Arthropod-Plant Interactions (2023) 17:765–776
https://doi.org/10.1007/s11829-023-10007-8

ORIGINAL PAPER

Temporal variation of floral reward can improve the pollination success of a rare flowering plant

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Received: 16 May 2023 / Accepted: 13 September 2023 / Published online: 18 October 2023

Abstract

Many pollinating animals visit a variety of flowering plant species. Rare plant species pollinated by such generalists may experience a low quality or quantity of pollination, depending on the pollinators' foraging behaviour. How plants cope with this rarity disadvantage is not well understood. One possibility would be to offer a higher floral reward, for example, a higher nectar sugar concentration. However, since nectar production is costly, rare plants may only be able to increase their nectar concentration for a limited time and offer little reward afterwards. In this study, we performed a laboratory experiment with bumblebees (*Bombus terrestris*) foraging on artificial flowers of two colours to investigate whether the bees' foraging behaviour produces a rarity disadvantage and if so, whether the rare flower type could improve its pollination success through temporal variation of its nectar sugar concentration, i.e. a temporary increase of nectar sugar followed by a period with low concentration. We found that when both flower colours offered equal rewards, the rare colour received only slightly fewer visits per flower, but had a considerably lower expected pollination success based on the bumblebees' visitation sequences. Temporal variation of the rare colour's sugar concentration increased both the quantity and quality of visits it received. This positive effect was reduced when there were fewer rare flowers or when two bumblebees foraged simultaneously. Our results suggest that temporal variation of floral rewards can alleviate, but not completely eliminate the rarity disadvantage.

Keywords Nectar · Bumblebee · Artificial flower · Frequency dependence · Co-flowering

Introduction

Species abundances are dynamic in space and time. Both natural and anthropogenic factors can cause shifts in species' relative abundances, with some populations declining, while others increase (e.g. Li et al. 2015). Such changes in abundance can be further amplified or dampened if the organisms' survival or reproductive success depends on their abundance. While processes which reduce the fitness of abundant species promote the maintenance of biodiversity (Chesson 2000), a fitness disadvantage for rare species may lead to their further decline and eventual extinction. Since rare-species fitness disadvantages occur under a wide range of circumstances (Schreiber et al. 2019, and references therein), it is important to understand which traits and strategies species may have evolved to cope with such disadvantages.

For the majority of plant species which are pollinated by animals, being less abundant than other co-flowering species can be a disadvantage. Most pollinating animals such as bees, hoverflies and hummingbirds visit flowers of more than one plant species, often within the same foraging bout (Waser et al. 1996; Brosi 2016, and references therein). If these generalist pollinators visit flowers as they encounter them, a rare plant species may receive few conspecific and many heterospecific pollen grains because its visitors have most recently been on flowers of other more abundant species (e.g. Levin and Anderson 1970; Kunin 1993; Runquist and Stanton 2013). By contrast, when pollinators temporarily specialize on a single flower type,

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Handling Editor: Ek del-Val.

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they deliver the same amount of conspecific pollen regardless of plant species abundance, but the visitation rate to a rare plant species may be low since most animals tend to specialize on abundant flowers to maximize their foraging efficiency (Kunin and Iwasa 1996; Smithson 2001; Schmid et al. 2016). Thus, depending on the pollinators' foraging behaviour, rare flowering plants may suffer from reduced quality or quantity of pollination, or a combination of both.

One possible way to overcome the rare-species disadvantage could be to offer a greater floral reward than co-flowering abundant species. Many pollinating animals can learn to associate floral traits such as colours, shapes or odours with specific rewards (Goulson 1999; Jones and Agrawal 2017, and references therein) and show a preference for more rewarding flowers, for example, flowers with higher nectar sugar concentration (e.g. Roberts 1996; Cnaani et al. 2006; Amaya-Márquez and Wells 2008). A high reward therefore has the potential to increase both the quantity and quality of flower visits to rare flowering plants. However, due to the energetic cost of bypassing less rewarding, but more abundant flowers, economically foraging pollinators should only completely specialize on a more rewarding rare flower type if the high reward and the absence of switching costs compensate for the increased travel cost (Stephens and Krebs 1986). Therefore, depending on the rare species' abundance and its floral reward relative to more abundant plant species, offering a higher reward may not always suffice to completely eliminate the rarity disadvantage. Moreover, since reward production can be costly for plants (Southwick 1984; Pyke 1991; Harder and Barrett 1992; Ordano and Ornelas 2005), rare plant species may only be able to increase their floral reward to a limited degree or for a limited time. If a rare plant increases its reward for a short period and offers little or no reward afterwards, it may benefit from the fact that foragers continue to sample its flowers to investigate whether the reward has increased again (e.g. Keasar et al. 2013).

