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RESEARCH ARTICLE



Nectar preferences in male bumblebees

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Abstract

Social insect males are relatively understudied, but knowledge of their biology is increasingly important for conservation of declining groups. Bumblebees are important pollinators in temperate, sub-arctic, and Alpine regions, but many species are in decline across the globe. Agri-environment schemes have been designed to support female bumblebees, but free-living males may also need support. Male bumblebees have an energetically expensive lifestyle, and so understanding their foraging choices may provide a first step towards designing interventions to support them in the wild. Using a series of controlled laboratory choice experiments, we demonstrate that males prefer sugar concentrations of between 50 and 60% when under either simple (binary) or complex (octanary) choice conditions when presented with a broad range of sugar concentrations. When presented with concentrations within this preferred range, males exhibit a clear preference for sugar solutions of 56% w/w sucrose when solutions differ by 4%. These results suggest that males maximise their rate of energy intake, as predicted by theoretical models, rather than minimise their water consumption. In the future, male preferences for high sugar concentrations can be combined with knowledge of baseline nectar concentrations and flower phenology to maximise the value of conservation interventions for this neglected sex.

Keywords *Bombus* · Foraging choice · Optimal foraging · Males

Introduction

The study of social insects has largely, and understandably, focused on the biology of workers and queens. Males, as transient members of the population, have often been viewed as ‘flying sperm’ and have elicited comparatively little study (Baer 2003; Boomsma et al. 2005). However, male biology is as important as female biology for understanding reproductive success in most species, and thus is particularly important to investigate in groups of conservation concern.

Bumblebees are a species-rich genus of annual social insects that play an important role as pollinators in temperate, Alpine, and sub-arctic ecosystems (Alford 1975). Over the last 30–40 years, it has become clear that many species of bumblebee are suffering severe declines across Europe (Williams 1982; Fitzpatrick et al. 2007; Nieto et al. 2014), North America (Cameron et al. 2011), South America (Morales et al. 2013), and Asia (Xie et al. 2008). These declines are

driven by a range of factors, including habitat loss, agricultural intensification, climate change, invasive species, and parasites (Goulson et al. 2008; Williams and Osborne 2009; Williams et al. 2009; Goulson et al. 2015; Arbetman et al. 2017). Given their importance as pollinators, and their charismatic and appealing nature, conservation programmes to support their populations in agricultural landscapes have been developed (Carvell et al. 2007; Goulson et al. 2008; Lye et al. 2009). While such schemes can work (Carvell et al. 2017), they have been designed and focused solely for workers and queens (Carvell et al. 2007; Lye et al. 2009). As such, how to approach supporting male populations, which are key to the reproductive success of queens, in this important group of pollinators remains unexplored.

Bumblebee males generally leave the nest approximately 3 days after emergence (Alford 1975), at which point they start to perform precopulatory sexual behaviours to find and attract mates (reviewed in Baer 2003). These behaviours are often energetically costly, as they involve considerable amounts of active flight (Bertsch 1984; Baer 2003). In a cage study, Bertsch (1984) showed that males of *Bombus lucorum* flew approximately 17 km in 4 h every day, largely in the morning. Consuming sufficient sugar to support such activity

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requires over-consumption of water, which then needs to be voided (Bertsch 1984), and thus, there should be significant selective pressure on males to optimise their choice of nectar sources to maximise sugar intake and minimise water intake. Modelling based on maximising the rate of energy intake suggested that bumblebees, as ‘viscous dipping’ feeders (where nectar is extracted by dipping the tongue into and then removing it from, viscous nectar), should have an optimal preference of 52% sugar concentration in nectar (Kim et al. 2011). However, these models ignored the issue of water management (Bertsch 1984). Currently, apart from records of male bumblebees on particular flowering plants (e.g. Benton 2006), nothing is known about nectar preferences in male bumblebees. In contrast, studies of workers have shown that they make clear foraging choices based on sugar concentration (e.g. Bailes et al. 2018), which appear to trade-off choosing higher concentration sources versus the time taken to consume the nectar (which increases with concentration due to increases in viscosity; Harder 1986). However, extrapolating from worker foraging preferences to the decisions that males may make is not straightforward, as workers are foraging for the colony, rather than just for themselves, and must also make trade-offs between nectar and pollen foraging (Konzmann and Lunau 2014).

