

1 Major article

2 TITLE: Salt sweetens the deal: bumble bees prefer sodium-enriched nectar when its
3 sugar concentration is low

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11 RUNNING HEAD: Adding salt enhances low-quality nectar

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23 ABSTRACT

24 Foraging decisions often depend on net energy intake, but the need for specific
 25 micronutrients means that foods are not always comparable based on energy content.
 26 Although sodium is essential for many physiological functions, many organisms face
 27 challenges obtaining it, especially those relying on a plant-based diet. Flowering plants
 28 often lure pollinators by manipulating nectar carbohydrate content, but nectar sodium
 29 might also influence pollinator choice. We experimentally tested how sodium addition
 30 and nectar carbohydrate concentration interact to affect bumble bee foraging decisions
 31 by allowing bees to forage on artificial flowers containing either low- or high-sucrose
 32 nectar, with or without sodium. We also explored whether sugar and sodium content in
 33 floral nectar trade-off across plant species. Bees preferred sodium-enriched nectar and
 34 preference nearly doubled when sucrose concentration was low. Furthermore, bees
 35 switched more often from flowers without sodium to those with sodium when sucrose
 36 concentration was low. Given increased fidelity for artificial flowers with nectar
 37 sodium, sodium may enhance plant fitness by increasing conspecific pollen receipt. Yet
 38 despite behavioral evidence that sodium enhances the perceived quality of low-sucrose
 39 nectar for bees, we found no evidence for a nectar sugar-sodium trade-off across plant
 40 species. We discuss implications for plant-pollinator interactions and flower evolution.

41

42 INTRODUCTION

43 Animals require a variety of nutrients to achieve a nutritional balance that
 44 maximizes growth, survival and reproduction (Raubenheimer and Simpson 2018).
 45 However, achieving this balance is challenging because nutrient composition varies
 46 among food types (Raubenheimer and Simpson 2004, Filipiak et al. 2023). To
 47 overcome this challenge, animals often regulate how much of each food type they eat,
 48 including consuming micronutrient-rich food types that simultaneously contribute little
 49 or not at all to energetic intake (Simpson and Raubenheimer 1993). Sodium is one such
 50 essential micronutrient that is necessary for many physiological functions, including
 51 osmoregulation, muscle contraction and relaxation, conduction of nerve impulses, and
 52 DNA stability (Fraústo da Silva and Williams 2001, Kaspari 2021). Despite its
 53 physiological importance, obtaining sodium is difficult for many organisms, especially
 54 for those relying on a plant-based diet (Welti et al. 2019, Kaspari 2020, Demi et al.
 55 2021). This limitation in acquiring sodium affects animal physiology, behavior, and
 56 performance (Snell-Rood et al. 2014, Raubenheimer and Simpson 2018). For example,
 57 to acquire sodium, herbivorous mammals are frequently observed licking salt from
 58 minerals and consuming soil (Duvall et al. 2023) and herbivorous arthropods are
 59 observed puddling (Molleman 2010, Demi et al. 2021), even though these nutrient
 60 sources do not contribute to dietary energy. Despite many studies showing that
 61 herbivorous animals can evaluate sodium content and exhibit sodium-seeking behaviors
 62 (Bonoan et al. 2017, Demi et al. 2021, De Sousa et al. 2022, Duvall et al. 2023), how
 63 sodium content affects choice of food types differing in nutritional content remains
 64 poorly understood (but see Clay et al. 2017, Borer et al. 2019)

65 In plant-pollinator mutualisms, flowering plants frequently offer carbohydrate-
 66 rich nectar to entice animals to visit and thereby acquire and transfer pollen (Nepi 2017,

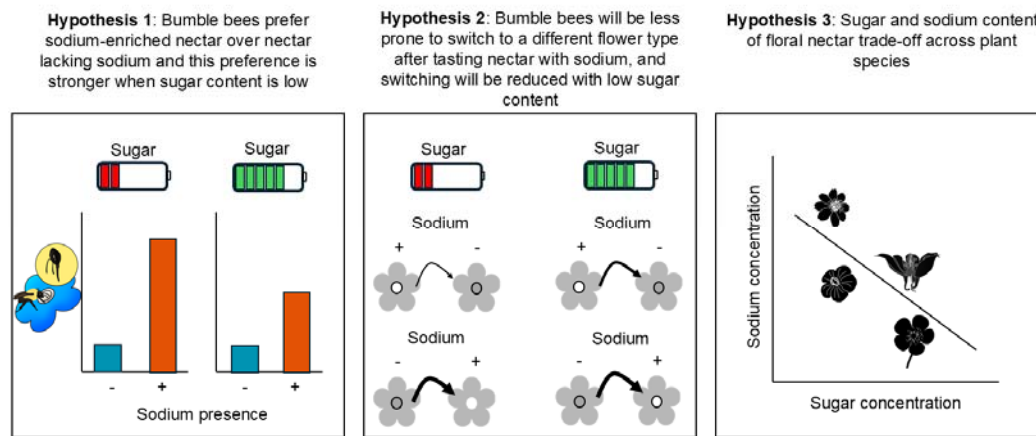
Ballarin et al. 2024). In contrast, the sodium content of floral nectar is very low, although highly variable across plant species, ranging from 0 to 35.7 mM (Hiebert and Calder 1983, Nicolson and W-Worswick 1990, Kaspari 2020, Filipiak et al. 2023). As a result of the low concentration of sodium in floral nectar, pollinators may suffer nutritional imbalance and sodium deprivation (Demi et al. 2021). For instance, honey bees allowed to self-select for the sodium concentration in their diet show a strong preference for high sodium concentrations, ranging from 21.7 to 43.5 mM (De Sousa et al. 2022), which are typically well above the concentrations found in most floral nectar (Hiebert and Calder 1983, Nicolson and W-Worswick 1990, Filipiak et al. 2023). As a result, pollinators are expected to employ foraging strategies to cope with sodium deprivation imposed by their plant diet. For example, pollinators might sample the floral nectar of multiple plant species and select those that meet their sodium intake requirements (Pyke 2010). In fact, recent field experiments have found that pollinators strongly prefer to forage on experimentally sodium-enriched nectar, resulting in an increase in the frequency of visits and the diversity of pollinators on sodium-enriched flowers (Finkelstein et al. 2022, Lovett and Carr 2024, VanValkenburg et al. 2024).