In the current study, we performed a laboratory experiment with buff-tailed bumblebees (*Bombus terrestris* L) foraging on two types of artificial flowers. Our aim was to (1) establish whether the bees forage in a way which may lead to lower pollination success of rarer plant species (due to low quantity and/or quality of flower visits), and if so (2) test whether a rare flowering plant could reduce its disadvantage or even gain an advantage through a temporary increase of its nectar sugar concentration. While plants could also offer a greater reward in terms of nectar volume or replenishment rate, we chose to manipulate sugar concentration because previous studies showed that bees can learn differences in concentration faster than differences in volume (Cnaani et al. 2006; but see Amaya-Márquez and Wells 2008), and differences in replenishment rate are generally more difficult to learn because the bees' encounter rate with empty flowers also depends on their own foraging patterns.

Here, we define a rare plant species as having low abundance and density, which results in a low encounter rate for flower visitors (Gaston 1994; Kondratyeva et al. 2019). For the experiment, we constructed arrays of two flower colours, one rare, one abundant, where each colour represented a plant species. We let single bumblebees forage on these floral arrays, and varied the sugar concentration of the rare colour while keeping the abundant colour's concentration constant. Each bee experienced two reward scenarios, a "constant reward" scenario in which both flower colours offered equal rewards (25% sucrose) and a "variable reward" scenario in which the rare colour's sucrose concentration was first increased to 40%, then decreased to 10%, while the abundant colour's concentration stayed at 25%. The "variable reward" scenario was chosen so that the average sugar concentration over both periods was equal for both flower colours (25%). While 25% and 40% are nectar sugar concentrations commonly found in bee-pollinated wild plants, 10% is an unusually low concentration (Pamminger et al. 2019). Previous experiments have shown that bumblebees visit flowers with such low concentrations, but quickly learn to avoid them if a more rewarding alternative is available (e.g. Cnaani et al. 2006). In addition to these reward scenarios, we varied the rarer flower colour's relative abundance (6/36 or 3/36) and the number of simultaneously foraging bees (one or two) between experimental trials to test the influence of these factors on the rare colour's visitation rate and expected pollination success. We expected that decreasing the rare colour's abundance should exacerbate its disadvantage and possibly reduce the positive effect of a temporarily increased reward. Likewise, we expected that with two simultaneously foraging bees the positive effect of increased sugar concentration on the rare colour's visitation and pollination success might be reduced, since in this case bees more frequently encounter recently depleted and not yet refilled flowers of the rare colour, which should shift their preference back to the abundant, less rewarding colour. On the other hand, if the two foragers partition the floral resources between themselves and each one specializes on a different flower colour, the rare colour should benefit from a high quantity and quality of visits, while the more abundant colour receives fewer visits per flower.

Materials and methods

Experimental setup

We conducted the experiment in a large indoor cage (4 × 4 × 2 m). The cage was illuminated with fluorescent lights and white LED strips in addition to daylight. These light sources combined provided a light intensity well above 1000 lx on the cage floor. The cage's sides were shielded from direct light to avoid biasing the bumblebees' direction of movement. For the experiment, we used the computer-controlled robotic flower system described by Kuusela and Lämsä (2016), modified for use with two microcontrollers to allow controlling a larger number of artificial flowers. 36 artificial flowers were placed on the floor of the cage in six rows and columns, with a distance of 50 cm between neighbouring flowers. The top of each flower was a flat circular surface of 9 cm diameter, which was covered with a disc made of rubber foam. We used white discs to train the bumblebees to forage on the artificial flowers and feed them before and after experimental trials, and blue and yellow discs for the experiment. The top of each flower had a circular opening (10 mm diameter, 15 mm deep) into which bees needed to crawl to access the reward consisting of a drop of sucrose solution in a "nectar cup" (top of a small cross-head screw) of approximately 2.5 µL. This nectar cup was connected to a motorized arm which could be lowered into a reservoir of sucrose solution to refill the reward. An infrared light barrier was integrated into the flowers' opening to register bumblebee visits. All artificial flowers were connected via cables to a control unit with two Genuino® microcontrollers which were programmed to refill flowers and record flower visits. Throughout the experiment, flowers were refilled after each visit, with a refill period of 15 s. For further details on the artificial flower system, see Kuusela and Lämsä (2016).