Here, we take the first steps towards understanding the nectar preferences of male bumblebees. Using controlled laboratory experiments, we allowed males of the common bumblebee *B. terrestris audax* to choose between different sugar concentrations, in order to determine their preferred concentration. Specifically, we first presented males with binary choices across a broad range of sugar concentrations to identify their general region of preference. We confirmed these experiments by presenting males with eight choices across this same range, to more closely mimic the complex choices males will face in the field. We then used further binary choice experiments, with sugar concentrations within the general region of preference identified in the initial experiments, to determine the precise concentration preferred by male bees. We discuss our results in the light of theory, previous studies of worker bumblebees, and in the broader context of how to support male bumblebees in the field.

Methods

General experimental protocol

The protocol for all four experiments followed the same basic format: male bumblebees sourced from commercial colonies (*Bombus terrestris audax*, Biobest, Belgium) that had been fed on an ad libitum diet of pollen and Ambrosia syrup (Thornes, UK) were placed individually in Folly cages

(described below) and offered a choice of varying sucrose solutions under a natural day/night regime in an air-conditioned laboratory (~21°C). Each trial lasted 48 h, after which the amount consumed was measured (see below). Any bees that died during the course of an experiment were removed and not included in analyses. Each experiment sourced males from a different colony. Each trial also included 2 control cages for each treatment, to account for evaporation of the feeding solutions (see below).

Folly cages were made from upside down, lidded, clear plastic cups (10 cm tall, 9 cm diameter at base, 6 cm diameter at top). A 1-cm layer of dust-free, paper-based animal litter was added to the bottom of each cage to absorb bee faeces. The top side of each cage had 15 × 2 mm diameter holes for ventilation. 12-mm-diameter holes were placed in the sides of the cage, ~1 cm above the base, to enable the insertion of feeding tubes (2 ml Eppendorf tubes), with the experimental trial determining the number of these holes and tubes. Feeding tubes had 4 × 2 mm diameter holes in a line on one side, to enable feeding—when in place, these holes were on the top side of the feeding tube.

Sucrose solutions of varying concentrations were made by percentage mass (w/w). To make the solutions, sucrose was weighed (Sartorius scale) and added to a weighed amount of purified deionised water (Pur1te Select). For example, to make 50 g of a 10% sucrose solution, 5 g of sugar was mixed with 45 g water. Once completely dissolved, 2 ml was pipetted into the relevant feeding tubes. Feeding tubes were weighed prior to placement and then at the end of the experimental trial (Ohaus scale). To calculate consumption, differences between pre- and post-experimental weights were corrected for evaporation using mean differences from the relevant evaporation controls. In each experiment, we measured consumption from each feeding tube, which enabled us to compare the consumption of both liquid and sugar by males within binary choices, across multiple choices, and across trials.

All bees were frozen after experimental trials and then measured, using thorax width as a proxy for body size. Each bee was measured three times using Mitutoyo digital callipers to generate a mean thorax width for statistical analyses.

Experiment 1: binary preference trials for sugar concentrations from 0 to 68%

To determine where, across the broad range of potential sugar concentrations, male preferences lie, each male bee was offered a choice of two sucrose concentrations, which differed by 10% (or 8% for the final treatment, as 68% is the saturation point for sucrose solutions). Seven treatments, each with 10 bees and 2 control cages, were set up as follows: 0% versus 10%, 10% versus 20%, 20% versus 30%, 30% versus 40%, 40% versus 50%, 50% versus 60%, 60%

versus 68%. We compared choices within each binary trial, as well as liquid and sugar consumption across all trials. These latter comparisons enabled us to determine whether males could compensate for low sugar concentrations by consuming more liquid.

Experiment 2: octanary preference trials for sugar concentrations from 0 to 68%

To determine whether males would express the same preference when presented with a more complex choice, representative of the diversity of nectar concentrations available in the field, 10 males were placed in Folly cages with 8 feeding tubes, each containing one of the concentrations (0, 10, 20, 30, 40, 50, 60, 68%) used in *Experiment 1*. Consumption patterns were analysed to determine which sugar concentration males preferred under these more complex conditions.

