



## Research Article

# Nectar drinking efficiency in lonchophylline and glossophagine bats: are “pump-like” or “mop-like” tongues better?

Diana Gamba<sup>1,3</sup>, Rossana Maguiña-Conde<sup>1,4</sup>, Camilo A. Calderón-Acevedo<sup>1,5</sup>, Santiago F. Burneo<sup>2</sup>, Nathan Muchhala<sup>1,\*</sup><sup>1</sup>Department of Biology, University of Missouri–St. Louis, St. Louis, MO 63121, United States<sup>2</sup>Museo de Zoología, Pontificia Universidad Católica del Ecuador, EC170143, Quito, Ecuador<sup>3</sup>Present address: Department of Biology, Pennsylvania State University, University Park, PA 16802, United States<sup>4</sup>Present address: Integrative Biology Department, University of Texas at Austin, Austin, TX 78712, United States<sup>5</sup>Present address: Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Republic of Panamá\*Corresponding author: Department of Biology, University of Missouri–St. Louis, St. Louis, MO 63121-4400, United States. Email: [muchhala@umsl.edu](mailto:muchhala@umsl.edu)

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## Abstract

Nectarivory has independently evolved twice in the bat family Phyllostomidae, resulting in elongated tongues with 2 contrasting morphologies. Glossophagines have lapping “mop-like” tongues with terminal papillae, while lonchophyllines have non-lapping “pump-like” tongues that pull nectar through lateral grooves. Using flight-cage experiments, we measured maximum tongue extension and compared the nectar extraction efficiency of glossophagines and lonchophyllines in flowers with different morphologies and nectar depths. We studied 3 co-existing species in a cloud forest in the Ecuadorian Andes: 2 glossophagines (*Anoura caudifer* and *A. cultrata*), and 1 lonchophylline (*Lonchophylla robusta*). We found that maximum tongue extension is associated with nectar extraction efficiency across the 3 species in that *L. robusta*, with an intermediate tongue extension, was also intermediate in extraction efficiency. Additionally, within the 2 species of *Anoura*, individuals with greater tongue extension had greater extraction efficiency. We also found that, across all species, extraction efficiency declined at a similar rate with increasing nectar depths. However, the mechanism behind this decline was different for the glossophagines—which increased visit duration the deeper the nectar—versus *L. robusta*, which instead decreased visit duration with deeper nectar but simultaneously showed a much sharper decrease in amount of nectar consumed per visit. Our results suggest that bats with “pump-like” and “mop-like” tongues have comparable nectar extraction abilities across a variety of floral shapes, despite the large differences in behavior and tongue morphology. Instead, tongue extension appears to be a better predictor of nectar extraction efficiency, although data from more species are needed to be able to generalize these results.

**Key words:** flight-cage experiments, Glossophaginae, Lonchophyllinae, nectar extraction efficiency, Phyllostomidae, tongue morphology.

## Eficiencia de extracción de néctar en murciélagos loncofilinos y glosofaginos: ¿son mejores las lenguas en forma de “bomba” o de “trapeador?”

### Resumen

La nectarivoría ha evolucionado de forma independiente 2 veces en murciélagos de la familia Phyllostomidae, lo que ha dado como resultado lenguas alargadas con dos morfologías contrastantes. Los glosofaginos tienen lenguas en forma de “trapeador” con papilas terminales, mientras que los loncofilinos tienen lenguas en forma de ‘bomba’ que bombean néctar a través de surcos laterales. Mediante experimentos en jaulas de vuelo, medimos la extensión máxima de la lengua y comparamos la eficiencia de extracción de néctar de glosofaginos y loncofilinos en flores con diferentes morfologías y profundidades de néctar. Estudiamos 3 especies coexistentes en un bosque nublado de los Andes ecuatorianos: 2 glosofaginos (*Anoura caudifer* y *A. cultrata*) y un loncofilino (*Lonchophylla robusta*). Encontramos que la máxima extensión de la lengua se asocia con la eficiencia de extracción de néctar en las 3 especies, ya que *L. robusta*, con una extensión intermedia de la lengua, también fue intermedia en la eficiencia de extracción. Además, dentro de las 2 especies de *Anoura*, los individuos de mayor extensión de la lengua tuvieron una mayor eficiencia de extracción. En todas las especies, la eficiencia de la extracción disminuyó a un ritmo similar con el aumento de las profundidades del néctar. Sin embargo, el mecanismo detrás de esta disminución fue diferente para los glosofaginos, que aumentaron la duración de la visita cuanto más profundo era el néctar, frente a los loncofilinos, que disminuyeron la duración de la visita con el néctar más profundo, pero al mismo tiempo mostraron una disminución mucho más pronunciada en la cantidad de néctar consumido por visita. En general, nuestros resultados sugieren que los murciélagos con lenguas en forma de “bomba” y en forma de ‘trapeador’ tienen capacidades comparables de extracción de néctar en una variedad de formas florales, a pesar de las grandes diferencias en el comportamiento y la morfología de la lengua. La extensión de la lengua parece ser un mejor predictor de la eficiencia de la extracción de néctar, aunque se necesitan datos de más especies para poder generalizar estos resultados.

