>Diglossa lafresnayii</i>	primary robber	66	22
Total		297	100
Legitimate		143	48
Robbing		154	52

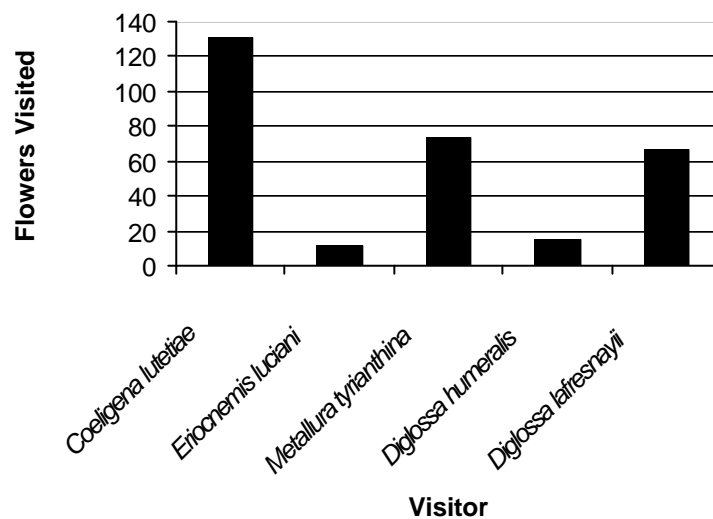


Figure 4. Number of *Fuchsia* Flowers fed on by avian visitors in 18 h of observation.

In addition to direct observations of the robbing behavior, the illegitimate activities of primary nectar robbers were examined through a search for holes in the base of the corollas of open flowers. This data is summarized in Table 3. All the blooming flower species observed being robbed had holes in them, moreover, holes were found in several species for which the act of robbing was never observed. Holes in the base of *Tropaeolum sp* were similar in size and shape to the holes left in other species of flowers, particularly *Salvia humboldtiana*, and there is a strong possibility that flowerpiercers are also acting as a primary nectar robber for this species.

Holes were also found in *Cavendishia* flowers, which the flowerpiercers regularly gape-feed from. These holes were very regular, small and round, one per flower, and in at least 3 examples the holes were located far from the base of the flower, closer to the corolla opening. *M. tyrianthina* and *E. luciani* were observed using these holes to presumably access nectar.

Table 3. Hole counts of flowers with holes per plant, and number of holes per flower. Average number of holes per flower was calculated from only flowers with holes.

	Flowers Examined	Flowers with Holes	% Flowers with Holes	Number Holes	AVG no. Holes/ Flower	St. Dev
<i>Fuchsia sp</i>	68	29	43	76	2.6	1.1
<i>Centropogon sp</i>	65	14	22	19	1.4	0.5
<i>Cavendishia sp</i>	119	26	19	27	1.0	0.20
<i>Tropaeolum sp</i>	36	7	19	9	1.3	0.49
<i>Salvia humboltiana</i>	69	28	41	32	1.1	0.35
<i>Siphocampylus giganteus</i>	37	26	70	49	1.9	0.51
<i>Aetanthus cf nodulus</i>	25	10	40	19	1.9	0.99
<i>Passiflora mixta</i>	5	5	100	21	4.2	1.8

Table 4. Hummingbird-flower relationships. Hummingbird bill lengths and corolla lengths to nectar are compared. Length to nectar of the corolla was obtained from measurements in the field, bill lengths are recorded in Ridgely & Greenfield (2001). LF = legitimate feeding; R = nectar robbing.