Experiment 3: binary preference trials for sugar concentrations from 50 to 60% at 2% intervals

After determining the range of sugar concentrations within which the preferred sugar concentration must lie in *Experiments 1* and *2*, we used binary choice trials (as in *Experiment 1*) to determine where between 50% and 60% male preferences lie. We repeated *Experiment 1*, but with the following choices: 50% versus 52%, 52% versus 54%, 54% versus 56%, 56% versus 58%, 58% versus 60%. As per *Experiment 1*, we examined both binary choices and liquid and sugar consumption across trials.

Experiment 4: binary preference trials for sugar concentrations from 50 to 62% at 4% intervals

Given results from *Experiment 3*, which suggested that males were incapable of differentiating between 2% differences in sugar concentration, we repeated this experiment, but using 4% differences in the sugar concentration of solutions offered to individual bees, as follows: 50% versus 54%, 52% versus 56%, 54% versus 58%, 56% versus 60%, 58% versus 62%. Again, we examined both binary choices and liquid and sugar consumption across trials.

Statistical analyses

Total consumption of liquid and sugar in Experiments 1, 3, and 4 was analysed using ANOVA with treatment (0 vs. 10, 10 vs. 20, etc.) as the fixed factor and bee size as a covariate. In Experiments 1 and 4, liquid consumption was log-transformed to meet the assumptions of the analysis, and in Experiment 4, sugar consumption was similarly transformed. To determine whether male bees showed a preference in pairwise choice tests, paired *t* tests were used, with

significance values being corrected using the adjusted Bonferroni correction. To determine whether male bees showed a preference in the eight choice trials, a Chi-square test was used, to test whether males' preferred sugar concentration was different from a random expectation. SPSS 23 was used for all statistical analyses.

Results

Experiment 1: pairwise choices across 0–68% sugar solutions

Treatment significantly affected the total liquid consumption of bees ($F_{6,54} = 2.674$, $p = 0.024$, Partial $\eta^2 = 0.229$), with males drinking most in the 10 versus 20 sugar treatment (Fig. 1a). There was no effect of bee size on total liquid consumption ($F_{1,54} = 3.434$, $p = 0.069$, Partial $\eta^2 = 0.06$). There was also an effect of treatment on the total amount of sugar consumed by bees ($F_{6,54} = 8.628$, $p < 0.001$, Partial $\eta^2 = 0.489$), with the least sugar being consumed in the 0 versus 10 sugar treatment, and the most in the 40 versus 50 sugar treatment (Fig. 1a). In contrast to results for total liquid consumption, body size did affect sugar consumption ($F_{1,54} = 5.279$, $p = 0.025$, Partial $\eta^2 = 0.089$), with larger bees consuming more sugar.

Within each test, the male bees expressed a clear preference for both solution and actual sugar consumption across every pairwise choice apart from in the 50 versus 60 treatment (Tables 1, 2). In all tests where the maximum solution concentration was 50% or less, the bees chose to drink from the higher concentration test solution (Fig. 1b), and thus consumed more sugar from this solution (Fig. 1c), whereas in the 60 versus 68 treatment, they chose the lower concentration solution (Fig. 1b) and consumed most sugar from the 60% solution (Fig. 1c).

Experiment 2: 8-choice experiment

Male bees consumed a mean of 1.12 ± 0.136 g of liquid, and $0.47 + 0.064$ g of sugar during the course of the 8-choice trials. Six of the ten bees preferentially consumed the 60% sugar solution, while three preferred the 50% solution, and one preferred the 20% solution (Chi-square = 36.4, $p < 0.01$; Table 3).