**Palabras clave:** eficiencia de extracción de néctar, experimentos en jaulas de vuelo, Glossophaginae, Lonchophyllinae, morfología lingual, Phyllostomidae.

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Animals specialized to a specific food type often exhibit strategic adaptations for exploiting those resources, such as the New World leaf-nosed nectar-feeding bats (family Phyllostomidae; von Helversen and Winter 2003; Fleming et al. 2009; Muchhala and Tschapka 2020). These bats hover when feeding, which allows them to visit a wide variety of flowers without needing a landing platform. Their elongated rostrums and long, protractible tongues enable them to reach deep within the flowers, similar to hummingbirds (Winter and von Helversen 2003; Muchhala 2006). However, their foraging style is energetically expensive and exposes them to predators, hence nectar extraction is typically very rapid. Consequently, increasing nectar extraction efficiency, or amount of nectar obtained per second, is critical for the survival of these bats (von Helversen and Winter 2003).

Phylogenetic reconstructions based on morphological and molecular data suggest that nectar feeding has evolved independently 2 times in the New World, in 2 clades in the family Phyllostomidae (Griffiths 1982; Datzmann et al. 2010; Dávalos et al. 2014). Despite convergent evolution in terms of longer snouts, extensible tongues, and the ability to hover, these clades are strikingly different in tongue morphology and feeding behavior. Specifically, species in the subfamily Glossophaginae have papillary tongues, while those in the subfamily Lonchophyllinae have grooved tongues, with dramatically different mechanisms of nectar uptake (Tschapka et al. 2015). Glossophagines have “mop-like” tongues, which lengthen during nectar extraction through a muscular hydrostatic mechanism and then fill with blood when they reach the nectar, causing the long, keratinized papillae covering the tip to become erect (Harper et al. 2013). The bats extend and retract tongues via lapping movements, capturing nectar within the erect papillae and pulling it back into the mouth (Tschapka et al. 2015). In contrast, tongues of lonchophyllines are characterized by deep longitudinal grooves on either side (Griffiths 1982; Tschapka et al. 2015) that pull nectar up in a pump-like fashion. Rather than lapping, these bats keep their tongues inside the nectar for the entire feeding duration, actively pumping it into their mouths, likely via a combination of peristaltic contractions and capillary forces (Tschapka et al. 2015). Lonchophylline and glossophagine species commonly co-exist across their range (Tschapka 2004; Sperr et al. 2011), thus these tongue differences could play an important role in resource partitioning, allowing the bats to specialize on different flower types.

Here, we compared the nectar extraction efficiency of glossophagine and lonchophylline bats for different types of natural and artificial flowers. Given their striking difference in lingual morphologies and corresponding nectar uptake mechanisms, we hypothesized that they should differ in nectar extraction efficiency depending on the morphology of flowers visited. Specifically, given that glossophagine tongues require lapping, we predicted that their nectar extraction efficiency will show a sharper decline at deeper flowers as greater amounts of time will be spent extending and retracting the tongue. Additionally, we predicted that lonchophylline tongues will perform better with wide corollas and ample nectar, such that the tongue can be fully submerged and the corolla walls do not impede the pumping mechanism—while glossophagine tongues will perform better with narrow corollas and small amounts of nectar tucked into corners, which might be better absorbed by a “mop.” Alternatively, differences in nectar extraction efficiency could be primarily determined by tongue length, independent of tongue morphology. We tested these hypotheses in 3 co-occurring bat species in the Amazonian slope of the Ecuadorian Andes: 1 lonchophylline (*Lonchophylla robusta*) and 2 glossophagines (*Anoura caudifer* and *A. cultrata*).

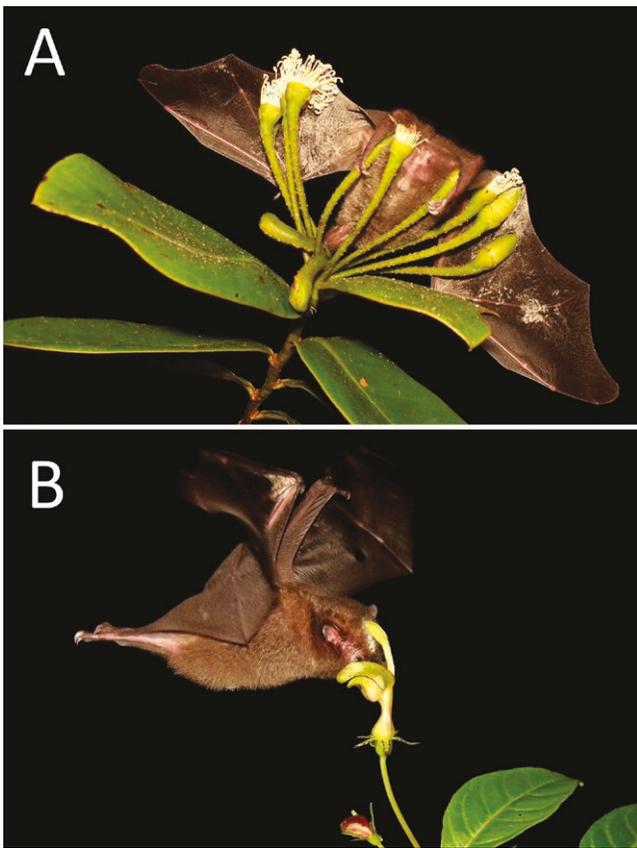
## Materials and methods.