	Bill Length (mm)	<i>Barnadesia spinosa</i>	<i>Centropogon sp.</i>	<i>Tropaeolum sp.</i>	<i>Rubus robusta</i>	<i>Castilleja sp.</i>	<i>Vaccinium floribundum</i>	<i>Salvia Humboltiana</i>	<i>Cavendishia sp.</i>	<i>Fuchsia sp.</i>	<i>Aetanthus cf. nodulus</i>	<i>Siphocampylus giganteus</i>	<i>Passiflora mixta</i>
Effective length of corolla (mm)		35 n=9	31 n=25	24 n=25	6 n=6	27 n=20	7 n=25	30 n=25	22 n=25	47 n=74	14 n=25	34 n=25	90 n=5
<i>Colibri coruscans</i>	25											LF	
<i>Aglaeactis cupripennis</i>	18	LF							LF		LF	LF	
<i>Lafresnaya lafresnayi</i>	25		LF			LF		LF	LF			LF	
<i>Pterophanes cyanopterus</i>	30									LF	LF	LF	
<i>Coeligena lutetiae</i>	33		LF						LF	LF		LF	R
<i>Ensifera ensifera</i>	90-100												LF

<i>Eriocnemis luciani</i>	20	LF		LF				LF	LF & R	LF		LF & R	
<i>Eriocnemis mosquera</i>	20		LF						LF				
<i>Metallura tyrianthina</i>	11			LF	LF		LF		LF & R	R	R?	R	
<i>Chalcostigma herrani</i>	12						LF						

The short-billed *M. tyrianthina* is unable to access the nectar from flowers with long corollas without access holes. It feeds legitimately on flowers with corollas with 6-24 mm length to nectar, a reachable distance for a 11 mm bill. The longer-billed *C. lutetiae* had many more legitimate feeding interactions, and only acts as a secondary nectar robber with *P. mixta* (90 mm effective corolla length).

COMPETITIVE INTERACTIONS

Table 5: Competitive interactions between two individual birds. The species name of the aggressor is written in the box indicating the two species involved. A #W indicates the number of wins for the aggressor, a #L indicates the number of losses for the aggressor, a ? indicates uncertainty in the outcome.

Species:	<i>Diglossa lafresnayii</i>	<i>Diglossopsis cyanea</i>	<i>Metallura tyrianthina</i>	<i>Aglaeactis cupripennis</i>	<i>Pterophanes cyanopterus</i>
<i>Diglossa humeralis</i>	<i>D. lafresnayii</i> 3W		<i>D. humeralis</i> W		
<i>Diglossa lafresnayii</i>	8 interactions				
<i>Diglossopsis cyanea</i>	<i>D. lafresnayii</i> 3W	1 interaction			
<i>Metallura tyrianthina</i>	<i>M. tyrianthina</i> ? <i>D. lafresnayii</i> W		14 interactions		
<i>Aglaeactis cupripennis</i>			<i>A. cupripennis</i> s 7W	1 interaction	
<i>Pterophanes cyanopterus</i>			<i>M. tyrianthina</i> L		1 interaction
<i>Coeligena lutetiae</i>			<i>C. lutetiae</i> 2W		
<i>Lafresnaya lafresnayi</i>			<i>L. lafresnayi</i> W		
<i>Colibri coruscans</i>			<i>C. coruscans</i> 2W	<i>C. coruscans</i> W	
<i>Eriocnemis mosquera</i>	<i>D. lafresnayii</i> 3W				
<i>Eriocnemis luciani</i>	<i>E. luciani</i> W <i>E. luciani</i> L		<i>E. luciani</i> W	<i>E. luciani</i> ?	<i>E. luciani</i> ?

All intraspecific and interspecific aggressive interactions while one bird was feeding were recorded during walking transects and stationary observations, the results are summarized above in Table 5. The aggressor was defined as the bird who initiated the confrontation, usually by diving in to the target bird's location. When the target bird was successfully disrupted from feeding by the aggressor the interaction was considered a win for the aggressor, and when the target bird continued with its feeding it was counted as a loss for the aggressor.

The bold *E. luciani* was a frequent aggressor, particularly when defending a *Siphocampylus giganteus*. The *C. coruscans* (Sparkling Violetear) interactions also took place at a *S. giganteus* it was defending. The small *M. Tyrianthina* was the most frequent target bird, and its aggressors were successful at driving off this secondary nectar robber.