At the same time, the sugar content of nectar varies greatly including among flowers of a single plant (Herrera et al. 2006), across plant populations, and among species (Nicolson 2022, Liu et al. 2024). For instance, nectar sugar concentration is as low as 159.74 mM in *Lutheria splendens* (Bromeliaceae) and as high as 2707.80 mM in *Billbergia euphemiae* (Bromeliaceae) (Göttlinger and Lohaus 2022b). Although environmental factors (Brito Vera and Pérez 2024) and even floral microbes (Vannette 2020) can contribute to variation in nectar sugar concentration, the cost of floral nectar production may also play a role (Southwick 1984, Pyke 1991, Ornelas et al. 2007, — but see Pyke and Ren 2023). As a result, there is often strong selection for plants to

manipulate their pollinators, such as by secreting colored or even pharmacologically active secondary metabolites into nectar (Nepi 2017, Parachnowitsch et al. 2019). Such manipulators can increase pollinator preference and consecutive conspecific visitations that can facilitate plant reproduction (i.e., floral fidelity) (Stevenson 2020). Could nectar sodium content also act as a manipulant of pollinator behavior? Accordingly, we might expect that pollinator preference and fidelity for a flower type may be enhanced when sodium content of its nectar increases, even when its sugar content decreases (Kaspari 2020). Yet pollinators often exhibit strong preferences for increased nectar sugar content (Nicolson et al. 2007, Fowler et al. 2016). An alternative possibility is thus that increased sodium content could enhance perceived nectar quality regardless of sugar content (Petanidou et al. 2006, Kaspari et al. 2008, Kaspari 2020).

In this laboratory study, we experimentally tested how nectar quality affected bumble bee (*Bombus impatiens* Cresson 1863) foraging decisions, by manipulating sucrose concentration and sodium presence in the nectar of artificial flowers. We hypothesized that if sodium is a floral nectar manipulant, sodium-enriched nectar will be preferred by bees over nectar lacking sodium, and this preference should be stronger when sugar content is low (Hypothesis 1; Figure 1). We therefore predicted that bumble bees will be more prone to (a) land and reject flowers with a low sugar content and no sodium when compared to flowers with a low sugar content and sodium; (b) reject nectar with low sugar content lacking sodium relative to nectar with high sugar content, regardless of sodium content, and (c) forage preferentially on sodium-enriched nectar and this preference will be stronger when bees are offered nectar with low sugar content. Accordingly, we hypothesized that bumble bees will be less prone to switch to a different flower type (i.e., exhibit greater floral fidelity) after tasting nectar with sodium, and switching will be reduced when bees are offered nectar with low sugar

117 content (Hypothesis 2; Figure 1). Finally, we quantified the relationship between nectar
118 sugar and sodium concentration across plant species using published data. We
119 hypothesized that plant species that offered less sugar in their nectar would offer more
120 sodium in their nectar (Hypothesis 3; Figure 1), as part of an evolved strategy to
121 enhance the quality of their nectar and manipulate their pollinators.
122



123
124 **Figure 1.** Schematic representation of the three proposed hypotheses. Hypothesis 1:
125 sodium-enriched nectar will be preferred by bees over nectar lacking sodium, and this
126 preference will be stronger when nectar sugar content is low. Hypothesis 2: bees will
127 exhibit greater floral fidelity to flowers with sodium-enriched nectar, with floral fidelity
128 being greatest when nectar sugar content is low. Hypothesis 3: plant species that offer
129 less sugar in their nectar offer more sodium in their nectar.