In the experiment, we successively tested bees of two colonies of *B. terrestris* obtained from BioBest through Katz Biotech (Baruch, Germany). The colony's nest box was placed on a table in a corner of the cage and connected to a gated wire mesh tunnel to control the movement of bees out of and into the nest. The bumblebee colony was fed pollen directly into the nest box every second day. Sucrose solution (25% w/w) was provided ad libitum in artificial flowers every day before and after experimental trials. Foragers of each new colony were trained to collect sucrose solution from artificial flowers in several steps. Initially, bees learned to forage on eight flowers containing an Eppendorf cup full of honey solution in the opening, with the scent of the honey acting as an olfactory cue. Once several bees had started making regular foraging trips to the flowers, the honey was replaced by sucrose. In the next step, we replaced the Eppendorf cups by a wick which hung down into a reservoir of sucrose solution. These flowers were also used to feed the colony between experimental trials. Finally, foragers were given access to the 36 electronically controlled flowers with a small, automatically refilling nectar cup at the bottom of the opening. Every morning before the start of experimental trials, all bees were allowed to collect sucrose solution from the electronic flowers for at least 30 min. New foragers (bees making regular trips to the flowers and back to the nest) were caught, sedated by cooling in a fridge at 4 °C and individually marked with a colour code.

Experimental trials were conducted between April and July 2019. Each trial consisted of a series of foraging bouts (trips to the artificial flowers and back to the nest) of one or two individually marked test bees (Supplementary Material, Fig. S1). All other bees were confined to the nest during experimental trials. To avoid pseudoreplication, each individual bee was only used once in an experimental trial. Trials began with a training phase in which the test bee was allowed to make two foraging bouts on 36 flowers of one colour (blue or yellow), then two foraging bouts on 36 flowers of the other colour. The order of colours was alternated between bees. We trained bees in this way to reduce possible effects of innate colour preferences on their behaviour, since our aim was to test the effect of flower colour abundance, not of colour per se. Directly after the training phase, the test bee was allowed to forage on the test array with one rare (3 or 6 flowers) and one abundant flower colour (33 or 30 flowers, respectively). The positions of the rare colour's flowers were determined by a random number generator separately for each test bee. The identity of the rare colour (blue or yellow) was alternated between bees. We let the test bee make three foraging bouts on the test array with 25% sucrose in all flowers, then three foraging bouts on the same array with increased concentration in the rare colour's flowers (40% sucrose), and finally three foraging bouts with decreased concentration (10% sucrose) in the rare flower type. The abundant flower colour stayed at 25% sucrose throughout each experimental trial. The flowers' coloured discs were wiped with 70% ethanol between trials of different bees to remove scent marks which might influence the behaviour of bees in following trials. In total, we tested 67 bumblebees in 51 experimental trials with one of three treatments: one bee foraging on six rare and 30 abundant flowers, one bee with three rare and 33 abundant flowers and two simultaneously foraging bees with six rare and 30 abundant flowers (see Table 1 for sample sizes for each combination of treatment, rare colour and colony). Due to the limited availability of

Table 1 Number of replicates (bee individuals) per treatment (number of flowers of the rare colour and number of simultaneously foraging bumblebees), rare colour and colony

Treatment	3 rare flowers, 1 bee		6 rare flowers, 1 bee		6 rare flowers, 2 bees	
Rare colour	Yellow	Blue	Yellow	Blue	Yellow	Blue
Colony A	4	4	4	5	5	3
Colony B	4	4	5	5	4	4

active foragers in the two colonies, we did not test the fourth possible combination (two bees foraging on three rare and 33 abundant flowers).