DISCUSSION

EFFECT ON AVIAN FLOWER VISITORS—The role of primary nectar robbers *Diglossa humeralis* and *D. lafresnayii* is important to the structure of Yanacocha's nectar feeding community. For *M. tyrianthina*, as a secondary nectar robber, the flowerpiercers have opened up 3-4 flower species as additional nectar sources, which would be otherwise unharvestable. The benefit of feeding from larger flowers appears to outweigh the downside of being driven off by other hummingbird species. *M. tyrianthina* individuals were chased off from *S. giganteus* flowers by four species of larger hummingbirds and one flowerpiercer. These are species that were not observed feeding on flowers that *M. tyrianthina* accesses from the corolla opening, such as the tiny *Pernettya sp.* or *Rubus robusta*. While *M. tyrianthina* was invariably chased off from *S. giganteus* flowers when challenged, it had the highest percentage of flower visits (33%) of any nectar feeding species.

M. tyrianthina have been observed piercing corollas, along with other hummingbird species summarized in Vogt (unpubl. Manusc.). During my observations I was never convinced that *M. tyrianthina* was capable of piercing the tough corollas of *S. giganteus* or *Fuchsia sp.* The thinner, more delicate corollas of *Salvia humboldtiana* may be pierced by this hummingbird, but this was never observed. In addition to the thickness of the corollas, *M. tyrianthina* was repeatedly seen landing upon a *Fuchsia* or *S. giganteus* flower and looking to either side of the corolla, but not inserting its bill into a hole. I hypothesize that in these cases the bird was looking for a hole and when it did not find one, it moved on to another flower, behavior that suggests it is incapable of piercing the corolla.

E. luciani and *C. lutetiae* appear to be opportunistic nectar robbers. They feed on a majority of their food sources in a legitimate manner. In the case of *E. luciani* on *S. giganteus*, only 5 out of the 72 flowers visited were robbed, and these 5 visits were all to the same plant. *E. luciani* is capable of visiting *S. giganteus* in a legitimate manner. However, perching on the corolla to steal nectar is potentially more energy efficient than hovering to access the nectar through the normal opening.

Both the robbing activities of the *Diglossa* flowerpiercers and the secondary nectar robbers have increased competition for legitimate pollinators. *D. lafresnayii* were observed in aggressive interactions with five other species, with a mixture of wins and losses. Birds like *C. coruscans* initiated aggressive interactions with the nectar robbers, expending energy chasing off the competitors.

EFFECT ON FLOWERS—The effects of nectar robbing on the plants themselves are not clear, and probably vary from species to species. Equal numbers of studies have described nectar robbing having a positive effect, a neutral effect or a negative effect (Inouye & Maloof 2000). Negative effects of nectar robbing can include: damage to the corolla and to plant reproductive tissues (Navarro 1999), the energetic cost of replacing nectar, and a decrease in the flower's attraction to legitimate visitors because of a potentially lower amount of available nectar and a higher level of competition (Mcdade & Kinsman 1980).

Damage to plant reproductive tissue has been infrequent in other studies (Navarro 1999), and there are other effects that are potentially positive or neutral. By robbing nectar, a flowerpiercer or hummingbird creates a variation in nectar availability, forcing a legitimate pollinator to visit more flowers, and potentially travel greater distances, enhancing gene out-crossing for the plant as has been suggested in Navarro (1999). Graves (1982) has described an incidence where *Diglossa brunneiventris* and *Diglossa humeralis* acted as pollinators for *Tristerix* mistletoe by jostling and coming into contact with the stamens and pistons while reaching the base of the flower corolla. Arizmendi et al. (1996) found flowerpiercers to function as low efficiency pollinators while nectar robbing. A nectar robber may function as a commensal with the flowers it pierces if the cost of nectar production is low for the plant and no damage occurs to the reproductive tissue (Arizmendi 2001).

