

RESEARCH ARTICLE

Drinking made easier: honey bee tongues dip faster into warmer and/or less viscous artificial nectar

Lianhui Shi^{1,2}, Susan W. Nicolson³, Yunqiang Yang², Jianing Wu^{1,*}, Shaoze Yan⁴ and Zhigang Wu¹

ABSTRACT

Optimal concentrations for nectar drinking are limited by the steep increase in the viscosity of sugar solutions with concentration. However, nectar viscosity is inversely related to temperature, which suggests there are advantages to foraging from flowers that are warmer than the surrounding air. The honey bee (*Apis mellifera* L.) dips nectar using a hairy tongue. However, the microscopic dynamics of the tongue while the bee ingests nectar of varying concentration, viscosity and temperature are unknown. In this study, we found that honey bees respond to the variation of nectar properties by regulating dipping frequency. Through high-speed imaging, we discovered that the honey bee traps warmer sucrose solutions with a quicker tongue. The honey bee dips the warmest and most dilute solution (40°C and 25% w/w sucrose) 1.57 times as fast as the coldest and thickest solution (20°C and 45% w/w sucrose). When the viscosity of different sucrose concentrations was kept constant by adding the inert polysaccharide Tylose, honey bees dipped nectar at constant frequency. We propose a fluid mechanism model to elucidate potential effects on sucrose intake and show that higher dipping frequency can increase the volumetric and energetic intake rates by 125% and 15%, respectively. Our findings broaden insights into how honey bees adapt to foraging constraints from the perspective of tongue dynamics, and demonstrate that elevated intrafloral temperatures and lower nectar viscosity can improve the volumetric and energetic intake rates of pollinators.

KEY WORDS: Pollinator, *Apis mellifera*, Temperature, Viscosity, Dipping frequency

INTRODUCTION

The optimal nectar concentrations for pollinators of different functional groups have been a source of much interest to pollination biologists, with one of the best known examples being the contrast between the dilute nectars of bird-pollinated flowers and the more concentrated nectars of bee-pollinated flowers (Pyke and Waser, 1981). Studies on the fluid mechanics of drinking show that optimal concentrations depend on the drinking mechanism used (Heyneman, 1983; Kim et al., 2011; Kim and Bush, 2012); this may be active

suction in butterflies, capillary suction in nectar-feeding birds, or viscous dipping in most bees and in bats (Kim et al., 2011). Because viscosity increases sharply with sugar concentration, animals employing these different techniques have different optimal nectar concentrations.

The honey bee is arguably the most important pollinator worldwide, and its mouthparts and drinking strategies have been studied extensively (Goodman, 2003; Krenn et al., 2005; Wu et al., 2019). The mouthparts include paired galeae and labial palps which enclose a segmented glossa covered by long, distally pointing hairs, also known as microtrichia (Fig. S1). When the glossa is extended into nectar, the hairs snap outward, remaining erect as the bee withdraws its tongue, so that they play an important role in trapping nectar. At the end of each dipping cycle, the hairs flatten as nectar is taken into the food canal (Zhu et al., 2016; Yang et al., 2017). Combined experimental observation and mathematical modelling demonstrate that this specialized viscous-dipping technique can meet the contradicting demands of both high sugar intake and low energy consumption (Wu et al., 2015, 2018). Our previous work revealed that the dipping frequency can be employed to characterize functional adaptation in honey bees, such as the compensation in nectar intake rate induced by structure deterioration: older honey bees with shorter glossal hairs dip nectar faster (Wu et al., 2019).

While the energy content of nectar increases linearly with sugar concentration, its viscosity increases exponentially; in addition, the viscosity of a sucrose solution decreases, although less steeply, with increased temperature (Pieter, 1953; Heyneman, 1983; Nicolson and Thornburg, 2007; Telis et al., 2007). Nicolson et al. (2013) offered artificial nectar of different temperatures and viscosities to honey bees in a natural setting, finding that both parameters affected the crop loads of individual bees and the consumption of sucrose solutions by colonies. These preferences of honey bees for warmer and less viscous nectar may facilitate reduced thermoregulatory costs and faster ingestion times (Nicolson et al., 2013). Extensive studies have reported effects of nectar viscosity on volumetric intake rate among a variety of insect species (Kingsolver and Daniel, 1983; May, 1985; Josens and Farina, 2001; Borrell, 2006; Kim et al., 2011; Yang et al., 2014); however, intrinsic connections among nectar temperature, nectar viscosity and dipping frequency remain unexplored. In this paper, we quantified the dipping frequency using high-speed imaging techniques while feeding honey bees artificial nectars of varying temperatures and concentrations, or with viscosity adjusted using the inert polysaccharide Tylose. Then, we built a mathematical model to analyse the key parameters that determine the nectar intake rate and energy reward. We predicted that temperature and viscosity effects on dipping frequency can enhance both volumetric and energetic intake rates, which may be one reason why bees are attracted to warm flowers (Dyer et al., 2006; Kovac and Stabentheiner, 2011).

¹School of Aeronautics and Astronautics, Sun Yat-Sen University, Guangzhou 510006, People's Republic of China. ²School of Engineering and Technology, China University of Geosciences (Beijing), Beijing 100083, People's Republic of China. ³Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa. ⁴Division of Intelligent and Biomechanical Systems, State Key Laboratory of Tribology, Department of Mechanical Engineering, Tsinghua University, Beijing 100084, People's Republic of China.