### Experimental setup.

We set mist-nets and captured bats at the Wildsumaco Biological Station (0.67°S, 77.59°W; at ~1,400 m) in Napo, Ecuador, during June to August 2014. Nectarivorous species included *A. caudifer* (7 individuals) and *A. cultrata* (4 individuals) in the subfamily Glossophaginae, and *L. robusta* (6 individuals) in the subfamily Lonchophyllinae. We recorded their body mass with a Pesola Spring scale ( $\pm 0.3\%$  precision) and held them temporarily inside flight cages (1 bat at a time) where we trained them to feed on test tubes with ~20% artificial nectar (i.e., 20% sugar and 80% water, by volume). Individuals that did not feed within 2 h were released, while those that fed were held for several days to run experiments. Before starting experiments, we first measured tongue length by offering the sugar solution in a modified drinking straw, which was closed off at the base to hold the liquid. The narrow opening of the straw did not allow bats to insert their snouts, allowing us to isolate tongue length. After every 30 min we measured the depth of the solution consumed since the last check and then replaced approximately half of it. When distance to the surface of the solution was the same for 3 consecutive visits, we considered this to be maximum tongue extension length (sensu Muchhala 2006). All bats were released after experiments, and we followed the American Society of Mammalogist’s guidelines for conducting research on wild mammals for our bat captures and experimental work (Sikes 2016).

### Experimental design.

In order to compare the nectar extraction efficiency of glossophagine and lonchophylline bats, we presented individuals in the flight cages with 8 treatments or “flower types.” Treatments consisted of 2 species of natural flowers—*Burmeistera glabrata* (Fig. 1A) and *Marcgravia* spp. (Fig. 1B)—which were locally abundant during our study, and 6 types of artificial flowers of different lengths and widths. We removed any remaining nectar from these flowers with a syringe before filling with 0.2 ml (almost to the top of the corolla for *B. glabrata* and the nectary for *Marcgravia* spp.) of 10% artificial nectar (10% sugar and 80% water, by volume). For *B. glabrata*, stems of individual flowers were placed in a microcentrifuge tube filled with water (to maintain freshness) and a small piece of cotton (to fix it in place)—while for *Marcgravia* spp. a single nectary (of which each inflorescence has 2 to 4; Fig. 1B) was placed in the tube. Wire was used to affix the tube to a 1.5-m wooden pole positioned in the corner of the flight cage, with the wire “stem” holding the flower approximately 10 cm from the pole to facilitate nectar bat access during their hovering visits. The artificial flowers were similarly affixed to the pole with a wire, and included straws (4.75 mm diameter, 150 cm length) to simulate narrow corolla tubes, with 3 levels of artificial nectar depth (0, 15, and 30 mm), and test tubes (11 mm diameter, 120 mm length) to simulate wide corolla tubes, again with 3 levels of artificial nectar depth (15, 30, 45 mm). We increased these depths by 15 mm relative to those of the straws given that nectar bats have been shown to insert their snout around 15 mm into floral tubes with a similar diameter (Winter and von Helversen 2003). Both straws and tubes were much longer than tongue extensions previously recorded for these bats (Winter and von Helversen 2003; Muchhala 2006) and those recorded in this study, such that bat tongues did not reach the bottom during visits. We performed a total of 10 repetitions per bat per treatment, allowing only a single visit to each “flower” in a randomized order (see below), while recording with a high-definition Sony digital camcorder with night vision to determine visit duration (from when the snout entered until it exited the “flower”). Treatments were run for 2 to 3 days per



**Fig. 1.** *Anoura cultrata* visiting a *Marcgravia* spp. inflorescence (A) and a *Burmeistera glabrata* flower (B). Photos by NM.

bat, beginning at nightfall (~18:00 PM) until ~1:00 AM. For artificial flowers we alternated treatment order, presenting 3 test tubes followed by 3 straws, with the 3 depths within each of these groups randomly assigned. For *B. glabrata* and *Marcgravia* spp., treatments were performed as flowers were available, with the 10 visits per species consisting of 2 visits to each of 5 different individual flowers. To quantify amount of nectar consumed, we weighed each natural and artificial flower before and after a visit with a battery-operated balance with an accuracy in grams to 3 decimal points. We defined nectar extraction efficiency as the amount of nectar extracted per visit (g) divided by the duration of each visit (s).

### Statistical analyses.

To compare nectar extraction efficiency among species, we used generalized linear mixed-effects models or GLMM (normal distribution logarithmic link function) in the R package “lme4” (Bates et al. 2015). We ran a separate model for each of the 4 “flower types”: *B. glabrata*; *Marcgravia* spp.; straws; and tubes. For *B. glabrata* and *Marcgravia* sp., bat species were treated as fixed effects. For the straws and tubes, fixed effects included bat species and nectar depth, with the species  $\times$  nectar depth interaction as an additional term. Individual bat identity was included as a random effect in all models. When species was a significant effect in our models, we used the R package “emmeans” to perform post hoc comparisons implementing the Tukey’s HSD (honestly significant difference) test (Lenth et al. 2020). We performed similar analyses to investigate whether species were different in the amount of nectar extracted per visit and in the duration of floral visits for each “flower type.”