A number of plant species were found to be nectar sources for primary and secondary nectar robbers in Yanacochoa, with between 19-70% of flowers showing holes (depending on species). Observation periods of *S. giganteus* and *Fuchsia sp.* found that 69 and 52%, respectively, of flowers visited were visited by avian nectar robbers. Both these flowers were also visited by a number of legitimate pollinators, and it is probable that the effect of Yanacochoa's nectar robbers on the flowers is determined more by the cost of producing nectar than by a lack of pollinators. *Diglossa* species were rarely observed initiating aggressive encounters with pollinators, and *M. tyrianthina* was routinely driven off by legitimate pollinators. This data indicates that the nectar robbers were not directly denying legitimate pollinators floral access.

Flowers examined for holes did not exhibit damage to their reproductive parts, only the corolla wall and occasionally the bract showed damage. It is likely that nectar robbing is not preventing these flowers from producing seeds or fruit. However, the amount of nectar consumed by the nectar robbers must have been significant, and I hypothesize that it is the cost of nectar production and the indirect effect of a reduced appeal to legitimate pollinators that is the most important effect of nectar robbing on the flowers of Yanacochoa.

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Pollination by a Nectar Robber: Gape-feeding behavior of the Glossy Flowerpiercer (*Diglossa lafresnayii*) on *Cavendishia* sp. (Ericaceae)

ABSTRACT

Diglossa flowerpiercers "gape-feed" from flowers by inserting their lower mandible into the natural corolla opening, potentially acting as pollinators for species with tubular corollas adapted for ornithophily. This study was conducted at Yanacocha Reserve, Ecuador in cloud forest vegetation. Stationary observation periods and walking transects were used to record *Diglossa lafresnayii* (Glossy Flowerpiercer) feeding behavior. *D. lafresnayii* is described gape-feeding on flowers of a *Cavendishia* sp. The flowerpiercer made up 756 of 1143 visits to *Cavendishia* flowers, and is likely an important pollinator for this species. Aspects of *Cavendishia* flower morphology and *Diglossa* behavior make *D. lafresnayii* a suitable and efficient pollinator for this flower species.

Los pichaflores *Diglossa* algunas veces comen el néctar de flores en una manera legítima, ponen su mandíbula inferior adentro de la corola y usan su lengua para extraer el néctar. Es posible que estas aves sean polinizadores de estas flores con corolas tubulares. Hice este estudio en la Reserva de Yanacocha, Ecuador, en un bosque

nublado. Observé el comportamiento de los pinchaflores durante periodos de observación y cuando caminaba por los senderos. Describí *D. Lafresnayii* comiendo el néctar de las flores *Cavendishia* en una manera legítima. El pinchaflores visitó a las flores de *Cavendishia* 756 veces de 1143 visitas en total, y probablemente es un polinizador importante para esta especie. *D. lafresnayii* es un polinizador eficiente y apropiado para esta especie porque de aspectos de la morfología de *Cavendishia* y el comportamiento de *Diglossa*.

INTRODUCTION

Diglossa flowerpiercers possess a uniquely adapted hook-shaped bill that makes them formidable nectar robbers (Vogt 2006). However, Stiles et al. (1992) described a flowerpiercer feeding behavior where the bird does not pierce the corolla wall, instead, the lower mandible and the tongue are inserted into the natural opening at the distal end of relatively short, tubular corollas, while the upper mandible rests against the outside of the corolla. This method of obtaining nectar puts the flowerpiercer's chin and bill into contact with the anthers and stamen, and it has been hypothesized that in this way the flowerpiercers act as pollinators (Stiles 1992). This behavior, here termed "gape-feeding", has been recorded for *Diglossa lafresnayii* (Glossy Flowerpiercer) and *Diglossa humeralis* (Black Flowerpiercer) feeding on two species of *Brachyotum* in SW Columbia, and for *Diglossa* and birds of the similar genus *Acanthidops* feeding legitimately on the short and wide flowers of *Vaccinium* in Costa Rica (Stiles 1992). This report describes gape-feeding behavior of *D. lafresnayii* on an abundant, and tubular species of *Cavendishia* (Ericaceae) observed in a cloud forest in Yanacocha Reserve, Ecuador. The purpose of this paper is to describe this behavior and to discuss the role of the *D. humeralis* as a legitimate pollinator of *Cavendishia*.