We checked that the artificial flower system was working correctly each morning before the start of experimental trials, and exchanged any malfunctioning parts. To test the reliability of the artificial flower recordings, for a subset of five haphazardly selected experimental trials, we compared the visits registered by the artificial flowers with video recordings. Only three out of several thousand automatically recorded visits did not correspond to the videos. Prior to the analysis of the data, all automatically recorded flower visitation sequences were checked for plausibility. In 23 out of a total of 153 visitation sequences, we removed one or more visits of implausible length (more than 30 s) or repeated shorter visits registered by the same artificial flower which overlapped in time with visits to other flowers.

Data analysis

To assess the likely consequences of bumblebee behaviour for the rare flower type's pollination success, we summarized the flower visitation sequences recorded by the artificial flower system in several ways. First, we counted the number of visits to each flower colour. In the case of trials with two bees, we included only those parts of the visitation sequences when both bees were actively foraging, since we were interested in the effects of higher encounter rates with depleted flowers due to the activity of the second forager. These parts of the visitation sequences were determined by comparing the visits' time stamps with video recordings.

To account for the expected effects of transitions between the two flower types on plant pollination success, we calculated a measure of theoretically expected pollination success using Bateman's (1947) model of pollen carryover. This model is based on the assumption that pollinators take up one unit of pollen in each flower visit and deposit a fraction λ of the pollen taken up during earlier visits (see also Montgomery 2009). Thus, pollen carryover was modelled as a geometric decay function, in accordance with several empirical studies (e.g. Thomson and Plowright 1980, Campbell 1986, Thomson 1986). Based on the observed visitation sequence, we calculated each flower colour's expected amount of conspecific pollen received for two rates of pollen deposition ($\lambda = 0.3$ and $\lambda = 0.8$). However, since the values of theoretically expected pollination success were highly correlated (Pearson's $r > 0.98$), we only analysed the data for $\lambda = 0.3$. As the artificial flowers did not record the identity of visiting bees, we could not reconstruct individual visitation sequences from the data of trials with two simultaneously foraging bees. Therefore, we calculated theoretically expected pollination success only for trials with a single forager.

Beside their effect on conspecific pollen receipt, bee movements between flower types could also negatively affect plant pollination success through clogging of stigmas with heterospecific pollen. However, since empirical evidence suggests that conspecific pollen loss has a much stronger influence on plant pollination success compared to heterospecific pollen deposition (Morales and Traveset 2008), we did not account for possible effects of stigma clogging in our calculations of theoretically expected pollination success.

To be able to compare numbers of visits and expected pollination success of the rare and abundant flower colour between trials with different durations and total numbers of bumblebee visits, we calculated indices which quantify the rare colour's visitation or pollination success, respectively, relative to the abundant colour, while taking into account the rare colour's relative abundance. Specifically, for flower visits we calculated the rare colour's relative visitation rate V as

$$V = \frac{P_{\text{obs}}}{P_{\text{obs}} + P_{\text{exp}}}, \tag{1}$$

where P_{obs} is the observed proportion of visits to the rare colour and P_{exp} is the expected proportion based on the rare colour's relative abundance (i.e. either 6/36 or 3/36). This is the preference index used by Fründ et al. (2010) and Schmid et al. (2016), which is based on the forage ratio of Krebs (1989). For pollination, we calculated the rare colour's relative expected pollination success in an analogous way, with P_{obs} representing the theoretically expected proportion of conspecific pollen received by the rare colour. With both indices, a value of 0.5 indicates that the rare colour received the same number of visits or amount of conspecific pollen per flower as the abundant colour. Values below 0.5 indicate a rare-colour disadvantage, and values above 0.5 a rare-colour advantage. We calculated these indices both for the complete visitation sequence of each individual and sucrose concentration and for the last 1/3 of each visitation sequence, which roughly corresponds to the last of the bumblebees' three foraging bouts. The behaviour of bumblebees in this last foraging bout should reflect their foraging decisions after an initial learning period during which they collected information about the distribution of flower types and floral rewards.

To investigate how the rare colour's relative visitation rate and pollination success varied between experimental trials, we fitted two regression models to each data set, one with relative visitation rate as response variable and one for relative expected pollination success. Both models included two main categorical predictors, floral reward of the rare colour (either constant or variable), treatment (combination of number of rare flowers and number of simultaneously foraging bees) and their interaction. For the "variable reward" scenario, we calculated the response using the sum of numbers of visits or expected conspecific pollen receipt of visitation sequences with 40% and 10% sucrose in the rare flowers. Treatment had three levels (6 or 3 rare flowers with one bee, 6 rare flowers with two bees) in the model of relative visitation rate and two levels (6 or 3 rare flowers with one bee) in the model of relative expected pollination success.

