

COMMENTARY

On the feeding biomechanics of nectarivorous birds

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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 (μ CT) 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.

KEY WORDS: Aves, Nectarivory, Drinking, Suction feeding, Fluid collection

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 (Pauw, 2019), 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 (Zweers, 1982). Given that the quantities of nectar concealed inside flowers are small (on the order of microliters; Pyke, 1978; Reed Hainsworth and Wolf, 1972) 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 (Rico-Guevara et al., 2019a).

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 (Nicolson and Thornburg, 2007), 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. Heyneman, 1983). 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 μ l⁻¹) (Heyneman, 1983; Pivnick and McNeil, 1985). In more concentrated nectar, the bird acquires more calories per microliter, but the increased viscosity reduces the volumetric uptake rate (μ l s⁻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 (Rico-Guevara et al., 2021; Sargent et al., 2021). Therefore, understanding the process of how nectar-feeding birds drink, and the links between mechanisms and ecology (e.g. Higham et al., 2021) and behavior (Green et al., 2021) for nectar drinking has implications for our understanding of nectarivore biology and coevolution with flowers (e.g. Wei et al., 2020). 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 (Pauw, 2019), 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.

How do hummingbirds drink nectar?

The distal portions of hummingbird tongues that make initial contact with nectar are primarily made of β -keratin (Rico-Guevara, 2017). 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

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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.

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 (Rico-Guevara and Rubega, 2017). These morphological characteristics determine the range of biomechanical possibilities for liquid collection and transport (e.g. Samy et al., 2019).

Initial stage: nectar collection

One of the first avian fluid intake hypotheses was that the hummingbird tongue functions as a 'drinking straw' (Gadow, 1883; Liversidge, 1967; Lucas, 1891; 1895; Weymouth et al., 1964) and terms of this nature (e.g. suction) are still used today to describe hummingbird feeding (Iwasaki et al., 2019). 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. Weymouth et al., 1964), 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) (Lucas, 1891; Weymouth et al., 1964).

The hummingbird tongue has also been hypothesized to function as a capillary tube (Lucas, 1891, 1895; Weymouth et al., 1964), and some have used the term 'capillary suction' (e.g. Kim et al., 2011). 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

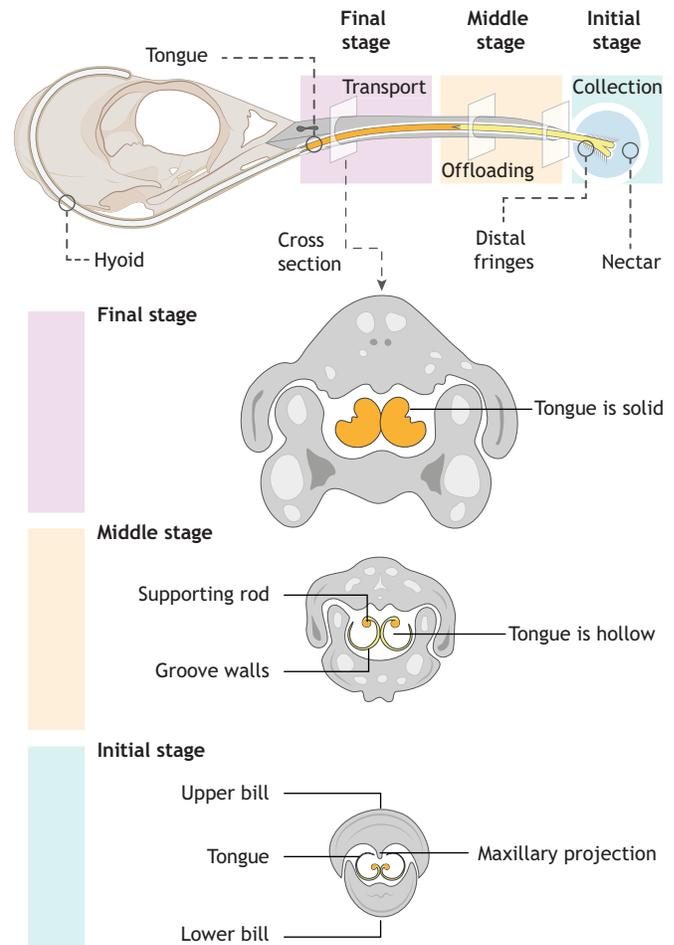


Fig. 1. Diagram of a hummingbird skull and feeding apparatus (highlighting the bill, hyoid bone and tongue). The initial stage (collection), middle stage (offloading) and final stage (transport) of nectar drinking are labelled. The stages are primarily referred to as successive points in time; however, 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.