Previous studies on nectar extraction efficiency among bats adjusted efficiency by dividing it by the species-specific daily energy expenditure (DEE in  $\text{kJ day}^{-1}$ ), which is a function of body mass

(von Helversen and Reyer 1984; von Helversen and Winter 2003; Gonzalez-Terrazas et al. 2012; Tschapka et al. 2015). These authors reasoned that different-sized animals have different daily energetic requirements (i.e., smaller bats have lower daily energetic requirements than bigger bats), thus this adjustment provides more biologically meaningful comparisons (Gonzalez-Terrazas et al. 2012; Tschapka et al. 2015). In our study, we use unadjusted measurements because we were specifically interested in comparing raw extraction rates (i.e., amount of nectar per unit of time) between the 2 tongue morphologies, which should not be affected by daily energetic requirements. However, we also report analyses with adjusted measurements (Supplementary Data SD1) for comparison with these previous studies.

Finally, we compared tongue length of study species with a 1-way analysis of variance (ANOVA) using the R function “aov.” We then used the “TukeyHSD” R function to perform pairwise comparisons between species. To investigate the extent to which differences in nectar extraction efficiency are explained by tongue length, we ran a separate GLMM (normal distribution logarithmic link function) with extraction efficiency as the response variable, tongue length as a fixed effect, and “flower type” as a random effect. We performed 1 interspecific test (i.e., using data from the 2 glossophagine species, with species as an additional random effect) and 3 intraspecific tests (i.e., using data for each species separately), which allowed us to check if patterns were consistent across and within species. We did not include *L. robusta* in the interspecific test given that this species is in a separate clade. Because tongue length covaried with body mass in our study species, we also evaluated whether nectar extraction efficiency was better explained by tongue length or body mass. To this end, we performed similar analyses with body mass as a fixed effect.

### Results

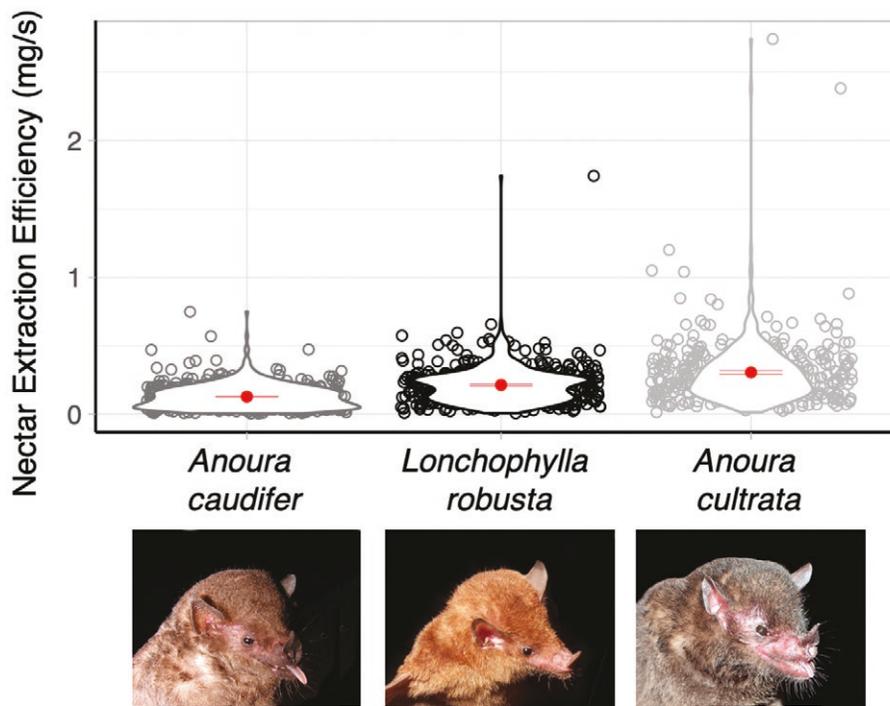
After removing 6 visits for which estimates of nectar removal were 0 or negative, and 9 visits for which the video camera failed to record, our total sample size included 1,332 flower visits: 401 for *A. caudifer*; 409 for *A. cultrata*; and 398 for *L. robusta* (Supplementary Data SD2 and SD3). Across all “flower types,” the larger *A. cultrata* (mean body mass  $\pm$  standard deviation [SD];  $16.75 \pm 0.96$  g,  $n = 4$  individuals) had on average a higher nectar extraction efficiency than did the intermediate-sized *L. robusta* ( $14.67 \pm 1.75$  g,  $N = 6$ ), followed by the smaller *A. caudifer* ( $10.07 \pm 0.45$ ,  $n = 7$ ; Fig. 2; Supplementary Data SD4). Below we detail how differences between species vary between the “flower” types that we tested.