*Author for correspondence (wujn27@mail.sysu.edu.cn)

 J.W., 0000-0003-0902-4466

MATERIALS AND METHODS

Honey bees

Honey bees (*Apis mellifera* L.) were obtained from an outdoor beehive on the east campus of Sun Yat-Sen University, Guangzhou, China (23.09°N, 113.30°E). Workers used for the experiments were captured at the colony entrance from 10:00 h to 12:00 h as they returned from foraging (Free, 1967). In total, we captured 100 honey bees individually in centrifuge tubes (10 ml), 20 for each experimental temperature, and we collected a further 20 bees for the viscosity experiment. For each temperature, 20 bees were caged in two glass beakers (500 ml) covered by a piece of cotton gauze for ventilation, 10 in each beaker. The specimens were kept in the dark in an incubator with a temperature of 25°C and starved for 24 h before observation of their dipping cycles (Li et al., 2016). Each bee was used for one video recording only. The laboratory temperature and humidity were 20°C and 65%, respectively. We recorded the feeding behaviour of bees at each temperature on one day and spent one day observing feeding behaviour of the 20 bees for the viscosity experiment.

Dipping nectar at different temperatures

Dipping cycles were visualized using a setup mainly composed of a high-speed camera (Phantom, Miro LC310) and a microscope (Olympus, CX33; Fig. S2a,b). Before the experiments, honey bees were placed in a refrigerator (KONKA, BCD-180GY2S) until they ceased moving and could be individually harnessed on the positioner (Mota et al., 2011). A cuboid feeder fabricated from two glass slides (75×50×3 mm; 1 mm apart) was placed under the microscope connected to the high-speed camera (Li et al., 2016) (Fig. S2a). Taking the 40°C temperature experiment as an example, we first prepared 25%, 30%, 35%, 40% and 45% w/w sucrose solutions and injected them into the five feeders. After being marked, the feeders were put in the refrigerator to attain an initial temperature of 5°C. Next, we placed one glass feeder on the heating pad (Smart-M) set at a temperature of 40°C (Fig. S2a). We wore latex gloves to prevent contamination from the fingers. To ensure the honey bees remained fixed in place and to encourage them to ingest solutions continuously, the magnetic base was used as the positioner (Fig. S2a). We glued the thorax of the bee to the positioner and moved it to approach the glass feeder for capturing dipping cycles using the high-speed camera (Wu et al., 2019).

Dipping nectar with a constant viscosity

To determine the effect of viscosity on dipping frequency, independent of concentration, we used small amounts of the inert polysaccharide Tylose (carboxymethyl cellulose) to increase the viscosity of the sucrose solutions without adding nutritional value (Josens and Farina, 2001; Nicolson et al., 2013). Honey bees were fed 25%, 30%, 35%, 40% and 45% w/w sucrose solutions, at a constant temperature of 25°C. Various amounts of Tylose HS 30000 YP2 (Shin-Etsu Chemical Co., Ltd) were added to maintain the viscosity at 7.2 mPa s⁻¹, the same as that of 45% w/w sucrose at 25°C. The amount of Tylose added to each sucrose concentration is shown in Table 1. The viscosity of the solutions was measured with a digital viscometer (NDJ-5S, MINCEE). Observations on dipping cycles were made using the method above.

Statistical analysis

We recorded 90 videos of the dipping cycles of individual honey bees (75 and 15 videos, respectively, for the temperature and viscosity experiments; data for dipping frequencies are in Tables S1 and S2). During drinking, the glossa first protracts, then retracts

Table 1. Amount of Tylose added to sucrose solutions

Sucrose concentration (%)	Initial dynamic viscosity (mPa s)	Tylose added (% w/w)	Dynamic viscosity with Tylose (mPa s)
25	1.9	0.094	7.2
30	2.7	0.085	7.2
35	3.8	0.056	7.2
40	5.3	0.031	7.2
45	7.2	0	7.2

through the feeding tube formed by the galeae and labial palpi. A feeding cycle lasts for time t (ms), and the dipping frequency can be calculated as $f=1000/t$ (Hz). The nectar solution has a viscosity μ (mPa s⁻¹), a sucrose mass concentration s (%) and a temperature T (°C). Linear regression analysis was used to determine the relationship between the dipping frequency, mass concentration of sucrose solution and temperature. Origin software (Origin2018, OriginLab) was used for data analyses and correlations. We introduced a mathematical model which we had built previously to determine the relationship between dipping frequency, volumetric flux and energetic intake rate, using the Matlab software (R2016a, MathWorks) (Shi et al., 2020).

RESULTS

Dipping frequency at different nectar temperatures

We obtained the dipping frequency of honey bees for sucrose solutions at a variety of concentrations and temperatures by analysing high-speed videos (Table S1). The feeding cycle is illustrated in Fig. 1; the frames in the two rows show the dipping frequency of two honey bees fed with 35% w/w sucrose solution at 20 or 40°C. The drinking process remained the same, consisting of the glossa extension phase (Fig. 1A–C and G–I), the glossal hair erection phase (Fig. 1C–D and I–J) and the glossa retraction phase (Fig. 1D–F and J–L). However, the durations differed. The dipping cycle lasted 208 ms for a honey bee drinking 35% sucrose at 20°C (Fig. 1A–F), with a dipping frequency of only 4.81 Hz. For a honey bee drinking 35% sucrose solution at 40°C, the feeding cycle shortened to 153 ms (Fig. 1G–L) with an increased dipping frequency of 6.54 Hz.