130

131 METHODS

132 Test subjects

133 To evaluate how bumble bee foraging decisions are affected by nectar quality
134 and sodium addition, we maintained two colonies (Plant Products: Biobest Group,
135 Canton, MI, U.S.A.) of the common eastern bumble bee *Bombus impatiens* following

136 Russell et al. (2017), and Russell et al. (2020). In brief, we allowed colonies to forage
137 freely on 20% w/v sucrose solution from artificial feeders within enclosed foraging
138 arenas (length, width, height: 82 × 60 × 60 cm) set to a 14 h : 10 h light : dark cycle.
139 Each foraging arena contained two artificial feeders. Each feeder's plastic lid was half
140 blue and half yellow to familiarize foraging bees with these colors. Pulverized
141 honeybee-collected pollen (Koppert Biological Systems) was deposited within colony
142 boxes (2g / day).

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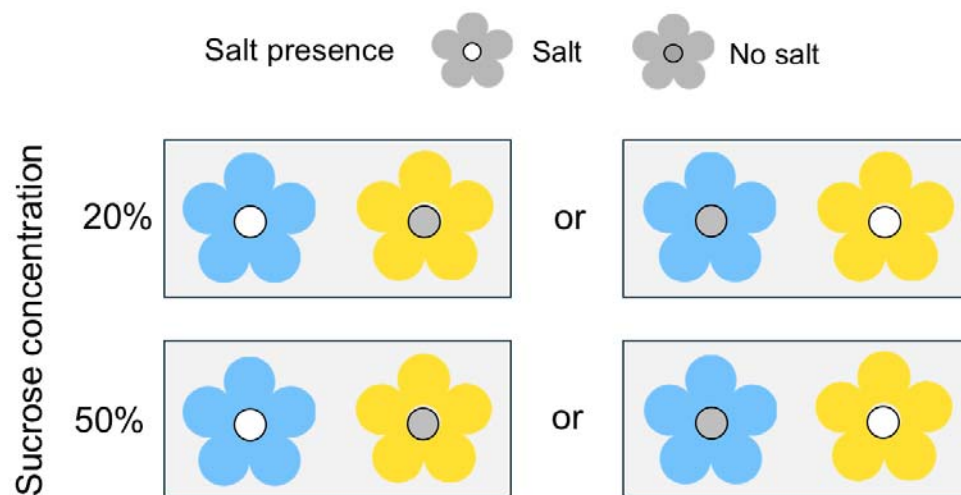
144 *Experiment*

145 To identify appropriate test subjects and accustom bees to foraging for nectar on
146 our experimental set, we captured bees that foraged on the artificial feeders and marked
147 them with non-toxic oil markers (Sharpie, CA) and returned them to their colonies. We
148 considered that they were appropriate for experiments when marked bees were observed
149 foraging again on the artificial feeders.

150 To assess how sodium and sucrose concentration of nectar affected bee foraging
151 behavior, we divided 36 marked flower-naïve bees into two treatment groups, each with
152 two sub-treatments. Both colonies were equally represented per treatment and sub-
153 treatment. Across all trials we set up a 5 × 4 horizontal array of equal numbers of
154 cleaned (wiped with 70% ethanol between trials and air dried) yellow and blue colored
155 plastic flowers on the test arena floor (20 flowers total). Each flower received an
156 artificial nectary (a sterile 1.5 mL microcentrifuge cap), into which 3 µL of sterile
157 artificial nectar solution was added into the center of the cap. The two treatment groups
158 differed in terms of which sucrose concentration was present (20% or 50% w/v; 584.3
159 mM or 1460.7 mM, respectively; Figure 2). The sub-treatments differed in terms of
160 which one of the two flower colors (i.e., flower types) offered nectar with 0.1% NaCl

161 w/v (17.11 mM) (Fisher Scientific) (Figure 2). We chose these ecologically realistic
 162 sucrose and salt concentrations based on the range of sucrose and NaCl concentrations
 163 found in the nectar of live plants (sugar concentration reported in nectar of live flowers
 164 ranges from 159.74 mM to 2707.80 mM (Göttlinger and Lohaus 2022b); while sodium
 165 concentration ranges from 0 to 35.7 mM; Hiebert and Calder 1983, Nicolson and W-
 166 Worswick 1990, Kaspari 2020, Filipiak et al. 2023; see results). The flower color type
 167 that offered NaCl was systematically alternated between behavioral trials. We used two
 168 flower colors in each horizontal array of 20 flowers to facilitate bees being able to
 169 choose between the nectar solution types (i.e., by associating a given flower color with
 170 NaCl or no NaCl; bumble bees rapidly learn simple flower color-nectar reward
 171 associations - Guiraud et al. 2025). We used a water purification system (Millipore,
 172 Sigma Aldrich) to prepare deionized purified sterile water for solutions.

173



174

175 **Figure 2.** Experimental set up. Each bumble bee ($N = 36$) was individually tested using
 176 an array of 20 artificial flowers with either all low-sugar (20% w/v sucrose treatment;
 177 584.3 mM) or all high-sugar nectar (50% w/v sucrose treatment; 1460.7 mM). Within

each treatment, bees had access to equal numbers of both flower color types alternating by position in the array, one type with 0.1% w/v NaCl salt (17.11 mM) and the other type with no NaCl in their nectar. The color of the flower (blue or yellow) associated with NaCl differs among sub-treatments.