Experiment 3: pairwise choices between 2% sugar differences

There was no significant effect of treatment on liquid consumption when the solutions presented to male bees ranged between 50 and 60% sugar concentration ($F_{4,29} = 2.592$, $p = 0.057$, Partial $\eta^2 = 0.263$; Fig. 2a), but size mattered

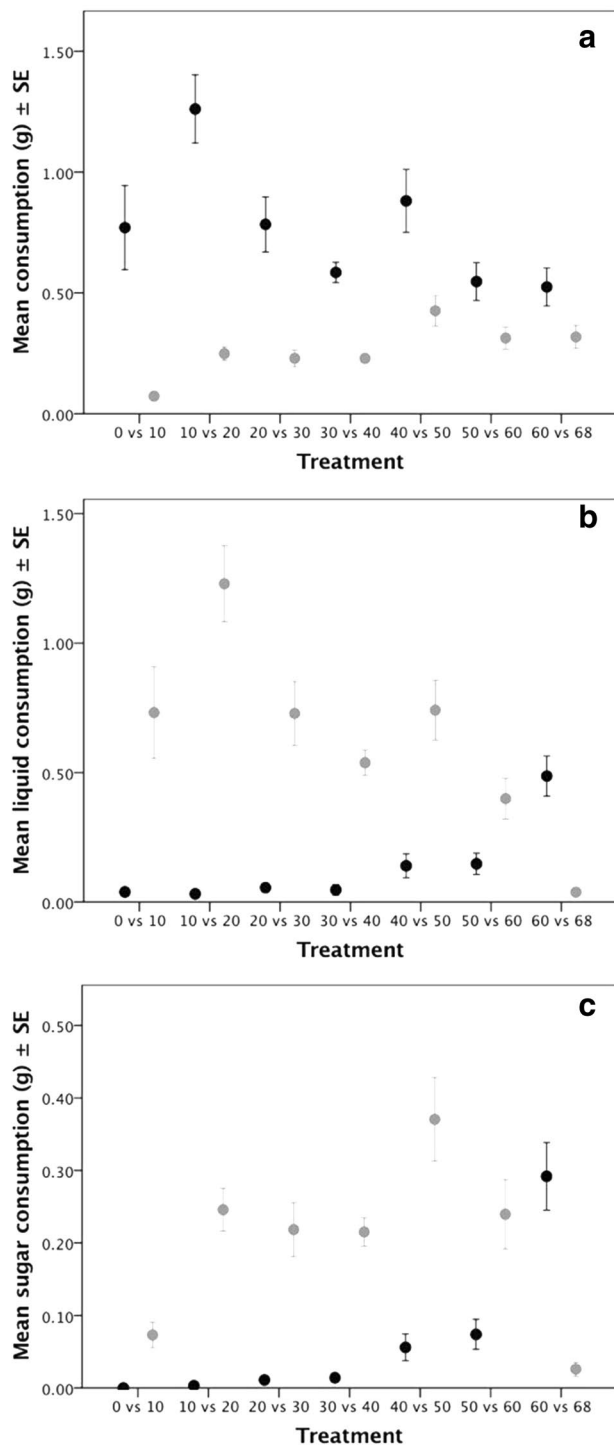


Fig. 1 Results from Experiment 1. **a** Mean liquid (black) and sugar (grey) consumption \pm standard error for each treatment group; **b** mean liquid consumption of the low (black) and high (grey) options in each binary choice treatment group \pm standard errors; **c** mean sugar consumption of the low (black) and high (grey) options in each binary choice treatment group \pm standard errors

Table 1 Pairwise choices of solution consumption made by male bees

Pairwise choice	<i>N</i>	<i>T</i> statistic	<i>p</i> value
0 versus 10	9	-3.807	0.005
10 versus 20	9	-7.796	<0.001
20 versus 30	9	-4.962	0.001
30 versus 40	10	-7.826	<0.001
40 versus 50	10	-5.086	0.001
50 versus 60	9	-2.511	0.036
60 versus 68	6	5.652	0.002

Significant *p* values after adjusted Bonferroni correction are shown in bold

Table 2 Pairwise choices of sugar consumption made by male bees

Pairwise choice	<i>N</i>	<i>T</i> statistic	<i>p</i> value
0 versus 10	9	-4.121	0.003
10 versus 20	9	-8.072	<0.001
20 versus 30	9	-5.250	0.001
30 versus 40	10	-8.517	<0.001
40 versus 50	10	-5.414	<0.001
50 versus 60	9	-2.882	0.02
60 versus 68	6	5.560	0.003

Significant *p* values after adjusted Bonferroni correction are shown in bold

($F_{1,29} = 12.849$, $p = 0.001$, Partial $\eta^2 = 0.307$), with bigger bees drinking more solution. In contrast, there was a significant effect of treatment on the amount of sugar bees consumed ($F_{4,29} = 3.112$, $p = 0.03$, Partial $\eta^2 = 0.3$), with males in the 50 versus 52 treatment group consuming less sugar than males presented with the other pairwise choices (Fig. 2a). There was a similar impact of bee size ($F_{1,29} = 13.14$, $p = 0.001$, Partial $\eta^2 = 0.312$), with bigger bees again consuming more sugar.