A histogram of mean dipping frequency for a range of concentrations with respect to nectar temperature is plotted in Fig. 2. The dipping frequency of the glossa was positively correlated with the temperature of the sucrose solution ($R=0.934$, $P<0.0001$). The average dipping frequency was 5.02±0.18 Hz for honey bees drinking 25% sucrose at 20°C. When this solution was warmed to 40°C, the average dipping frequency was 7.06±0.46 Hz, an increase of 40.8%. We also found that the dipping frequency was negatively correlated with sucrose concentration ($R=-0.309$, $P<0.0001$). At each temperature, honey bees dipped dilute nectar at higher frequency than more concentrated nectar (Movies 1 and 2). For instance, at 25°C, the mean dipping frequency was 5.29±0.53 Hz for the 25% sucrose solution, decreasing to 4.73±0.28 Hz for the highest concentration of 45%.

Dipping frequency at different food viscosities

We measured the dipping frequency of honey bees fed different concentrations of sucrose with the viscosity maintained at 7.2 mPa s⁻¹ (Table S2). Fig. 3 shows the dipping frequencies for 25–40% sucrose solutions with added Tylose and 45% sucrose with no added Tylose. The polynomial fitted equation $f(s)=7.14\times 10^{-5}s+4.73$ ($R^2=0.712$; Fig. 3) is consistent with the dipping frequency of 4.73±0.28 Hz obtained when honey bees drank 45% sucrose solution at

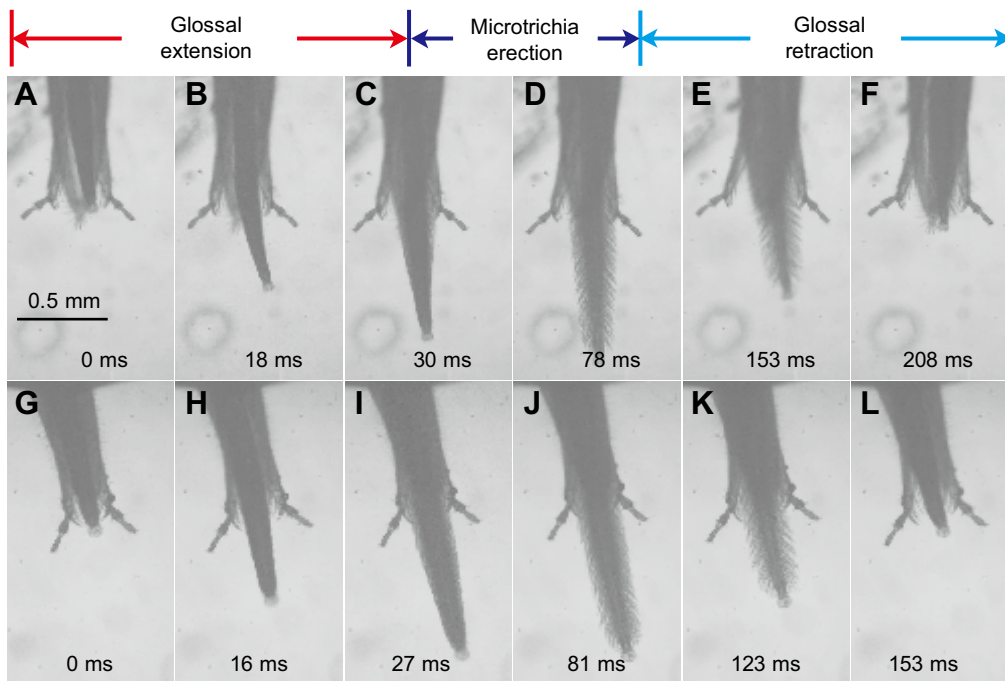


Fig. 1. Honey bee tongues dipping cooler and warmer sucrose solutions. Typical dipping cycle of a honey bee drinking 35% w/w sucrose solution at 20°C (A–F) or 40°C (G–L).

25°C. The dipping frequency remained stable at 4.73 Hz when the viscosity of the sucrose solutions was maintained at 7.2 mPa s⁻¹, independent of changes in sucrose concentration.

Fluid transport model

In accordance with viscosities of sucrose solutions from the literature (Pieter, 1953), we selected information for sucrose concentrations from 25% to 45% w/w and temperatures from 20 to 40°C (as used in the experiments). The equation for viscosity μ against concentration s and temperature T was fitted by Matlab using robust methods and is shown in Fig. S3:

