Investigating the convergent evolution of nectar-feeding birds through the lens of biomechanics

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Abstract

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Nectar-feeding birds employ highly specialized mechanisms to collect minute liquid rewards hidden within floral structures. There are over 20 independent evolutionary origins of nectarivory amongst birds, but little is known about how most of these lineages ingest nectar. In this dissertation, I examine the feeding mechanics of two distantly related nectarivorous bird groups and investigate the effects of nectar concentration on energy intake rates. In Chapter 1, I review what is known about avian nectar-drinking mechanics and define the knowledge gaps that should be addressed to understand how the multitude of nectar-feeding birds are able to consume their liquid food. In Chapter 2, I investigate if convergent morphologies underlie convergent biomechanics of nectar-feeding in two distantly related bird clades: sunbirds (family *Nectariniidae*) and hummingbirds (family *Trochilidae*). In Chapter 3, I describe the drinking mechanics of a morphologically unique group of nectar-feeding birds, the hanging parrots (genus *Loriculus*), and compare them with the mechanics of birds with more "typical nectarivore" feeding apparatus morphologies. In Chapter 4, I use the liquid-ingestion mechanics that I described for sunbirds to predict the nectar consumption rate and energy intake rate of multiple species feeding from a

range of nectar concentrations. Using biomechanics to examine the variety of nectar-feeding mechanisms in birds unveils unique biological solutions to complex physical challenges. In turn, these mechanisms can be used to predict and test how different nectar-feeding birds interact with the variety of plant species they encounter in nature and what environmental factors shape their ecological interactions and evolutionary trajectories.

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0.2 Dedication

This thesis is dedicated to the animals that made it possible. Whether captured, recorded, and released, or museum specimens that were used for morphological studies this project is nothing without them. I hope that the work I do honors them as the beautiful, complex, living things they are and contributes to their continual protection. I would also like to dedicate this to my friend Neil Karpe who never got the opportunity to go to graduate school but would have helped the world with his engineering gifts. I will always miss you.

Chapter 1

On the feeding biomechanics of nectarivorous birds

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1.1 Abstract

Nectar-feeding birds employ unique mechanisms to collect minute liquid rewards hidden within floral structures. In recent years, techniques developed to study drinking mechanisms in hummingbirds have prepared the groundwork for investigating nectar feeding across birds. In most avian nectarivores, fluid intake mechanisms are understudied or simply unknown beyond hypotheses based on their morphological traits, such as their tongues, which are semi-tubular in sunbirds, frayed-tipped in honeyeaters and brush-tipped in lorikeets. Here, we use hummingbirds as a case study to identify and describe the proposed drinking mechanisms to examine the role of those peculiar traits, which will help to disentangle nectar-drinking hypotheses for other groups. We divide nectar drinking into three stages: (1) liquid collection, (2) offloading of aliquots into the mouth and (3) intraoral transport to where the fluid can be swallowed. Investigating the entire drinking process is crucial to fully understand how avian nectarivores feed; nectar-feeding not only involves the collection of nectar with the tongue, but also includes the mechanisms necessary to transfer and move the liquid through the bill and into the throat. We highlight the potential for modern technologies in comparative anatomy [such as microcomputed tomography (µCT) scanning] and biomechanics (such as tracking BaSO4-stained nectar via high-speed fluoroscopy) to elucidate how disparate clades have solved this biophysical puzzle through parallel, convergent or alternative solutions.

1.2 Introduction

As a clade, birds consume a variety of liquids for hydration or as a food source. Efficient consumption of liquids has had a significant impact on the morphological and physiological traits of many avian groups. Nectarivory, in particular, continues to play an integral role in the evolution of approximately 30 avian clades (1), leading to a large diversity of forms. To drink a liquid (usually water), most birds submerge their bills to some extent into a reservoir and enclose a mouthful of fluid (2). Given that the quantities of nectar concealed inside flowers are small (on the order of microliters; 3, 4) and the narrow floral corolla (petals) limits the bill's ability to scoop, capturing mouthfuls of nectar with just the bill is not a plausible solution for avian nectarivores (see Glossary). Instead, nectar-feeding birds use their tongues to entrap fluids, while their bills guide the tongue and allow access to the nectar chamber (5).

A nectarivore's ability to handle nectar is not only affected by the morphology and function of the feeding apparatus (e.g. bill and tongue), but is also significantly influenced by the characteristics of the liquid reward (e.g. composition, volume, concentration). Within the context of nectar-feeding biomechanics, sugar concentration is a particularly important characteristic of nectar. The viscosity of nectar increases exponentially with increasing sugar concentration (6), whereas its caloric content increases linearly with concentration, resulting in a trade-off between speed of volume extraction and caloric intake, with optimal values that depend on the details of the feeding mechanism at work (e.g. 7). At lower sugar concentrations, a bird can extract liquid faster (their tongues move faster through the liquid, and the liquid moves inside the tongue and bill more rapidly), but it obtains fewer calories per microliter (cal µl−1) (7, 8). In more concentrated nectar, the bird acquires more calories per microliter, but the increased viscosity reduces the volumetric uptake rate (µls−1). Ultimately, nectarivores are expected to use energy gain rates (cal s−1), which are influenced by the coupling between floral/nectar characteristics and the nectarivore's morphology/mechanics, to make foraging decisions (9, 10). Therefore, understanding the process of how nectar-feeding birds drink, and the links between mechanisms and ecology (e.g. 11) and behavior (12) for nectar drinking has implications for our understanding of nectarivore biology and coevolution with flowers (e.g. 13). The physical challenges (e.g. narrow corollas and varying nectar viscosities) that nectarivores face when collecting concealed and minute liquid rewards have led to unique biomechanical solutions and morphological adaptations of their feeding apparatus.

Here, we focus on biomechanical hypotheses of avian nectar drinking at each of the three following stages: (1) the initial stage: liquid collection by the tongue from the nectar source; (2) the middle stage: offloading the aliquot of nectar from the tongue; and (3) the final stage: intraoral transport of the fluid to the throat for swallowing (Fig. 1). Although there are approximately 30 independent origins of nectarivory amongst birds (1), research on nectar-feeding mechanics has almost solely focused on hummingbirds (Trochilidae); therefore, we will use these as a case study. We also present mechanisms proposed for other avian nectarivores, highlight current knowledge gaps and suggest methods to test a variety of hypotheses at each drinking stage.

1.3.1 How do hummingbirds drink nectar?

The distal portions of hummingbird tongues that make initial contact with nectar are primarily made of β-keratin (14). Their tongues are solid at the base, bifid at the tip, and each side of this bifurcated region consists of a semi-tubular groove with a dorsal supporting rod and distal fringes (see Glossary) (Fig. 1). Hummingbird bills are narrow, long, keratinous structures formed like sheaths around mandibular and maxillary bones (see Glossary). Their bills taper internally such that the empty space within the bill decreases longitudinally, forming a funnel near the tip (15). These morphological characteristics determine the range of biomechanical possibilities for liquid collection and transport (e.g. 16).

1.3.2 Initial stage: nectar collection

One of the first avian fluid intake hypotheses was that the hummingbird tongue functions as a 'drinking straw' (17–21) and terms of this nature (e.g. suction) are still used today to describe hummingbird feeding (22). The idea that the hummingbird tongue functions as a straw assumes the involvement of suction (see Glossary), specifically hermetic suction (Box 1, Fig. 2A), through the lingual grooves (see Glossary). However, even though the hummingbird tongue possesses tube-like grooves (Fig. 1) (e.g. 21), it is not plausible that they function as straws. This is because the tongue is not hollow for its entire length, and the open nature of the grooves precludes the pressure gradient needed to pull nectar into the tongue via hermetic suction (Fig. 2A) (19, 21).

The hummingbird tongue has also been hypothesized to function as a capillary tube (19–21), and some have used the term 'capillary suction' (e.g. 23). The use of the word suction alongside capillary forces is confusing because, within the context of vertebrate feeding, suction implies that the expansion of a structure is used to pull a liquid into a cavity (Box 1). Surface tension draws the meniscus of the liquid up structures, a process called capillarity. The surface tension at the liquid–air–solid interface imparts a force on the structure to pull it in towards the liquid as opposed to expanding it. We therefore recommend that researchers discontinue using the term capillary suction. Instead, we use capillary filling (Fig. 2B), which occurs when a liquid enters a hydrophilic tube, and the surface tension at the meniscus pulls the liquid through the tube until an antagonistic force, such as gravity, equals the capillary force, halting the movement of the fluid (24, 25). The expectations for a capillarity-based mechanism include: (1) empty lingual grooves that form nearly closed tubes (capillary filling primarily works with enclosed tubes/structures), traveling to contact the nectar; (2) a constant or decreasing (due to surface tension forces) capacity of the tongue throughout the nectar-loading process, as opposed to flattened grooves recovering their cylindrical configuration during the process; and (3) the existence of a concave meniscus inside the tongue moving proximally and filling the grooves (26). Although capillary filling has been the dominant theory for decades, experimental data have only supported this mechanism under artificial conditions that hummingbirds never experience when drinking from wildflowers, specifically restricting them to feed at unnaturally long distances between the bill tip and nectar surface (27).

Recent high-speed video evidence (26, 28) has demonstrated that the hummingbird tongue fills with two different mechanisms: fluid-trapping and elastic filling. Fluid trapping (Fig. 2C) occurs when surface tension applies a force to the distal fringes, causing them to roll medially and trap fluid within the tongue tip (fig. 2 in 28). Elastic filling (Fig. 2D) relies on the compression and expansion of the lingual grooves during the licking cycle (26). The tongue is dorsoventrally compressed by the bill tips as it is protruded, and then expands and fills once it contacts the nectar (26). Most notably, there is no concave meniscus observed during elastic filling, suggesting that capillary filling is not the predominant mechanism. Additionally, the elastohydrodynamic mathematical model outlined by Rico-Guevara et al. (2015) fits their experimental data collected from feeding in live birds and results in a filling rate that is an order of magnitude faster than in previous laboratory tests with hummingbirds (27). When hummingbirds are forced to feed at unnaturally long distances, the elastic energy stored in the tongue due to compression in the bill tips is released before the tongue contacts the nectar. The grooves recover their cylindrical configuration and fulfil the conditions for capillary filling to occur, hence capillary filling is a physically plausible but biologically irrelevant mechanism of nectar collection for hummingbirds.

The unlikelihood of lingual capillary filling as an important mechanism of drinking in hummingbirds is also borne out by their elevated licking rates. Whereas capillary filling would fill the tongue too slowly (over 25 ms, 26) to match the tongue reciprocation rates recorded in wild hummingbirds (14-17 Hz, 29, 30), the elastic filling mechanism fills the tongue at an appropriate rate (~15 ms, 26). Interestingly, previous capillary filling mathematical models found ‘optimal concentrations’ of nectar that closely matched those commonly offered by flowering plants in nature (7, 23, 24, 31). However, these studies exploring optimal concentrations focused solely on the collection stage of nectar feeding, as opposed to the entire process (see sections below). For example, a later stage may have a greater impact on caloric uptake rates than the initial stage depending on the specifics of fluid transport (through tongue and bill) and nectar properties (i.e. viscosity). Thus, our ability to determine optimal concentrations for caloric uptake depends on our ability to model all the feeding stages and finding the one that is limiting under particular conditions.

1.3.3 Middle stage: offloading nectar into the bill

A nectar-feeding bird must rapidly transfer the minute aliquots captured in each lick to the bill. This offloading stage is critical, because without further action, a bird cannot swallow the aliquot or clear the tongue to restart the collection process. Based on manipulation of museum specimens, inferences from morphology and observations of feeding in captive birds, several authors proposed hypotheses regarding nectar offloading in hummingbirds (17, 32–35). Gadow (1883) suggested that oropharyngeal and hyobranchial muscles (see Glossary) cyclically raise and depress the basal portion of the tongue to generate a vacuum between the tongue and the palate; nectar then flows into the oral cavity, after which the tongue resets at the top of the palate (17). This pumping action inside the bill would be enabled by tomial overlap (see Glossary) at the margin of the upper and lower jaws, potentially making the internal bill space hermetically sealed (see Glossary). A different mechanism was proposed by Moller (1930), who suggested that the beak was used as a pump through a combined action of the tongue base moving diagonally downward and backward; in this model, the tongue is likened to a piston and the bill to a cylinder (32, 33). Steinbacher (1935) further proposed that the rapid pharyngeal movements observed in captive birds (cf. 32) could create a suction force at the bill base.

A consensus hypothesis emerged, stating that hummingbirds offload nectar with hermetic suction (Box 1, Fig. 2E) generated by an expansion of the mouth at the bill base from a pumping action created both by tongue and pharynx movements and made possible by a sealed, tube-like middle portion of the bill (cf. 36, fig. 11 in 37). Furthermore, the flexibility of hummingbird mandibular rami (see Glossary) (38–40) raises the possibility of basal mandible expansion as a suction generator. These suction-based offloading hypotheses, however, seem incompatible with the morphology of hummingbird tongues and bills. Generating suction in the oral cavity (via any of the aforementioned mechanisms) would generate a negative pressure differential, but nectar could not be pulled through the hummingbird tongue because the longitudinal grooves are open. Air would be drawn through open spaces at the bill tip or exposed grooves (if there is no distal opening, suction could not operate) and would flow over the open grooves into the bill cavity instead of applying a force to the nectar and offloading it from the tongue. This process can be likened to drinking liquid using a straw with a hole in the side – the liquid cannot easily flow through the straw because it is not fully sealed. If the tongue was completely inside the bill, then there would be no pressure differential across the tongue, because the hermetically sealed intraoral cavity would increase and decrease in pressure uniformly, and thus no liquid would flow.

Eventually, with the advent of high-speed videography, Ewald and Williams (1982) showed that the hummingbird tongue was compressed by the bill tips during protrusion, in a process we call tongue wringing (Fig. 2F). Upon each lick, the tongue collects liquid, which is then physically extruded and funneled for collection when the tongue is pushed through a small opening at the bill tips to begin the next lick; compression of the tongue structures releases the nectar trapped inside. As the tongue is retracted into the bill after collecting nectar, the bill tips are kept separate to avoid squeezing out any nectar. For hummingbirds, detailed studies (e.g. 15, 41) have not only supported this finding, but also revealed what seem to be intricate morphological adaptations to enhance the nectar-offloading process. Near the bill tip, there is a reduction in oral cavity volume before the external narrowing of the bill (by thickening of the mandibular floor), which creates an internal, funnel-like arrangement (14). Additionally, in the middle of the funnel, prong-like structures project inward and forward from longitudinal ridges on both the upper and lower bills (Fig. 1, 15). These projections and longitudinal change in oral cavity cross section are hypothesized to enhance the nectar-offloading process by guiding the tongue through the intraoral-squeezing zone of the bill during tongue wringing, but mechanistic models of their functioning have not yet been tested. It is worth highlighting the multiple connections between stages and mechanisms. For example, compression of the tongue during protrusion is useful to both wring it and reset the grooves for the next cycle of elastic filling (Fig. 2D).

1.3.4 Final stage: intraoral transport of nectar

Most birds move water to the throat by tipping their head back after enclosing a mouthful of the liquid with their bill (2, 5). Although nectar-feeding birds are potentially capable of doing the same, the time needed to allow gravity to pull the fluid to the throat would greatly decrease foraging efficiency; additionally, the small internal diameters of nectarivore bills may generate high surface tension forces relative to the weight of the liquid, preventing the liquid from flowing to the throat.

One hypothesis has proposed that the base of the tongue could adhere to the offloaded nectar and bring it towards the pharynx as the tongue is retracted (29, 33, 34, 42). This mechanism, which we have called cohesive pulling (Fig. 2G) (41), utilizes liquid adhesive forces to hold a small layer of nectar to the tongue, and liquid cohesive forces to pull the rest of the nectar with the tongue. Additionally, hummingbirds have flattened keratinous structures (alae linguae, fig 7C in 14, 21) at the proximal end of their tongue shaped similar to a spatula, which may be used to pull or push the nectar into the throat as the tongue is retracted (41). The cohesive pulling hypothesis does not require hermetic sealing of the intraoral space.

Another kind of pulling mechanism may operate by expansion at the bill base. If all the spaces at the proximal end of the oral cavity are filled with nectar and the base expands, there will be a net backwards displacement of the liquid column. This mechanism, which is like the suction-feeding mechanism in fish (43), is a form of cohesive suction driven by proximal oral expansion (Box 1, Fig. 2H). Cohesive suction generates force via enlargement of an internal cavity that is already filled with liquid. There are non-exclusive options to generate this basal bill expansion: (1) the base of the mandibular rami could bow and separate laterally, bending outwards (38–40); (2) the maxilla and mandible could separate dorsoventrally with the latter displacing downwards; and/or (3) the throat can be expanded through depression of the hyoid apparatus (see Glossary) or involving associated musculature. These mechanisms function like expanding bellows to generate a suction force and draw nectar toward the throat.

Along similar lines, Ewald and Williams (1982) suggested the existence of a suction component after observing bulging in the throat region during tongue protrusion of hummingbirds (cf. 32, 35). The mechanism implied in their suggestion, hermetic suction, generates pressure using air in the oral cavity and requires that the basal and medial portions of the bill remain hermetic to allow for vacuum production (Box 1, Fig. 2I). Hermetic suction has also been proposed to be generated by the depression of the tongue, creating a vacuum between its base and the palate (Fig. 2J) (17).

The last mechanism, hydraulic displacement, depends on the use of tongue wringing for nectar offloading, as described above. While the nectar is offloaded from the tongue via repeated cycles of wringing, a new aliquot of nectar fills the tip of the bill and pushes back the nectar that was collected in previous licks (Fig. 2K) (41). After the last tongue reciprocation, the remainder of liquid left in the oral cavity could be brought back to the throat via one of the other mechanisms described above. Notably, cohesive pulling could work in tandem with hydraulic displacement as it would not require any change in bill or tongue movements to continue to bring nectar to the throat. It is relevant to note that, while feeding on flowers, hummingbirds continue to lick even when the nectar has been depleted (9). This could be a byproduct of delayed sensory information at their high licking rates – part of their behavioral strategy – to ensure that all the nectar has been collected. Additionally, this action may be used to draw the remaining nectar in the bill back to the throat through some of the mechanisms described above, such as cohesive pulling or hydraulic displacement.

1.3.5 How do other nectarivorous birds drink nectar?

Thus far, we have used hummingbirds as a case study to review the biomechanics of avian nectarivory. The feeding mechanics in other avian nectarivores remain mostly unknown. In Table 1, we present the current hypotheses inferred from the morphology of the feeding apparatus, by nectar-feeding stage, for four other major clades of avian nectarivores. We posit plausible drinking mechanisms for groups currently lacking hypotheses for any given feeding stage. However, we caution that these hypotheses must be evaluated using experimental data, as there are dynamic processes involved in feeding that cannot be inferred from morphology alone.

Some groups share significant morphological similarities to hummingbirds in their feeding apparatus. Sunbirds, for instance, have long, tubular, fimbriated (fringed with hair-like structures) tongues that could use similar elastic filling mechanisms to those of hummingbirds (Fig. 2D, 44). Their bills are also relatively long and narrow, and possess similar internal features such as mandibular grooves and prongs (15, 18, 42), which may guide the tongue through the intraoral-squeezing zone of the bill during tongue wringing (Fig. 2F, 15). Additionally, Gadow suggested that sunbirds use suction by cyclically expanding and contracting their oral cavities using oropharyngeal and hyobranchial muscles (Fig. 2A,E), and that honeyeaters use the same pumping action for generating suction to draw in nectar (17). Honeyeaters have brushed-tipped tongues that may trap liquid among the bristles using surface tension (e.g. 16), which could be drawn close together to effectively create an enclosed capsule of liquid at the tongue tip (45). Honeyeaters also have lingual grooves, which could use capillary filling to draw the nectar into the rest of the tongue body (Fig. 2B, 45). Hawaiian honeycreepers have tubular tongues (46–51), which may lend themselves to surface tension-based mechanisms such as capillary filling or fluid trapping (Box 1). Nectarivorous parrots have complex, muscular tongues ending in many filiform papillae (see Glossary) that can be used for fluid trapping (52, 53), similar to those of mammalian nectarivores (e.g. 54), where surface tension holds liquid between adjacent papillae (55). Although other groups of avian nectarivores have nearly no study of their nectar-feeding mechanisms, many have frayed-tipped tongues (e.g. 56), such that they could rely on surface tension based mechanisms for nectar collection.