After correction for multiple testing, no significant choices were made between different sugar concentrations (Table 4), and this was also true for sugar consumption (Table 5). However, the trend was for bees to drink more of the higher concentration solution, and to consume more sugar from it as a result, until the 58 versus 60 trial, when the lower concentration solution elicited more consumption (Tables 4, 5; Fig. 2b, c).

Experiment 4: pairwise choices between 4% sugar differences

There were significant effects of both treatment ($F_{4,42} = 7.364$, $p < 0.001$, Partial $\eta^2 = 0.412$) and male size ($F_{1,42} = 10.051$, $p = 0.003$, Partial $\eta^2 = 0.193$) on liquid consumption. Male bees consumed least in the 56 versus

Table 3 Liquid consumption by male bees (shown as per cent of total consumption) when presented with a choice of 8 sugar concentrations

Bee	0%	10%	20%	30%	40%	50%	60%	68%
1	3	12	11	9	10	6	47	2
2	9	12	0	1	1	0	77	0
3	0	0	7	5	17	9	33	29
4	8	8	8	6	4	41	22	3
5	16	17	5	10	17	12	23	0
6	8	5	0	10	5	33	24	15
7	1	9	15	12	5	14	42	2
8	0	13	25	13	0	9	25	15
9	0	1	18	10	4	37	26	4
10	11	12	32	24	6	0	8	7

The most preferred concentration is shown in bold for each bee

60% sugar choice treatment (Fig. 3a) and, as seen in previous experiments, larger bees drank more liquid. Mirroring these results, there were also significant effects of both treatment ($F_{4,42} = 6.165$, $p = 0.001$, Partial $\eta^2 = 0.37$) and male size ($F_{1,42} = 10.471$, $p = 0.002$, Partial $\eta^2 = 0.2$) on sugar consumption, with the lowest consumption in the 56 versus 60% choice (Fig. 3a) and larger males consuming more sugar.

Male bees significantly preferred to consume liquid and consumed more sugar as a result, from the higher concentration solution when it was 56% or less (Tables 6, 7; Fig. 3b, c). No preference was expressed when the choice was between 54 and 58% solutions, whereas when the low concentration was 56% or above, it was always preferred over the higher concentration solution (Tables 6, 7; Fig. 3b, c).

Discussion

Overall, in our laboratory experiments, male bumblebees showed a preference for a sugar concentration of 56%, measured both in the amount of liquid consumed and the actual consumption of sucrose. In addition, patterns of consumption of liquid and sucrose suggest that sucrose consumption may be constrained by the ability to consume or process water. Together, these results suggest that male behaviour in the field is likely to be constrained by the availability of high-quality nectar sources.

Theoretical analyses have categorised worker bumblebees as using ‘viscous dipping’ to collect nectar and consequently suggested that the optimal concentration of sugar that would maximise their rate of energy intake was 52% (Kim et al. 2011). This concentration is lower than the preference expressed by males for 56% sucrose solution in our experiments, which may reflect differences between males and workers in tongue structure or dipping mechanics. Energy intake depends upon the impact of viscosity on feeding rate and the concentration of sugar in solution. Harder (1986) showed that the impact of viscosity on feeding rate