#### Amount of nectar extracted per visit.

We found that the amount of nectar extracted per visit did not differ significantly between bat species for any of the treatments. Specifically, our GLMMs found no differences between species for straws ( $F_{(2,455)} = 3.73$ ,  $P = 0.15$ ; Fig. 3A), tubes ( $F_{(2,441)} = 0.12$ ,  $P = 0.87$ ; Fig. 3D), *B. glabrata* flowers ( $F_{(2,181)} = 2.37$ ,  $P = 0.26$ ; Fig. 3G), or *Marcgravia* spp. flowers ( $F_{(2,99)} = 1.56$ ,  $P = 0.31$ ; Fig. 3J). Nectar depth level exhibited a significant main effect, with less nectar extracted per visit the deeper the starting level in the artificial flowers (straws:  $F_{(2,455)} = 86.41$ ,  $P < 0.0001$ ; tubes:  $F_{(2,441)} = 61.55$ ,  $P < 0.0001$ ; Fig. 3A and D). Furthermore, we found a significant interaction between species and nectar depth level (straws:  $F_{(2,455)} = 8.21$ ,  $P < 0.0001$ ; tubes:  $F_{(2,441)} = 6.53$ ,  $P < 0.0001$ ): *A. caudifer* and *L. robusta* exhibited steeper declines in the amount of nectar extracted over the 3 nectar depths than did *A. cultrata* (Fig. 3A and D).

#### Duration of floral visits.

GLMM models showed that the duration of floral visits did not differ significantly between species when visiting *B. glabrata* ( $F_{(2,181)} = 0.30$ ,



**Fig. 2.** The mean rate of nectar extraction across all “flower types” was higher in *Anoura cultrata* ( $n = 5$ ), followed by *Lonchophylla robusta* ( $n = 6$ ), and lastly by *A. caudifer* ( $n = 7$ ). Open circles represent raw data, closed circles represent species means, and surrounding bars correspond to standard errors. Photos by CAC-A (*A. cultrata*), NM (*L. robusta*), and Carlos Boada (*A. caudifer*).

$P = 0.87$ ; Fig. 3H) or *Marcgravia* spp. flowers ( $F_{(2,99)} = 0.99$ ,  $P = 0.46$ ; Fig. 3K). For the straw treatments (Fig. 3B), there were similarly no main effects on visit duration for species ( $F_{(2,455)} = 5.04$ ,  $P = 0.21$ ), nor for levels of nectar depth ( $F_{(2,455)} = 1.17$ ,  $P = 0.29$ ). However, there was a significant interaction between species and nectar depth ( $F_{(2,455)} = 2.63$ ,  $P = 0.02$ ): *A. caudifer* and *A. cultrata* increased their hovering duration slightly for the deepest nectar (30 mm depth), while *L. robusta* decreased duration slightly (Fig. 3B). For the tube treatments (Fig. 3E), GLMM models found no main effect of species on visit duration ( $F_{(2,441)} = 7.87$ ,  $P = 0.13$ ), but did find a significant main effect of levels of nectar depth ( $F_{(2,441)} = 6.14$ ,  $P = 0.001$ )—visits lasted longer, on average, at deeper flowers. As in the straw treatments, we also detected a significant interaction between species and nectar depth levels in the tube treatments (GLMM:  $F_{(2,441)} = 7.96$ ,  $P < 0.0001$ ), in that *L. robusta* actually decreased hovering duration for deeper nectar, while the 2 *Anoura* species followed the overall trend of increased duration at deeper flowers (Fig. 3E).

### Nectar extraction efficiency.

Nectar extraction efficiency, or amount of nectar extracted per second, combines data from the previous 2 sections. We found that species were not significantly different in their nectar extraction efficiency when visiting *B. glabrata* ( $F_{(2,181)} = 1.27$ ,  $P = 0.54$ ; Fig. 3I) or *Marcgravia* spp. flowers ( $F_{(2,99)} = 0.005$ ,  $P = 0.99$ ; Fig. 3L). In contrast, for both treatments with artificial flowers (Fig. 3C and F) nectar extraction efficiency was significantly different among species (straws:  $F_{(2,459)} = 28.64$ ,  $P < 0.0001$ ; tubes:  $F_{(2,445)} = 31.97$ ,  $P < 0.0001$ ) and levels of nectar depth (straws:  $F_{(2,459)} = 49.06$ ,  $P < 0.0001$ ; tubes:  $F_{(2,445)} = 66.48$ ,  $P < 0.0001$ ). Post hoc tests revealed that in the straw treatments, *A. caudifer* was significantly less efficient than both *A. cultrata* and *L. robusta* ( $P \leq 0.0002$ ), but the latter 2 were not different from each other ( $P = 0.23$ ), while in the tube treatments all 3 species were significantly different from each other ( $P \leq 0.01$ ). Finally, we did

not find a significant interaction between species and levels of nectar depth for either treatment (straws:  $F_{(2,455)} = 0.73$ ,  $P = 0.55$ ; tubes:  $F_{(2,441)} = 1.45$ ,  $P = 0.20$ ); that is, the slopes of the declines in efficiency with increasing nectar level depth were similar among species (Fig. 3C and F).