$$\mu(s, T) = 10^{(s^4 + (1.56(s+B))/(T+C))} - 1.48, \quad (1)$$

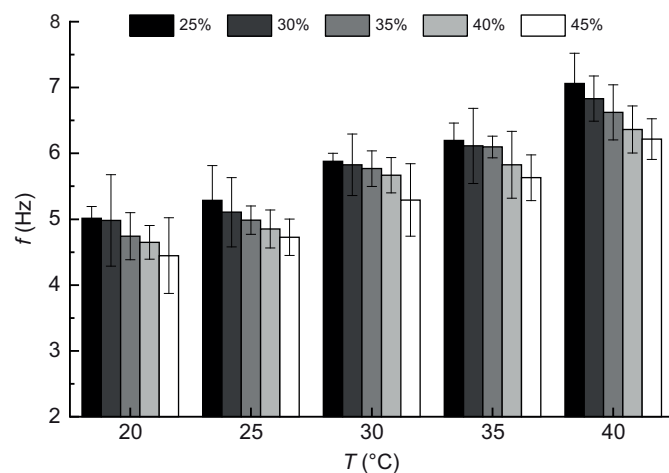


Fig. 2. Effect of temperature and sucrose concentration on dipping rate. Honey bees ingested 25%, 30%, 35% and 45% w/w sucrose solutions maintained at a temperature T of 20, 25, 30, 35 and 40°C. Mean dipping frequency f ($n=10$ drinking cycles from 3 bees) is shown for each combination of concentration and temperature, and error bars are presented as 95% confidence intervals (see Table S1).

where A – C are constant coefficients ($A=-26$, $B=-0.497$, $C=48$) and the coefficient of determination is $R^2=0.9998$.

To calculate the volumetric intake rate of honey bees at different glossal dipping frequencies, we fitted the relationship between dipping frequency, mass concentration and temperature using the experimental data in Table S1 to give:

$$f = 3.257 + 0.09372s - 0.031T, \quad (2)$$

where the coefficient of determination was $R^2=0.9688$. To verify the veracity of Eqn 2, we analysed the relative error Er between calculated values and experimental values for the honey bees' dipping frequencies. We found that the maximum $|Er|$ was less than 3.67%. The results of the fitted Eqn 2 were roughly consistent with the real dipping frequencies of honey bees.

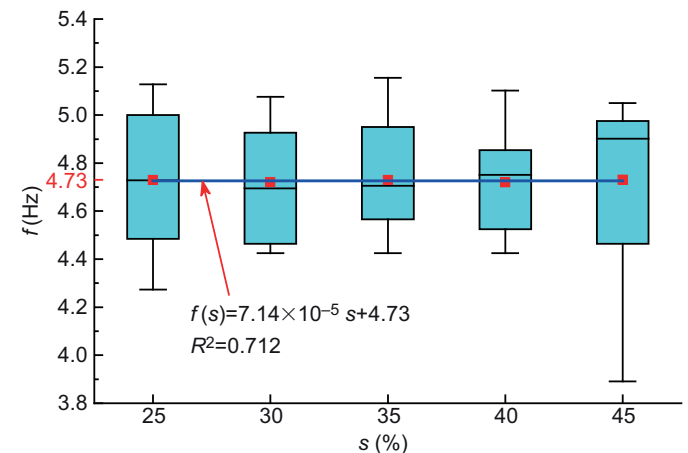


Fig. 3. Effect of viscosity on dipping rate. Dipping frequency f remains constant when bees are fed different sucrose concentrations s at 25°C with a constant viscosity of 7.2 mPa s⁻¹ as a result of added Tylose. Red squares represent mean values ($n=10$ drinking cycles from 3 bees) for dipping frequency, cyan boxes indicate the interquartile range and whiskers indicate minimum and maximum values. The blue line represents the best fit to the experimental data (see Table S2).

In the viscous dipping model of honey bees, we obtained the intake volume of a dipping cycle as follows (Shi et al., 2020):

$$\dot{Q}(s, T) = \left[\pi h \sin \theta (2a + h \sin \theta) v T_1 - \frac{2}{3} \pi^2 n a d^2 h v T_1 \right] \cdot f, \quad (3)$$

where \dot{Q} is the average volumetric flux, f is the dipping frequency, T_1 is the duration of glossal protraction, v is the protraction speed of the glossa and a is the average radius of the glossa. Here, the glossal hairs have length h , erection angle θ , distribution density n and diameter at the base d .

Then, we introduced the assumption that the power rate applied in viscous dipping of honey bees remains constant with respect to concentration. This assumption leads to $v \approx k\mu^{-1/2}$, where μ is the viscosity and the coefficient k indicates the relative value of work power. We also used the assumption that the honey bees maintain erection angle θ constant in solutions of different viscosity in our experiments. The energetic intake rate \dot{E} is then derived from the product of the energy content per unit mass of sugar c and density ρ (Kingsolver and Daniel, 1979):

$$\dot{E}(s, T) = \rho s c \dot{Q} / 100. \quad (4)$$

DISCUSSION

According to our experiments, the dipping frequency of the honey bee glossa is proportional to the temperature, inversely proportional to the sucrose concentration and independent of concentration if

viscosity is kept constant with Tylose. This is the first investigation of the effects of temperature and viscosity of sucrose solutions on the kinematics of drinking in honey bees; both are critical factors in the drinking process.

To elucidate the effect of changes in dipping frequency on nectar consumption, we combined Eqn 1 and the mathematical model to evaluate the volumetric flux and energetic intake rate for nectar of different temperatures and viscosities (Fig. 4A,B). Fig. 4A shows the theoretical volumetric flux of the honey bee in terms of the temperature and viscosity of nectar. The volumetric flux reaches a maximum value of $\dot{Q}_{\max} = 1.64 \mu\text{l s}^{-1}$ when the bee dips nectar at a high temperature and low viscosity (red region in Fig. 4A). Conversely, at lower temperature and higher viscosity, the volumetric intake decreases (blue region). The theoretically optimal volumetric flux of honey bees calculated by this model occurs at a high nectar temperature (40°C) and low viscosity ($\mu = 1.24 \text{ mPa s}^{-1}$, equivalent to $s = 25\% \text{ w/w}$), which matches well with the experimental results reported by Nicolson et al. (2013).