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 (Kingsolver and Daniel, 1983; Rowlinson and Widom, 2013). 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 (Rico-Guevara et al., 2015). Although capillary filling has been the dominant theory for decades, experimental data have only supported this

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.

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 (Kim et al., 2012).

Recent high-speed video evidence (Rico-Guevara and Rubega, 2011; Rico-Guevara et al., 2015) 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 Rico-Guevara and Rubega, 2011). Elastic filling (Fig. 2D) relies on the compression and expansion of the lingual grooves during the licking cycle (Rico-Guevara et al., 2015). The tongue is dorsoventrally compressed by the bill tips as it is protruded, and then expands and fills once it contacts the nectar (Rico-Guevara et al., 2015). 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 (Kim et al., 2012). 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, Rico-Guevara et al., 2015) to match the tongue reciprocation rates recorded in wild hummingbirds (14–17 Hz, Ewald and Williams, 1982; Rico-Guevara and Rubega, 2012), the elastic filling mechanism fills the tongue at an appropriate rate (~15 ms, Rico-Guevara et al., 2015). Interestingly, previous capillary filling mathematical models found ‘optimal concentrations’ of nectar that closely matched those commonly offered by flowering plants in nature (Heyneman, 1983; Kim et al., 2011; Kingsolver and Daniel, 1983; Pyke and Waser, 1981). 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.

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 (Döhling, 1931; Gadow, 1883; Moller, 1930; Scharnke, 1931; Steinbacher, 1935). 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 (Gadow, 1883). 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 (Moller, 1930; Döhling, 1931). Steinbacher (1935) further proposed that the rapid pharyngeal movements observed in captive birds (cf. Döhling, 1931) 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. Böker, 1927; fig. 11 in Zusi, 2013). Furthermore, the flexibility of hummingbird mandibular rami (see Glossary) (Chaparro-Herrera et al., 2019; Smith et al., 2011; Yanega and Rubega, 2004) 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

