Nectar preferences in male bumblebees

M. Brown & M. J. F. Brown

Insectes Sociaux
International Journal for the Study of Social Arthropods

ISSN 0020-1812
Volume 67
Number 2

Insect. Soc. (2020) 67:221-228
DOI 10.1007/s00040-020-00751-y
Your article is published under the Creative Commons Attribution license which allows users to read, copy, distribute and make derivative works, as long as the author of the original work is cited. You may self-archive this article on your own website, an institutional repository or funder’s repository and make it publicly available immediately.
Nectar preferences in male bumblebees

M. Brown · M. J. F. Brown

Received: 6 August 2019 / Revised: 2 January 2020 / Accepted: 25 January 2020 / Published online: 7 February 2020
© The Author(s) 2020

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...
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’ feed-
ers (where nectar is extracted by dipping the tongue into and
then removing it from, viscous nectar), should have an opti-
mal 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 prefer-
ences 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 concentra-
tions to identify their general region of preference. We con-
firmed these experiments by presenting males with eight
differences across this range, to more closely mimic the
complex choices males will face in the field. We then used
further binary choice experiments, with sugar concentra-
tions within the general region of preference identified in
the initial experiments, to determine the precise concentra-
tion 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-condi-
tioned 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 diam-
eter 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 experi-
mental trial (Ohaus scale). To calculate consumption, dif-
ferences between pre- and post-experimental weights were
corrected for evaporation using mean differences from the
relevant evaporation controls. In each experiment, we mea-
sured 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 calli-
pers 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 trial, 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 ($F_{6,54} = 2.674, p = 0.024, \text{Partial } \eta^2 = 0.229$), with males drinking most in the 10 versus 20 sugar treatment (Fig. 1a). There was no effect of bee size on total liquid consumption ($F_{1,54} = 3.434, p = 0.069, \text{Partial } \eta^2 = 0.06$). There was also an effect of treatment on the total amount of sugar consumed by bees ($F_{6,54} = 8.628, p < 0.001, \text{Partial } \eta^2 = 0.489$), 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 ($F_{1,54} = 5.279, p = 0.025, \text{Partial } \eta^2 = 0.089$), 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. 1a), and thus consumed more sugar from this solution (Fig. 1b), 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 $1.12 \pm 0.136$ 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 ($F_{4,29} = 2.592, p = 0.057, \text{Partial } \eta^2 = 0.263$; Fig. 2a), but size mattered.
M. Brown, M. J. F. Brown

13 (F1,29 = 12.849, p = 0.001, Partial Eta2 = 0.307), with bigger bees drinking more solution. In contrast, there was a significant effect of treatment on the amount of sugar bees consumed (F4,29 = 3.112, p = 0.03, Partial Eta2 = 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 (F1,29 = 13.14, p = 0.001, Partial Eta2 = 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 (F4,42 = 7.364, p < 0.001, Partial Eta2 = 0.412) and male size (F1,42 = 10.051, p = 0.003, Partial Eta2 = 0.193) on liquid consumption. Male bees consumed least in the 56 versus

---

**Table 1** Pairwise choices of solution consumption made by male bees

| Pairwise choice | N  | T statistic | p 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 | N  | T statistic | p 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

---

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

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 $R^2 = 0.37$) and male size ($F_{1,42} = 10.471, p = 0.002$, Partial $R^2 = 0.2$) 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% (Pouvreaux 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...
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. 2 Results from Experiment 3. a Mean liquid (black) and sugar (grey) consumption ± standard error for each treatment group; b mean liquid consumption of the low (black) and high (grey) options in each binary choice treatment group ± standard errors; c mean sugar consumption of the low (black) and high (grey) options in each binary choice treatment group ± standard errors](image)

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

| Pairwise choice | N | T statistic | p 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 | N | T statistic | p 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
Nectar preferences in male bumblebees

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...