The results of the mathematical model show the energetic intake rate of honey bees, which is plotted against the nectar temperature and viscosity in Fig. 4B. We found that the energetic intake rate reaches a maximum value (red area in Fig. 4B; $\dot{E} = 7.00 \text{ J s}^{-1}$) under conditions of higher temperature and lower viscosity. In contrast, when the nectar temperature is lower with higher solution viscosity, the energetic intake rate approaches minimum levels (blue area in Fig. 4B; $\dot{E} = 3.22 \text{ J s}^{-1}$). The theoretically optimal energetic intake rate

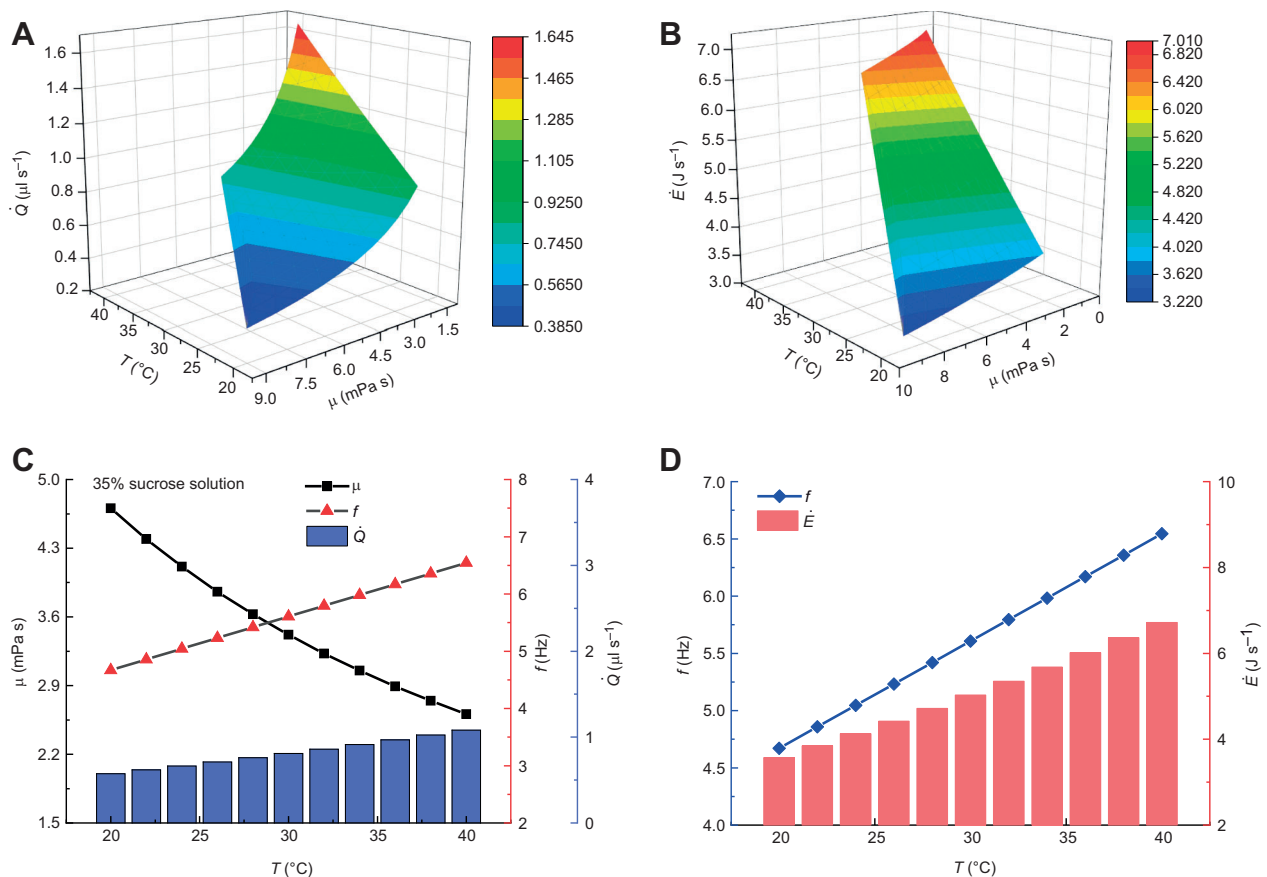


Fig. 4. Theoretical model and implications. (A) Relationship of nectar intake rate \dot{Q} , nectar viscosity μ and temperature T . The colour gradient ranging from blue to red indicates the minimum to maximum intake rate. (B) The energetic intake rate \dot{E} of honey bees plotted against the solution temperature T and viscosity μ . (C) Mapping of volumetric intake rate \dot{Q} , dipping frequency f and viscosity μ in a typical situation in which a honey bee feeds on 35% sucrose solution at different temperatures. (D) When a honey bee dips 35% sucrose solution, the energetic intake rate \dot{E} increases with respect to temperature T .

of honey bees calculated by this model occurs at a high temperature (40°C) with low viscosity ($\mu=1.24 \text{ mPa s}^{-1}$, $s=25\% \text{ w/w}$).