METHODS

Diglossa lafresnayii was observed in Yanacocha Reserve, where it is the most abundant of three flowerpiercer species. Yanacocha Reserve is located on the Western slope of Pichincha volcano 12 km west of Quito, Ecuador. This 1,030 ha reserve stretches from 2,800-4,000 m in elevation and encompasses páramo, *Polylepis* forest, and cloud forest vegetation (Jocotoco). This study was conducted from the main trail system located at 3,300 m altitude and lying in the cloud forest; observations on gape-feeding were also collected on *Cavendishia* sp. in the *Polylepis* forest. Data was collected from 7 April- 28 April 2007, during the wet season. Plant identification was done at the University of San Francisco, Quito, with assistance from Professor Vlastimil Zak.

D. lafresnayii gape-feeding behavior and plant use were observed during walking transects and stationary observation periods. Walking transects took place on the main trail system between 07:00 h and 11:00 h and lasted from 2-4 h. Data was recorded on any feeding behavior, gape-feeding or nectar robbing by *D. lafresnayii*.

Stationary observational periods lasted from 1-3 hours and took place between 07:00 h and 10:00 h (13h total) and 10:00 h and 18:30 h (5h total). These observations were made from a distance of 4-6 m and were focused on an individual *Cavendishia* or group of *Cavendishia*. Flowerpiercer behavior was watched at four sites for a total of 18 h observation.

Data was recorded on each avian floral visitor, including the time spent per flower, the number of flowers visited, and the method of feeding (nectar robbing, gape-

feeding or legitimate feeding). Nectar robbing was defined as any time a flowerpiercer grabbed the base of a flower corolla with its bill, or any time a hummingbird inserted its bill into a hole in the base of the corolla. Legitimate feeding was defined as any time a hummingbird put its bill into the corolla through the normal opening. Gape-feeding was defined as any time a *D. lafresnayii* put its lower mandible into the corolla opening while its upper mandible remained outside lying against the corolla.

The total length of the flower, measured from the base of the bract to the farthest corolla point, and the effective corolla length, measured as the shortest distance between the corolla opening and the nectar were measured for 25 *Cavendishia* flowers. Twenty-five corollas with holes were located and the number of flowers with holes per plant and the number of holes per flower was recorded. A specimen of *Cavendishia* was collected from along the trail system and identified to genus at the University of San Francisco de Quito, in Cumbaya, Ecuador.

RESULTS

Diglossa lafresnayii was observed gape-feeding from *Cavendishia sp.* *Cavendishia* flowers are 26.2 ± 2.1 mm in total length (n=25), and 22.1 ± 1.7 mm in effective length (n=25), measured as the shortest length from the corolla opening to the nectary (Stiles 1992). The flowers hang in clusters with the corolla opening down from the ends of branches. The style hangs down from *Cavendishia* flowers past the corolla opening, which would put the stamen in direct contact with the throat plumage of *D. lafresnayii*, while the anthers are clustered inside the corolla where a disturbance by the lower mandible and tongue of *D. lafresnayii* causes a release of pollen. *D. lafresnayii* accessed the natural corolla opening in a variety of methods; by perching on a nearby branch, by perching on a lower inflorescence, or by hanging onto flower corollas with its feet, hanging down, and then stretching its head upwards to feed from neighboring corollas. *D. lafresnayii* inserted its lower mandible briefly (1-2 s) into each open flower, while the upper mandible remained outside the corolla, lying against its side. When the bill was inserted the flowerpiercer would often pull the flower to a new angle or position, depending on where *D. lafresnayii* was reaching from. Upon withdrawing its bill, the flower was jostled again, and six times when the flower was released pollen puffed out from the corolla opening.