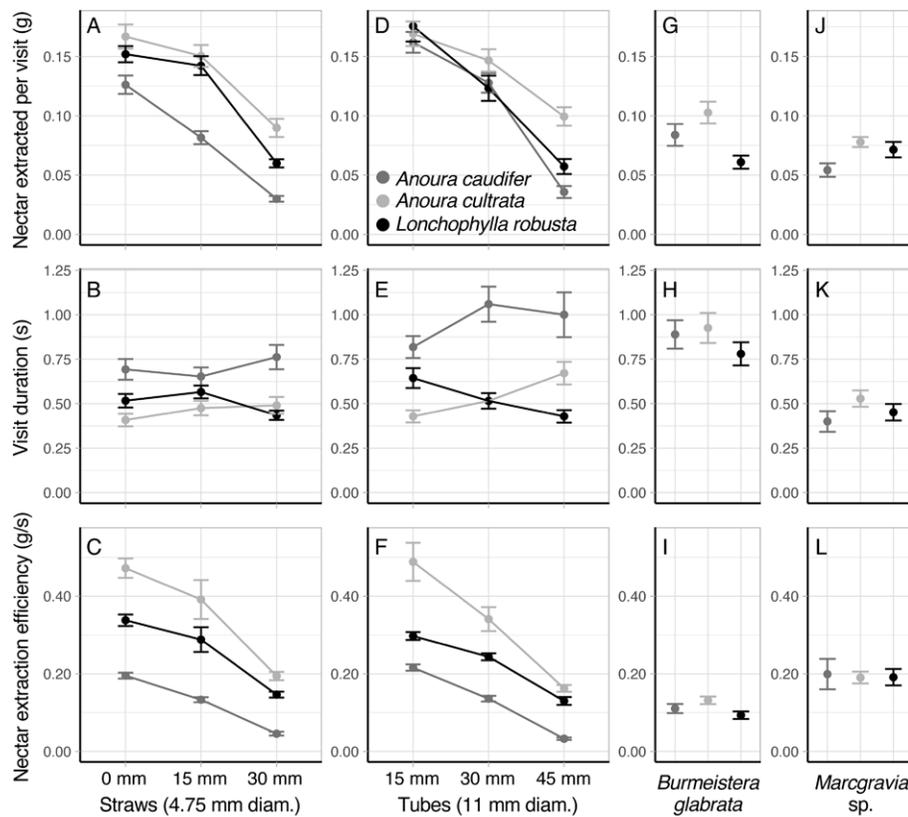
### Tongue length and nectar extraction efficiency.

Our measurements showed that *A. cultrata* was capable of the greatest maximum tongue extension (mean length  $\pm$  SD;  $49.4 \pm 4.5$  mm,  $n = 4$  individuals), followed by *L. robusta* ( $38.5 \pm 1.8$  mm,  $n = 9$ ) and lastly by *A. caudifer* ( $34.6 \pm 2.9$  mm,  $n = 6$ ). The overall differences were significant (ANOVA:  $F_{(2,16)} = 34.13$ ,  $P < 0.0001$ ), and a post hoc Tukey HSD test indicated that all pairwise comparisons were also significant (*A. caudifer* vs. *A. cultrata*:  $P < 0.0001$ , *A. caudifer* vs. *L. robusta*:  $P = 0.045$ , *A. cultrata* vs. *L. robusta*:  $P < 0.0001$ ).

We found a positive relationship between tongue length and nectar extraction efficiency for the 2 glossophagine species (GLMM:  $F_{(1,728)} = 6.43$ ,  $P < 0.0001$ ). When analyzing each species separately, this relationship remained significant for *A. caudifer* ( $F_{(1,389)} = 4.16$ ,  $P < 0.0001$ ) and *A. cultrata* ( $F_{(1,337)} = 4.35$ ,  $P < 0.0001$ ). It was not significant for *L. robusta* ( $F_{(1,396)} = -1.058$ ,  $P = 0.29$ ) (Fig. 4A). We found no relationship between body mass and nectar extraction efficiency for the 2 glossophagine species ( $F_{(1,728)} = 0.061$ ,  $P = 0.95$ ). When analyzing each species separately, there was a positive and significant relationship for *A. caudifer* ( $F_{(1,399)} = 2.036$ ,  $P = 0.042$ ), but not for *A. cultrata* ( $F_{(1,327)} = -0.174$ ,  $P = 0.86$ ) or *L. robusta* ( $F_{(1,396)} = -0.029$ ,  $P = 0.98$ ; Fig. 4B).

### Discussion

Nectarivory has evolved independently 2 times in the bat family Phyllostomidae, resulting in strikingly different tongue morphologies and nectar-drinking techniques—glossophagine “mop-like” and lonchophylline “pump-like” tongues (Griffiths 1978, 1982;