in worker bumblebees only occurred at sugar concentrations above 40%, with an ~18% reduction in rate at 50% solutions, and a further ~35% reduction at 65% solutions. As these reductions in rate do not scale isometrically with increasing sugar concentration, they result in reductions of both liquid and sugar consumption. Similar patterns were reported for stingless bees (*Melipona* spp.) and honey bees (*Apis mellifera*) by Roubik and Buchmann (1984). While we did not measure the time spent consuming sugar solution, these results suggest that male bees must have spent significantly more time feeding on the higher concentration solutions to demonstrate the preferences we observed. If males are time constrained in the wild, it is possible that they might actively choose to consume lower concentration nectars. However, Bertsch (1984) showed that males of *B. lucorum*, which have similar behaviour to males of our study species, are unlikely to be time constrained in this way, as most mating flight behaviour occurs in the morning, leaving the rest of the day free for foraging. Interestingly, despite the need to manage over-consumption of water (Bertsch 1984), males did not choose the highest concentration of sugar solution in our study, suggesting that they are optimising rate of energy intake rather than minimising water load. We note, however, that our study was conducted under laboratory conditions where males were limited in their ability to express natural behaviour. Consequently, it would be valuable to test nectar preferences under more natural conditions, where they may be modified by both costs of flight and environmentally induced dehydration.

In the wild, bumblebee workers show foraging preferences that match those expected by the nectar value in flowers (Pleasants 1981). Laboratory studies of consumption at the colony level have suggested a preference by workers for sugar concentrations of between 30 and 50%, when presented with choices ranging from 10 to 70% (Pouvreau 1974). In contrast, individual workers have been shown to prefer 60% over 45% concentrations, based on consumption (Konzmann and Lunau 2014), or 55% over 40%, with

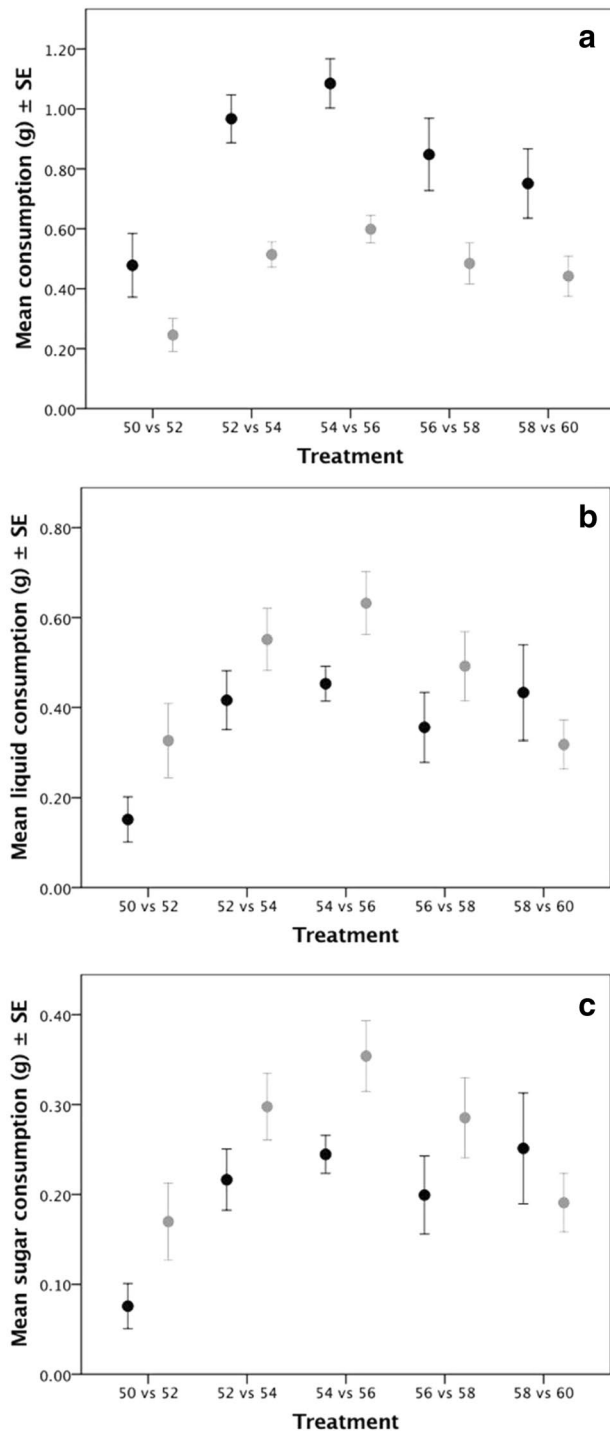


Fig. 2 Results from Experiment 3. **a** Mean liquid (black) and sugar (grey) consumption \pm standard error for each treatment group; **b** mean liquid consumption of the low (black) and high (grey) options in each binary choice treatment group \pm standard errors; **c** mean sugar consumption of the low (black) and high (grey) options in each binary choice treatment group \pm standard errors