To initiate a behavioral trial, freshly cleaned flowers and nectaries were set up and a single marked worker bee was gently captured from the foraging arena using a 40 dram vial (Bioquip, CA) and immediately released in the center of the test arena following Russell et al. (2017). We recorded three flower visiting behaviors: ‘landing’, when the bee visited the flower (touched the flower with at least 3 of its legs simultaneously), but did not extend its proboscis into the nectary; ‘tasting’, when the bee visited and extended its proboscis into the nectary only briefly (<1 second; leaving most of the nectar); and ‘drinking’, when the bee visited and extended its proboscis into the nectary for more than 1 second (removing all of the nectar).

Immediately after each visit that involved drinking, we refilled the artificial nectary with the appropriate nectar solution, such that flowers were never depleted within a trial. Bees made on average 29.6 ± 13.5 flower visits (mean $\pm$ standard deviation) within their single trial. To ensure trials were comparable, we terminated a trial when the bee did not approach any flower for a period of 5 min. To terminate a trial, we turned off the overhead arena lights and captured the bee in a vial. After a bee completed its trial, it was euthanized to prevent it from returning experimental nectar to its colony. After each trial, flowers were wiped clean with 70% ethanol and artificial nectaries were soaked in 70% ethanol for at least 30 minutes and then rinsed repeatedly in sterile water and allowed to air dry before being reused.

203 *Literature review*

204 To evaluate whether plants increase the amount of sodium available in their
 205 nectar to improve the quality of a nectar with low sugar content, we searched for papers
 206 quantifying the amount of sodium and sugar in the nectar of live flowers under field and
 207 cultivated conditions. For that, we conducted a systematic search on Web of Science
 208 (main core collection) for published papers between 1945 (first year available on Web
 209 of Science) and May 14th, 2026. We used the following keywords: (1) salt AND floral
 210 nectar; (2) sodium AND floral nectar; (3) NaCl AND floral nectar; (4) (sodium OR salt
 211 OR NaCl or ion) AND floral nectar composition; and (5) floral nectar AND (sodium
 212 OR salt OR NaCl or ion). We also included in our database all studies that cited Hiebert
 213 and Calder (1983) and Nicolson and W-Worswick (1990), because these studies
 214 represent the foundation of understanding sodium availability on flowers. We also
 215 included studies that cited Finkelstein et al. (2022), since this is one of the first studies
 216 to manipulate sodium content of floral nectar in a natural community. Finally, to be as
 217 thorough as possible, we searched through the references of these studies. Therefore,
 218 our final database comprised 149 studies. We read these studies and included in our
 219 dataset only studies that provided data on sodium and sugar content on floral nectar. For
 220 studies that manipulated sodium or sugar content, we only included those that provided
 221 data for the control conditions (no sodium or sugar manipulation). For each study, we
 222 collected plant species, sugar and sodium content. We synonymized plant species names
 223 using Plants of the World Online (POWO 2024).

224

225 *Statistical analysis*

226 All data were analyzed using R v. 4.1.3 (R Core Team 2022). We checked
 227 model assumptions using *DHARMa* v. 0.4.6 package (Hartig 2020) and conducted

228 visual diagnostics with *sjPlot* (Lüdecke 2023). For figures, we used *ggplot2* v. 3.5.1
229 (Wickham 2016).

230 To evaluate whether sodium and sugar concentration affected bee foraging
231 preference, we specified three generalized linear mixed effects models (GLMMs). As
232 the response variable, we used the (1) proportion of landings (for a given trial: total
233 visits with landing / total visits with landing plus total visits with drinking), (2)
234 proportion of tasting (for a given trial: total visits with tasting / total flower visits with
235 drinking plus total visits with tasting), or (3) the proportion of drinking (for a given
236 trial: total visits with drinking / total flower visits). Each response variable was used in
237 one GLMM. To evaluate whether bees switched to a different flower type while
238 foraging, we conducted a GLMM using the proportion of switching to a different flower
239 type compared to the immediate previous visit as the response variable. We used the
240 interaction between sucrose concentration and the presence of salt as the predictor
241 variable in all models. We included the identity of the bee as a random variable in all
242 models.

243 For all models, we considered a binomial family distribution using the
244 *glmmTMB* function available in *glmmTMB* v. 1.1.7 package (Brooks et al. 2017). To
245 generate p-values, we specified type II Wald χ^2 -tests via the *Anova* function available in
246 *car* v. 3.1-2 package (Fox and Weisberg 2019). If we found an effect of the predictor
247 variable, we used an adjusted Tukey's post-hoc test to evaluate the difference between
248 the levels of the predictor using the *emmeans* function available in the *emmeans* v. 1.8.8
249 package (Lenth et al. 2025). We calculated effect sizes using the *emmeans* package
250 (Lenth 2025) and reported Cohen's d in all cases.