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

| Pairwise choice | N  | T statistic | p 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 | N  | T statistic | p 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

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

Acknowledgements We would like to thank Judit Bagi and Emily Bailes for support in the laboratory.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Alford DV (1975) Bumblebees. Davis Poynter, London
Arbetman MP, Gleiser G, Morales CL, Williams P, Aizen MA (2017) Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. Proc R Soc B 294:20170204
Baer B (2003) Bumblebees as model organisms to study male sexual selection in social insects. Behav Ecol Sociobiol 54:521–522
Bailies EJ, Patrick JG, Glover BJ (2018) An analysis of the energetic reward offered by field pea (Vicia faba) flowers: nectar, pollen, and operative force. Ecol Evol 8:3161–3171
Baude M, Kunin W, Boatman ND, Conyers S, Davies N, Gillespie MA, Morton RD, Smart SM, Memmott J (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature 530:85–88
Benton T (2006) Bumblebees. Collins, London
Bertsch A (1984) Foraging in male bumblebees (Bombus lucorum L.): maximizing energy or minimizing water load? Oecologia 62:325–336
Boomsma J, Baer B, Heinze J (2005) The evolution of male traits in social insects. Ann Rev Entomol 50:395–420
Brown MJF, Schmid-Hempel R, Schmid-Hempel P (2003) Strong context-dependent virulence in a host-parasite system: reconciling genetic evidence with theory. J Anim Ecol 72:994–1002
Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL (2011) Patterns of widespread decline in North American bumblebees. PNAS 108:662–667
Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. J Appl Ecol 44:29–40
Carvell C, Osborne JL, Bourke AFG, Freeman SN, Pywell RF, Heard MS (2011) Bumble bee species’ responses to a targeted conservation measure depend on landscape context and habitat quality. Ecol Apps 21:1760–1771
Carvell C, Bourke AFG, Dreier S, Freeman SN, Hulmes S, Jordan WC, Redhead JW, Sumner S, Wang J, Heard MS (2017) Bumblebee family lineage survival is enhanced in high-quality landscapes. Nature 543:547–549
Fitzpatrick Ú, Murray TE, Paxton RJ, Breen J, Cotton D, Santorum V, Brown MJF (2007) Rarity and decline in bumblebees: a test of causes and correlates in the Irish fauna. Biol Cons 136:185–194
Freeman RB (1968) Charles Darwin on the routes of male humble bees. Bull Br Mus (Nat Hist) Hist Ser 3:177–189
Goulson D, Lye GC, Durvill B (2008) Decline and conservation of bumblebees. Ann Rev Entomol 53:191–206
Goulson D, Nicholls E, Bottia C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347:1255957
Harder LD (1986) Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. Oecologia 69:309–315
Kim W, Gilet T, Bush JWM (2011) Optimal concentrations in nectar feeding. Proc Natl Acad Sci USA 108:16618–16621
Konzmann S, Lunau K (2014) Divergent rules for pollen and nectar foraging bumblebees: a laboratory study with artificial flowers offering diluted nectar substitute and pollen surrogate. PLoS ONE 9:e91900
Lye G, Park K, Osborne J, Holland J, Goulson D (2009) Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). Biol Cons 142:2023–2032
Morales CL, Arbetman MP, Cameron SA, Aizen MA (2013) Rapid ecological replacement of a native bumble bee by invasive species. Front Ecol Env 11:529–534
Nieto A, Roberts SP, Kemp J, Rasmont P, Kuhlmann M, García Criado M, Bissemjejer JC, Bogusch P, Dathe HH, De la Rúa P, De Meulemeester T, Dehony M, Dewulf A, Ortiz-Sánchez FJ, Lhomme P, Pauly A, Potts SG, Praz C, Quaran M, Radchenko VG, Scheucll E, Smit J, Straka J, Terzo M, Tomozii B, Windom J, Michez D (2014) European red list of bees. Publication Office of the European Union, Luxembourg
Pleasants JM (1981) Bumblebee response to variation in nectar availability. Ecology 62:1648–1661
Pouvreau A (1974) Le comportement alimentaire des bourdons (Hymenoptera, Apoidea, Apis mellifera scruetes. Apidologie 5:247–270
Roubik DW, Buchmann SL (1984) Nectar selection by Melipona and Apis mellifera (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. Oecologia 62:1–10
Williams PH (1982) The distribution and decline of British bumble bees (Bombus L.). J Apic Res 21:236–245
Williams PH, Osborne JL (2009) Bumblebee vulnerability and conservation worldwide. Apidologie 40:367–387
Williams P, Colla S, Xie Z (2009) Bumblebee vulnerability: common correlates of winners and losers across three continents. Cons Biol 23:931–940
Xie Z, Williams PH, Tang Y (2008) The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan Plateau of Sichuan. J Insect Cons 12:695–703