Figure 1. *Diglossa lafresnayii* gape-feeding on *Cavendishia sp.*

On many occasions, individuals of *D. lafresnayii* were observed with white-yellow patches directly underneath the bill. On the 5 individuals closely observed with this whitish patch, the patch was variable in size, although it was always located directly under the bill.

When *D. lafresnayii* fed on a number of *Cavendishia sp.* it occasionally dislodged the corolla from its bract (22 out of 756 flowers visited, 3%). Either the corolla would fall when the flowerpiercer withdrew its bill, or the corolla would dislodge and catch on the lower mandible, the flowerpiercer would then open its mouth and shake its head to get rid of the corolla caught on its bill.

Many small scars and indents, less than 1mm in size were found on the outside of 5 out of 18 *Cavendishia* flowers examined. Small round holes were found in 26 out of 119 flowers examined (19%), average 1.0 ± 0.2 holes/flower.

Table 1. 18 hours of flower visitor data for *Cavendishia sp.*

Visitor	Type of Visit	Number of Flowers Visited	Percent of Total Visits (%)
<i>Aglaeactis cupripennis</i>	legitimate	21	2
<i>Eriocnemis mosquera</i>	legitimate	281	25
<i>Eriocnemis luciani</i>	legitimate	36	3
<i>Metallura tyrianthina</i>	legitimate	49	4
<i>Diglossa lafresnayii</i>	gape-feeding	756	66
Total		1143	100

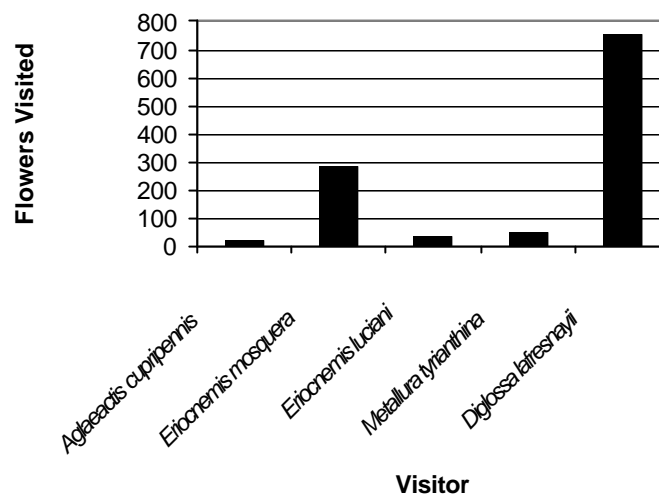


Figure 1: The number of flowers visited by each floral visitor to *Cavendishia sp.*

D. lafresnayii was the most common floral visitor to *Cavendishia* flowers, and of the eight aggressive interactions observed at a *Cavendishia* plant, six of them were between two *D. lafresnayii*. An aggressive interaction was defined as any time a target bird was feeding and an aggressor bird came in and tried to disrupt the feeding of the target bird, usually by diving at the target, or chasing it in the air. *D. lafresnayii* was also the aggressor in an interaction with *Eriocnemis mosquera* (Golden-breasted Puffleg), the *D. lafresnayii* was successful in disrupting the feeding of the hummingbird. The last aggressive interaction witnessed was initiated by an *Eriocnemis sp.* aggressor, which dived at a *D. lafresnayii* feeding in a *Cavendishia*. This attack was unsuccessful at interrupting the flowerpiercer gape-feeding. Only eight aggressive interactions were recorded in 18 hours of observation, and two *D. lafresnayii* were repeatedly witnessed feeding from a large clump of *Cavendishia* concordantly without having any altercations.