251 To evaluate the relationship between sodium and sugar concentration in the
252 nectar of live plants, we conducted a phylogenetic generalized least square (PGLS)

model to account for evolutionary relationships among plant species. We used the mean values of sodium (mM) and sugar concentration (mM) for each species. We used the largest dated angiosperm phylogenetic tree at the species level by Janssens et al. (2020). This tree was reconstructed using 36,101 angiosperm species based on two plastid barcoding genes, *matK* and *rbcL*. It was dated using 56 angiosperm fossils as calibration points. Before running the analysis, we pruned all phylogenetic trees to species whose sodium and sugar concentrations were simultaneously quantified. We used this approach because nectar concentration is highly variable not only across individual plants populations, but also across individual flowers (Parachnowitsch et al. 2019). To create our regression model, we used the *phylolm* in *phylolm* v. 2.6.2 (Tung Ho and Ané 2014). To account for phylogenetic relatedness, we incorporated a correlation structure in our regression. This structure assumes that the variance of trait values increases linearly with time. To conduct all analysis, we also used *phytools* v. 1.9-16 (Revell 2012), *ape* v. 5.7-1 (Paradis and Schliep 2019), *geiger* v. 2.0.11 (Pennell et al. 2014) and *caper* v. 1.0.1 (Orme et al. 2018).

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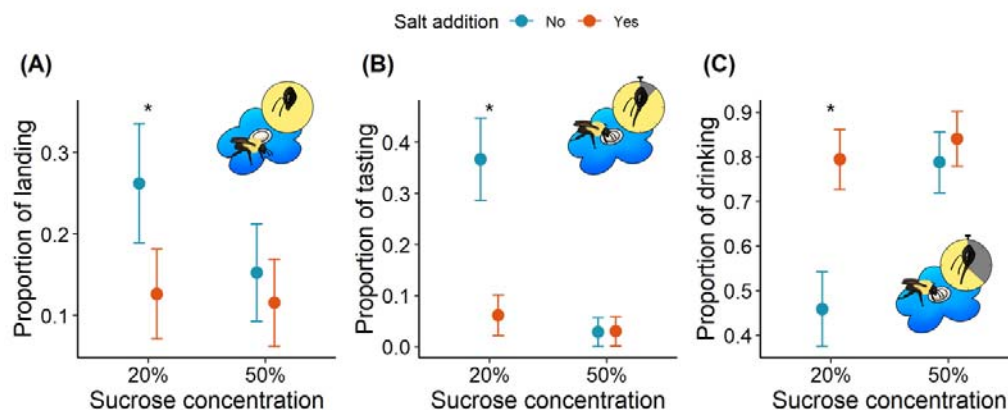
269 RESULTS

270 *Bumble bees prefer sodium-enriched flowers*

Bumble bees rejected artificial flowers (landing on them without drinking or tasting) that lacked salted nectar much more frequently than flowers with salt (0.1% NaCl) nectar. This pattern only became very strong when the sucrose concentration of nectar was low (20% vs 50%) (Figure 3a; GLMM: sugar effect: $\chi^2_1 = 4.735$, $P = 0.029$; salt presence effect: $\chi^2_1 = 12.494$, $P < 0.0001$; sugar $\times$ salt presence effect: $\chi^2_1 = 3.184$, $P = 0.074$; effect size_{low sugar} = 0.876; effect size_{high sugar} = 0.289; Table S1). In fact, bees were 2.08 times as likely to reject flowers with low sucrose concentration lacking salt

278 versus those with salt. Likewise, bees rejected nectar lacking salt after tasting much
 279 more frequently when the sucrose concentration of that nectar was low (Figure 3b;
 280 GLMM: sugar effect: $\chi^2_1 = 20.269$, $P < 0.0001$; sodium presence effect: $\chi^2_1 = 34.347$, P
 281 < 0.0001 ; sugar $\times$ salt presence effect: $\chi^2_1 = 18.139$, $P < 0.0001$; effect size_{low sugar} =
 282 2.323; effect size_{high sugar} = -0.269; Table S1). Overall, bees were 5.93 times as likely to
 283 reject nectar lacking salt versus nectar with salt when sucrose concentration was low.
 284 Altogether, bees preferred to drink from flowers with salt, but this effect became much
 285 greater (1.73 times as likely) when sucrose concentration of the nectar was low (Figure
 286 3c; GLMM: sugar effect: $\chi^2_1 = 18.860$, $P < 0.0001$; salt presence effect: $\chi^2_1 = 40.855$, P
 287 < 0.0001 ; sugar $\times$ salt presence effect: $\chi^2_1 = 19.802$, $P < 0.0001$; effect size_{low sugar} = -
 288 1.574; effect size_{high sugar} = -0.259; Table S1).