Next, we examined the typical example in which the honey bee dips the optimal concentration of 35% sucrose solution (Yang et al., 2014; Shi et al., 2020) at different temperatures. The relative error between theoretical and experimental dipping frequency [Er] was less than 3.07% in this case, which validates the model. The volumetric flux \dot{Q} (Fig. 4C) increased with dipping frequency (which rose from 4.67 to 6.54 Hz as the temperature increased from 20 to 40°C). The volumetric flux at the highest dipping frequency (6.54 Hz) was up to $1.08 \mu\text{l s}^{-1}$, which is 1.89 times that derived from dipping at 4.67 Hz, i.e. $0.57 \mu\text{l s}^{-1}$ (Fig. 4C). The viscous dipping model shows theoretical values for the energetic intake rate in Fig. 4B. As shown in Fig. 4D, when a honey bee forages on 35% w/w nectar, the energetic intake rate also increases with higher solution temperatures and faster dipping frequencies.

The influence of nectar viscosity on drinking rate is also seen in bird pollinators, which utilize a licking mechanism for drinking (Rico-Guevara et al., 2015). In a study of the whitebellied sunbird (*Cinnyris talatala*), Köhler et al. (2010) found that lick frequency, tongue load and volumetric intake rate were inversely proportional to nectar viscosity. However, these parameters remained constant when Tylose was used to maintain constant viscosity in sucrose concentrations ranging from 0.25 to 1.5 mol l^{-1} (8–42% w/w). In both honey bees and sunbirds, as well as other insect nectarivores such as hawk moths and orchid bees (Josens and Farina, 2001; Borrell, 2006), viscosity modification with Tylose has clearly shown that consumption of sugar solutions is constrained by their viscosity. Our fluid transport model confirms that ingesting dilute nectar facilitates both higher volumetric flux and greater energetic intake rate, revealing the specific kinematic regulation for increasing energy intake rate (Fig. 4A,B).

What are the rewards for nectarivores from drinking warmer and less viscous nectar? Faster drinking of low viscosity nectar helps to explain the relatively dilute nectars of bird-pollinated plants (Köhler et al., 2010). Moreover, for avian nectarivores, which must ingest high nectar volumes to maintain energy balance, there are thermal benefits to drinking warmer nectar, because it is more easily warmed to body temperature (Lotz et al., 2003). In honey bees, lower nectar viscosity also enables faster drinking. This work with immobilized bees in the laboratory is in good agreement with previous work on colonies in a natural setting (Nicolson et al., 2013). In that study, it was necessary to use dilute nectar (10–20% w/w) to prevent overcrowding at feeders during winter food scarcity, and it is significant that the temperature effect on viscosity will be substantially more pronounced at the higher nectar concentrations on which honey bees usually forage (Fig. S3). Warm nectar also offers thermoregulatory benefits for honey bees, which must maintain high thoracic temperatures during foraging (Waddington, 1990; Roberts and Harrison, 1999; Kovac and Stabentheiner, 2011). The preference of stingless bees (*Trigona carbonaria*) for warm nectar increases at low ambient temperatures (Norgate et al., 2010). Associated with faster drinking, crop loads are higher in honey bees feeding on warm and less viscous nectars, which may maximize energetic efficiency (Afik and Shafir, 2007; Nicolson et al., 2013). In demonstrating that older honey bee workers with worn glossal hairs compensate by dipping nectar at a higher frequency, Wu et al. (2019) found that the wear rate increased in more viscous nectar. There are apparently multiple and interacting benefits to drinking warm and less viscous nectar.

While it is often assumed that nectar is at air temperature, intrafloral temperature may be several degrees higher than air

temperature (Corbet, 1990; Herrera, 1995; Kovac and Stabentheiner, 2011). Flower colour, size, shape, orientation and movement are among the factors that influence the microclimate in flowers, often leading to heat gain from solar radiation (reviewed by Van der Kooi et al., 2019). Floral warming provides thermoregulatory benefits to pollinators (Herrera, 1995; Kovac and Stabentheiner, 2011) and increases nectar volume and sugar production (Nicolson, 1995; Petanidou and Smets, 1996). Bees can distinguish differences in temperature between and within flowers (Whitney et al., 2008; Harrap et al., 2017). Tests of the foraging preferences of bumblebees (*Bombus terrestris*) show that they perceive floral warmth as a reward (Dyer et al., 2006; Whitney et al., 2008). Floral warmth may act as a cue for pollinators, signalling improved nectar rewards as well as a direct metabolic reward (Rands and Whitney, 2008). Honey bees associate temperature differences with food, especially warm temperature differences, as shown by proboscis extension when a warm surface is touched to the antenna (Hammer et al., 2009).

In conclusion, we provide a mechanistic explanation, from the point of view of tongue dynamics, for the preference of bees for warm nectar. By selecting flowers with warm and therefore less viscous nectars, honey bees increase the dipping frequency of their tongues and imbibe the nectar faster. Other bees, with similar mouthparts (Krenn et al., 2005), will have similar opportunities to enhance their energy gains when drinking warm nectar.