For offloading the tongue, we hypothesize that most nectar-feeding birds that drink with the bill nearly closed or cyclically opening and closing (like hummingbirds) will wring their tongues with the bill tips. This is the most parsimonious process that has been described – it requires little to no specialized bill morphology beyond an internal oral cavity and the ability to compress the bill tips together when protruding the tongue and separate them when retracting the tongue. Nectar-feeding parrots, meanwhile, feed with their strongly hooked bills wide open while reciprocating their tongues (53), and thus cannot use tongue wringing (44). However, given their ability to manipulate tongue papillae (53), we hypothesize that nectar-feeding parrots may wring their tongues of nectar by compressing their papillae together, to squeeze the nectar out from between them once the tongue is retracted within the bill.

Finally, sunbirds have been proposed to use a suction-based mechanism, lowering their tongue to the bottom of their oral cavity to facilitate intraoral transport of nectar (17, 18, 57). We hypothesize that most nectarivorous birds use hydraulic displacement as part of their intraoral transport of nectar (Fig. 2K). Additionally, the tongue reciprocating in and out of the bill aids in nectar transport via cohesive pulling of the liquid along the structure of the tongue, as it moves toward the back of the bill (Fig. 2G). These mechanisms entail the most parsimonious solutions: nectarivores only need to have a relatively closed medial and proximal portion of the bill to allow the previously collected aliquots of nectar to travel into the throat via hydraulic displacement. Moreover, nearly any tongue will be able to pull a portion of liquid to the back of the bill with it via cohesion, assuming its outer surface is not hydrophobic.

1.4 Discussion

Out of the four ways in which birds interact with nectar or any other liquid for drinking (Box 1), all the nectar-feeding mechanisms reported to date involve fast tongue reciprocation, a form of displacement of feeding structures. The other three core methods are utilized in the specific mechanisms detailed in the previous sections (and illustrated in Fig. 2). The geometry of feeding structures influences capillary filling, fluid trapping, elastic filling and cohesive pulling. The compression of feeding structures influences fluid trapping, elastic filling (its preparation), tongue wringing and hydraulic displacement. Finally, expansion of feeding structures influences elastic filling and hermetic and cohesive suction. Fig. 3 illustrates how these specific mechanisms can work together for different stages of the nectar-feeding process, and which core method is at work for each. Certain methods do not work successively or simultaneously together because some methods require hermetically sealed bills, whereas others require pathways for air to exit the bill while nectar is being introduced and/or displaced. Of the mechanisms described, the initial and middle stage hermetic suction mechanisms (Fig. 2A,E) require a hermetic seal along the full length of the bill. The final stage hermetic suction mechanisms (Fig. 2I,J) require a hermetic seal of the portion of the bill proximal to where the liquid is in or on the tongue. Capillary filling (Fig. 2B), tongue wringing (Fig. 2F), cohesive pulling (Fig. 2G), cohesive suction (Fig. 2H) and hydraulic displacement (Fig. 2K) require non-hermetically sealed bills to allow the mechanisms to work properly.

The knowledge gaps in the field of nectar-feeding biomechanics are substantial (Table 1), and many of the nectar-drinking hypotheses (Fig. 2) must be tested and refined with further research. We suggest laboratory and in natura experiments, using high-speed macro videography to capture the rapid movements of the nectarivore's feeding apparatus, both in artificially transparent (26) or wild backlit-translucent flowers (9). Although some aspects of the nectar offloading and intraoral transport stages of feeding can be observed from external cameras (e.g. backlit filming of translucent bills, 41), much of the mechanisms would remain hidden within opaque/thick bills. High-speed fluoroscopy could offer visualization of $BaSO_4$ (barium sulfate)-stained nectar as it travels from the tongue to the bill, inside the oral cavity and even through the throat, thereby illuminating what mechanisms are occurring inside those structures (58, 59). We also suggest coupling the aforementioned dynamic visualization methods with 3D morphological studies [e.g. microcomputed tomography (μCT) scanning] to fully understand and explicitly model the functioning of the complex structures of nectar-feeding birds' tongues and bills, as well as volumetric flow through them (e.g. to determine optimal concentrations for caloric uptake).

1.5 Conclusion

In the pursuit of understanding the evolutionary pressures of avian nectarivory, we hope to have shown the importance for researching all stages of the process of drinking nectar. Although the nectar-collection stage has been the most researched, a single stage alone provides inadequate information to encompass all the constraints and challenges to the biomechanics of nectar drinking, given the rest of the steps that must be undertaken to transfer and transport nectar from the tongue to the throat. Similarly, as we study the complete nectar-feeding cycle we will likely find that each stage interacts with nectar differently, and thus the mechanism of a particular stage may not appear ideally suited for a given set of nectar characteristics, such as viscosity, but it might when all the parts and stages of the cycle are considered.

Once we have a better understanding of the exact mechanisms involved in nectar feeding across birds, we can consider broader ecological and evolutionary questions of interest. Nectarivory has evolved in a variety of ecological contexts, from tight coevolutionary relationships (e.g. some hummingbirds, 9) to more generalized systems (e.g. honeyeaters, 60, 61). Unique ecological circumstances are likely to influence the evolution of feeding mechanics (and vice versa), as the vast array of mechanisms described herein are likely to differ in their volumetric uptake rate, and depending on the nectar composition, their caloric intake rate. Future research should aim to understand: (1) how nectar-feeding biomechanics vary across avian nectarivore systems and how that variation relates to differences in ecological context (i.e. the plant–pollinator relationships), and (2) how avian nectar-feeding clades have evolved alternative or convergent solutions, since convergence in the face of different ecological scenarios could elucidate what biophysical aspects of nectar feeding are truly ubiquitous. Additionally, efforts could build upon the understanding of nectar drinking, such as finding explicit links to the ecological pressures that nectarivorous birds face. As nectar is a very poor source of protein (62–64), all nectar-feeding birds require additional food sources. Therefore, studying each groups' proportional reliance upon nectar compared with their other food sources and their associated selective pressures and mechanical challenges, is necessary to fully understanding the convergent evolution and evolutionary constraints across nectarivorous groups. To tackle these larger questions about avian nectarivory, we must first improve our understanding of the feeding biomechanics of many taxa.

Tables

Table 1. Hypotheses of nectar-feeding biomechanics at each stage of the feeding process in five groups of nectarivorous birds

	Group	Nectar concentration (%w/v)	Initial stage: liquid collection	Middle stage: offloading nectar into the bill	Final stage: intraoral transport of nectar
1	Trochilidae (Hummingbirds)	25.4% average (Pyke and Waser, 1981)	Elastic filling* (Rico-Guevara et al., 2015) Fluid trapping* (Rico-Guevara and Rubega, 2011)	Tongue wringing* (Ewald and Williams, 1982; Rico-Guevara and Rubega, 2017)	Hydraulic displacement‡ and cohesive pulling‡ (Rico-Guevara, 2014)
2	Nectariniidae (Sunbirds)	19–49% range (Bartoš et al., 2012)	Elastic filling‡ and/or capillary filling‡ (Liversidge, 1967; Rico Guevara et al., 2019a,b) Hermetic suction‡ (Cheke and Mann, 2008; Gadow, 1883)	Tongue wringing	Hydraulic displacement and cohesive pulling
3	Meliphagidae (Honeyeaters)	23.4% average (Pyke and Waser, 1981)	Capillary filling‡ and fluid trapping‡ (Paton and Collins, 1989) Hermetic suction‡ (Gadow, 1883)	Tongue wringing and/or compressing tongue against upper mandible	Hydraulic displacement and cohesive pulling
4	Psittacidae (Parrots)	15–35% range (Fleming et al., 2008)	Fluid trapping‡ (Churchill and Christensen, 1970; Homberger, 1980)	Squeezing of tongue hairs or pressing tongue against upper mandible	Short-term nectar storage during feeding using pharyngeal papillae‡ (Homberger, 1980)
5	Others	Unknown	Fluid trapping‡ in frayed tips and capillary filling‡ of tubular structures [e.g. Fleischer, 2008 (Hawaiian honeycreepers); Chang et al., 2013 (white-eyes)]	Tongue wringing	Hydraulic displacement and cohesive pulling

*Hypotheses with strong supporting evidence. ‡Hypotheses previously proposed (citations provided) but not experimentally investigated. Hypotheses proposed here for the first time have no marks added and are formulated based on what can be inferred from morphological characteristics, previous proposals and/or data for hummingbirds. The numbers in the first column match the numbers in Fig. 3 indicating which group uses a particular mechanism.

Glossary

Glossary

Distal fringes
Fringed, keratinous, lateral edges on the distal tips of the tongue, formed by lacerations of the groove walls, sometimes also called lamellae.

Hermetically sealed
Refers to a seal that is complete and airtight.

Hyoid apparatus
The bones attached to the proximal portion of the tongue that allow for the extension and retraction of the tongue including associated musculature.

Lingual grooves
Longitudinal grooves or channels in many elongated avian tongues, which extend from the distal portions of the tongue to the middle or the base of it (shown in Fig. 1).

Mandibular bones/rami
The jawbones inside of the lower bill, the rami make up the two halves of the jaw.

Maxillary bones
Bones inside the upper bill.

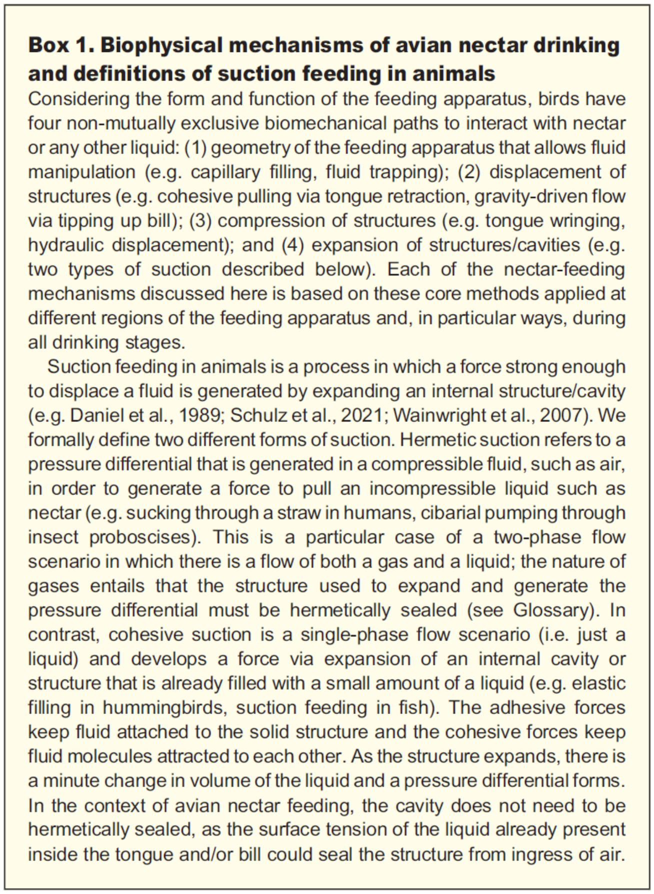
Nectarivore
An animal that has specialized to consume floral nectar, which exhibits morphological, physiological and behavioral adaptations for nectar feeding.

Oropharyngeal and hyobranchial muscles
Muscles in the front and back of the throat (respectively) that can be used to expand or contract the internal volume of the proximal oral cavity and throat.

Suction
Production of a negative pressure differential by expanding a cavity to generate force on fluids.

Tomia
The 'cutting edges' of the upper and lower bills; when they overlap, they could produce a somewhat airtight seal between the upper and lower bill.

Box 1. Biophysical mechanisms of avian nectar drinking and definitions of suction feeding in animals



Box 1. Biophysical mechanisms of avian nectar drinking and definitions of suction feeding in animals

Considering the form and function of the feeding apparatus, birds have four non-mutually exclusive biomechanical paths to interact with nectar or any other liquid: (1) geometry of the feeding apparatus that allows fluid manipulation (e.g. capillary filling, fluid trapping); (2) displacement of structures (e.g. cohesive pulling via tongue retraction, gravity-driven flow via tipping up bill); (3) compression of structures (e.g. tongue wringing, hydraulic displacement); and (4) expansion of structures/cavities (e.g. two types of suction described below). Each of the nectar-feeding mechanisms discussed here is based on these core methods applied at different regions of the feeding apparatus and, in particular ways, during all drinking stages.

Suction feeding in animals is a process in which a force strong enough to displace a fluid is generated by expanding an internal structure/cavity (e.g. Daniel et al., 1989; Schulz et al., 2021; Wainwright et al., 2007). We formally define two different forms of suction. Hermetic suction refers to a pressure differential that is generated in a compressible fluid, such as air, in order to generate a force to pull an incompressible liquid such as nectar (e.g. sucking through a straw in humans, cibarial pumping through insect proboscises). This is a particular case of a two-phase flow scenario in which there is a flow of both a gas and a liquid; the nature of gases entails that the structure used to expand and generate the pressure differential must be hermetically sealed (see Glossary). In contrast, cohesive suction is a single-phase flow scenario (i.e. just a liquid) and develops a force via expansion of an internal cavity or structure that is already filled with a small amount of a liquid (e.g. elastic filling in hummingbirds, suction feeding in fish). The adhesive forces keep fluid attached to the solid structure and the cohesive forces keep fluid molecules attracted to each other. As the structure expands, there is a minute change in volume of the liquid and a pressure differential forms. In the context of avian nectar feeding, the cavity does not need to be hermetically sealed, as the surface tension of the liquid already present inside the tongue and/or bill could seal the structure from ingress of air.

Figures

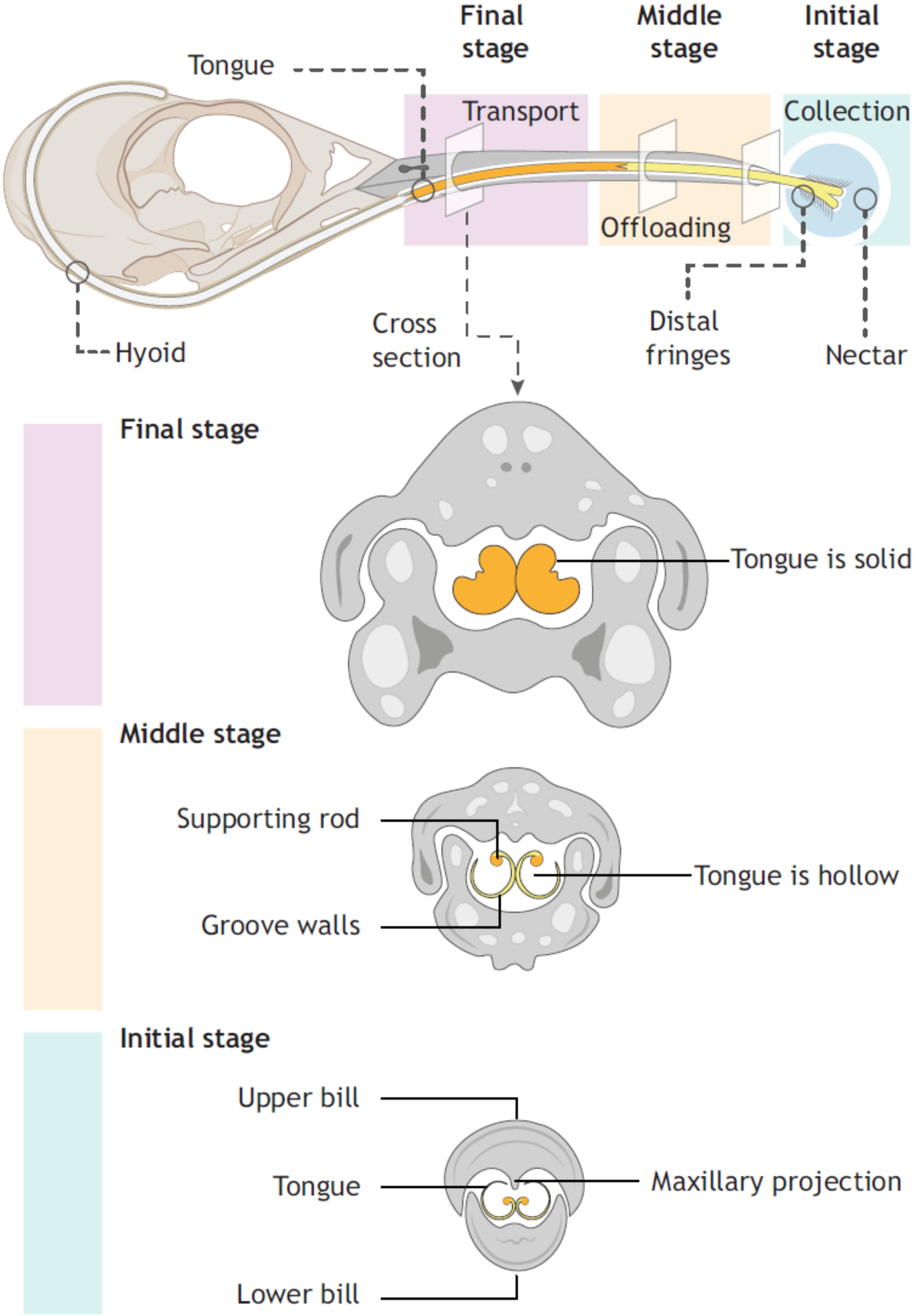


Fig. 1. Diagram of a hummingbird skull and feeding apparatus (highlighting the bill, hyoid bone and tongue). The initial stage (collection), middle stage (offloading) and final stage (transport) of nectar drinking are labelled. The stages are primarily referred to as successive points in time; however, they can be visualized as regions along the bill and tongue as the locations where most of the proposed mechanisms in each stage occur spatially. The cross sections portray how the bill and tongue change along the length of the bill.

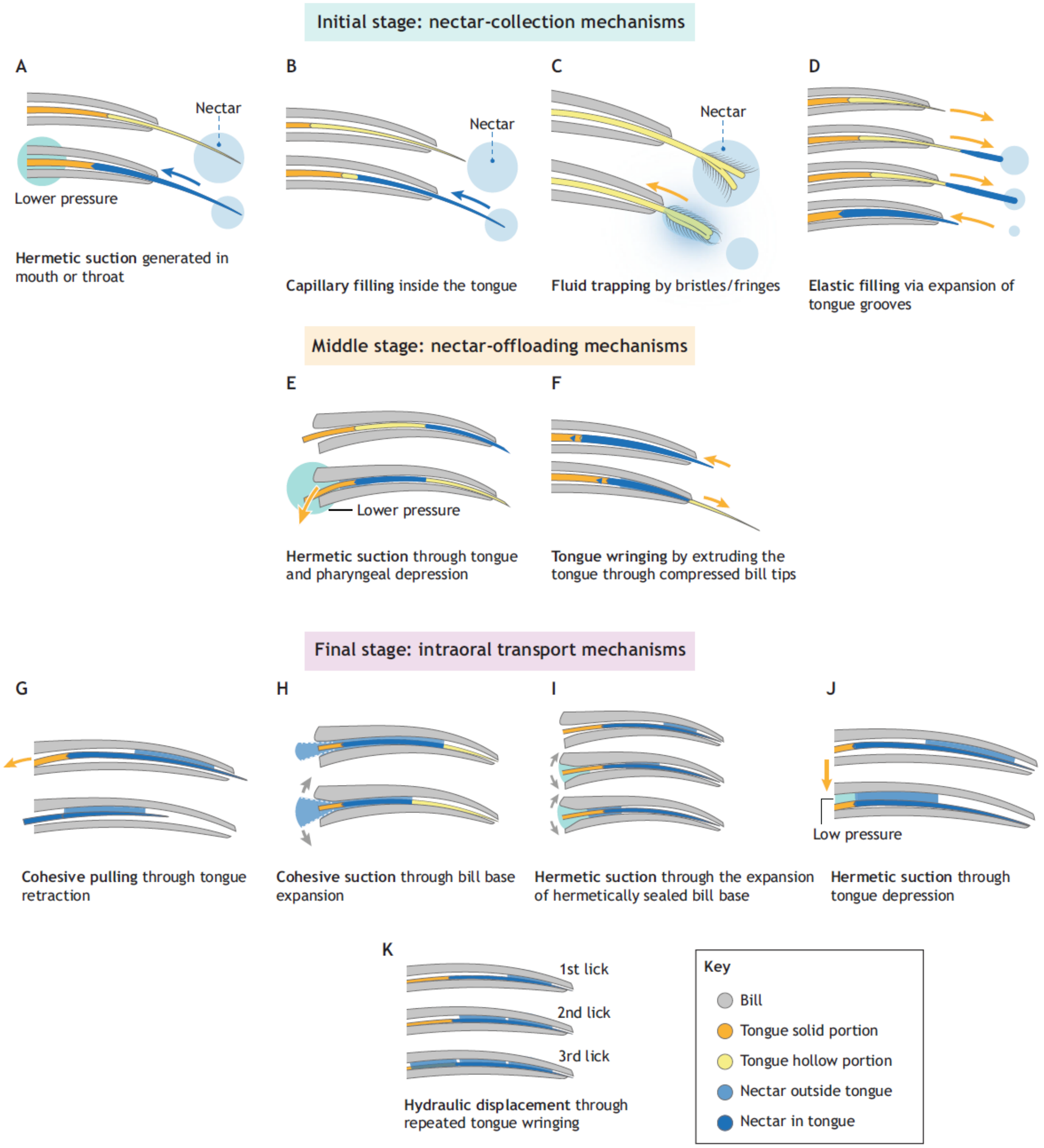


Fig. 2. Biomechanical methods of nectar drinking at different stages of the process. Each panel depicts a different mechanism hypothesized to be a part of avian nectar feeding organized by the stage of the nectar-feeding process in which they occur: (A–D) initial stage, (E,F) middle stage or (G–K) final stage. In each panel, the successive steps of the mechanism are shown in chronological order from the top down, and the bill, tongue, nectar and low-pressure areas (when applicable) are shown to illustrate how each mechanism could contribute to the collection, offloading or transport of nectar. Blue arrows indicate movement of nectar, orange arrows movement of the tongue and grey arrows movement of the bill.