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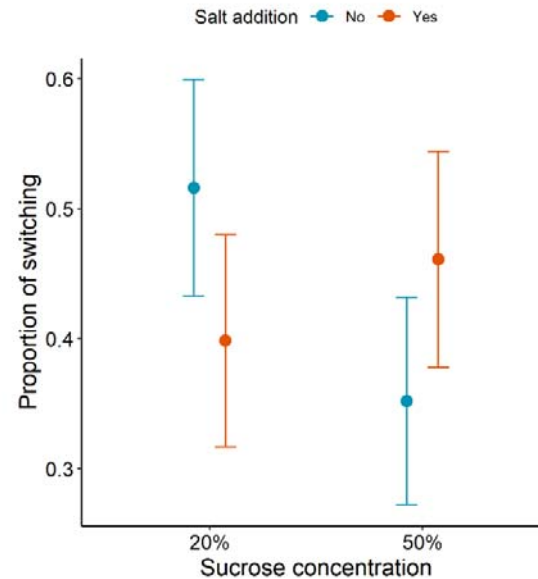


290

291 **Figure 3.** Effect of sucrose concentration (20% or 50% w/v; 584.3 mM or 1460.7 mM,
 292 respectively) and NaCl (0.1% w/v; 17.11 mM) presence on the proportion of (A)
 293 landings (visits without drinking or tasting), (B) tasting (visits without drinking), and
 294 (C) drinking by bumble bees (*Bombus impatiens*). A 'landing' was when the bee visited

the flower (touched the flower with at least 3 of its legs simultaneously) but did not extend its proboscis into the nectary; ‘tasting’, when the bee visited and extended its proboscis into the nectary only briefly ($<<1$ second); and ‘drinking’, when the bee visited and extended its proboscis into the nectary for more than 1 second, removing all of the nectar. $N = 18$ bees for each treatment. Dots represent the mean values and lines represent the standard errors. Asterisks indicate significant differences in mean proportions among flower types for a given treatment at $p < 0.05$ according to a Tukey’s post hoc test. Illustrations by Matheus Siqueira.

The probability of switching to a different flower type was affected by sucrose concentration and salt presence (Figure 4; GLMM: sugar effect: $\chi_1^2 = 0.505$, $P = 0.477$; salt presence effect: $\chi_1^2 = 0.018$, $P = 0.89$; sugar $\times$ salt presence effect: $\chi_1^2 = 4.848$, $P = 0.003$; effect size_{low sugar} = 0.340; effect size_{high sugar} = 0.317; Table S1). Bees were 1.30 times more prone to switch from a flower lacking salt to a flower with salt when the sucrose concentration was low.



311

312 **Figure 4.** Effect of sucrose concentration (20% or 50% w/v; 584.3 mM or 1460.7 mM,
 313 respectively) and NaCl (0.1% w/v; 17.11 mM) presence on the proportion of switching
 314 to a different flower type (one with versus without NaCl in its nectar) by bumble bees
 315 (*Bombus impatiens*). $N = 18$ bees for each treatment. Dots represent the mean values
 316 and lines represent the standard errors.

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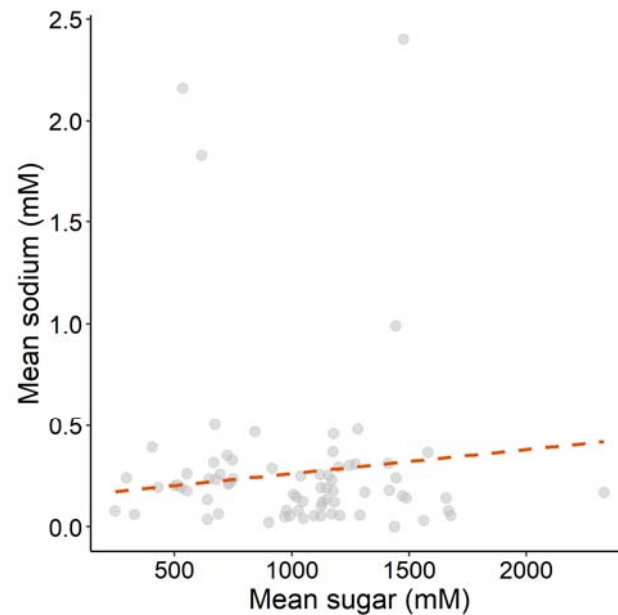
318 *No phylogenetic relationship between sugar and sodium content*

319 Most studies did not provide data on floral nectar composition. Only 15 of the
 320 149 studies recovered in our literature search provided data on nectar sodium and/or
 321 sugar content available in live flowers. Of these, only eight studies provided data on
 322 both sodium and sugar content. These studies collectively reported sodium and sugar
 323 concentration of nectar for 215 plant species across 40 genera and nine families. The
 324 most common species studied were *Pitcairnia recurvata* (Bromeliaceae) ($k = 7$
 325 observations), followed by *P. corallina*, *P. longissimiflora*, *P. maidifolia* and *P.*
 326 *wendlandii* ($k = 6$ observations for each species). The most common genera studied
 327 were *Pitcairnia* ($k = 121$ observations), *Aechmea* (Bromeliaceae) ($k = 37$), *Tillandsia*

(Bromeliaceae) ($k = 36$). The most commonly studied family was Bromeliaceae ($k =$
 347 observations) and Solanaceae ($k = 22$ observations). Unfortunately, two studies
 reported concentration of sugar using g/100 mL, but did not specify which sugar type
 was available in the sample (Nicolson 1990, Nicolson and W-Worswick 1990). Since
 we need sugar composition to convert this data to mM, we removed these studies from
 our analysis.