Table 4 Pairwise choices of solution made by male bees when presented with 2% differences

Pairwise choice	<i>N</i>	<i>T</i> statistic	<i>p</i> value
50 versus 52	6	−2.046	0.096
52 versus 54	8	−1.247	0.252
54 versus 56	10	−2.313	0.046
56 versus 58	5	−1.423	0.228
58 versus 60	6	0.933	0.393

Significant *p* values after adjusted Bonferroni correction are shown in bold

Table 5 Pairwise choices of sugar consumption made by male bees when presented with 2% differences

Pairwise choice	<i>N</i>	<i>T</i> statistic	<i>p</i> value
50 versus 52	6	−2.131	0.086
52 versus 54	8	−1.415	0.200
54 versus 56	10	−2.542	0.032
56 versus 58	5	−1.578	0.190
58 versus 60	6	0.838	0.440

Significant *p* values after Bonferroni correction are shown in bold

no differentiation between 55 and 68% when measured by number of visits (Bailes et al. 2018). To our knowledge, the current study is the first to assess male preferences for different sugar concentrations, mimicking the variation in nectar quality they will experience under natural conditions (e.g. Pleasants 1981). Our experimental protocol explicitly measured choice by consumption under conditions of no competition and low energy demand (although we note that males were observed trying to fly in their cages), and thus differs from previous studies on colonies or workers. However, males, who forage only for themselves and probably only for nectar (Bertsch 1984), have fundamentally different foraging priorities to workers, who have to forage both for themselves and for the colony, and have to combine foraging for nectar and pollen (Konzmann and Lunau 2014). Our results suggest that males may have more precise preferences, or possibly preferences for higher sugar concentrations than workers, reflecting a need to maximise energy intake rather than optimise the return of energy to the nest. Direct comparisons under the same experimental conditions are needed to test this interpretation.

Male bumblebees showed clear preferences when they were given choices that differed by 10%, 8%, and 4% in concentration. However, we could find no evidence for preferences when the offered solutions differed by only 2%. While this may be an artefact of experimental power, given that more replicates were lost from this experiment than the others, or reflect a lack of perceptual ability in the particular