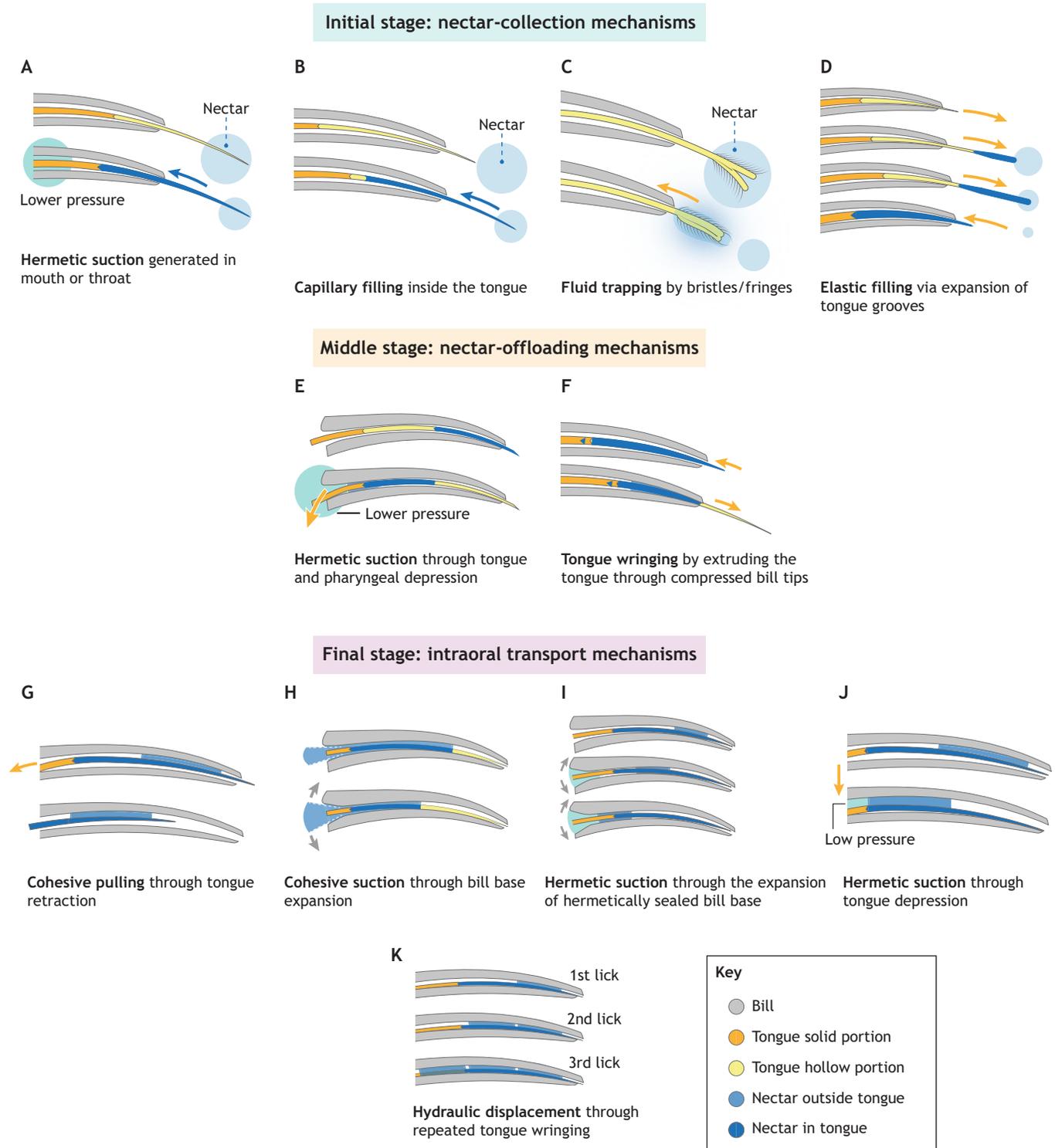


Fig. 2. Biomechanical methods of nectar drinking at different stages of the process. Each panel depicts a different mechanism hypothesized to be a part of avian nectar feeding organized by the stage of the nectar-feeding process in which they occur: (A–D) initial stage, (E, F) middle stage or (G–K) final 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.

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. Rico-Guevara, 2014; Rico-Guevara and Rubega, 2017) 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 (Rico-Guevara, 2017). 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, Rico-Guevara and Rubega, 2017). 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).

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 (Rico-Guevara et al., 2019a; Zweers, 1982). 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 (Downs, 2004; Ewald and Williams, 1982; Moller, 1930; Scharnke, 1931). This mechanism, which we have called cohesive pulling (Fig. 2G) (Rico-Guevara, 2014), 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 Rico-Guevara, 2017; Weymouth et al., 1964) 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 (Rico-Guevara, 2014). 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 (Muller and Osse, 1984), 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 (Chaparro-Herrera et al., 2019; Smith et al., 2011; Yanega and Rubega, 2004); (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. Döhling, 1931; Steinbacher, 1935). 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) (Gadow, 1883).

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) (Rico-Guevara, 2014). 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 (Rico-Guevara et al., 2021). 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.

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, Rico-Guevara et al., 2019b). Their bills are also relatively long and narrow, and possess similar internal features such as mandibular grooves and prongs (Downs, 2004; Liversidge, 1967; Rico-Guevara and Rubega, 2017), which may guide the tongue through the intraoral-squeezing zone of the bill during tongue wringing (Fig. 2F, Rico-Guevara and Rubega, 2017). 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

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.

same pumping action for generating suction to draw in nectar (Gadow, 1883). Honeyeaters have brushed-tipped tongues that may trap liquid among the bristles using surface tension (e.g. Samy et al., 2019), which could be drawn close together to effectively create an enclosed capsule of liquid at the tongue tip (Paton and Collins, 1989). Honeyeaters also have lingual grooves, which could use capillary filling to draw the nectar into the rest of the tongue body (Fig. 2B, Paton and Collins, 1989). Hawaiian honeycreepers have tubular tongues (Beecher, 1951; Fleischer et al., 2008; Gardner, 1925; Gardner, 1927; Raikow, 1976; Ziegler et al., 2002), 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 (Churchill and Christensen, 1970; Homberger, 1980), similar to those of mammalian nectarivores (e.g. Harper et al., 2013), where surface tension holds liquid between adjacent papillae (Nasto et al., 2018). Although other groups of avian nectarivores have nearly no study of their nectar-feeding mechanisms, many have frayed-tipped tongues (e.g. Sustaita et al., 2018), 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 (Homberger, 1980), and thus cannot use tongue wringing (Rico-Guevara et al., 2019b). However, given their ability to manipulate tongue papillae (Homberger, 1980), 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 (Cheke and Mann, 2008; Gadow, 1883; Liversidge, 1967). 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.