DISCUSSION

Stiles (1992), found that gape-feeding behavior by two *Diglossa* species on *Brachyotum* flowers was depositing pollen on the throat of *Diglossa* and hypothesized that the flowerpiercers were acting as legitimate pollinators for *Brachyotum*. My observations suggest that *Diglossa lafresnayii* is acting as an important pollinator for *Cavendishia* flowers as well. The flowerpiercers account for 66 percent of all visits to these flowers and their gape-feeding method puts their throats and bills in contact with

the reproductive parts of the flower. Pollen has been observed being released during gape-feeding behavior, and several individual birds carried a whitish-yellowish patch on their throat, I hypothesize that this patch is from the pollen of *Cavendishia sp.*, although pollen samples from the birds would be needed to determine exactly what species of pollen the flowerpiercers are carrying.

Several aspects of *Diglossa* behavior make it a suitable pollinator. *Diglossa* flowerpiercers hold territories (Moynihan 1962) but do not vigorously defend small groups of individual plants, as some hummingbirds do. By defending individual plants, these hummingbirds restrict gene flow, with negative effects for the pollination of the plant (Lasio & Naranjo 2003). The infrequent aggressive interactions observed were usually between two *D. lafresnayii*, and the observations of multiple individuals feeding from the same bush indicate that they are not excluding other potential pollinators from flowers. *D. lafresnayii* visited a number of flowers on the same plant, but was also observed visiting multiple plants in sequence.

Diglossa species are famous for their nectar robbing behavior, and this behavior potentially makes them a more effective pollinator than the hummingbirds with whom they share *Cavendishia* flowers. The hummingbird species visiting *Cavendishia* were observed legitimately feeding on nine other species of flowers, while the *Diglossa* flowerpiercers are more likely to have only *Cavendishia* pollen, or few grains from other species. In pollen samples taken from hummingbirds and flowerpiercers in Stiles (1992), relatively few *Diglossa* individuals were carrying pollen grains from species they were not gape-feeding from. On average, the hummingbirds carried pollen from more species.

Flowerpiercers are also known to feed from the natural opening of *Vaccinium* flowers (Stiles & Hespenheide 1972, personal observation) but the flower morphology makes it unlikely that they are effective pollinators for this genus. *Vaccinium floribundum* have short (7 mm effective corolla length $n=25$), and wide corollas. Their effective corolla length is shorter than the length of flowerpiercer bills, so it is unlikely that the flowerpiercers plumage regularly comes into contact with pollen or stamens of these flowers.

Stiles (1992) has hypothesized that aspects of *Brachyotum* morphology favor pollination by *Diglossa* species and may reflect a long evolutionary history for these two genera. *Cavendishia* flower morphology may also promote pollination by *Diglossa* species over nectar robbing behavior. The tubular corollas are situated in hard bracts, from which the corollas sometimes become dislodged. In the process of gape-feeding, some corollas were observed to dislodge easily. It may be that a more forceful entry by piercing the corolla would cause the corolla to fall off, once the corolla is gone, the nectar supply would dry up. Because *Diglossa* flowerpiercers defend territories and revisit flowers, it would be detrimental for them to be knocking off many corollas. However, it is also likely that the delicacy of the corolla-bract connection is also dependant on the age of the flower and the flowerpiercers could just be dislodging old corollas that would fall off eventually on their own.

The hard bracts themselves are certainly a deterrent to piercing the corolla, and the position of the flowers, bunched together in thick clumps with leaves on top, would make access to the base of the corolla difficult. However, *D. lafresnayii* has demonstrated great dexterity when reaching the corolla opening from underneath, often hanging by its feet from other corollas. Research into the geographical extent of "gape-feeding" behavior and its presence or absence in other *Cavendishia spp.* will hopefully improve our understanding of the evolutionary implications of the flowerpiercers' relationship with *Cavendishia*.