The mean sodium concentration found in the nectar of live flowers was $1.70 \pm$
 4.44 mM (mean $\pm$ standard deviation) (median = 0.26 mM), whereas mean sugar
 concentration was 939 ± 432 mM (median = 894 mM). However, in our phylogenetic
 analysis we only included studies that measured the concentration of sodium and sugar
 in the same flower. Thus for studies included in our phylogenetic analysis, the mean
 sodium concentration was 0.61 ± 1.13 mM (median = 0.21 mM) while the mean sugar
 concentration of nectar was 935 ± 429 mM (median = 892 mM). To account for the
 phylogenetic relatedness among species, we pruned the angiosperm tree to our data
 (Janssens et al. 2020). Only 73 of the 215 species with data on sodium and sugar
 concentration of floral nectar were present on the tree. We found no significant
 relationship between sodium and sugar concentration in nectar across plant species
 (Figure 5A; PGLS with Brownian motion correlation structure: intercept = 0.14, $P =$
 0.70; slope = 0.00012, $P = 0.38$). Accounting for nectar volume, flower nectar had on
 average 7.65 ± 21.6 ng of sodium ($N = 8$ species).

348



349
350 **Figure 5.** Correlated evolution between mean sugar and sodium concentration (mM) on
351 live flowers of 73 plant species. Each dot represents the mean value of a plant species.
352 Darker dots indicate overlapping data points. The orange dashed line represents the
353 regression line estimated from the phylogenetic generalized least squares model in
354 which the p-value of the slope is greater than 0.05.

355

356 DISCUSSION

357 Because pollinators are expected to evaluate the nutrient qualities of their foods
358 to achieve nutritional balance (Welti et al. 2019, Kaspari 2020, Demi et al. 2021), we
359 hypothesized that access to a rare nutrient (i.e., sodium) would act as a manipulant of
360 pollinator behavior and thus affect the perceived quality of nectar differing in energetic
361 content (sucrose, a common nutrient). We found that bumble bees prefer sodium-
362 enriched nectar of artificial flowers, consistent with recent studies conducted under field
363 (Finkelstein et al. 2022, VanValkenburg et al. 2024) and experimental conditions (De
364 Sousa et al. 2022). Furthermore, as we hypothesized, we found that the magnitude of

sodium preference depended on sugar content (consistent with Hypothesis 1; Figure 1). In addition to affecting bee preference, sodium-enrichment also affected bee movement among artificial flower types (i.e., floral fidelity), partly consistent with Hypothesis 2 (Figure 1). When flowers offered only nectar with low sugar content, bees switched more often when encountering flowers without sodium (i.e., exhibited greater floral fidelity to flowers with sodium). Conversely, when flowers offered only nectar with high sugar content, bees switched more often when encountering sodium enriched nectar, suggesting that higher energetic content of the nectar reward may result in sodium presence being perceived as mildly aversive. Finally, despite the clear effect of sodium enhancing the perceived quality of nectar with low sugar content, we found no evidence for a negative relationship between nectar sugar and sodium content across taxonomically diverse plant species (inconsistent with Hypothesis 3; Figure 1). Thus, plants likely do not reduce the sugar provision of their nectar while simultaneously increasing its sodium content as a strategy to enhance the quality of nectar and thereby manipulate their pollinators.

Overall, our results strengthen the case for sodium to be considered a floral reward offered in exchange for pollination services (see Kaspari 2020), adding sodium to a growing list of non-energetic nutrients that act as floral reward (Lau and Nieh 2016, Bonoan et al. 2017). To be considered a floral reward, the floral component must be used by animals and ensure repeated visitation to flowers (Simpson and Neff 1981). We found that bees preferred sodium-enriched flowers, which also required bees to discriminate which flower color was associated with sodium-enriched nectar. Our results thus suggest that bees may have learned to associate sodium-enriched nectar with flower color, although future work will be required to categorically demonstrate associative learning in this context. Likewise, Finkelstein et al. (2022) and

390 VanValkenburg et al. (2024) showed that sodium-enriched flowers increased pollinator
391 visitation at the community level. Our study extends their foundational work by
392 showing that in addition to consumption, bees frequently rejected (i.e., tasted but did not
393 consume) low-sucrose nectar when it lacked sodium; however, when sucrose
394 concentration was high, nectar rejection was very rare regardless of sodium content. A
395 similar result was found when phenylalanine, an essential amino acid not produced by
396 bees, was added to nectar with low sugar content (Hendriksma et al. 2014). Taken
397 together, components of nectar that contribute to nutritional requirements, but not
398 energetic content, appear to manipulate pollinators into foraging for nectar with low
399 energetic content.