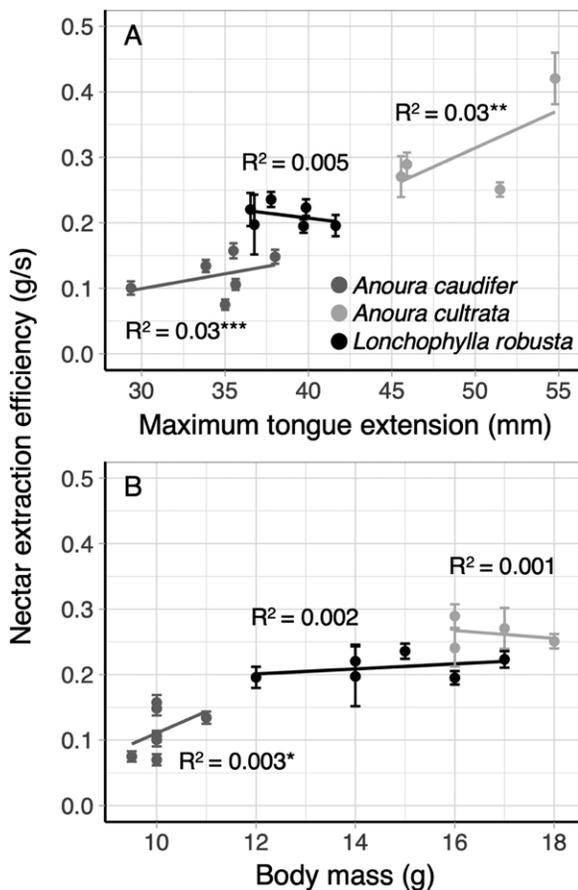
**Fig. 3.** Feeding behavior of 3 species of bats for straw (A–C) and tube (D–F) treatments, at 3 nectar depth levels, and for flowers of *Burmeistera glabrata* (G–I) and *Marcgravia* spp. (J–L). Top panels show the mean  $\pm$  SE amount of nectar (g) consumed per visit, middle panels show the mean  $\pm$  SE duration (s) of the visits, and lower panels show the overall mean  $\pm$  SE of nectar extraction efficiency (g/s).

Datzmann et al. 2010; Dávalos et al. 2014; Tschapka et al. 2015). Few studies have compared the effect of such divergent morphologies on foraging efficiency (but see Tschapka et al. 2015). Our results show that the different tongues do not, in fact, correspond to clear differences in nectar extraction efficiency across the various flower shapes; rather, the “pump-like” tongue of *L. robusta* consistently performs intermediate to the “mop-like” tongues of *A. caudifer* and *A. cultrata* (Figs. 2 and 3). This pattern held for both wide “flowers” (our tube treatments) and narrow “flowers” (our straw treatments), contrary to our prediction that lonchophylline tongues should perform better with wide tubes containing large pools of nectar. Thus, convergent evolution of nectarivory in New World bats seems to have resulted in tongues with comparable efficiency. Results instead suggest that tongue extension is an important determinant of feeding efficiency. Across and within the 2 glossophagine species, bats capable of greater tongue extension are more efficient at extracting nectar across a wide variety of flowers (Fig. 4). And *L. robusta*, whose tongue length was intermediate to the 2 *Anoura* species, also was intermediate in feeding efficiency. Overall, our study suggests that the striking differences between lonchophylline and glossophagine tongues likely play a less important role than overall tongue extension in resource partitioning where these bats co-occur. Future comparative studies on more species from each clade would be useful to further explore the role of tongue morphology and tongue length in feeding efficiency.

The only previous study to compare glossophagine and lonchophylline nectar extraction efficiency found that *Glossophaga soricina* was significantly less efficient than the larger *L. robusta*, even after standardizing nectar extraction efficiency by the species-specific daily energy expenditure (Tschapka et al. 2015).

Given that *G. soricina* also has a shorter tongue (Winter and von Helversen 2003), this result supports the idea that tongue length might be more important than tongue morphology in determining nectar extraction efficiency. A comparison of extraction efficiency across 3 glossophagine species (Gonzalez-Terrazas et al. 2012) further supports this idea, in that the shorter-tongued *G. soricina* was consistently less efficient than the other 2 species, and the longer-tongued *Musonycteris harrisoni* was more efficient than the intermediate-tongued *Leptonycteris yerbabuenae* at most nectar depths.

The idea that the feeding mechanism is not important for niche partitioning is further bolstered by the similarity of diets of lonchophylline and glossophagine bats when they co-occur. For instance, Delavel et al. (2005) found very high niche overlap values between 2 lonchophyllines and a glossophagine (0.825 to 0.883) in a rainforest site in French Guiana. Similarly, of the 19 flower species visited by our 3 study species in Wildsumaco, *L. robusta* visited 17, and visitation proportions were similar to those of the 2 *Anoura* species (see supplementary materials of Muchhala et al. 2024). On the other hand, Tschapka (2004) found that the diet of *L. robusta* was relatively specialized on the flowers of *Matisia cordata* compared to the diets of 3 co-occurring glossophagines in a Costa Rican rainforest, but also noted that the difference only occurred during peak flowering months, suggesting that the large size of *L. robusta* allows it to commute long distances to target high-energy food sources such as *M. cordata*. Along these lines, other differences among nectar bats such as body size, wing morphology, tongue length, and rostrum length may be more important in niche partitioning and coexistence than “mop-like” versus “pump-like” feeding mechanisms (Tschapka 2004; Gonzalez-Terrazas et al. 2012).