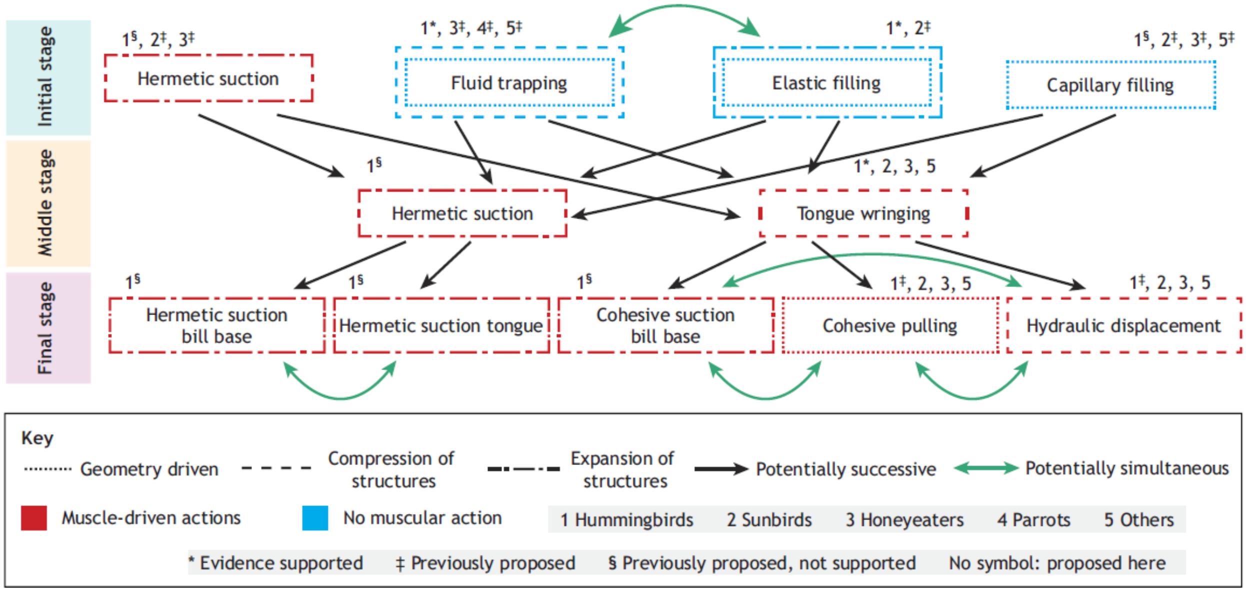


Fig. 3. Hypothesis flowchart showing how the proposed biomechanical methods could interact. Interactions show how feeding mechanisms could either occur successively across different stages (black, single-headed arrows) or simultaneously in the same stage (green, double-headed arrows). The box outline of each mechanism indicates if the core mechanism is geometry driven (small dashes) or involves compression (medium dashes) or expansion of structures (large and small dashes). The color of the box specifies if the hypothesis requires muscular action (red) or no muscular action (blue). The numbers above boxes indicate which nectarivorous groups have been proposed to use each mechanism, and correspond to entries in Table 1. The requirement for hermetic sealing of the bill is the major factor determining if mechanisms can or cannot work together (successively or simultaneously). See Table 1 for references.

Chapter 2

Biomechanical divergence underlies morphological convergence: sunbirds feed via intralingual suction

Authors: David Cuban, Cynthia Wang-Claypool, Yohanna Yohanna, Colleen T. Downs, Rauri C. K. Bowie, Fabian Brau, Steven D. Johnson, Alejandro Rico-Guevara

2.1 Abstract

Nectarivory has independently evolved many times among birds, yet little is known about the diversity of feeding mechanisms that enable specialized taxa to efficiently collect this energy-rich resource. Multiple avian groups have converged on evolving elongated bills and tube-like tongues adapted for nectar extraction. Old World sunbirds (family Nectariniidae) stand out as having the greatest degree of convergence in bill and tongue morphology with the well-studied and highly specialized New World hummingbirds (family Trochilidae) which fill their tongues via elastic filling. However, using museum specimens, high-speed video, and fluid modeling, we show that sunbirds use a unique drinking mechanism not found in any other animal: intralingual suction through the inside of hollow tubular tongues, a remarkable feat for animals without lips or cheeks. We show how this feeding mechanism is used and how we can model it mathematically. We anticipate that our results will be used to evaluate both food capture mechanisms and feeding efficiencies. For example, understanding the feeding mechanism enables the predictions for energy intake rates which, in turn, can be accurately predicted and tested, leading to more precise energy budget models and minimum energy requirements that in turn circumscribe more complex ecological interactions.

2.2 Introduction

Feeding is a fundamental need of all organisms, and a variety of food acquisition mechanisms have been studied for centuries (65–69). Although most vertebrates use lapping or licking to drink, a few groups can suck from large pools of liquid by creating a small oral opening connected to an expandable oral cavity (*e.g.*, some mammals) (70), which requires their lips to be in contact with the liquid. Only one vertebrate, a species of bat, has been reported to transport liquid along the length of its tongue, using lateral grooves on the surface of their tongues (71). For these bats, however, suction is not possible because the edges of the tongue grooves do not overlap to form a seal, and their tongues are not hollow but rather muscular. For vertebrates without lips or cheeks, suction is an even greater challenge. In birds, suction feeding is restricted to a few taxa (*e.g.*, filter feeders, pigeons) and it is accomplished with the bill being submerged in water and the tongue acting as a piston (5). There are no known examples of vertebrates able to move liquids through their tongues using active suction, which involves generation of an internal pressure differential. Nectar-feeding insects (e.g., lepidopterans), and other invertebrates that feed on liquids via suction, have evolved proboscides and other mouthparts analogous but developmentally distinct from tongues. Additionally, they require muscular pumps inside their heads for which there are no homologous to any vertebrate structure (72–76). The dietary niche of nectar feeding is a prime candidate for novel feeding mechanisms to be discovered as the animals rely upon efficient consumption of small and hard-to-reach amounts of liquid food to offset the elevated caloric needs of this demanding lifestyle (feeding while hovering, constant commute among flowers, and/or intense resource defense)(9, 10).

Vertebrates are responsible for 3-25% of plant pollination across habitats, and amongst them, birds are the most diverse pollinators, with over 920 species pollinating a plethora of plant groups (60, 77–80). Within birds, specialized nectar feeding has evolved independently in approximately 30 clades (1, 81), which exhibit varying degrees of morphological, functional, and behavioral convergence (47, 81–84). Some of the most identifiable convergent traits to this specialized dietary niche occur in the feeding apparatus. Bill and tongue similarities are evident among taxa in distant geographic regions; for example, hummingbirds (Trochilidae) in the Americas, honeycreepers (Thraupidae) in Hawaii, sunbirds (Nectariniidae) in Africa and Asia, asities (Philepittidae) in Madagascar, and honeyeaters (Meliphagidae) in Australia (42, 45, 81, 85). Of the many nectar-feeding birds across the world, the nectar drinking mechanisms are best known for hummingbirds (15, 26, 86). A taxon morphologically similar to hummingbirds, yet phylogenetically distinct, are the sunbirds whose feeding mechanism has not been previously experimentally investigated (45).

There are 142 species of nectarivorous sunbirds, and their ranges span Africa, southern Asia, and the Malay Archipelago (87, 88). For over a century, hypotheses about their feeding mechanics have been proposed (17, 18, 42, 87), with capillarity as the most recently noted (23, 89), yet these ideas have not been tested (84). The mechanics of drinking nectar have been explored across a diversity of hummingbird species, and given that both sunbirds and hummingbirds have elongated and narrow bills, housing equally long and distally hollow, bi-cylindrical tongues (14, 42), we expected that these groups would employ similar feeding mechanisms. To test this hypothesis, we studied sunbirds from both Africa and Asia, sampling seven species from multiple clades across the phylogeny, as well as species across a wide range of body and bill sizes. To comprehensively study sunbird feeding mechanics and the structures involved in the process, we used micro-computed tomography (μCT) scans and microscope image analysis, high-speed videos of sunbirds drinking from transparent artificial flowers, kinematic analyses, and fluid dynamics models.

2.3 Methods

2.3.1 Experimental Design

We used high-speed cameras to capture the nectar, tongue, and bill movement of nine individuals from seven sunbird species (Table 1) while they fed on nectar from artificial flowers (described below). Sunbird species in South Africa (n = 5, Table 1) were captured in the Umgungundlovu district of KwaZulu Natal in grassland areas with aloes and foothill areas with proteas between June and August of 2022 and 2023. Experiments with these species were conducted at the University of KwaZulu-Natal Pietermaritzburg in the outdoor Animal House aviaries (Permits: DAFF Section 20, 12/11/1/5/2418(HP); EKZNW, OP 3034/2022; AREC, AREC/00004060/2022; AREC, AREC/00006760/2024). Sunbird species from Indonesia (n = 2, Table 1) were captured on Gunung Ambang and Gunung Klabat in North Sulawesi, Indonesia in July 2023. Experiments with these species were conducted in field camps established at each site (Permits: BRIN, 346/SIP/IV/FR/6/2023; IACUC, 4498-05). The artificial flower (Fig. S2) consisted of a red plastic ring attached to the end of a clear rectangular tube made of 4 glass microscope slides: one on the bottom, two glued on top of the bottom one with ~6mm separating them, and the fourth glued on top of those to form a 5.9 mm width x 1.5 mm height rectangular tube. The apparatus was oriented horizontally and filled with artificial nectar (20% w/w sugar concentration, within range of local flower nectar). When birds fed from the artificial flower, they partially inserted their bills through the red disk into the tube and extended their tongues to feed. Two high-speed cameras (Chronos 1.4, Krontech) were used, one oriented to film the clear tube from above, and a second filming the side of the bird's bill and head. The artificial nectar was dyed red with food coloring to help visualize the nectar moving inside of the sunbird tongues. The cameras used Nikkor 105 mm macro lenses (Nikon) with film settings of 1000 frames/second (fps) at 1280x1024 pixel resolution for videos of the head, bill, and throat in addition to 4500 fps at 1280x240 pixels for videos of the nectar moving through the tongue..

2.3.2 Video Analysis

We analyzed the video data using dltdv8a (90), tracking the tongue tips, bill tips, nectar meniscus in the corolla of the artificial flower, and nectar menisci inside the tongue for multiple licks across multiple feeding bouts for each individual sunbird recorded in the experiment. Corolla nectar meniscus is defined as the edge of the nectar in the clear prismatic chamber at roughly the midpoint of the tube’s width. The tongue nectar menisci are defined as the leading surface of nectar as it is drawn into the tongue and the trailing surface of the column of nectar as it moves through the tongue (these are found at different times in the feeding process, Movies 1, 2, 3). The video data was calibrated using the known width of the nectar reservoir (5.9 mm) and the recording frame rate.

2.3.3 Morphological analysis of bills and tongues

We took measurements of dissected tongues using light microscopes to input the effective internal tongue diameter into the fluid model equation. We also used micro-computed tomography (microCT) scans of an olive sunbird, *Cyanomitra olivacea,* at ~20 micron resolution to compare morphology and measured internal tongue and oral cavity volumes to validate our light microscope measurements. The CT scanner (NSI X5000) x-ray source voltage and current were 42 kV and 560 microAmps, respectively. We analyzed the scan using the 3D Slicer software and the SlicerMorph package (91, 92). Transverse section images were taken along the bill and tongue at six points that showed relevant anatomical features of interest.

2.3.4 Derivation of fluid models

The equation of motion of a liquid flowing into a vertical tube with a circular cross-section of radius R_T is given by the Bosanquet equation (93, 94):

$$\rho \frac{d}{dt}\left[h\frac{dh}{dt}\right] + \frac{8\mu}{R_T^2} h \frac{dh}{dt} + \rho g h = \frac{2\gamma \cos\theta}{R_M} + \Delta p, \quad (1)$$

where ρ, μ and γ are the density, viscosity and surface tension of the liquid respectively. h and R_M are the height and radius of curvature of the air-liquid meniscus inside the tube and θ is the contact angle between the liquid and the tube. The terms on the left-hand side of this equation represents, respectively, inertial forces, viscous forces and hydrostatic pressure and are balanced on the right-hand side by the capillary forces and an applied difference of pressure Δp. In our case, because the inner part of the tongue (tube) is wet, we assume θ = 0. In addition, because the radius R_T of the tongue ($\simeq$ 0.15 mm) is much smaller than the capillary length $\ell_c = [\gamma/\rho g]^{1/2} \simeq$ 2.7 mm, the radius of curvature of the meniscus is equal to the radius of the tube $R_M = R_T$.

In the absence of applied pressure, this equation admits a stationary solution, i.e. dh/dt = 0, corresponding to the maximum height reachable by the meniscus, i.e. the so-called Jurin's height: $h_\infty = 2\gamma/(\rho g R_T) \simeq 9$ cm. Since, h at t_∞ is significantly larger than the height reached by the meniscus in the data we analyzed, gravity can be neglected. In addition, in our case, a time-dependent applied pressure is considered which makes the role of gravity completely negligible. Therefore, Eq. (1) becomes

$$\rho \frac{d}{dt}\left[h\frac{dh}{dt}\right] + \frac{8\mu}{R_T^2} h \frac{dh}{dt} = \frac{2\gamma}{R_T} + \Delta p, \quad (2)$$

It is usual to neglect inertia to describe a capillary rise since its effects are noticeable only at very short time. In this case, in the absence of applied pressure, Eq. (2) becomes

$$h\frac{dh}{dt} = \frac{\gamma R_T}{4\mu}. \quad (3)$$

Using the initial condition $h(0) = h_0$, the solution reads

$$h_C^2(t) = h_0^2 + \frac{\gamma R_T}{2\mu}, \quad (4)$$

This square-root behavior does not describe well the data as shown in Fig. 3. Taking into account inertia without applied pressure, i.e. $\Delta p = 0$ in Eq. (2), together with $h'(0) = 0$ leads to the following solution

$$h_{CI}(t)^2 = h_C(t)^2 - \frac{\gamma\rho R_T^3}{16\mu^2}\left[1 - e^{-t/\tau}\right], \quad (5)$$

where $\tau = \rho R_T^2/(8\mu)$ gives the typical time below which inertia dominates the viscous effects. Fig. 3 shows that adding inertia does not improve the description of the data since the curve is always below the curve without inertia as seen in Eq. (5). This indicates that the capture of nectar by sunbirds is not passive.

Finally, solving Eq. (2) with an applied pressure varying linearly in time, i.e. $\Delta p(t) = \alpha t$, leads to

$$h_{CIP}(t)^2 = h_{CI}(t)^2 + \mathrm{K}\left[\frac{t}{\tau}\left[\frac{t}{\tau} - 2\right] + 2\left[1 - e^{-t/\tau}\right]\right], \quad (6)$$

where $K = \alpha\rho^2 R_T^6/(8\mu)^3$. Note that, in our case, τ is quite small (about 1.5 ms) and Eq. (6) can be simplified by expanding h_{CIP} for $t >> \tau$:

$$h_{CIP}(t) \simeq Vt + C, \quad V = R_T\left[\frac{\alpha}{8\mu}\right]^{1/2}, \quad C = \frac{\gamma}{[2\mu\alpha]}\left[1 - \frac{\alpha\rho R_T^3}{16\gamma\mu}\right], \quad (7)$$

where V is the speed at which the liquid rises in the tongue and which results from the competition between the applied pressure driving the motion and the viscosity slowing down the dynamics. The constant C is a small offset resulting from the competition between all effects involved at small time $t << \tau$ (inertia, capillarity, viscosity and applied pressure) as seen by the presence of ρ, γ, μ and α in its expression.

Eqs. (4)-(6) are compared to in vivo measurements in Fig. Z with $\gamma = 0.07$ N/m, $\mu = 0.002$ Pa s, $\rho = 1085$ kg/m³ and the values of R_T and α reported in Table 2 for each species. The difference of pressure applied by the birds during the time interval where the data have been measured is small compared to the atmospheric pressure.

With the values of the parameters mentioned above and reported in Table 2, V given in Eq. (7) varies between 0.4 and 0.8 m/s.

2.4 Results

2.4.1 Tongue morphology, kinematics, and nectar flow

We used microscope photography and µCT scans of dissected sunbird tongues, including some of the same specimens we filmed, to detail their morphology (Fig. 1, A and B). The sunbird tongue can be described along three distinct sections: 1) distally, the tongue is bifurcated, and made of medially curling, keratinous, and very thin walls that form two hollow cylinders (Fig. 1C, cross section [XS] 6); 2) in the middle section, the tongue is no longer bifurcated, the walls are less curled inward with their edges open toward each other, forming a single elliptical cylinder, hollow across its entire length (Fig. 1C, XS 4-5); 3) in the proximal section, the walls of the lingual cylindrical groove are much thicker, and the tongue opens to form a “U”-shaped channel with its edges flared out laterally (Fig. 1C XS 1-3).

To visualize the nectar flow and tongue movement of sunbirds feeding on artificial nectar, we fed birds *ad libitum* with red-dyed (to enhance flow visualization) sucrose solutions of 20% w/w. Dorsal and lateral videos, captured using synchronized high-speed cameras, showed that all sampled sunbirds (nine individuals across seven species, Table 1) fed in similar ways. 1) They protruded their tongue past the open bill tips until the distal portion of the lingual cylinders entered the nectar. 2) They kept their tongue inserted while nectar flowed towards the mouth, filling the internal tongue capacity. 3) They retracted the tongue only partially to swallow, leaving the distal cylinders partly protruded from the bill and filled with nectar. And 4) without squeezing the tongue with the bill tips, they re-extended it for the next lick cycle (*e.g.*, Movie 1). Using the dorsal videos of the transparent nectar chamber, we tracked the tongue motion and fluid flow during the lick cycle for all individuals (e.g., Fig. 2A). Figure 2 shows the data for a malachite sunbird (*Nectarinia famosa*). The position of the tongue tip, nectar meniscus in the reservoir, and nectar meniscus in the tongue are measured relative to a fixed point at the base of the artificial flower (Fig. 2A) over multiple tongue extensions and retractions per feeding bout (*e.g.* Fig. 2B). After initial videography experiments, we did not focus on recording or tracking the bill tips as they remained open and relatively stationary during feeding; we determined that, surprisingly, the bill tips were not actively involved in the sunbird nectar collection biomechanics (*e.g.*, Movie 1). By subtracting the position of the reservoir meniscus from the tongue tip position, we found the immersion depth to be limited to a narrow band (between 1.3 and 2.1 mm), despite the receding reservoir meniscus and the high tongue reciprocation rate, with an average lick period of ~0.11 s (Fig. 2C). Notably, sunbirds did not immerse their tongues in the expected way relative to other nectar-feeding birds; e.g., hummingbirds and honeyeaters dip their tongues deep inside the nectar and continuously reciprocate them faster in and out the nectar except for some honeyeaters (28, 95). Sunbirds immersed only the very distal portion of their tongue tips in the nectar and kept them stationary at the point of maximum protrusion, performing long “pauses”, which comprised roughly half of the entire lick cycle. We subtracted the reservoir meniscus position from the tongue meniscus position to calculate the nectar column position in the tongue relative to the nectar reservoir, h (Fig. 2D). Each of the licks were overlaid with each other relative to the tongue insertion time comparing the position, h, of the nectar meniscus in the tongue (Fig. 2E). We averaged all the tongue meniscus positions for each lick, at the same relative time in the lick cycle, and found a linear relationship between meniscus position and time (Fig. 2F).