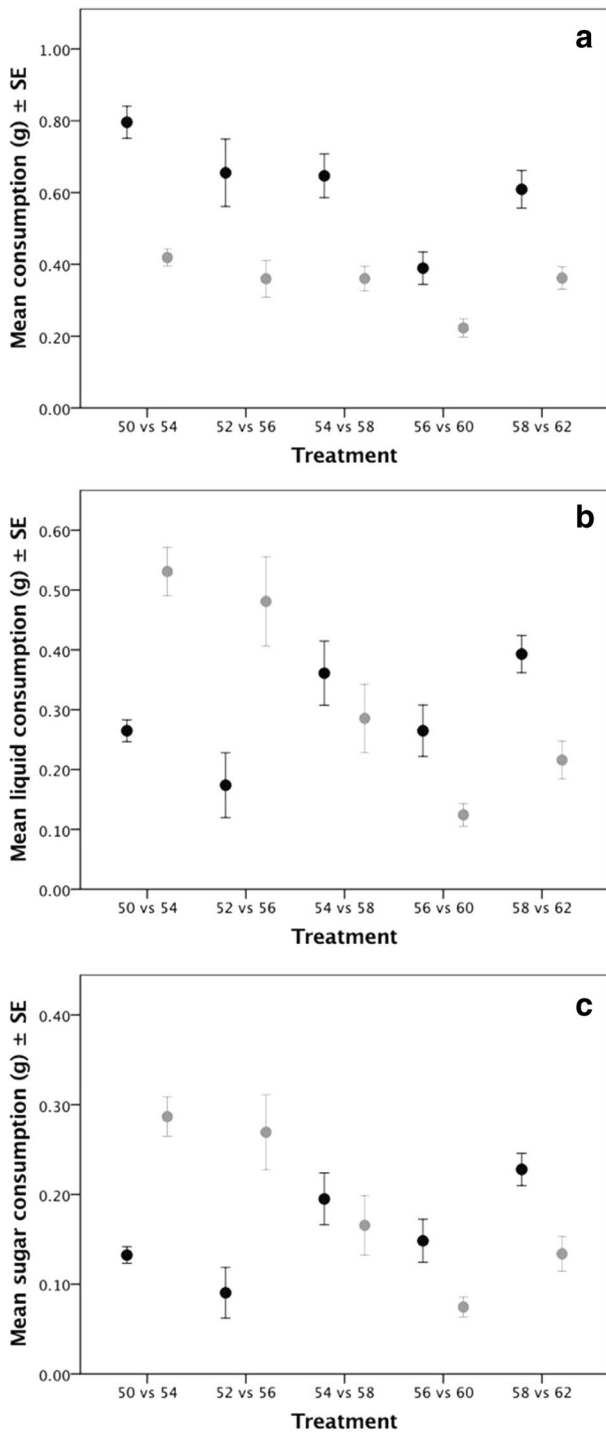


Fig. 3 Results from Experiment 4. **a** Mean liquid (black) and sugar (grey) consumption \pm standard error for each treatment group; **b** mean liquid consumption of the low (black) and high (grey) options in each binary choice treatment group \pm standard errors; **c** mean sugar consumption of the low (black) and high (grey) options in each binary choice treatment group \pm standard errors

Table 6 Pairwise choices of liquid consumption made by male bees when presented with 4% differences

Pairwise choice	<i>N</i>	<i>T</i> statistic	<i>p</i> value
50 versus 54	10	-6.031	< 0.001
52 versus 56	10	-3.383	0.008
54 versus 58	9	0.817	0.438
56 versus 60	9	2.871	0.021
58 versus 62	10	5.134	0.001

Significant *p* values after Bonferroni correction are shown in bold

Table 7 Pairwise choices of sugar consumption made by male bees when presented with 4% differences

Pairwise choice	<i>N</i>	<i>T</i> statistic	<i>p</i> value
50 versus 54	10	-6.553	< 0.001
52 versus 56	10	-3.605	0.006
54 versus 58	9	0.566	0.587
56 versus 60	9	2.652	0.029
58 versus 62	10	4.537	0.001

Significant *p* values after Bonferroni correction are shown in bold

colony used for this experiment, it does warrant further work to determine what the sensory limits are of both males and workers in terms of making choices in the field between different nectar concentrations.

As well as showing preferences for specific sugar concentrations, male bumblebees demonstrated significant differences in their consumption depending upon the food that was available to them. Most intriguingly, when presented with choices ranging from 0% + 10% to 60 + 68%, males appeared unable to compensate for sugar concentrations below 40% by increasing consumption, and this effect was particularly stark when they were presented with only 10% sugar solution. In a laboratory study, Bertsch (1984) suggested that males might forage, not to maximise their energy consumption, but to minimise their water load. Water loss in bumblebees occurs via evaporation and defecation (Bertsch 1984), and our results show that at low sugar concentrations the need to maintain water balance via these processes may significantly constrain the consumption of sugar which is required for active flight. That these effects emerge even in laboratory conditions, where males have no constraints on time or energy consumption, is particularly striking. As male mating success is presumably related to their activity on flight paths (Freeman 1968), low sugar concentrations in nectar may limit male reproductive success. It would be interesting to quantify how sugar concentration in available nectar relates to flight activity in males.

Bumblebee males forage on a range of flowering plants (Benton 2006) that have been recorded as having nectar

concentrations of up to 49% (Baude et al. 2016). Given that males largely forage in the afternoon, when nectar becomes more concentrated (Bertsch 1984), it seems likely that they will encounter nectar concentrations towards the upper end of the range we examined. Consequently, maximising the abundance of those preferred male forage plants with higher nectar concentrations will support male populations as they attempt to mate with new gynes, and lower the costs of managing water balance (Bertsch 1984). Currently, however, bumblebee conservation efforts largely focus on supporting spring queens and workers (e.g. Carvell et al. 2011). Even though males are produced in much higher numbers than gynes (e.g. Brown et al. 2003), interventions that maximise their activity and lifespan can only help in producing the fertilised gynes that are required to produce the next generation of colonies.

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