Acknowledgements

We thank Mr Yue Chen from China University of Geosciences (Beijing) for his assistance with honey bee anatomy.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Methodology: L.S., S.W.N., J.W.; Software: L.S.; Investigation: S.W.N., J.W.; Resources: J.W., Z.W., S.Y.; Writing - original draft: J.W., L.S.; Writing - review & editing: S.W.N., J.W.; Visualization: S.Y.; Project administration: J.W., Y.Y., Z.W.

Funding

This work was supported by the research grant of Sun Yat-Sen University for Bairen Plan (grant no. 76200-18841223), and the National Natural Science Foundation of China (grant no. 51905556).

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.229799.supplemental>

References

- Afik, O. and Shafir, S. (2007). Effect of ambient temperature on crop loading in the honey bee, *Apis mellifera* (Hymenoptera: Apidae). *Entomol. Gen.* **29**, 135–148. doi:10.1127/entom.gen/29/2007/135
- Borrell, B. J. (2006). Mechanics of nectar feeding in the orchid bee *Euglossa imperialis*: pressure, viscosity and flow. *J. Exp. Biol.* **209**, 4901–4907. doi:10.1242/jeb.02593
- Corbet, S. A. (1990). Pollination and the weather. *Israel J. Bot.* **39**, 13–30.
- Dyer, A. G., Whitney, H. M., Arnold, S. E. J., Glover, B. J. and Chittka, L. (2006). Bees associate warmth with floral colour. *Nature* **442**, 525. doi:10.1038/442525a
- Free, J. B. (1967). Factors determining the collection of pollen by honeybee foragers. *Anim. Behav.* **15**, 134–144. doi:10.1016/S0003-3472(67)80024-1
- Goodman, L. J. (2003). *Form and Function in the Honey Bee*. Cardiff: International Bee Research Association.
- Hammer, T. J., Hata, C. and Nieh, J. C. (2009). Thermal learning in the honeybee, *Apis mellifera*. *J. Exp. Biol.* **212**, 3928–3934. doi:10.1242/jeb.034140
- Harrap, M. J. M., Rands, S. A., Hempel de Ibarra, N. and Whitney, H. M. (2017). The diversity of floral temperature patterns, and their use by pollinators. *eLife* **6**, 1–18. doi:10.7554/eLife.31262
- Herrera, C. M. (1995). Floral biology, microclimate, and pollination by ectothermic bees in an early-blooming herb. *Ecology* **76**, 218–228. doi:10.2307/1940644