In addition to the two main predictors, we also included bumblebee colony (A or B) and colour of the rare flower type (blue or yellow) as population-level (fixed) effects in both models. To account for the non-independence of flower visitation sequences of the same bee or pair of bees, bee identity was included in the models as a group-level (random) effect.

Statistical models were fitted in a Bayesian framework, using the "brms" package (Bürkner 2017) in R (R Core Team 2021) as an interface to Stan (Stan Development Team 2019). Since the response variables had continuous values between zero and one and some values were exactly zero, we used a zero-inflated beta model, and modelled both the beta distribution's location parameter and the zero-inflation parameter as a function of all predictors. To prevent overfitting while avoiding the drawbacks of variable selection (e.g. Hastie et al. 2009; Harrell 2015), we performed penalized regression using a regularized horseshoe prior with three degrees of freedom for the Student t prior of the local shrinkage parameters (Piironen and Vehtari 2017; van Erp et al. 2019). We used non-informative priors for all other model parameters: a non-standardized Student t distribution (3, 0, 2.5) for the intercept of non-zero values and the standard deviation of group-level effects, a Gamma distribution (0.01, 0.01) for the beta distribution's precision parameter and a logistic distribution (0, 1) for the intercept of the zero-inflation term. To account for the different numbers of flower visits used to calculate relative visitation rate or relative expected pollination success, we performed weighted regression with number of visits as weights. Posterior estimates were obtained using Markov Chain Monte Carlo (MCMC) sampling with four chains of 4000 iterations each. The first 2000 iterations of each chain were discarded as warm-up. Convergence diagnostics indicated that the models had fully converged: all $\hat{R}$ values were smaller than 1.01, effective sample sizes were larger than 1500, and no divergent transitions occurred. We checked for patterns in the residuals by comparing the observed data to posterior predictive simulations from the fitted model using the R package "DHARMa" (Hartig 2020). Population-level effects were considered significant when their 95% credible intervals did not overlap zero.

To help us interpret the findings of the main analyses, for the visitation sequences with 40% sucrose in the rare flower type, we calculated the proportion of visits to the rare colour in which the floral reward had been recently depleted and not yet refilled. We modelled this proportion of visits to empty rare flowers as a function of treatment (number of rare flowers and simultaneously foraging bees), rare colour and colony, using a generalized linear mixed model with binomial errors and logit link. The model was fitted using the function "glmer" from the R package "lme4" (Bates et al. 2015), with an observation-level random effect to account for overdispersion.

Results

When both flower colours were equally rewarding (25% sucrose, "constant" reward scenario), single bumblebees avoided the rare colour on average, i.e. they showed positive frequency dependence of flower choice (Figs. 1a, 2a). This rare-colour avoidance was significantly stronger when there were only three rare flowers compared to six (Table 2). By contrast, two simultaneously foraging bees did not show a clear rare-colour avoidance, although the difference to single foragers was not significant. Overall, there was considerable variation between individuals, with some bees visiting the rare colour much less than expected by chance, while others even showed a slight preference for the rare colour. On the other hand, the rare colour's theoretically expected pollination success in the "constant" reward scenario was consistently lower than that of the abundant colour, especially with only three rare flowers (Figs. 1a, 2b, Table 3).

As expected, the average relative visitation rate and pollination success of the rare colour increased when its flowers offered 40% sucrose and decreased with 10% sucrose (Fig. 1a). When analysing the visitation sequences with 40% and 10% sucrose combined as one "variable" reward scenario, we found a significant increase of relative visitation rate and expected pollination success compared to the "constant" reward scenario (Fig. 2, Tables 2 and 3). The positive effect of a variable reward on relative visitation rate was slightly, but significantly weaker when there were only three rare flowers or when two bees foraged simultaneously. In the model of relative expected pollination success, the positive effect of variable reward markedly and significantly decreased with three rare flowers (Table 3). Both relative visitation rate and expected pollination success were significantly higher for yellow rare flowers compared to blue flowers. Bumblebee colony only had a significant effect on relative expected pollination success, but not on relative visitation rate.