2.4.2 Fluid dynamic modeling

We compare the nectar meniscus rise in the tongue averaged across multiple licks (e.g., Fig 2) among individuals from each species (Table 1) with three feeding mechanics fluid models of increasing complexity. To inform the models (Table 2), we collected all of the specimens for which we obtained feeding performance data, and measured their tongues via dissections and µCT scans (e.g., Fig. 1, Fig. S1). First, as the recently favored model (17, 18), we present the expectations from the capillarity model, accounting for the surface tension of the sucrose solution at the air-nectar interface inside the tongue and the viscosity of the nectar. As the model shows significant deviation relative to the measured meniscus position, especially after a few initial milliseconds, capillarity on its own does not explain our observations (Fig. 3). Second, also modeling capillarity, but including the inertial effects of accelerating the fluid from a static position, brings the initial meniscus position closer to that of the observed values, especially during the initial fluid climb (first few milliseconds), after which the empirical data still mismatch (Fig. 3). Third, we included a time-varying applied difference of pressure in the model, which resulted in a satisfactory fit of the output with our empirical measurements, and provided support for active suction being the primary mechanism at play (Fig. 3). See “Derivation of fluid models” in the Supplementary Materials for detailed derivations of the fluid models.

The slope, or velocity, of the nectar meniscus in the birds’ tongues matched the predicted slope of a pressure-dominated flow, especially during the portions of the tongue filling process where capillarity is too slow to account for the observed flow. The applied difference of pressure itself is found to increase linearly with time, implying that whatever internal motion the bird is doing to generate suction must be happening continuously during the period of linear advance of the intralingual nectar meniscus. One individual, the brown-throated sunbird *Anthreptes malacensis* (the species with the shortest bill and tongue in the study, Table 1), showed evidence of using suction during one of its feeding bouts, and of a second mechanism (capillary filling only) when its tongue was extended near its maximum during a separate feeding bout (Fig. 3). This observation sheds light on the intraoral mechanism of suction generation as we discuss further down.

2.4.3 Mechanistic hypothesis testing of the tongue filling process

In addition to the fluid dynamics modeling, other lines of evidence also support the intralingual suction hypothesis. In several videos, bubbles can be seen moving inside the tongue when a bird does not make complete contact between its tongue tips and the nectar reservoir (e.g., Movie 2). If capillarity was the sole mechanism used by sunbirds then no bubbles would be present inside the cylinders, as the surface tension at the distal end of the tongue would not allow bubbles to pass into the tongue. Moreover, in several instances, we observed that the nectar columns inside the tongue cylinders from the previous lick moved mouthwards before the tongue tips contacted the nectar reservoir (see trailing menisci in Movies 1, 3). This occurs whenever there is sufficient distance between the bill tip and the nectar reservoir, as the suction mechanism can begin while the tongue is being extended, regardless of its position relative to the nectar reservoir. In these instances, when the tongue is being extended, and its tips are not in contact with the nectar yet, there is a nectar-air interface at both the distal and proximal end of the tongue tubes. The distal interface creates a surface tension force pulling the nectar in the tongue towards the tip of the tongue which opposes surface tension forces applied at the unseen proximal end of the tongue cavity. The cancellation of surface tension forces means that by capillarity alone (in the absence of any external shape change) the nectar column would not rise (96). Inertial forces at this small scale can also be safely disregarded as the cause of the intralingual displacement of the nectar columns. Since the nectar does, in fact, move toward the mouth before the tongue contacts the reservoir, an additional force must be applied to result in the observed motion. Additionally, an amethyst sunbird *Chalcomitra amethystina* was recorded while its tongue suddenly dropped down from contact with its upper bill resulting in nectar flowing out of its oral cavity (Movie 4). We hypothesize this unusual event resulted from the failure of a hermetic seal between the tongue and upper bill (see Discussion) as the bird moved its tongue too far out/down while feeding. Lastly, in all feeding events, we observed throat motions that would correspond to displacement of the hyoid apparatus (bones supporting the tongue). This displacement would allow the controlled tongue depression inside the mouth to generate suction (as we discuss in our biomechanical hypothesis below).

2.5 Discussion

For over two centuries, it was believed that passive capillary force was the main mechanism for nectar feeding in birds (23, 45, 65, 97). Using fluid dynamic models, Kim and collaborators (23) showed correspondence between the optimal concentration for caloric ingestion, using published data, and the predicted energy intake peak based on feeding mechanism. In their study, three bird groups – hummingbirds, honeyeaters, and sunbirds – were assumed to use capillarity, which they termed “capillary suction”, as their drinking mechanism (23). Since then, the capillary filling mechanism has been disproved for hummingbirds (26, 28, 30, 44), and for most honeyeaters—only one out of five species exhibited tongue kinematics consistent with capillarity (95); other avian nectarivores have not been studied until now. Hummingbirds and most honeyeaters employ fluid trapping with their fimbriated tongue tips and an expansive filling mechanism to load up their tongue grooves with nectar; the latter mechanism is enabled by the dorso-ventral compression of their tongues upon protrusion, such that once in contact with the nectar reservoir, the elastic energy stored restores their shape drawing nectar in (26, 28, 95). To offload the nectar inside the bill and swallow it, they wring their tongues with their bill tips—which compresses the grooves—at the beginning of the subsequent lick (86, 95, 98). Our initial hypothesis was that sunbirds, with convergent traits in their feeding apparatus morphology, would also use similar techniques. However, our results were not consistent with this initial hypothesis. Unexpectedly, sunbirds do not use their bill tips to compress their tongues while feeding. In contrast, sunbirds keep their bills slightly open during the entire nectar feeding process, with the tongue reciprocating along the maxilla, keeping the mandible apparently disengaged from the drinking mechanism (as can be seen in Movie 4). Tongue kinematics, nectar flow observations, and fluid dynamics models demonstrated that a simple capillary filling mechanism cannot explain the nectar uptake patterns reported here for sunbirds. Instead, sunbirds move nectar through their tongues with shallower licks, over relatively longer immersion times, and at a slower licking rate than hummingbirds and honeyeaters (86, 95). The only mechanistic model that matched the collected data was the one that included a difference of pressure within the tongue cylinders.

We propose that sunbirds use active suction to generate a pressure gradient when drinking nectar. We present a biomechanical hypothesis for intralingual suction feeding, aided by cross-section diagrams of the feeding apparatus across the lick cycle, depicting the tongue motions that could generate such a pressure differential (Fig. 4). Initially, the tongue lies centered inside the slightly open bill; a ridge in the roof of the oral cavity matches the dorsal tongue shape (Fig. 4A XS 1) and would help to maintain the tongue laterally centered as it slides along the upper bill. When the tongue is extended to reach the nectar reservoir, its base is lifted, pressing against the mouth's roof (Fig. 4B). We hypothesize that pressing the base upwards results in a partial flattening of the "U"-shaped (in cross section) proximal tongue region (Fig. 4B XS 2 and 3) that pushes out the air trapped between the tongue dorsal surface and the oral roof. The flexible tongue edges would create a hermetic seal against the maxilla producing a "suction cup" effect (Figs. 1B, 4B XS 2-3). Meanwhile, when the tongue tips contact the nectar reservoir, capillary forces initiate the wetting of the inner tongue spaces at the fringed tip and a rising meniscus can form via capillarity inside the tongue cylinders (which have a ventrolateral longitudinal slit). Although initially, portions of the intralingual nectar flow fit capillarity expectations, the overall meniscus advancement rate can only be explained by the addition of active suction (Fig. 3). We hypothesize that suction begins when the tongue base is depressed after being pressed against the roof of the oral cavity. Using synchronized side views, we observed a downward motion of the throat while nectar was simultaneously flowing inside the tongue cylinders, as observed in the top view (e.g., Movie 1). This downward motion of the throat corresponded to the area where the hyoid bones that support the tongue base move through, thus consequently corresponding with the "U"-shaped cross-section of the tongue (Figs. 1C XS 1-2, 4B-C XS 2-3) being depressed within the oral cavity. The increasing space between the tongue and oral roof (sealed at the back by the proximal tongue edge, Fig. 1B) creates a region of lower pressure relative to the atmosphere which draws nectar through the tubular-shaped distal and middle regions of the tongue (Fig. 4C XS 3-4). It is important to note that although there are narrow gaps formed by the longitudinal slits along the tongue, the tightly curled and sometimes overlapping tongue edges could allow the tongue to work as a straw in the presence of a strong suction action. Next, the tongue is pulled proximally towards the throat and as it is retracted, it unseals from the maxilla, allowing the bird to swallow the nectar now in the proximal end of the oral cavity (Fig. 4D). The nectar column breaks near the proximal end of the semi-cylindrical section of the tongue, leaving some nectar trapped in the middle and distal portions of the tongue, where the internal lingual cylinders are thin enough for surface tension forces to prevent dislodging of the liquid inside (Fig. 4D). The tongue is now back at its approximate initial position—although it is not entirely retracted as in other nectarivores (13, 71, 95, 99)—but still contains some nectar within the lingual cylinders (Fig. 4E). To complete the ingestion of the entire nectar aliquot, as the lick cycle begins again, the tongue is extended and its proximal portion is pressed into the roof of the mouth before being pulled down to generate negative pressure. The nectar already in the lingual cylinders flows mouthwards because of the pressure differential at the tongue base (Fig. 4F). In some cases, this occurs even before the tongue tip makes contact with the nectar reservoir if the tongue needs to be extended far to reach it.

In summary, several lines of evidence support the existence of a novel vertebrate feeding mechanism in sunbirds: 1) they do not immerse their tongues deep inside the nectar to use fluid trapping; 2) they do not wring their tongues with their bill tips, precluding expansive filling of the lingual cylinders; 3) the nectar flow in the tongues is closest to the fluid model for active suction, and does not decrease in flow rate over time as predicted with other models; 4) while feeding, sunbirds sometimes draw in bubbles of air into their tongues if they do not make complete contact with the nectar reservoir, meaning that capillarity alone is not responsible for the nectar flow; 5) sunbirds depress their tongues and hyoid apparatus inside their mouths simultaneously with the flow of nectar, pointing to use of tongue depression to generate a pressure differential leading to active suction; 6) as seen in an individual *C. amethystina*, when the tongue is overextended and depressed, the hermetic seal can be broken and the nectar load is lost (Movie 4); and 7) as observed in an *A. malacensis* (Fig. 3), only when the tongue is extended much further than normal to make contact with the nectar reservoir the tongue base will not be in the appropriate position to generate a pressure differential and thus capillary filling is the dominant mechanism for those lick cycles. This last line of evidence shows that sunbird tongues, as shown in hummingbird tongues, have the architecture that can allow for capillary filling (26, 27, 30). However, this only occurs when the distance between the bill tip and nectar reservoir is farther than would be found in any flower it visits in nature. The fact that a mechanism is physically possible does not make it biologically relevant, and here we have demonstrated that suction is used in realistic conditions by sunbirds for nectar-feeding. Our findings provide potential implications for how these birds select the flowers they pollinate, as plant species have diverse floral morphology and nectar traits which would directly affect nectar intake rates of sunbirds given the biomechanics of their feeding methods. Their suction feeding mechanism is greatly influenced by the viscosity of the nectar offered by the plants they visit, which opens the door to predictions on the evolutionary interplay between floral nectar concentrations, bird preferences, and optimal energy extraction rates.

The mechanistically unique feeding style of sunbirds adds another interesting physical solution to the evolutionary challenge of feeding on small quantities of nectar concealed in flowers. While some insects are known to use suction through separately evolved structures (13, 72–74, 99), we have described a method to generate suction through a straw-like tongue in vertebrates without cheeks or lips. This discovery opens new avenues of investigation for other vertebrate and invertebrate groups that have solved the challenge of extracting small-volume and hard-to-reach liquid food with the many diverse materials, structures, and physics phenomena of which the biological world is composed.

Tables

Table 1. Data for individual sunbirds included in the study.

Individual	Genus	Species	Date caught (dd-mm-yy)	Location caught	Sex	Mass (grams)	Exposed culmen (mm)	Tongue insertion depth (mm)	Tongue insertion duration (s)	Licks digitized (n)
AMSB-10	*Chalcomitra*	*amethystina*	27-07-22	RWAN	M	16	28.6	2.48+-0.14	0.12+-0.01	4
GDCS-03	*Cinnyris*	*afer*	24-08-22	RWAN	M	12	26.5	5.16+-0.27	0.11+-0.01	4
OLSB-05	*Cyanomitra*	*olivacea*	19-07-24	RWAN	U	12	25.6	1.48+-0.09	0.11+-0.003	4
WBSB-01	*Cinnyris*	*talatala*	27-07-22	RWAN	M	8.5	21	0.89+-0.22	0.08+-0.01	3
MASB-01	*Nectarinia*	*famosa*	05-08-22	ZF	M	18.5	33.7	1.79+-0.14	0.08+-0.004	5
MASB-04	*Nectarinia*	*famosa*	22-08-22	ZF	M	19	31.5	0.94+-0.39	0.08+-0.007	7
MASB-09	*Nectarinia*	*famosa*	24-08-22	ZF	F	14.5	31.4	1.88+-0.23	0.07+-0.008	6
OBSB-01	*Cinnyris*	*jugularis*	19-07-23	BK	M	7.32	21.55	2.73+-0.12	0.07+-0.007	3
BTSB-01	*Anthreptes*	*malacensis*	24-07-23	GA	F	12.9	16.9	Capillary: 0.39+-0.08 Suction: 3.18+-0.26	Capillary: 0.11+-0.004 Suction: 0.08+-0.001	Capillary: 3 Suction: 4

Locations are RWAN: Rocky Wonder Aloe Nursery (-29.638591N, 30.491850E), ZuluFlora (-29.533766N, 30.353995E), Bongkudai (0.764167N, 124.441936E), and Gunung Klabat (1.437379N, 125.000389E). Exposed culmen is the straight line length between the bill tip and the most proximal portion of the exposed keratin on the upper bill. Tongue insertion depth is the maximum distance between the nectar reservoir meniscus and the tongue tip when submerged.

Table 2. Fluid dynamics model variables.

Individual	**Genus**	**Species**	**R_T (mm)**	**α (kPa/s)**	**Δt (ms)**	**$\Delta p/p_{atm}$**
MASB-01	*Nectarinia*	*famosa*	0.15	329	24	0.078
MASB-09	*Nectarinia*	*famosa*	0.15	110	12	0.013
GDCS-03	*Cinnyris*	*afer*	0.15	434	3.5	0.015
WBSB-01	*Cinnyris*	*talatala*	0.13	256	6.6	0.017
AMSB-10	*Chalcomitra*	*amethystina*	0.14	240	3.8	0.009
OLSB-05	*Cyanomitra*	*olivacea*	0.15	224	11	0.024
OBSB-01	*Cinnyris*	*jugularis*	0.13	199	13.5	0.027
BTSB-01	*Anthreptes*	*malacensis*	0.14	528	3	0.016

R_T is the effective radius of the tongue along the enclosed, tubular length. α is the pressure differential per second applied by the bird. Δt is the time period over which the bird applies the pressure differential. $\Delta p/p_{atm}$ is the total applied pressure relative to the ambient atmospheric pressure.

Figures

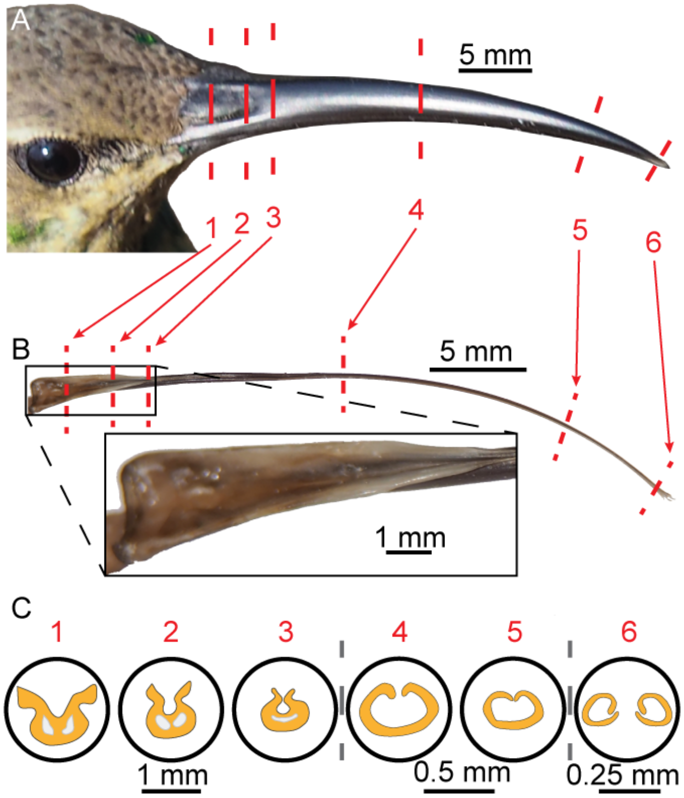


Figure 1. Sunbird bill, tongue, and cross-sections from microCT images. The sunbird tongue can convey fluid along its entire length, with the lateral edges of the tongue base capable of sealing against the inside of the upper bill. (A) Dorsolateral view of a *Nectarinia famosa* from the study. Red dashed lines correspond with the locations of the µCT cross-sections. (B) Dorsolateral view of the dissected tongue from the above *N. famosa* with cross-section lines marked. (Inset) magnified proximal portion of the tongue showing dorsal and lateral edges. (C) Enlarged cross-sections from different locations along the length of the sunbird bill and tongue. Cross sections (XS) 1-3 show the proximal portion of the tongue, the “U”-shaped section at the back that becomes narrower further down the tongue.Orange parts are keratin and light gray parts are the internal paraglossal bones located inside the thicker keratin which tapers down to very thin walls towards the distal end. XS 4 and XS 5 show the hollow middle section formed by the inward curling edges of the tongue walls, forming an elliptical space. XS 6 shows the bifurcated tip of the tongue, with the walls rolling inward to form tube-like structures.

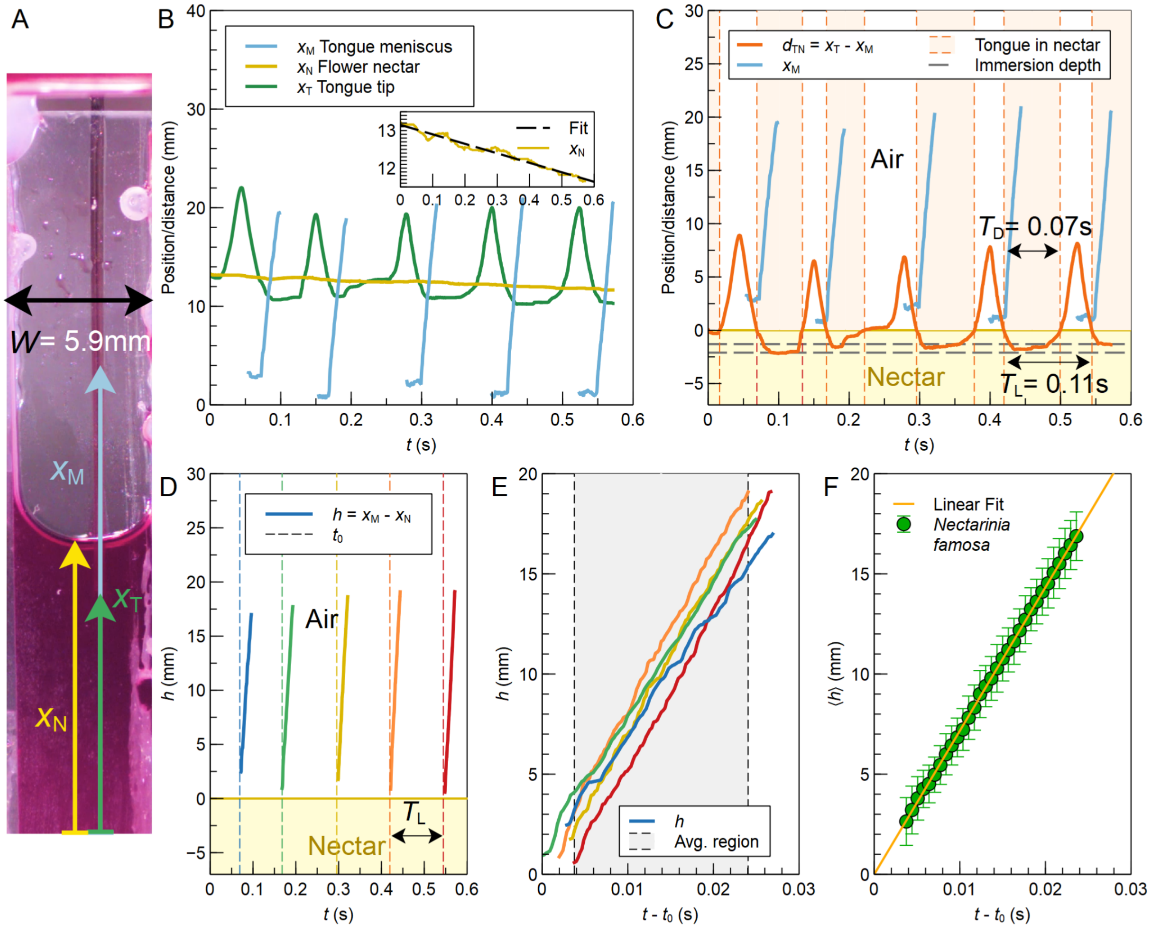


Figure 2. Kinematic measurements of a *Nectarinia famosa* tongue and red colored nectar during multiple lick cycles. (A) Video frame showing the nectar reservoir and the tongue tips immersed in the nectar (dyed magenta to improve visualization). Arrows indicate the position of the nectar meniscus of the reservoir, xN, the meniscus inside the tongue, xM, and the tongue tip, xT, with respect to an arbitrary fixed point. (B) Position of xN, xT and xM as a function of time. Inset: Position of xN as a function of time together with a linear fit. (C) Position of the tongue tip relative to the nectar reservoir, dTN, as a function of time. Tongue insertion depth varies between 1.3 and 2.1 mm. (D) Nectar position, h, in the tongue relative to the nectar reservoir as a function of time. t0 corresponds to the time at which the tip of the tongue touches the nectar in the extension phase for each capture process. (E) Position of h as a function of t − t0 for 5 licks and the time interval used to average h values. (F) Average and linear fit of h data in panel E.