- Heyneman, A. J.** (1983). Optimal sugar concentrations of floral nectars: dependence on sugar intake efficiency and foraging costs. *Oecologia* **60**, 198-213. doi:10.1007/BF00379522
- Josens, R. B. and Farina, W. M.** (2001). Nectar feeding by the hovering hawk moth *Macroglossum stellatarum*: intake rate as a function of viscosity and concentration of sucrose solutions. *J. Comp. Physiol. A*, **187**, 661-665. doi:10.1007/s00359-001-0238-x
- Kim, W. and Bush, J. W. M.** (2012). Natural drinking strategies. *J. Fluid Mech.* **705**, 7-25. doi:10.1017/jfm.2012.122
- Kim, W., Gilet, T. and Bush, J. W. M.** (2011). Optimal concentrations in nectar feeding. *Proc. Natl. Acad. Sci. USA* **108**, 16618-16621. doi:10.1073/pnas.1108642108
- Kingsolver, J. G. and Daniel, T. L.** (1979). On the mechanics and energetics of nectar feeding in butterflies. *J. Theor. Biol.* **76**, 167-246. doi:10.1016/0022-5193(79)90368-0
- Kingsolver, J. G. and Daniel, T. L.** (1983). Mechanical determinants of nectar feeding strategy in hummingbirds: energetics, tongue morphology, and licking behavior. *Oecologia* **60**, 214-226. doi:10.1007/BF00379523
- Köhler, A., Nicolson, S. W., Verburg, L. and Leseigneur, C. D.** (2010). Dilute bird nectars: viscosity constrains food intake by licking in a sunbird. *Am. J. Physiol.* **299**, 1068-1074. doi:10.1152/ajpregu.00208.2010
- Kovac, H. and Stabentheiner, A.** (2011). Thermoregulation of foraging honeybees on flowering plants: seasonal variability and influence of radiative heat gain. *Ecol. Entomol.* **36**, 686-699. doi:10.1111/j.1365-2311.2011.01313.x
- Krenn, H. W., Plant, J. D. and Szucsich, N. U.** (2005). Mouthparts of flower-visiting insects. *Arthropod Struct. Dev.* **34**, 1-40. doi:10.1016/j.asd.2004.10.002
- Li, C.-C., Wu, J.-N., Yang, Y.-Q., Zhu, R.-G. and Yan, S.-Z.** (2016). Drag reduction effects facilitated by microridges inside the mouthparts of honeybee workers and drones. *J. Theor. Biol.* **389**, 1-10. doi:10.1016/j.jtbi.2015.10.010
- Lotz, C. N., Martínez del Río, C. and Nicolson, S. W.** (2003). Hummingbirds pay a high cost for a warm drink. *J. Comp. Physiol. B* **173**, 455-462. doi:10.1007/s00360-003-0346-8
- May, P. G.** (1985). Nectar uptake rates and optimal nectar concentrations of two butterfly species. *Oecologia* **66**, 381-338. doi:10.1007/BF00378303
- Mota, T., Yamagata, N., Giurfa, M., Gronenberg, W. and Sandoz, J.-C.** (2011). Neural organization and visual processing in the anterior optic tubercle of the honeybee brain. *J. Neurosci.* **31**, 11443-11456. doi:10.1523/JNEUROSCI.0995-11.2011
- Nicolson, S. W.** (1995). Direct demonstration of nectar reabsorption in the flowers of *Grevillea robusta* (Proteaceae). *Funct. Ecol.* **9**, 584-588. doi:10.2307/2390148
- Nicolson, S. W. and Thornburg, R. W.** (2007). Nectar chemistry. In *Nectaries and Nectar* (ed. S. W. Nicolson, M. Nepi and E. Pacini), pp. 215-264. Dordrecht, The Netherlands: Springer.
- Nicolson, S. W., de Veer, L., Köhler, A. and Pirk, C. W. W.** (2013). Honeybees prefer warmer nectar and less viscous nectar, regardless of sugar concentration. *Proc. R. Soc. B-Biol. Sci.* **280**, 1-7. doi:10.1098/rspb.2013.1597
- Norgate, M., Boyd-Gerny, S., Simonov, V., Rosa, M. G. P., Heard, T. A. and Dyer, A. G.** (2010). Ambient temperature influences Australian native stingless bee (*Trigona carbonaria*) preference for warm nectar. *PLoS ONE* **5**, e12000. doi:10.1371/journal.pone.0012000
- Petanidou, T. and Smets, E.** (1996). Does temperature stress induce nectar secretion in Mediterranean plants? *New Phytol.* **133**, 513-518. doi:10.1111/j.1469-8137.1996.tb01919.x
- Pieter, H.** (1953). *Principles of Sugar Technology*. Amsterdam: Elsevier.
- Pyke, G. H. and Waser, N. M.** (1981). The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* **13**, 260-270. doi:10.2307/2387804
- Rands, S. A. and Whitney, H. M.** (2008). Floral temperature and optimal foraging: is heat a feasible floral reward for pollinators? *PLoS ONE* **3**, e2007. doi:10.1371/journal.pone.0002007
- Rico-Guevara, A., Fan, T.-H. and Rubega, M. A.** (2015). Hummingbird tongues are elastic micropumps. *Proc. R. Soc. B* **282**, 20151014. doi:10.1098/rspb.2015.1014
- Roberts, S. P. and Harrison, J. F.** (1999). Mechanisms of thermal stability during flight in the honeybee *Apis mellifera*. *J. Exp. Biol.* **202**, 1523-1533.
- Shi, L., Wu, J., Krenn, H. W., Yang, Y. and Yan, S.** (2020). Temporal model of fluid-feeding mechanisms in a long proboscis orchid bee compared to the short proboscis honey bee. *J. Theor. Biol.* **484**, 110017. doi:10.1016/j.jtbi.2019.110017
- Telis, V. R. N., Telis-Romero, J., Mazzotti, H. B. and Gabas, A. L.** (2007). Viscosity of aqueous carbohydrate solutions at different temperatures and concentrations. *Int. J. Food Prop.* **10**, 185-195. doi:10.1080/10942910600673636
- Van der Kooij, C. J., Kevan, P. G. and Koski, M. H.** (2019). The thermal ecology of flowers. *Ann. Bot.* **124**, 343-353. doi:10.1093/aob/mcz073
- Waddington, K. D.** (1990). Foraging profits and thoracic temperature of honey bees (*Apis mellifera*). *J. Comp. Physiol. B* **160**, 325-329. doi:10.1007/BF00302599
- Whitney, H. M., Dyer, A. G., Chittka, L., Rands, S. A. and Glover, B. J.** (2008). The interaction of temperature and sucrose concentration on foraging preferences in bumblebees. *Naturwissenschaften* **95**, 845-850. doi:10.1007/s00114-008-0393-9
- Wu, J., Zhu, R., Yan, S. and Yang, Y.** (2015). Erection pattern and section-wise wettability of honeybee glossal hairs in nectar feeding. *J. Exp. Biol.* **218**, 664-667. doi:10.1242/jeb.111013
- Wu, J., Shi, G., Zhao, Y. and Yan, S.** (2018). How to dip nectar: optimal time apportionment in natural viscous fluid transport. *J. Phys. D Appl. Phys.* **51**, 245401. doi:10.1088/1361-6463/aac0a5
- Wu, J., Chen, Y., Li, C., Lehnert, M. S., Yang, Y. and Yan, S.** (2019). A quick tongue: older honey bees dip nectar faster to compensate for mouthpart structure deterioration. *J. Exp. Biol.* **222**, jeb212191. doi:10.1242/jeb.212191
- Yang, H., Wu, J. and Yan, S.** (2014). Effects of erectable glossal hairs on a honeybee's nectar-drinking strategy. *Appl. Phys. Lett.* **104**, 263701. doi:10.1063/1.4886115
- Yang, Y., Wu, J., Zhu, R., Li, C. and Yan, S.** (2017). The honeybee's protrusible glossa is a compliant mechanism. *J. Bionic Eng.* **14**, 607-615. doi:10.1016/S1672-6529(16)60426-2
- Zhu, R., Lv, H., Liu, T., Yang, Y., Wu, J. and Yan, S.** (2016). Feeding kinematics and nectar intake of the honey bee tongue. *J. Insect Behav.* **29**, 325-339. doi:10.1007/s10905-016-9561-5