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Short Communication: New Hummingbird Diet Information from Yanacocha Reserve, Ecuador

Hummingbirds are famous for having specially adapted bills ideal for extracting nectar from long, tubular corollas while acting as pollinators for these flowers. The mutualism between the hummingbirds and the flowers they feed upon is well studied. Still, the diet information for many species of hummingbirds remains incomplete. In this paper I describe observations of new hummingbird-flower interactions (unlisted in del Hoyo 1999) obtained in a cloud forest in Yanacocha Reserve, Ecuador.

Located in the Ecuadorian Andes, on the Western slope of Pichincha volcano, Yanacocha Reserve is home to many species of hummingbirds, living in the cloud forest, *Polylepis* forest, and páramo vegetation within the park. Observations for this report were made along the main trail system of the 1, 030 ha reserve, lying within the cloud forest at an elevation of 3,300 m. Observations were conducted between 7 April 2007 and 28 April 2007, during the wet season, and plant identification was done at the University of San Francisco, Quito in the following days.

The first new observation was of an *Eriocnemis luciani* (Sapphire-vented Puffleg) feeding on a *Tropaeolum sp.* The bird hovered while feeding, sticking its bill briefly into the red corollas and visiting a string of flowers on the same plant. Another nectar source for *E. luciani* is *Cavendishia sp.*, an abundant, tubular ericad in Yanacocha. *E. luciani* was observed feeding from *Cavendishia* while hovering, inserting its bill into the distal corolla opening for 1-2 seconds. Once, an *E. luciani* acted as a secondary nectar robber for this species, inserting its bill into a large hole at the base of the corolla and presumably extracting nectar without coming into contact with the flower's reproductive anatomy.

Eriocnemis mosquera (Golden-breasted Puffleg) is a less-common Puffleg of Yanacocha's cloud forest. New diet observations for this species were made when it fed on a *Centropogon sp.*, inserting its bill legitimately in the natural corolla opening, and when it was frequently seen feeding on a *Cavendishia sp.* To reach the *Cavendishia* flowers *E. mosquera* would hover or perch on a nearby branch, leaf, or flower. Another feeding method of *E. mosquera* was to grasp onto a corolla opening with its feet and hang, reaching its bill into nearby corollas.

A third visitor to the *Cavendishia sp.* was *Metallura tyrianthina* (Tyrian metaltail). This short-billed hummingbird was capable of feeding legitimately from the *Cavendishia* flowers, but it was also observed acting as a secondary nectar robber

through pre-existing holes. *M. tyrianthina* fed from the *Cavendishia* in the same way as *E. mosquera*, hovering or grabbing on with its feet to a corolla opening and hanging to feed from neighboring flowers. *M. tyrianthina* are common in the reserve, they were observed feeding on *Vaccinium floribundum*, a *Pernettya sp.*, and a *Tropaeolum sp.* as well.

Vaccinium floribundum was also discovered to be an important food source for *Chalcostigma herrani* (Rainbow-bearded Thornbill), this flower was the only species *C. herrani* was seen feeding upon.

Coeligena lutetiae (Buff-winged Starfrontlet) fed from a variety of species, new records include *Siphocampylus giganteus*, *Salvia humboldtiana*, and a *Centropogon sp.* *C. lutetiae* few legitimately from all these flowers while hovering. *Aglaeactis cupripennis* was another previously unrecorded visitor to *S. giganteus*, it was seen feeding from the flowers by perching on the style, and inserting its head over the style and into the corolla. Although it does feed from the natural opening, because of its position above the anthers, I am unsure whether or not this species is a pollinator or a nectar thief of *S. giganteus*. *A. cupripennis* did feed legitimately from *Barnadesia spinosa*.

The last new interactions I observed involved *Pterophanes cyanopterus* (Great Sapphirewing) feeding legitimately on a *Fuchsia sp.* and *Aetanthus cf. nodosus*. This large hummingbird hovered while it fed.

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