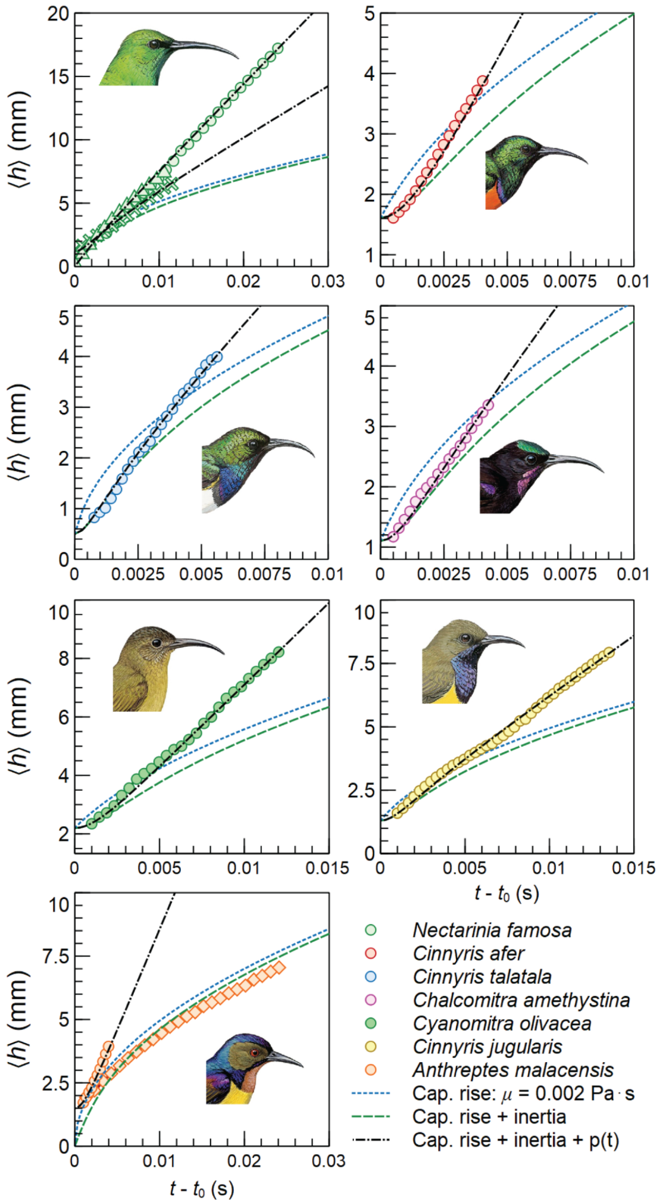


Figure 3. Intralingual suction across sunbird species. Change of ⟨h⟩, nectar position in tongue, as a function of time together with the change predicted by capillary rise only (blue dotted curve), by capillary rise and inertial effects (green dashed curve) and by capillary rise, inertial, effects, and a difference of pressure across the tongue's length varying linearly in time (black solid curve). These predictive models are adjusted based on the tongue morphology for each species. Data averaged across multiple licks from individuals from each species in the study are plotted (see Table 1). Differences in lick sequence duration (video frames) are due to different tongue lengths and bill tip to nectar reservoir distances. We only observed nectar distance motion typical of capillarity alone in one foraging bout of Anthreptes malacensis, and the same individual fed in the more common mode in another video where the tongue was much less extended (both plotted).

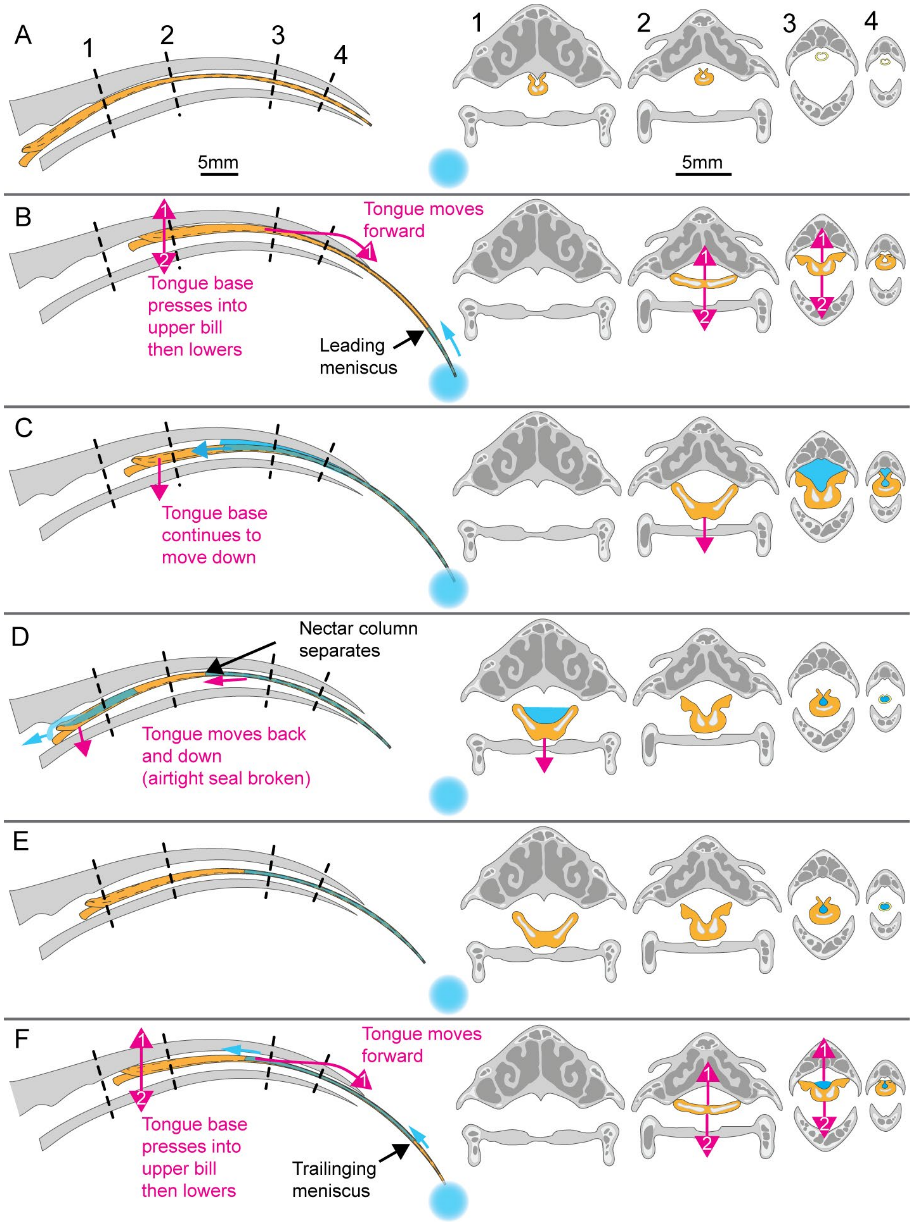


Figure 3. Biomechanical hypothesis of sunbird suction feeding. Sagittal cross sections of the bill and tongue of a feeding sunbird (left). Coronal cross sections (XS) of the bill and tongue while feeding (right). These cross sections combine anatomically accurate information from µCT scans, hypothetical motions, and deformations inferred from our external high-speed video observations. (A) Initial position of the tongue at the start of the first lick. (B) Tongue extension and base pressed into the mouth's roof before depression. (C) The tongue continues to depress while tongue edges are sealed against the upper bill. (D) Partial retraction of the tongue, proximal portion lowered from the oral roof. The hermetic seal is released and nectar can move from the back of the tongue to the proximal oral cavity and throat. (E) The tongue has completed a lick cycle. Some nectar often remains in the tubular portion of the tongue from the previous lick cycle. (F) During re-extension for the second lick, the nectar left over from the previous cycle is drawn back into the tongue via suction as the bird begins to generate a pressure differential across the length of the tongue before the tongue tips make contact with the nectar reservoir.

Chapter 3

Hanging parrots use surface tension and peristalsis to drink nectar

Authors: David Cuban, Sunghwan Jung, Maude Baldwin, Alejandro Rico-Guevara

3.1 Abstract

Nectar-feeding parrots' feeding apparatus morphology differs dramatically from most other nectarivorous birds, and hanging parrots (genus *Loriculus*) in particular have muscular and fleshy tongues unlike the keratinous tongues of the "typical" nectar-feeding birds. Despite their unique morphology for a nectar-feeder, little is known about how they consume the liquid food source or their volumetric intake rates. Here we test a hypothesis that blue-crowned hanging parrots (*L. galgulus*) lap with tongues to drink nectar like some mammals do when drinking liquids. Using micro-computed-tomography scans, high-speed videos, and mathematical models, we describe the nectar-feeding mechanics of hanging parrots and compare them with other nectarivorous bird families. Our results show that *L. galgulus* can use at least two different feeding mechanisms to drink nectar and that their volumetric intake rate is comparable to specialized nectar-feeding birds despite their differences in morphology and overall diet composition. Further, these findings show evidence for plasticity and choice in the feeding mechanism used by *L. galgulus* when feeding on nectar.

3.2 Introduction

Does form predict function? Convergent evolution of morphology in animals may imply that there is a selectively advantageous phenotype for animals to succeed in similar ecological niches (100–102). Nectar-feeding birds are an ideal study system to examine this phenomenon as there are over 20 evolutionarily independent origins of nectar-feeding across the avian clade (1, 81). Many of these nectar-feeding bird lineages share a common set of morphological traits, apparently evolved to better consume their liquid food source. The feeding apparatus, consisting of maxilla, mandible, and tongue, shows variable degrees of convergent evolution across nectar-feeding birds (81). Bills tend to be long, narrow, straight or slightly decurved, composed of a keratin sheath over a boney core. In most nectarivorous birds, the tongue is composed primarily of keratin from tip to base, terminating at the pharyngeal cavity where the hyoid bones and associated muscles are housed and extend around the back of the head (14, 45, 103). The lack of internal tongue musculature, especially at the distal lingual regions, results in the lack of active control of tongue shape, thus most nectar-feeding birds seem to rely solely on passive interactions between the nectar and the tongue tips for nectar collection (e.g., 26, 28, 95). Nectarivorous bird tongues often have bifurcations, fimbriations, and hollow channels running along their length that carry nectar towards the back of the mouth; however, nectar-feeding parrots' feeding apparatus morphology significantly differs from the norm (81). Their bills are short, hooked, and thicker than other nectar-feeders and their tongues (like other parrot tongues) are fleshy, muscular, and articulable all the way to tip, unlike other nectar-feeders and most other birds (Fig. 1; 104).

Hanging parrots in the genus *Loriculus* are small birds that feed on fruit, seeds, nectar, and some invertebrates. They are frequently observed feeding from flowers in nature and live in the Malay Archipelago where there are a variety of floral forms and other specialized nectar-feeding birds present (105–107). They visit flowers by inserting their bill into the corolla cup of wider flowers as well as piercing the base of longer flowers to apparently rob nectar (108). Beyond the few reports of their feeding behavior, little is known about how their tongues function and how they are able to feed on the small amount of liquid food hidden away within the flowers they visit (84). Like many other parrots, their tongues are composed of fleshy tissue along their entire length. The hanging parrot tongue differs from the other major clade of nectar-feeding parrots, lorikeets, that have brush-like papillae at the tip of the tongue (52). Hanging parrots' fleshy and muscular tongues are unique amongst other avian nectarivore tongues, and thus we expect that they would use them in distinct ways.

There are two fundamental mechanics of fluid transport, either a pressure induced flow such as suction or capillary action, or a boundary driven flow caused by motion of a surface in contact with a fluid such as lapping (98, 109–111). Cats, dogs, and other mammals have been observed drinking liquids by lapping with their tongues. They form their tongues into cupped or hooked shapes and plunge them in and out of the surface of a liquid reservoir - using fluid inertia and cohesive forces between the liquid and their tongue to draw the liquid up into their mouths (97, 112–114). For a similar mechanism to be possible for parrots drinking nectar, they would need to be able to deform their tongue shape at the same time as they move their tongues in and out quickly from the nectar reservoir.

We hypothesize that there may exist a functional difference in nectar intake rate between the typical parrot bill and tongue morphology (115, 116) compared with the specialized feeding apparatus morphology of other nectar-feeding birds (i.e. hummingbirds and sunbirds). We expected that the versatility of having a parrot bill and tongue able to handle tough items and produce substantial shearing and crushing forces but still small enough to fit on nectar chambers would result in lower drinking efficiency rate in nectarivorous parrots compared to other specialized nectar-feeding birds.

Here we describe the morphology and nectar-feeding behavior of the blue-crowned hanging parrot (*Loriculus galgulus*). By recording the parrots feeding on standardized artificial flowers with high-speed cameras, we can determine the mechanism they use, develop mathematical fluid dynamics models to describe the phenomena, and measure the feeding efficiency rate of these parrots to compare it with other specialized avian nectarivores. We present surprising findings of two unique feeding mechanisms employed by blue-crowned hanging parrots—distinct from mammalian methods—and show that their nectar-feeding efficiency is comparable to those of other specialized nectarivorous birds.

3.3 Methods

3.3.1 Animals

We studied three blue-crowned hanging parrots (*Loriculus galgulus*) housed at the Max Planck Institute for Biological Intelligence, Seewiesen, Germany. Animal housing and experiments were conducted in compliance with permits and protocols approved by the government of Upper Bavaria.

3.3.2 Morphological Analysis

Images of the *L. galgulus* tongue and bill were taken from video frames of the bird feeding to show it expanded and reshaped from its resting position. Micro computed tomography (microCT) scans were made from a museum specimen (UWBM 127652) from The Burke Museum of Natural History and Culture, Seattle, United States. The specimen was fixed using a 10% formalin solution and stained with 5% Lugol's iodine solution for 3 days. The x-ray source was set to 140 kiloVolts and 115 microAmps and the resulting scan had ~9.3 micron voxel resolution. We used the visualization software 3D Slicer and the SlicerMorph package to create cross-sectional images from the microCT scan of the bird's bill and tongue as well as measure key anatomical features of the feeding apparatus (92, 117).

3.3.3 Experimental Design

Individuals were held in testing cages with multiple perches available and an artificial nectar source presented within easy reach from a perch. The nectar reservoir was made from an optically clear photospectrometry cuvette that was shortened to only use the narrower portion at the bottom to improve fluid consumption estimation. The artificial nectar was a 20% sucrose solution by weight - a reasonable concentration to mimic natural nectars in the wild and comparable to other nectar-feeding bird experiments in the literature (e.g., 118–120). Three high-speed cameras (Chronos 1.4, Krontech) with Nikkor 105 mm macro lenses (Nikon) were used to film individual birds feeding from the nectar reservoir from anterior, lateral, and isometric views simultaneously at 1069 frames per second at a resolution of 1280x1024 pixels. The cameras were triggered remotely when the individual fed from the reservoir. All individuals fed ad libitum throughout multiple periods in the experiment cage over multiple days. The scale for each video was set using the known linear distance between the vertical edges of the nectar reservoir.

3.3.4 Kinematic Analysis

We used DLTdv8 for video kinematic analysis of the nectar meniscus, bill, and tongue during feeding sessions (90). Nectar uptake rate was calculated by marking the nectar reservoir meniscus each time the bird's tongue contacted the nectar (once per lick). This was repeated for every lick per feeding session, for all videos that were collected for each individual in the study (Table 1). Nectar-feeding mechanics were compared by plotting the size-corrected volumetric intake rate (microLiters per second) for the two observed *L. galgulus* mechanisms and the rates of hummingbirds and sunbirds using published data (119, 121).

3.4 Results

3.4.1 Feeding Apparatus Morphology

We analyzed the feeding apparatus morphology of the blue-crowned hanging parrot *L. galgulus* both with a microCT scan of a museum specimen and video frames of live individuals while they were feeding to see the tongue exposed and formed into different shapes while moving (Figs. 1 and 2). The hanging parrot tongue shows notable differences compared with most other nectar-feeding birds in its overall shape, size, and internal structures. The hanging parrot tongue measures approximately 7mm in length from its base with a resting width of 2.8 mm and an expanded width of 3.4 mm that we observed while it fed on nectar (Fig. 1A). Other nectar feeding birds tend to have relatively long and narrow tongues [hummingbirds: 27.94 mm long x 0.49 mm wide; sunbirds: 32.41 mm long x 0.29 mm wide (41, 42)] (Fig. 1B and 1C). Most other nectar-feeding bird tongues are composed of keratin with no distal musculature, vasculature, or innervation (e.g., 14, 81, 103). Blue-crowned hanging parrot tongue internal morphology shows muscle tissue oriented like the mammalian muscular hydrostat tongue (122, 123), connective tissues, and the underlying paraglossal bone located more distally compared to other nectar-feeding birds (Fig. 2B). The tongue has a longitudinal groove running medially on its dorsal surface with multiple smaller grooves running anterolaterally (Fig. 2C). The blue-crowned hanging parrot's bill is small (~13.5 mm exposed culmen length) and the inner surface of the maxilla (which interacts with the tongue during drinking) is concave with a small radius of curvature of 1.81mm at the tip (Fig. 2D).

3.4.2 Tongue Movements

Throughout all the observed feeding bouts we did not observe any typical "lapping" motions of the tongue that would be consistent with the hypothesis that hanging parrots feed on liquid like some mammals do. Two distinct patterns of tongue movement were observed during different instances of nectar-feeding across trials (Fig. 3, Video 1 and 2). We tested our results with a binary logistic regression to see if nectar depth affected the mechanism used but found no significant results $p = 0.916$. In the first pattern, the tongue extends such that it protrudes past the bill tip (Fig. 3A, Video 1). The tongue then oscillates in a sinusoidal-like manner, with the tongue tip slightly separated from the bill, the nectar fills the gap (Fig. 3A, Frames 1-4), then the tongue is pushed against the upper bill starting distally and continuing to the proximal most point visible to the camera (Fig. 3A, Frame 5), trapping and squeezing up the nectar between the tongue dorsal surface and the concave inner maxillary surface. Nectar travelled between the tongue and bill as the oscillations occurred at ~11.2 Hz. We call this mechanism peristaltic pumping due to the oscillations and the dynamic change in the nectar channel diameter formed between the tongue and upper bill.

For the second observed tongue motion pattern, the tongue was protruded to approximately half the length of the bill and never extended past the bill tip (Fig. 3B, Video 2). The tongue was first extended to contact nectar that had climbed via capillary action inside the concave cavity between the upper bill and the reservoir wall (Fig. 3B, Frames 1-2), then the tongue was retracted posteroventrally (Fig. 3B, Frames 3-5). A meniscus of nectar was observed between the upper bill and the tongue, moving back as the tongue was retracted and depressed. The tongue was then pushed to contact the proximal portion of the upper bill and slide forward while being compressed against the upper bill until it reached the nectar at the bill tip again (Fig. 3B, Frame 1). The entire pattern is repeated at ~8.5 Hz during feeding. We term this mechanism "surface tension drinking" as the bird makes use of its upper bill's small internal radius of curvature to initially draw up a small portion of nectar and then surface tension holds the nectar between the bill and the tongue as it is separated and then retracted. A version of surface tension feeding has been previously described within another bird group, phalaropes, that separate their bills to draw liquid (along with prey items entrapped in the water) up to their pharyngeal cavity (124, 125).