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

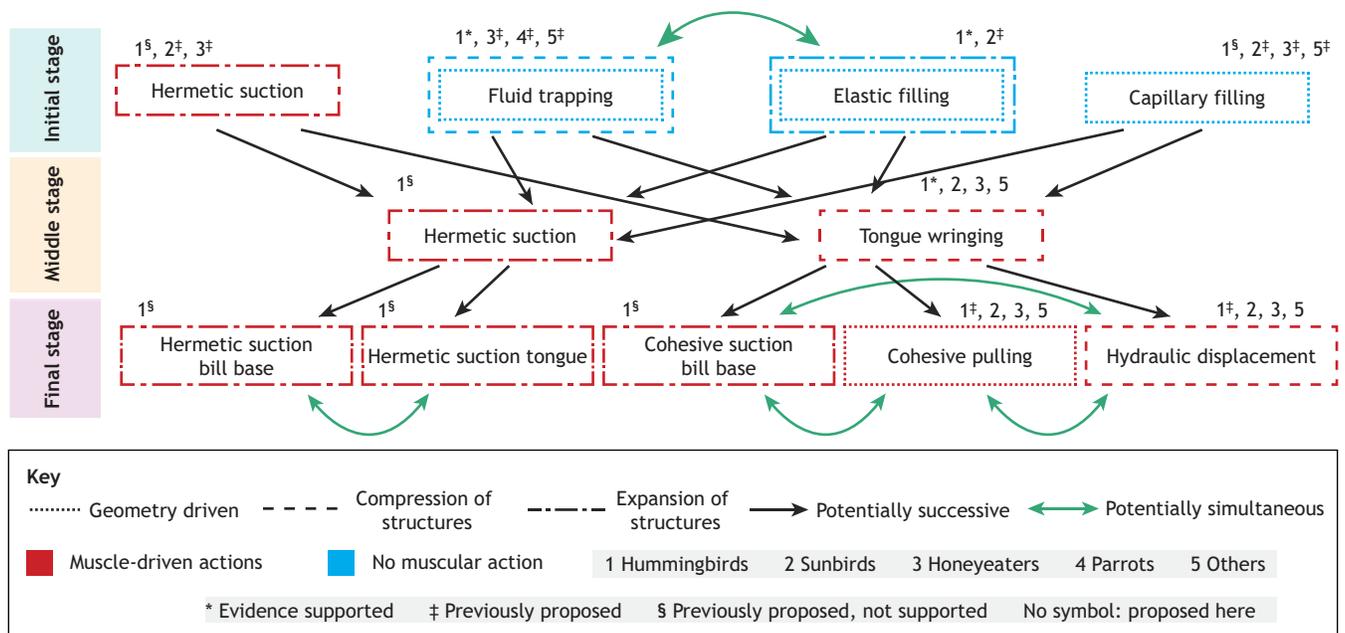


Fig. 3. Hypothesis flowchart showing how the proposed biomechanical methods could interact. Interactions show how feeding mechanisms could either occur successively across different stages (black, single-headed arrows) or simultaneously in the same stage (green, double-headed arrows). The box outline 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.

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 (Rico-Guevara et al., 2015) or wild backlit-translucent flowers (Rico-Guevara et al., 2021). 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, Rico-Guevara, 2014), much of the mechanisms would remain hidden within opaque/thick bills. High-speed fluoroscopy could offer visualization of BaSO₄ (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 (Doss et al., 2017; Vink-Nooteboom et al., 2003). 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).

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, Rico-Guevara et al., 2021) to more generalized systems (e.g. honeyeaters, Fleming and Muchhala, 2008; Zanata et al., 2017). 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 (Baker and Baker, 1983; Gartrell, 2000; Grant and Grant, 1968), 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 understand 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.

Acknowledgements

We would like to thank Nuria Melisa Morales García for her incredible work on Figs 1 and 2. Our goal to consolidate and examine the variety of nectar-feeding biomechanical methods would not have been possible without the suggestions, guidance and interest from Charlotte Rutledge, JEB Reviews Editor. We also thank Rosey Elting for discussions and general lab support. Morphological inspections of museum specimens have greatly improved our understanding of nectar-feeding structures; we thank the following institutions for access to their ornithological collections: Burke Museum of Natural History and Culture, American Museum of Natural History, Smithsonian National Museum of Natural History and the Instituto de Ciencias Naturales at the Universidad Nacional de Colombia.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.C., A.E.H., A.R.-G. Literature Search: D.C., A.E.H., A.J.S., D.J.E.G., A.R.-G. Writing – original draft preparation: D.C., A.E.H., A.R.-G. Critical Revision and Editing: D.C., A.E.H., A.J.S., D.J.E.G., A.R.-G.

Funding

This work was supported by a Walt Halperin Endowed Professorship and a Washington Research Foundation Distinguished Investigator award to A.R.-G.

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