400 Preference and learning can be powerful mechanisms driving selection on floral
401 traits (Schiestl and Johnson 2013) and even speciation (Takimoto et al. 2022). Given
402 that bees preferred sodium-enriched nectar and may even have learned to associate this
403 nutrient with flower color, nectar sodium content and associated floral traits might be a
404 target for pollinator-mediated selection (Parachnowitsch et al. 2019, but see
405 Abrahamczyk et al. 2017). For instance, plants offering nectar with low sugar content in
406 particular may experience strong pollinator-mediated selection for honest signals of
407 sodium content. Such signals would facilitate pollinators in reliably visiting flowers
408 with sodium-enriched nectar, similar to honest signals associated with other kinds of
409 floral rewards (Knauer and Schiestl 2015, Ortiz et al. 2020). Furthermore, while sodium
410 content of nectar is on average low, it is typically much higher in pollen (Nicolson,
411 1990). Given that bees can assess pollen lipid and protein content (Ruedenauer et al.
412 2016, Vaudo et al. 2016) and sodium content of floral nectar (De Sousa et al. 2022), it is
413 plausible to assume that bees can also assess pollen sodium content. We might therefore

414 expect pollinator-mediated selection on pollen sodium content and associated floral
415 traits to be even stronger than within the context of nectar foraging.

416 Pollinator foraging decisions are often driven by nutritional demands, which
417 could include visiting multiple plant species to acquire sufficient nutrients, resulting in
418 greater interspecific pollen transfer and reduced plant fitness (Morales and Traveset
419 2008). We should therefore expect plants to manipulate reward composition to promote
420 floral fidelity (Huang et al. 2015, Pyke 2016, Nepi et al. 2018). Consistent with this
421 hypothesis, we observed that fidelity to a given flower type was enhanced by adding
422 sodium to a low-sugar floral nectar. Why then did we not observe a negative
423 evolutionary relationship between sodium and sugar content in floral nectar across plant
424 species? There are at least two non-mutually exclusive mechanisms explanations. First,
425 although it is often assumed that the production and secretion of carbohydrate-rich
426 nectar is costly for the plant, this cost may be highly variable depending on the
427 ecological context (Pyke and Ren 2023). When photosynthetic metabolism is
428 constrained, such as water, light, or nutrient deficiency, carbohydrate production – and
429 thus nectar production – also becomes limited (Pacini and Nepi 2007). Conversely,
430 when photosynthetic metabolism is not constrained, nectar cost might be low or even
431 negligible (Pyke and Ren 2023). Understanding whether the cost of carbohydrate
432 production influences nectar sodium content will require studies evaluating flower
433 nectar sugar and sodium content for plant populations or species varying in constraints
434 of photosynthetic metabolism. Second, while pollinators are usually sodium-deprived,
435 so are herbivores (Kaspari 2020). While additional sodium in nectar attracts pollinators
436 (Finkelstein et al. 2022, VanValkenburg et al. 2024), potentially facilitating plant
437 fitness, additional sodium may also attract florivores that decrease plant fitness (Snell-
438 Rood et al. 2014). Extrapolating from studies demonstrating that increased leaf sodium

content increases folivory (Prather et al. 2018, Welte and Kaspari 2021), it is plausible that increased nectar sodium content also increases florivory. Thus, while pollinators may exert selective pressure for increased sodium in floral nectar, herbivory may exert a selective pressure in the opposite direction. How plants balance using sodium to lure pollinators while avoiding attraction of herbivores remains an open question.

Although biological mechanisms may explain the absence of a relationship between sodium and sugar investment in nectar, the absence of this relationship may also be due to limited data. While more than 200,000 plant species produce nectar as a floral reward (Ballarin et al. 2024), we were able to compile data on sodium and sugar content for only 215 species and only a third were represented in the currently most comprehensive phylogenetic tree at the species level (Janssens et al. 2020). Although floral nectar is one of the primary floral rewards, floral nectar composition beyond sugars is still relatively understudied (Nicolson and Thornburg 2007, Barberis et al. 2023).

Altogether, our study suggests that sodium-enriched nectar plays an important, but context-dependent role in plant-pollinator interactions. Additionally, given anthropogenic increases in soil salinity, such as via road salt and groundwater infiltration (Findlay and Kelly 2011, Ivushkin et al. 2019), understanding consequences for floral rewards, pollinator foraging, and animal-mediated pollination will become ever more important. Experiments manipulating soil salinity have shown that when soil salinity is high, nectar sodium content of at least some plant species increases, in turn attracting more pollinators (Lovett and Carr 2024). At the same time, our results suggest that enhanced pollinator preference may not always increase pollination success, given that when sugar content of nectar was high, fidelity to sodium-enriched flowers actually decreased. Furthermore, even if sodium-enrichment generally enhances pollination

(Snell-Rood et al. 2014), plants not adapted to salty soil conditions might overall have reduced fitness due to physiological stress (Equiza et al. 2017). Finally, although anthropogenic increases in soil salinity are common, the soil in some regions is naturally salty, especially in coastal areas (Jaiswal et al. 2022). Future phylogenetic and experimental studies will be required to understand how variation in soil salinity affects plant-pollinator interactions and potential tradeoffs among floral reward nutrient types.

ETHICS APPROVAL

All bumble bee experimentation was carried out in accordance with the legal and ethical standards of the USA.

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