3.4.3 Nectar-feeding Efficiency

The volumetric intake rate was measured for all three individuals in the study for a total of 75 feeding bouts defined as insertions of the bill and/or tongue into the nectar (Table 1). Interestingly, the average intake rate and standard deviation (microLiters per second) between the two observed feeding mechanisms was similar – peristaltic = 2.97±1.16 microLiters/second/gram; surface tension = 3.08±1.17 microLiters/second/gram – despite the notably different movement patterns observed in each (Fig. 4). By sorting out the efficiency data by mechanism and individual we notice behavioral idiosyncrasies (Fig. 4). Individual 1, a male, was only ever recorded feeding using the peristaltic pump mechanism, whereas individual 3, a female, only used the surface tension feeding method. Interestingly, individual 2, a male, used both mechanisms during different feeding bouts but primarily used the peristaltic pump mechanism. Comparing both observed blue-crowned hanging parrot feeding mechanism efficiencies with those of two other nectar-feeding birds, hummingbirds and sunbirds, we see that the size corrected feeding rate of hanging parrots is less than that of hummingbirds but greater than the sunbirds (Fig. 4).

3.5 Discussion

Fluid drinking in birds has been described for multiple groups, with most using a “scraping” technique with their tongue to drag liquid back towards their throats, and others generating suction with their tongue and oral cavity to pump liquid back (126, 127). Our findings disprove our hypothesis that hanging parrots lap when fluid-feeding, and additionally in context of natural bird-flower interactions, a lapping mechanism seems unlikely as natural nectar quantities and flower shapes would not result in deep pools of nectar that are reachable for the relatively short bills of hanging parrots. Despite this, nectar-feeding bats can employ this mechanism, because of the brush-like papillae on their tongues and the ability to extend their tongues far beyond their snouts (128, 129). Unexpectedly, we found that blue-crowned hanging parrots use at least two different drinking mechanisms when consuming nectar - neither of which has been previously reported before as a liquid feeding mechanism (Fig. 3). Similar to recent work on honeybees, both mechanisms have a similar volume intake rate (99). However, unlike with honeybees, nectar depth does not seem to affect the choice of feeding mechanism used. The nectar intake rate of blue-crowned hanging parrots employing either mechanism was less than that of hummingbirds but greater than that of sunbirds when corrected for size (Fig. 4). This finding is consistent with aspects of the hypothesis that the long, keratinous, and tubular tongue of specialized nectar-feeding bird species may be selected for to improve nectar intake rates, but that tongue morphotype is not the only way to drink nectar at high rates. Hanging parrots also have a diverse diet including fruits and seeds in addition to nectar and likely have multiple selective pressures influencing their feeding apparatus evolution aside from nectar-intake rate.

3.5.1 Nectar-feeding mechanisms of hanging parrots

We combined our findings on the hanging parrot feeding apparatus morphology with the observed tongue and nectar movements during feeding to describe the underlying fluid dynamics involved in the drinking process. The ventral surface of the upper bill and the longitudinal groove on the dorsal surface of the tongue both exhibit concave shapes with small radii of curvature (bill: 1.8 mm; tongue groove: 0.2 mm), suggesting enhanced surface tension effects, such as capillary rise. In the feeding videos, the nectar from the reservoir is seen attached to the bill in a cone shape from the nectar surface due to surface tension forces at the air-nectar-bill interface. Likewise, when the tongue is in contact with the reservoir, it draws nectar up its sides and when it breaks contact with the nectar surface some liquid is still attached to the tongue as it moves. This surface tension phenomena of wicking the nectar up the bill and tongue surfaces likely serves to “prime” the feeding apparatus with nectar like a mechanical water pump would, so that the tongue can then interact with and transport the liquid to the back of the mouth. We propose the following mathematical models to describe the nectar-feeding mechanics of blue-crowned hanging parrots that we observed in our study. Derivations and schematics for the models are available in the supplementary materials. The nectar meniscus height on the bill is determined by the fluid properties and geometry of the solid surface as follows (Fig. S1A):

$$y = \sqrt{\frac{\gamma}{\rho g} cot\, \theta_0 + \frac{1/R_0}{\rho g/\gamma}} \quad (1)$$

where $\rho = 1000$kg/m^3, $\theta_0 = 0$, $\gamma = 72$ mN/m, and g = 9.81 m^2/s are the fluid density, wetting angle, surface tension coefficient, and the gravitational acceleration, respectively. R_0 is the radius of curvature of the ventral surface of the upper bill which we found to be ~1.81mm. Notably, as R_0 decreases the nectar meniscus height would increase.

Once their feeding apparatus is primed, the individuals then use one of two observed mechanisms to drink the nectar. In the first, peristaltic pumping, the bird presses its tongue against its bill tip, capturing a small amount of nectar between the upper bill and tongue surface. Then the bird compresses the rest of its tongue to the upper bill, squeezing the nectar back towards its throat. Modelling the bill and tongue as flat plates, the nectar meniscus position measured from the bill tip along the length of the tongue can be described as (Fig. S1B):

$$x = \sqrt{\frac{V_0}{w \cdot tan\theta}} \quad (2)$$

and the meniscus velocity

$$\frac{dx}{dt} = -\frac{\sqrt{\frac{V_0}{w}} csc^2\theta}{2\sqrt{cot\theta}} \frac{d\theta}{dt} \quad (3)$$

V_0 is the initial volume captured in the tongue at the beginning of retraction. We find the mean microLiters/lick of a bird using peristaltic pumping feeding to be ~7.5 microLiters. w is the effective width of the nectar held between the upper bill and tongue, we conservatively estimate this as the width of the tongue when not flattened ~3 mm. θ is the angle measured between the upper bill and the tongue at the bill tip. This model makes the assumption that the nectar-bill and nectar-tongue contact angles are constant while the angle between the bill and tongue changes.

The second mechanism, surface tension feeding, utilizes the surface tension of the nectar and the adhesive forces between the nectar and solid surfaces in the mouth to hold the nectar in place. As the tongue is retracted and depressed the nectar moves back towards the throat and due to the incompressibility of water we can model the position of the nectar meniscus with the same mathematical expression, except that θ is measured between the bill and the tongue from the intersection of the two surfaces at near the throat. In this case x is measured from the point of intersection of the two plates representing the bill and tongue. The derivation results in the same equations for position and velocity as described in (2) and (3) but with the different definition of theta (Fig. S1C). V_0 is the initial volume captured in the tongue at the time the tongue tip makes contact with the bill tip. We find the mean microLiters/lick of a bird using surface tension feeding to be ~11 microLiters. w = ~3mm as above.

3.5.2 Ecological implications

The mechanisms observed in this study contribute to our understanding of how hanging parrots attain their daily energy needs when foraging for nectar (amongst the other components of their diet). Our study illustrates how these birds could drink from open, cup-like flowers, a morphotype approximated by the geometry of our experimental apparatus (106, 130). In addition, the mechanisms observed may still be applicable to scenarios when the hanging parrots are nectar-robbing from the base of long, thin flowers. Their sharp upper bills can pierce the base of flower corollas, and the small radius of curvature of the upper bill's internal surface may draw out nectar from the pierced hole. From here, the birds could use either of the observed mechanisms to move the nectar to their throats. Further studies, either field observations or lab experiments with different artificial flower geometries, would help test this hypothesis. Understanding the measured nectar extraction rate, or feeding efficiency - provided that the drinking behaviors observed in our lab experiments approximates hanging parrots feeding on flowers from their natural habitat – can help us understand the foraging behavior necessary for the birds to fulfill their daily metabolic costs.

3.5.3 Comparisons with other nectar-feeding birds

The results of our experiments suggest that hanging parrots, specifically *L. galgulus*, feed at intermediate levels of efficiency compared to two other specialized nectar-feeding bird groups (119, 121). An analysis of variance (ANOVA) revealed significant variation of the size-corrected intake rate between the three species F(2, 209) = 336.2, $p < 2e-16$. A post hoc Tukey test showed that *L. galgulus* intake rate was significantly lower than that of hummingbirds at $p < 2e-16$, and significantly higher than that of sunbirds at $p < 2e-16$. *Since L. galgulus* feeds on many different food types - seeds, fruit, nectar, flowers - the fact that they are still able to consume nectar at rates comparable to specialized nectar-feeders shows how well adapted and/or functionally plastic their feeding apparatus is (131–133). Hanging parrots and their relatives have recently been found to use their tongues to aid in gripping the substrate they climb on in addition to their bills and feet (134, 135). The evolution of an articulable appendage that is capable of numerous distinct actions raises many questions for the evolution and plasticity of phenotypes with multiple different selective pressures, as well as of potential trade-offs or behavioral workarounds as seen in the hanging parrots studied.

The small sample size (n = 3) of individuals in this study must be considered in our findings. The mechanistic descriptions of how these animals feed are backed up by repeated experiments per individual (3-6 feeding experiments per individual) as well as overlap in mechanisms observed between the individuals (Table 1). However, increasing the sample size and filming birds in the wild may reveal even more mechanisms and could expose the determinants of the choice between these drinking methods (e.g., as it has been shown for bees drinking nectar, 99). Additionally, further experiments should consider a variety of artificial flower geometries and/or use natural flowers in the studies. It is possible that these animals select a feeding mechanism based on the particular nectar-feeding challenge they encounter. This study has revealed some of the feeding biomechanics of the blue crowned hanging parrot, and raises questions about how other fleshy-tongued nectar-feeders drink nectar and at what rate, such as nectar-feeding bats, canids, geckos, and others (128, 136, 137). Investigating the similarities and differences between these groups' feeding mechanisms will expand our understanding of how soft tissue appendages can interact with liquid-solid-air interfaces in nature.

Tables

Table 1. Feeding bouts of *L. galgulus* per individual and feeding mechanism

Individual	Total number of feeding bouts	Number of peristaltic feeding bouts	Number of surface tension feeding bouts
1	34	34	0
2	16	13	3
3	25	0	25

Figures

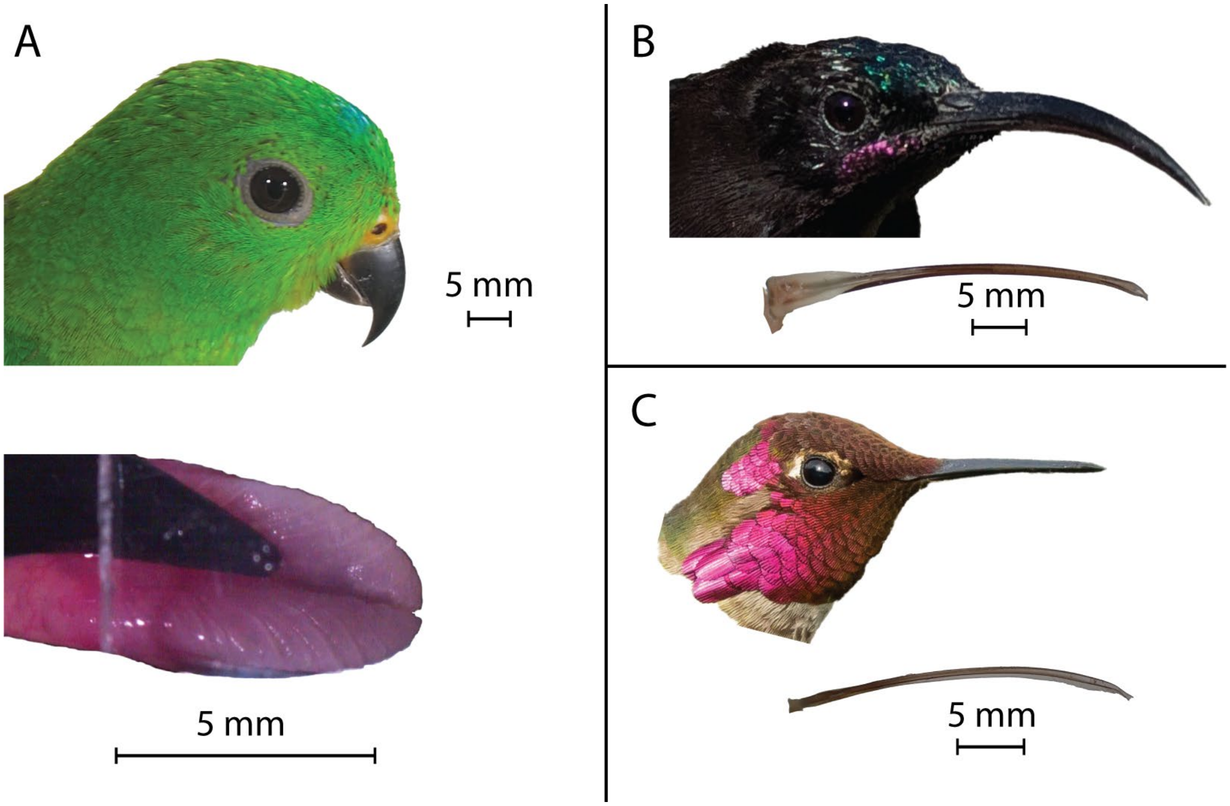


Fig. 1. Comparison of the blue-crowned hanging parrot (*Loriculus galgulus*) tongue with other nectar-feeding birds. (A) *L. galgulus* has a notably pink, fleshy, and muscularized tongue which can partially protrude past its bill tip. Its fleshy external surface and underlying musculature differ from most other nectarivorous birds. (B) Sunbirds (*Chalcomitra amethystina* shown here) and (C) hummingbirds (*Calypte anna* shown here), and most other nectarivorous birds have tongues composed of keratin from the base to the tip, with bifurcations, fimbriations, and hollow channels extending longitudinally. Photos taken by David Cuban.

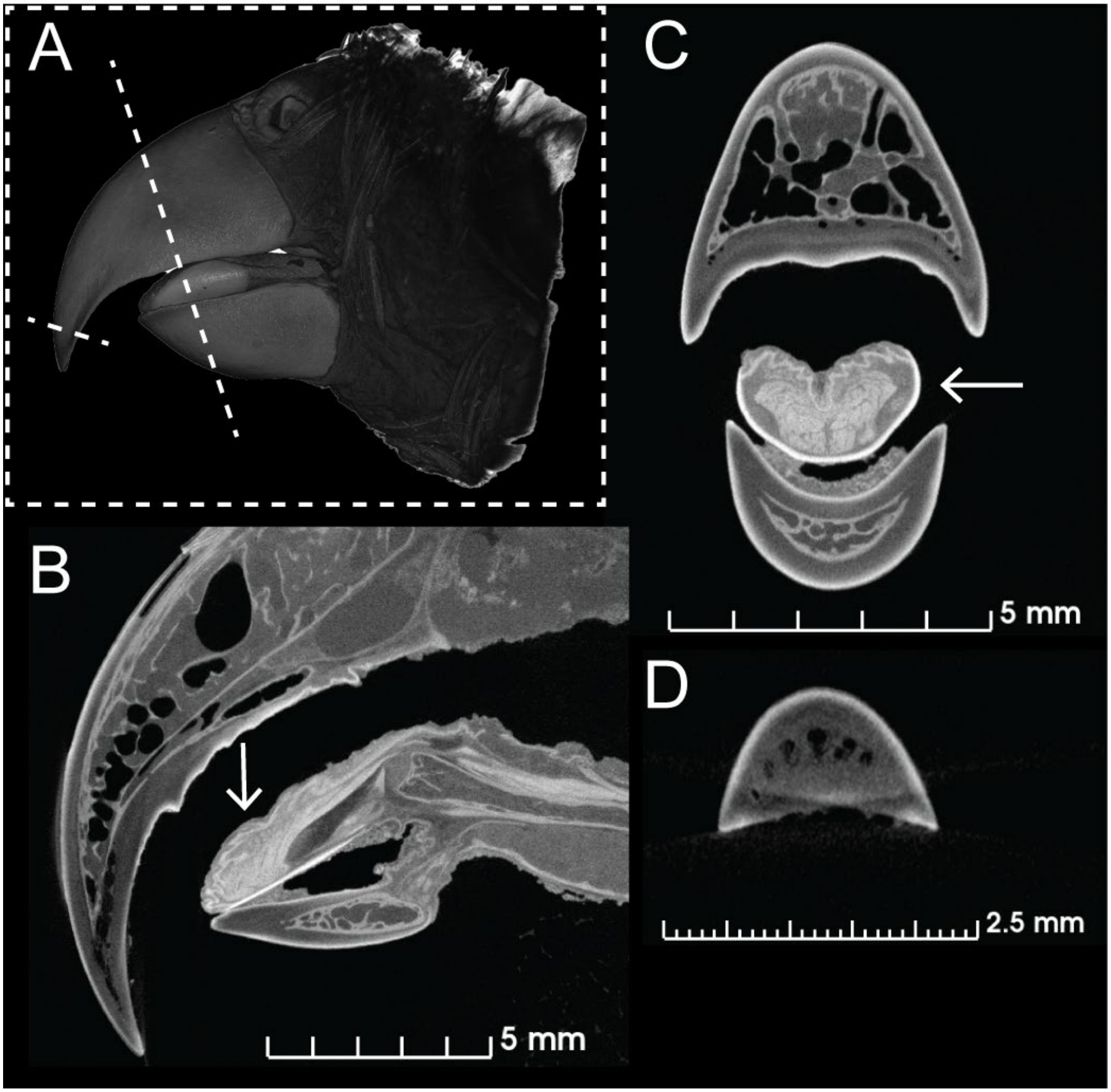


Fig. 2. micro Computed Tomography (microCT) scan of a *L. galgulus* specimen from Singapore. (A) Lateral view of the 3D scan with 3 different cross section planes indicated with white dashed lines. (B) Sagittal microCT cutaway showing the upper and lower bill with the muscular tongue (indicated by white arrow). (C) Coronal microCT cutaway showing the upper and lower bill with the muscular tongue (indicated by white arrow). (D) Coronal microCT cutaway at the tip of the bill portraying its small and concave inner surface.

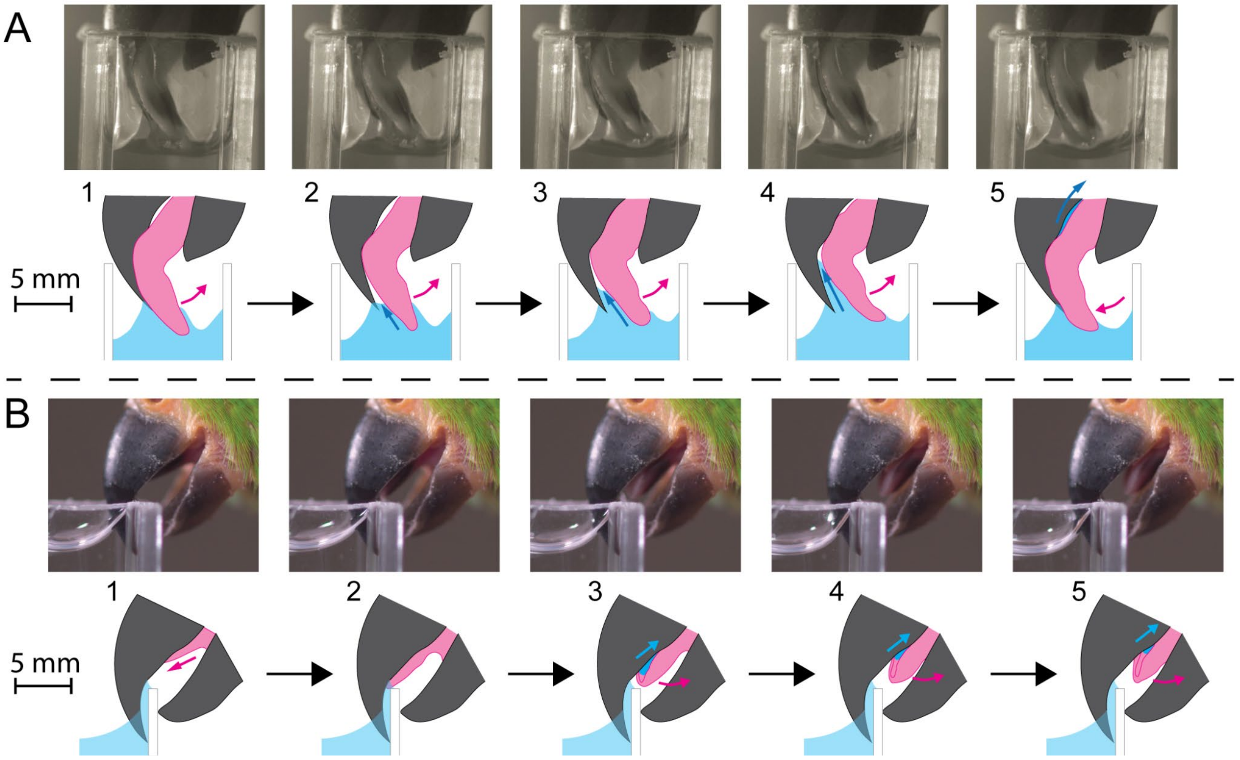


Fig. 3. Comparison of both observed nectar-feeding mechanisms. (A and B) Video frames (top) and schematic drawings (bottom) of lateral view of *L. galgulus* while feeding from the nectar reservoir. (A) Instance of a bird feeding on nectar using a peristaltic mechanism while feeding. The parrot pulls its tongue back partially, causing nectar to fill the empty space between the bill and tongue, then presses its tongue back into the bill, pumping the nectar back towards the throat. (B) Instance of bird using a surface tension mechanism to drink from the nectar reservoir. The parrot slides its tongue along the lower surface of its upper bill until it makes contact with the nectar held between the bill and the edge of the reservoir. Then it lowers its tongue and due to surface tension forces the nectar to stay adhered to the bill and tongue towards the proximal end while the nectar front retracts backwards towards the throat.