**Fig. 4.** Nectar extraction efficiency as predicted by tongue length (A) and body mass (B). Each point corresponds to the mean extraction efficiency across all experimental treatments for an individual bat.  $R^2$  values come from within-species linear models. GLMMs found significant positive relationships between tongue length and efficiency for *Anoura caudifer* ( $F_{(1,389)} = 4.16$ ,  $**P < 0.0001$ ) and *A. cultrata* ( $F_{(1,337)} = 4.35$ ,  $**P < 0.0001$ ), but not for *L. robusta* ( $F_{(1,396)} = -1.058$ ,  $P = 0.29$ ), while those between body size and tongue length were significant for *A. caudifer* ( $F_{(1,399)} = 2.036$ ,  $*P = 0.042$ ), but not for *A. cultrata* ( $F_{(1,327)} = -0.174$ ,  $P = 0.86$ ) or *L. robusta* ( $F_{(1,396)} = -0.029$ ,  $P = 0.98$ ).

Given that the glossophagine “mop-like” tongue requires lapping, we predicted that nectar extraction efficiency would show a sharper decline at deeper depths because most of the visit time would be used in extending and retracting the tongue. However, results show that all 3 species of bat experience similar declines in nectar extraction efficiency at deeper depths (Fig. 3). Further, these declines were similar among “straw” and “tube” treatments (compare Fig. 3C and F), suggesting that the fact that bats are able to insert their snouts in the latter does not affect these patterns. Interestingly, a closer look at the data suggests that the mechanisms behind these similar declines may differ among species. Specifically, there was a significant interaction between species in terms of hovering time per visit, in that while the *Anoura* species increased duration for deeper tubes/straws, *L. robusta* actually decreased duration (Fig. 3B and E). Thus, in glossophagine bats feeding efficiency declines with depth may be due to the extra time needed to extend and retract the tongue farther—while in lonchophylline bats the extreme muscular extension of the tongue might render the pumping force less efficient, resulting in less nectar consumed at deeper depths (see also Tschapka et al. 2015).

The positive and significant association between tongue extension and nectar extraction efficiency across and within our glossophagine bats suggests a role of tongue length on foraging efficiency (Fig. 4A). In contrast, the lack of such association within

*L. robusta* suggests that efficiency for “pump-like” tongues may not be impacted by length. Why longer “mop-tongues” are more efficient than those that are shorter, even at shallow nectar depths, is not immediately clear. One possibility is that overall tongue length is correlated with the length of the portion of the tongue covered in papillae, thus longer tongues provide larger “mops” with more surface area. Anecdotally, *A. fistulata*, with a tongue twice as long as other glossophagines, also has a patch of papillae twice as long (NM, personal observation; Supplementary Data SD5; Harper et al. 2013), suggesting that developmental constraints may lead to isometric increases in lengths of both. Our results also show that, although body mass correlates with tongue length, body mass is not a significant predictor of extraction efficiency across glossophagine species, nor within species for *A. cultrata* or *L. robusta* (although it is a significant predictor for *A. caudifer*; Fig. 4B).

Although we tested bats over a wide range of floral shapes and nectar depths, we likely did not cover the full diversity of bat-pollinated flower shapes and their corresponding nectar presentation. For instance, nectar quantity can vary greatly among different species, and it can be produced in small discrete amounts throughout the night or in large amounts only once during the night (Machado et al. 1998; Kays et al. 2012; Tschapka et al. 2015). Tschapka et al. (2015) hypothesized that a “mop-like” tongue could be more efficient at extracting nectar produced in very small amounts because a “pump-like” tongue needs to be completely submerged for nectar uptake to happen. Our data hint at this possibility, in that *L. robusta* only extracted 30% on average of the 0.2 g of nectar we placed in *Burmeistera* flowers (vs. 52% for *A. cultrata* and 42% for *A. caudifer*; Fig. 3G). These flowers have narrow constrictions above the larger nectar chamber, with nectar likely tucked away in the corners of this chamber—features that may favor “mop-like” tongues. On the other hand, *L. robusta* extracts comparable proportions of nectar as the *Anoura* species from the less complicated, tube-like nectaries of *Marcgravia* spp. (Fig. 3J). Along with accessibility, nectar viscosity could also be important, in that highly viscous nectar might be harder for “pump-like” tongues if they require more muscular effort from the lingual canals (as an analogy, consider drinking honey vs. water through a straw). For example, a recent study in honeybees showed that as nectar viscosity increases, honeybees facultatively switch from a “pump-like” mechanism to a “mop-like” mechanism of nectar intake (Wei et al. 2020). Data from more species of bat flowers would be useful to further explore the importance of nectar accessibility and viscosity for nectar extraction efficiency of glossophagine and lonchophylline bats.

## Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.** Appendix repeating nectar extraction analyses, in this case with efficiency for each bat divided by its species-specific daily energy expenditure.

**Supplementary Data SD2.** Table showing sample sizes for all bat species and treatments.

**Supplementary Data SD3.** Data obtained in this study and used for analyses.

**Supplementary Data SD4.** Violin plots of feeding efficiency per treatment plotted separately for each species.

**Supplementary Data SD5.** Image showing patch of papillae on distal tip of the tongue of *Anoura fistulata*.

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## Author contributions

DG performed analyses, created figures, and wrote the original draft. RM-C and CAC-A performed flight cage experiments and helped design the project. SFB aided logistics and project administration. NM conceptualized and oversaw the project, and all authors helped with revisions.

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## Conflict of interest

None declared.

## Data availability

Raw data can be found in [Supplementary Data SD3](#).

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