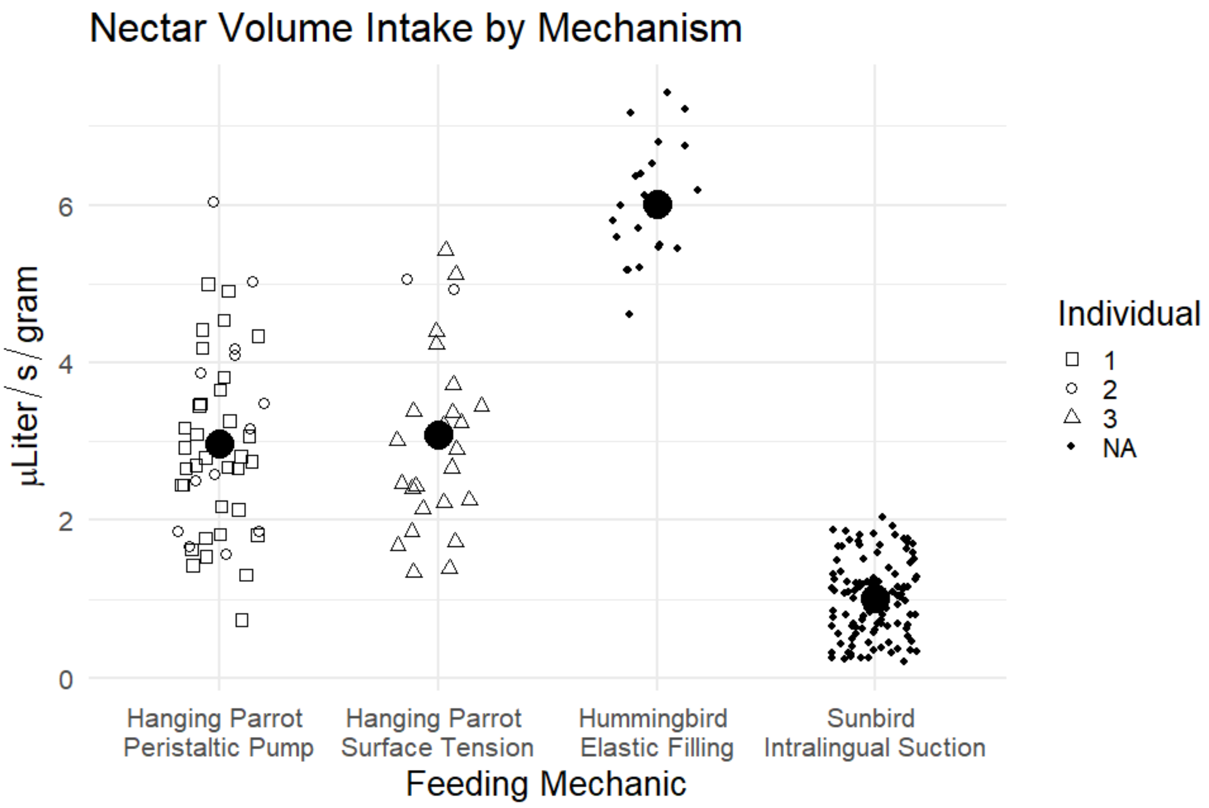
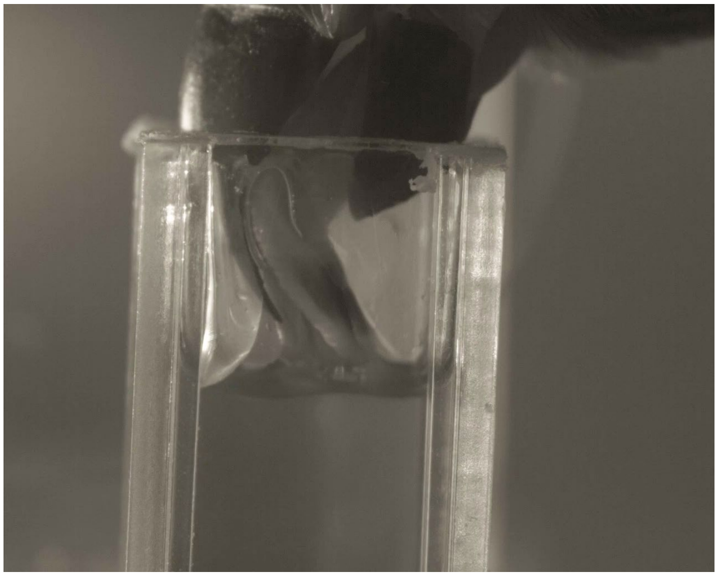


Fig. 4. Comparison of nectar intake rates between the two observed *L. galgulus* mechanisms, hummingbirds, and sunbirds. Experimental data collected by filming birds feeding from artificial flowers containing 20% sucrose solutions (by mass). Each point represents the average nectar uptake rate in microLiters per second for a single feeding event corrected for mass (insertion of bill and tongue into the artificial flower). Large black dots are the mean intake rates per mechanism. Hummingbird data from Tamm and Gass 1986. Sunbird data from Cuban 2025.

Videos



Video 1. ***Loriculus galgulus* using a peristaltic pump when feeding on nectar.**

Video 2. ***Loriculus galgulus* using surface tension when feeding on nectar.**

3.6 Supplementary Materials

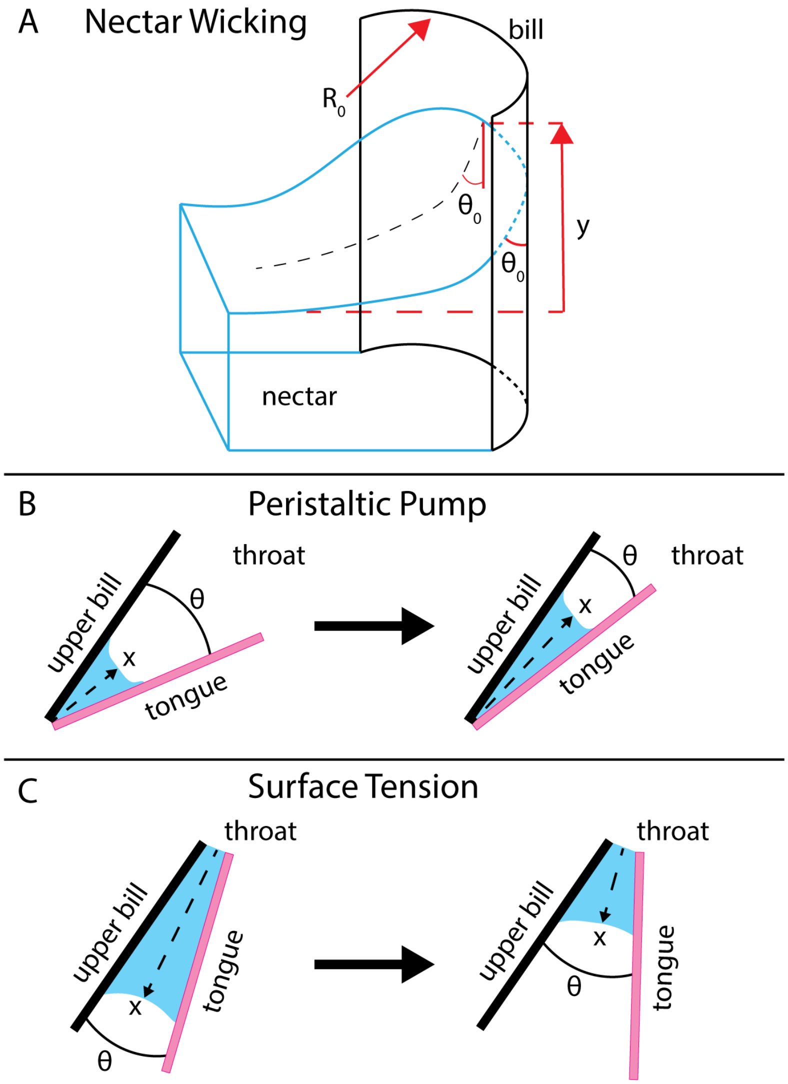


Fig. S1. Schematic representation of bill, tongue, and nectar used for mathematical models of feeding mechanisms. (A) a curved surface submerged in liquid representing the bill and nectar, respectively. y is the meniscus height relative to the surface of the nectar reservoir, θ_0 is the wetting angle of the nectar on the bill, and R_0 is the radius of curvature of the upper bill inner surface. (B) two plates represent the upper bill and tongue, with θ being the angle between the upper bill and tongue measured at the point of contact between the bill tip and tongue, x is the distance of the nectar front measured from the bill tip, w is the tongue width measured perpendicular to the page (not shown). (C) two plates represent the upper bill and tongue, θ is the angle between the upper bill and tongue measured from the point of intersection near the throat, x is the distance of the nectar front measured from the throat, w is tongue width measured perpendicular to the page (not shown).

3.6.1 Equation derivations

3.6.1.1 Nectar Wicking

The forces on the fluid are balanced with the force due to gravity on the left and the surface tension force on the right:

$$\rho g y = \gamma\left(\frac{1}{R_1} + \frac{1}{R_2}\right) \quad (1)$$

where ρ is density, g is gravitational acceleration, y is fluid height, γ is the surface tension coefficient. R_1 and R_2 are the radius of curvature of the fluid meniscus and internal bill surface, respectively. We use the definition of the parameterization of a planar curved surface to substitute for R_1:

$$\rho g y = \gamma\left(y" + \frac{1}{R_0}\right) \quad (2)$$

and reorganize to find:

$$y" = \frac{\rho g}{\gamma} y_0 - \frac{1}{R_0} \quad (3)$$

Solving for the second order differential equation we find:

$$y = y_0 exp\left(\sqrt{\frac{\rho g}{\gamma}} x\right) + \frac{1/R_0}{\rho g/\gamma} \quad (4)$$

Where x is the distance horizontally from the internal bill surface. Using the condition:

$$\frac{dy}{dx}|_{x=0} = cot\theta \quad (5)$$

we substitute:

$$cot\theta = y_0\sqrt{\frac{\rho g}{\gamma}} \quad (6)$$

into (4) to find that:

$$y = \sqrt{\frac{\gamma}{\rho g}} cot\theta_0 exp\left(\sqrt{\frac{\rho g}{\gamma}} x\right) + \frac{1/R_0}{\rho g/\gamma} \quad (7)$$

At the contact point (x = 0), the fluid height is

$$y(x=0)=\sqrt{\frac{\gamma}{\rho g}cot\theta_0+\frac{1/R_0}{\rho g/\gamma}} \quad (8)$$

3.6.1.2 Peristaltic Pump

We begin with an expression for the volume of nectar trapped between the upper bill and tongue once the tongue makes contact with the bill tip.

$$V_0 = \frac{1}{2}\cdot x\cdot h\cdot w \quad (1)$$

V_0 can be measured empirically from our high speed video experiments, w is known from videos and microCT scans, x is the distance of the nectar front that we are solving for, and h is the height of the right triangle formed by the bill or tongue and the x axis. As the system is represented by two plates, we find a trigonometric expression for h

$$h = 2\cdot x\cdot tan\theta \quad (2)$$

Substituting equation (2) into (1) results in

$$V_0 = x^2\cdot tan\theta\cdot w \quad (3)$$

Solving for x results in

$$x = \sqrt{\frac{V_0}{tan\theta\cdot w}} \quad (4)$$

We also show the nectar front velocity by taking the derivative of (4) with respect to time

$$\frac{dx}{dt}=-\frac{\sqrt{\frac{V_0}{w}}\cdot csc^2\theta}{2\sqrt{cot\theta}}\cdot\frac{d\theta}{dt} \quad (5)$$

3.6.1.3 Surface Tension

The derivation for the surface tension mechanism models are identical to those of the peristaltic pump, except that we begin with a different point of contact between the upper bill and tongue. This results in x being defined as the distance between the nectar front and the point of intersection of the upper bill and tongue at the throat and θ measured between the upper bill and tongue from the throat.

Chapter 4

Sunbird Feeding Efficiency and Comparison with Hummingbirds

Authors: David Cuban, Stevan Pekich, Yohanna Yohanna, Rauri C. K. Bowie, Steven D. Johnson, Alejandro Rico-Guevara

4.1 Abstract

Nectar-feeding birds consume nectar from a variety of plant species which offer nectars with different sucrose concentrations. Not only does sucrose concentration directly affect the caloric density of the nectar but it also increases the viscosity and thus limits the rate of fluid flow. We hypothesize that there will be a nectar concentration that maximizes energy intake dependent on the tongue morphology which differs across species. In this study, we present a quantitative analysis of feeding efficiency across a range of nectar sucrose concentrations for sunbirds (Nectariniidae), a diverse and ecologically important group distributed across Africa and Southeast Asia. Using high-speed videography and artificial nectar of varying sucrose concentrations (10–50% w/w), we measured volumetric and caloric intake rates in six sunbird species. We compared these data with predictions from a fluid dynamics model based on the Hagen–Poiseuille equation, using tongue morphology from micro-computed tomography (µCT) scans to estimate nectar flow under active suction feeding. Our results show that sunbirds exhibit a semi-parabolic energy intake curve, with optimal sucrose concentrations between 20–40% w/w, consistent with theoretical predictions. However, caloric intake rates were significantly lower than those observed in the North American hummingbird *Selasphorus rufus*, highlighting fundamental differences in feeding mechanisms—active suction in sunbirds versus elastic filling in hummingbirds. These findings shows how convergent evolution of the nectar-feeding niche – but unique nectar-feeding biomechanics – has shaped the physiological performance limits of avian nectarivores and provides a framework for comparing between phylogenetically distinct groups.

4.2 Introduction

Feeding efficiency has been investigated across many groups of animals as a way to validate mechanistic hypotheses, estimate caloric needs, and determine key animal-resource interactions (129, 138–141). Nectar-feeding animals provide an ideal study system to investigate feeding efficiency and its potential effect on plant-pollinator interactions and evolutionary trajectories as their high metabolisms and the small quantities of nectar spread throughout the landscape add selective pressures to efficiently uptake calories while minimizing energy expenditure during foraging. Many plants offer nectar composed of water, sugar, and other chemicals as a means of attracting and rewarding pollinators that visit a flower. Nectar traits differ between plant species such as volume per flower, sucrose concentration, and chemical composition (6, 142). One trait, sucrose concentration, has a significant direct effect on the ability of a nectar-feeding animal to consume the nectar and their feeding efficiency. As the sucrose concentration varies amongst different nectars, there is a linear relationship with the energy density, or calories per unit volume, and an exponential relationship with the viscosity, the resistance to fluid shear and thus its flow rate (7). This tradeoff affects the volumetric (and caloric) intake rate of a nectar-feeding animal based on the feeding mechanism it employs. Mathematical models have been developed for many different nectar-feeding animals to describe their energy intake rates across nectars of different sucrose concentrations (23, 24, 99, 143). These models predict that for a given feeding mechanism there should be an optimal nectar concentration that maximizes the energy intake rate, and consequently the feeding efficiency, of a nectar-feeding animal (23).

In recent years, the feeding mechanics of nectar-feeding birds have been experimentally studied and determined across multiple nectarivorous groups from independent evolutionary origins (26, 84, 95, 144). Not only has this increased our understanding of a large number of ecologically important pollinators (1, 60, 77, 78) but it has also set the foundation for investigating the feeding efficiencies of these animals in the context of nectarivory. One group of nectar-feeding birds, the sunbirds (Nectariniidae), has been found to use active suction when feeding on nectar (144).

Here we present the first nectar feeding efficiency study on sunbirds, an ecologically important group of pollinators spanning the African continent to the Malay Archipelago (57, 87). We use mathematical models and morphological measurements to predict the volumetric and caloric intake rate pattern of sunbirds using active suction and then compare it to experimentally determined feeding rates measured in the field. We consider sunbird feeding efficiencies relative to that of a common North American hummingbird species, Selasphorus rufus, to compare between two convergently evolved instances of avian nectarivory (119).

4.3 Methods

4.3.1 Nectar-feeding experiments

We measured the nectar consumption of 6 sunbird species feeding on different nectar concentrations from an artificial flower using high-speed video cameras. South African sunbird species (5, Table S1 were captured in Umgungundlovu district of KwaZulu Natal in grassland areas with aloes and foothill areas with proteas between June 2022 and August 2023. Experiments with these species were conducted at the University of KwaZulu-Natal Pietermaritzburg in the outdoor Animal House aviaries. The Indonesian sunbird species (1, Table S1) were captured on Gunung Ambang and Gunung Klabat in North Sulawesi, Indonesia in July 2023. These species were selected as they represent a species from the geographic extremes of the family distribution as well as a broad representation of species across the sunbird family phylogeny. Experiments with these species were conducted in field camps established at each site. The artificial flower (Fig S1) consisted of a clear tube of circular cross-section (4 mm diameter) and a red plastic ring attached to the tip. The tube was oriented horizontally and filled with artificial nectar at 10, 20, 30, 40, and 50% w/w (by mass) sucrose concentrations, consistent with the range of nectar concentrations that can be found in the wild from bird-visited plants. Feeding trials were run with artificial nectar presented in a random order of sucrose concentrations to each individual bird. Feeding bouts were recorded for each bird at each nectar concentration. One high-speed camera (Chronos 1.4, Krontech) was oriented laterally, filming the side of the clear artificial corolla tube at 500 frames/second.

4.3.2 Video analysis of nectar-feeding

We used dltdv8a (90) to track the nectar meniscus in the clear corolla tube as the bird drank. The videos were calibrated using known dimensions of the tube and the recording frame rate. We measured the consumed nectar volume using the position change of the nectar meniscus and multiplying the cross-sectional area of the tube. Volumetric intake rate was calculated by dividing the consumed nectar volume by the duration of each lick. We calculated energy consumed and energetic intake rate by using the sucrose solution energy density equation to calculate the joules/microliter of each nectar concentration.

4.3.3 Fluid Dynamics Model Predictions

We used the Hagen–Poiseuille equation to model the flow of nectar inside a sunbird's tongue during feeding. The equation:

$$Q = \frac{\Delta P \pi R^4}{8 \mu L} \quad (1)$$

can be used to model viscid (negligible inertia) fluid flow in a pipe due to a constant pressure differential. We used a micro-Computed Tomography (microCT) scanner (NSI X5000) to measure of the internal radius, R, and length, L, of the tubular portion of a *Cyanomitra olivacea* tongue (Fig. 1A). The viscosity, μ, was calculated using the equations in Heyneman 1983 for the different sucrose concentrations of nectar (Fig. 1B). We plotted the volume intake rate in units of microLiters per second across sucrose concentrations ranging from 0 to 60% w/w (Fig. 1C). Finally we calculated the energy density, joules per microLiter, from Heyneman and multiplied the values by the volume intake rate to plot the energy intake rate in units of joules per second (Fig. 1D). We use the model made from *C. olivacea* as an example of the expected volume and energy rates, but expect variation between sunbird species due to differences in tongue length and internal diameter.

4.3.4 Statistical analysis

To test if there were statistically significant maxima for each species' energy intake rate we ran pairwise Wilcoxon tests between the nectar concentrations used in the experiment. The results are plotted in Fig. 3. The results show that there are statistically significant differences between the energy intake rates of the birds at different nectar concentrations. All the sunbird species have a statistically significant maxima in energy intake rate for a sucrose concentration in the middle region of the tested range (20, 30, or 40% w/w) as all species had significantly lower energy intake rates for both 10% and 50% w/w nectar concentrations compared to the other treatments. Additionally, none of the sunbird species have a single nectar concentration that results in a statistically significant higher energy intake rate compared to other concentrations, but two or three concentrations that are not statistically different from each other, but different from concentrations on either end.

4.4 Results

4.4.1 Nectar-feeding Experiments

We measured the nectar volume intake rates for all sunbirds in the study (Table S1) across multiple nectar sucrose concentrations. Scatter plots of the data show a decreasing trend in flow rate (microLiters per second) as the sucrose concentration increases (Fig. 2A). There is some variation between the species in the study, potentially explained by the difference in tongue lengths and internal radii between the species. *Nectarinia famosa* is the largest species in Southern Africa in mass and tongue size, which may explain why it has a higher nectar volume intake rate than the other species for all sucrose concentrations (except for 40%). Likewise, the smallest species in the study, *Cinnyris talatala*, has the lowest volume intake rate of all the species for all tested sucrose concentrations. We calculated the caloric intake rate, in units of joules per second, by multiplying the volume intake rates by each nectar sucrose concentration's energy density. The scatter plot shows an approximate parabolic shape in the mean caloric intake rates per species across the tested sucrose concentrations (Fig. 2B). The nectar sucrose concentration value that maximizes the energy intake rate of each species varies between species.

4.4.2 Comparison with Hummingbirds

We compare the caloric intake rates of our study sunbirds with the previously collected data from a common North American species of hummingbird, *Selasphorus rufus* (Fig. 4). Tamm and Gass conducted a similar study measuring the volume and caloric intake rates of *S. rufus* across multiple nectar concentrations (from 20% to 60% w/w) (Tamm and Gass, 1986). At 20% sucrose concentration hummingbird caloric intake rate is similar to some of the larger sunbird species. However, for all higher concentrations tested the average hummingbird caloric intake rate is higher than the average for all the sunbirds in the study (Fig. 4). Notably, the *S. rufus* hummingbird's average mass is less than half of the smallest sunbird in the study, and its bill length, <20mm, is comparable to the smallest sunbird bill, 21mm (*C. talatala*).

4.5 Discussion

The feeding efficiency of nectarivorous birds has been studied by multiple methods for creating energy budget models and investigating ecological interactions of birds and the plants they visit (145, 146). Previous studies have hypothesized the optimal nectar concentration that would maximize caloric intake rate of nectar feeding birds (23, 24). We endeavored to test the hypotheses that these mathematical models suggest for a speciose group of nectar feeding birds, the sunbirds (Nectariniidae).

4.5.1 Optimal nectar concentrations for sunbirds

We experimentally measured nectar volume intake rate and the associated caloric intake rate of multiple sunbird species to test for an optimal nectar concentration. Our results showed that each species included in the study exhibits a semi-parabolic trend in caloric intake rate over the nectar sucrose concentrations tested. None of the species fed on a single concentration that resulted in a caloric intake rate greater than all other nectar concentrations with statistical significance. However, we found that the middle range (20, 30, and 40% w/w) of concentrations resulted in higher caloric intake rates for all species. This shows that there may be evidence of an optimal nectar concentration, or at least an optimal range of nectar concentrations, that maximize energy intake rates for sunbirds. The result of a non-specific optimal concentration may be due to one or more of multiple reasons. The active suction feeding mechanism that sunbirds use when feeding on nectar allows for variability in the specific ways the bird employs the mechanism - for instance the pressure generated by the bird can be controlled by different amounts of muscle activation. Other confounding factors that are not considered in our study may be related to a bird's desire to drink a particular nectar concentration if it can detect the level of sugar in the nectar or its level of hunger at the time it fed from the experimental flower.

4.5.2 Feeding efficiency of sunbirds versus hummingbirds

The results of our experiment show that at least one hummingbird species, *S. rufus*, feeds at a significantly higher energy intake rate than the sunbirds included in the study (Fig. 4). This difference is likely due to the different feeding mechanisms used by each group. Hummingbirds use elastic filling and fluid trapping (26, 28) when feeding on nectar while sunbirds use active suction (144). The fundamental physics governing these two distinct feeding mechanisms likely plays a significant role in the possible flow rates of nectar, but further development of mathematical models would help clarify which biophysical factors are the most important. Additionally, our study is primarily concerned with the rates of energy uptake, and thus does not consider the absolute volume consumed by each species when it visits a flower or the total it consumes throughout a day. Hummingbirds are on average much smaller than sunbirds by mass but also use a much more energetically costly means of locomotion and foraging - hovering. Sunbirds are known to usually perch when feeding from flowers, but have been observed to hover frequently when feeding from particular plant species (147, 148). Overall, this difference in feeding efficiency between these two convergently evolved groups provides a snapshot of how different evolutionary pressures and environmental traits may have shaped each lineage's form of nectarivory that they independently evolved over millions of years.

Tables

Table 1. Data for individual sunbirds included in the study.

Individual	Genus	Species	Date caught (dd-mm-yy)	Location caught	Sex	Mass (grams)	Exposed culmen (mm)
AMSB-08	*Chalcomitra*	*amethystina*	06-07-22	RWAN	M	14.5	29.4
AMSB-10	*Chalcomitra*	*amethystina*	27-07-22	RWAN	M	16	28.6
AMSB-15	*Chalcomitra*	*amethystina*	01-08-23	RWAN	M	14	29.3
GDCS-02	*Cinnyris*	*afer*	27-06-22	RWAN	M	NA	28.5
GDCS-03	*Cinnyris*	*afer*	24-08-22	RWAN	M	12	26.5
GDCS-04	*Cinnyris*	*afer*	03-08-23	ZF	M	11	27.5
OLSB-03	*Cyanomitra*	*olivacea*	19-07-24	RWAN	U	12	25.6
OLSB-04	*Cyanomitra*	*olivacea*	01-08-23	RWAN	U	12.5	24.2
WBSB-01	*Cinnyris*	*talatala*	27-07-22	RWAN	M	8.5	21
MASB-01	*Nectarinia*	*famosa*	05-08-22	ZF	M	18.5	33.7
MASB-03	*Nectarinia*	*famosa*	22-08-22	ZF	M	19	31.5
MASB-07	*Nectarinia*	*famosa*	24-08-22	ZF	F	14.5	31.4
OBSB-01	*Cinnyris*	*jugularis*	19-07-23	BK	M	7.32	21.55
OBSB-02	*Cinnyris*	*jugularis*	19-07-23	BK	M	7.5	20.5
WBSB-01	*Cinnyris*	*talatala*	24-07-23	RWAN	F	12.9	16.9

Locations are RWAN: Rocky Wonder Aloe Nursery (-29.638591N, 30.491850E), ZuluFlora (-29.533766N, 30.353995E), and Bongkudai (0.764167N, 124.441936E). Exposed culmen is the straight line length between the bill tip and the most proximal portion of the exposed keratin on the upper bill.

Figures

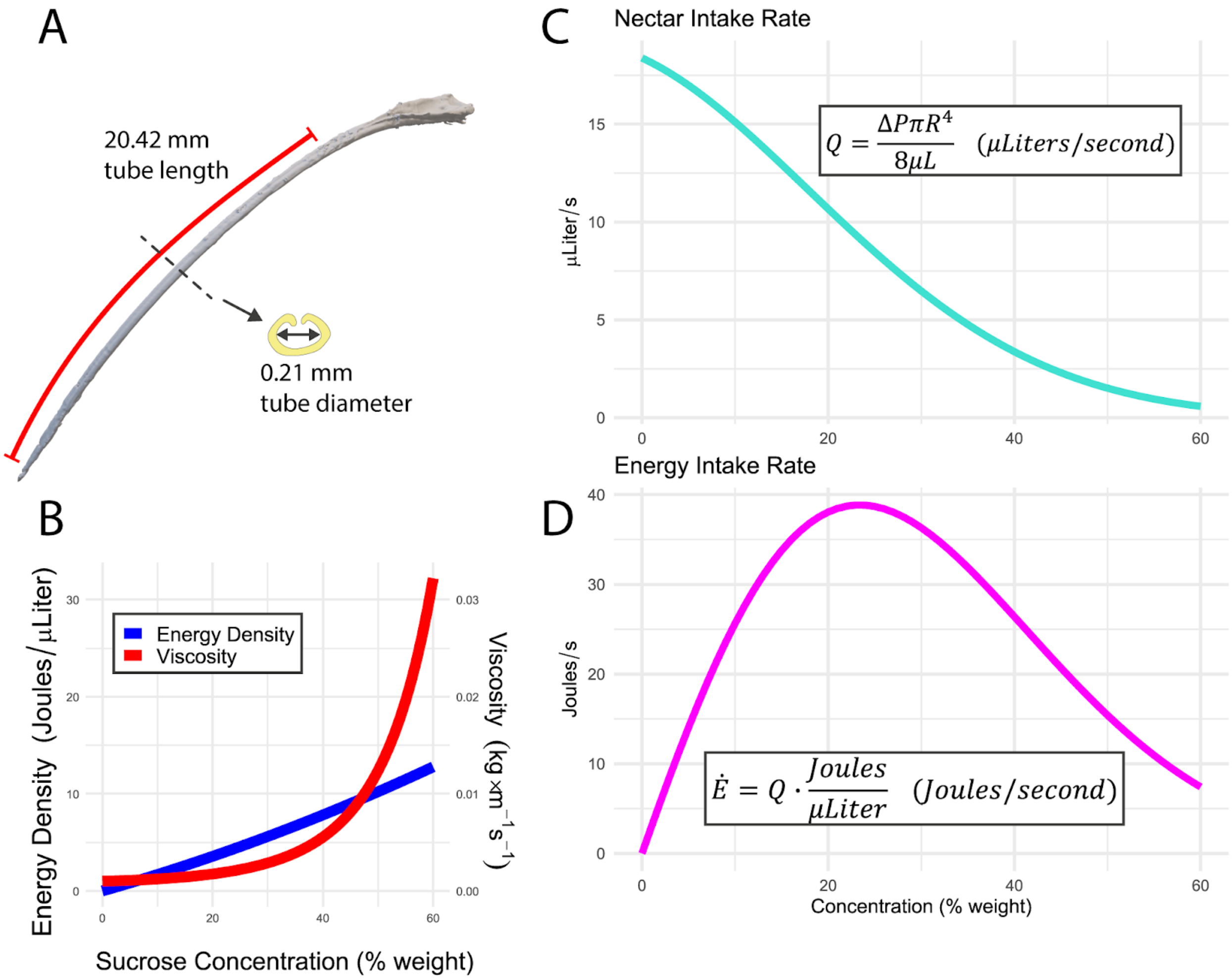


Fig. 1. Morphology, sucrose chemistry, and mathematical feeding models. (A) micro-Computed Tomography scan of a *Cyanomitra olivacea* tongue and cross-section of tube-like portion of the tongue. (B) Energy density and viscosity values plotted relative to the sucrose concentration of a solution (by percent weight w/w). (C) Volume flow rate (in microLiters per second) of the active suction feeding mechanism model plotted relative to nectar concentration. (D) Energy intake rate model (in Joules per second) plotted relative to nectar concentration.

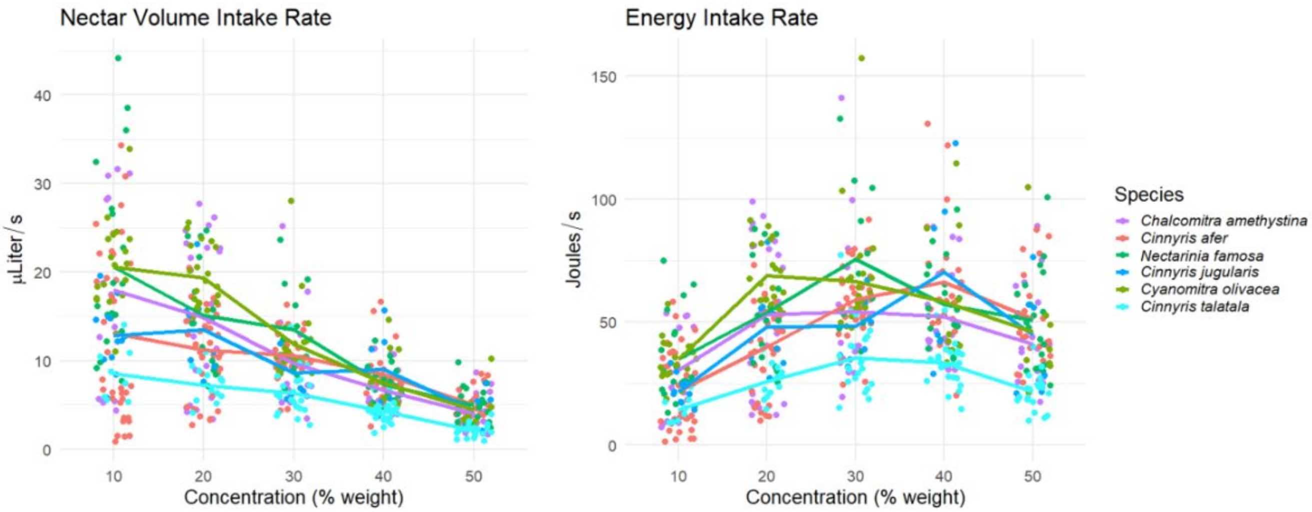


Fig. 2. Experimentally measured volume and energy intake rate. (A) Plot of the volume flow rates (in microLiters per second) of six sunbird species over five artificial nectar sucrose concentration treatments. (B) Plot of the energy intake rate (in Joules per second) of the six sunbird species.

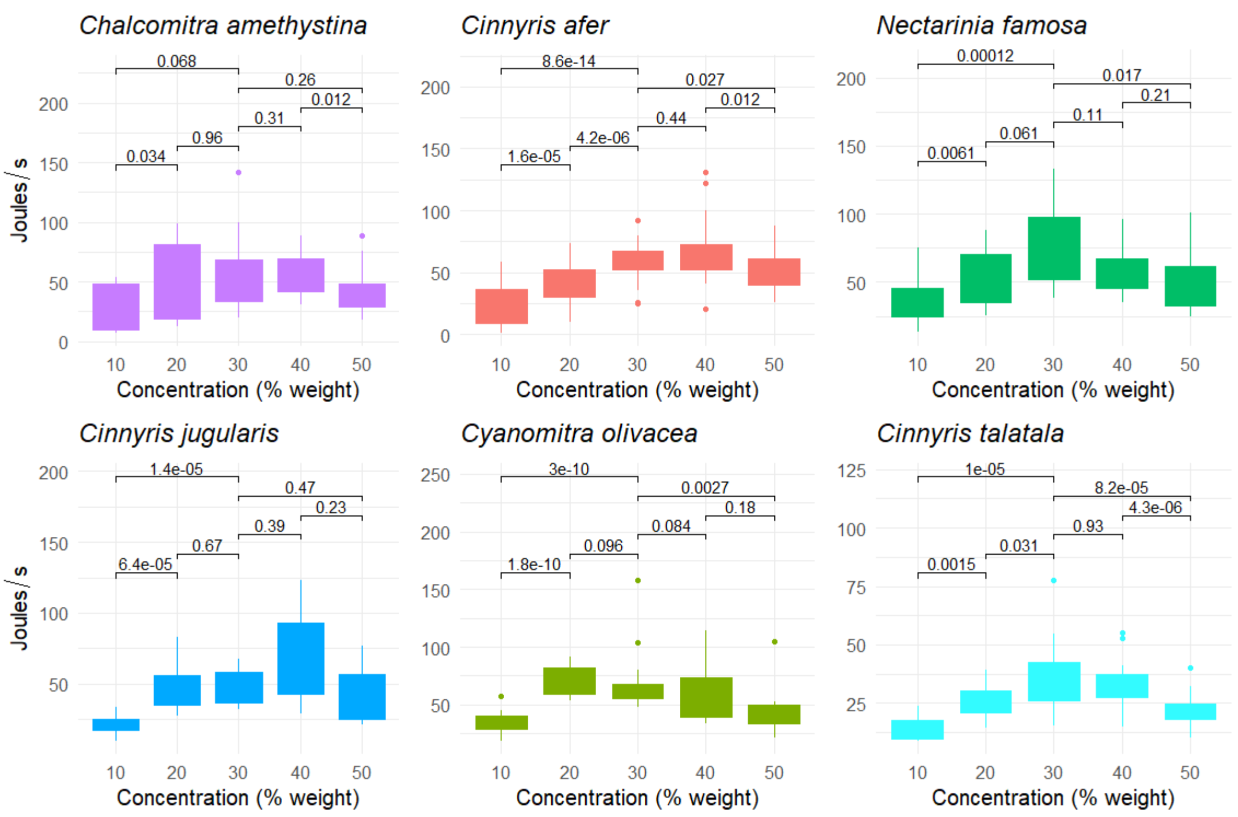


Fig. 3. Box plots and statistical analysis of sunbird optimal nectar concentration. Each species is tested to find the nectar concentrations at which the energy intake rate (in Joules per second) is significantly different from the other concentrations. Results show that there are statistically significant differences between nectar concentrations but none of the species have a single concentration for which its energy intake rate has a statistically significant maxima compared to all other concentration treatments.

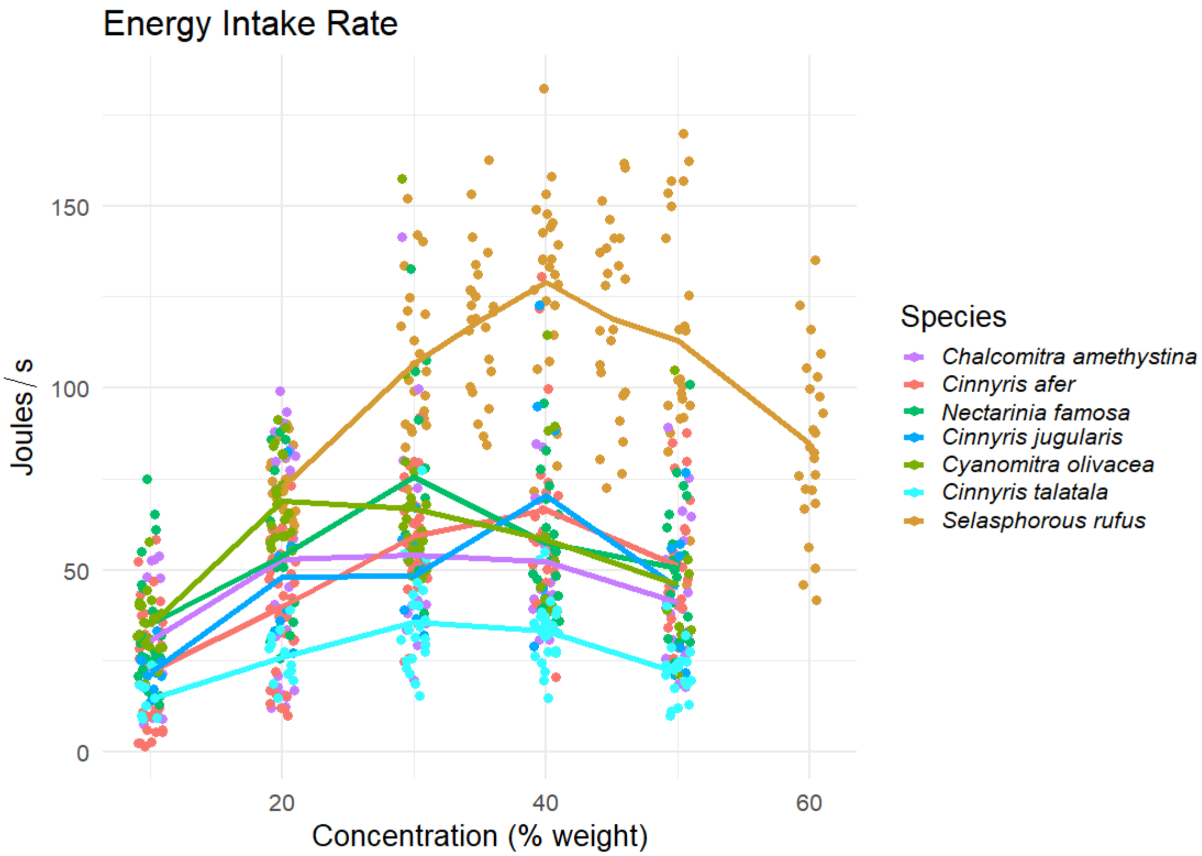


Fig. 4. Energy intake rate of sunbirds compared to a hummingbird. The energy intake rate (in Joules per second) of the sunbirds in this study are plotted with the *Selasphorous rufus* rate found by Tamm and Gass (1986). For all overlapping nectar concentrations tested the average energy intake rate of the hummingbird is greater than all the sunbird species.

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