Compared to the data set with all flower visits, when considering only the last part of each flower visitation sequence, there was a stronger increase and decrease of relative visitation and pollination with 40% sucrose and 10% sucrose in the rare flowers, respectively (Fig. S2). Whereas over all flower visits the weighted mean relative visitation rate and expected pollination success were higher at 10% sucrose than at 25%

Table 2 Results of a weighted zero-inflated beta regression of the rare flower colour's relative visitation rate ($N = 102$, 1 zero)

Predictor level	Mean estimate	2.5%	97.5%
Effect on mean of non-zero values			
Intercept	**– 0.54**	−0.75	−0.32
Reward "variable"	**0.54**	0.53	0.55
Treatment "3 rare, 1 bee"	**– 0.34**	−0.57	−0.11
Treatment "6 rare, 2 bees"	0.19	−0.06	0.42
Rare colour "yellow"	**0.20**	0.01	0.40
Colony "B"	0.18	−0.01	0.38
Reward variable × Treatment "3 rare, 1 bee"	**– 0.03**	−0.04	−0.02
Reward variable × Treatment "6 rare, 2 bees"	**– 0.05**	−0.06	−0.04
Effect on zero-inflation parameter			
Intercept	**– 19.88**	−36.61	−9.85
Reward "variable"	−1.03	−18.63	15.57
Treatment "3 rare, 1 bee"	8.17	−1.52	24.11
Treatment "6 rare, 2 bees"	−1.76	−21.27	16.68
Rare colour "yellow"	4.10	−2.69	12.14
Colony "B"	−4.05	−11.84	2.68
Reward "variable" × Treatment "3 rare, 1 bee"	−17.29	−40.55	2.88
Reward "variable" × Treatment "6 rare, 2 bees"	0.31	−24.34	26.35

Both the mean (location) of non-zero values and the zero-inflation parameter were modelled as a function of all predictors, with the number of flower visits of each visitation sequence as weights. The intercept is the estimated value for the "constant" reward scenario, treatment "6 rare, 1 bee", colony "A" and rare colour "blue". The table shows the mean value of each parameter's posterior distribution on the link (logit) scale together with its 95% credible interval (CI). Parameter values whose CI does not overlap zero are in bold. The estimated standard deviation for the group-level (random) effect of bumblebee individual was 0.35 [0.29, 0.43] (mean posterior estimate, 95% CI in square brackets) for the mean of non-zero values and 5.07 [3.00, 8.27] for the zero-inflation parameter. The scale parameter of the beta distribution of non-zero values was estimated as 124.66 [122.61, 126.74]

Table 3 Results of a weighted zero-inflated beta regression of the rare flower colour's relative expected pollination success ($N = 70$, 1 zero)

Predictor level	Mean estimate	2.5%	97.5%
Effect on mean of non-zero values			
Intercept	**– 2.91**	−3.47	−2.37
Reward "variable"	**1.61**	1.59	1.63
Treatment "3 rare, 1 bee"	**– 1.13**	−1.69	−0.58
Rare colour "yellow"	**0.62**	0.07	1.18
Colony "B"	**0.59**	0.04	1.17
Reward variable × Treatment "3 rare, 1 bee"	**– 0.15**	−0.18	−0.11
Effect on zero-inflation parameter			
Intercept	**– 17.02**	−29.07	−8.88
Reward "variable"	−1.06	−12.33	9.77
Treatment "3 rare, 1 bee"	5.93	−2.53	17.37
Rare colour "yellow"	4.05	−3.05	12.01
Colony "B"	−4.30	−12.48	2.81
Reward "variable" × Treatment "3 rare, 1 bee"	−15.18	−30.81	−2.37

The estimated standard deviation for the group-level (random) effect of bumblebee individual was 0.82 [0.64, 1.06] (mean posterior estimate, 95% CI in square brackets) for the mean of non-zero values and 5.34 [3.06, 9.02] for the zero-inflation parameter. The scale parameter of the beta distribution of non-zero values was estimated as 39.40 [38.57, 40.29]. See the legend of Table 2 for further details

Parameter values whose CI does not overlap zero are in bold

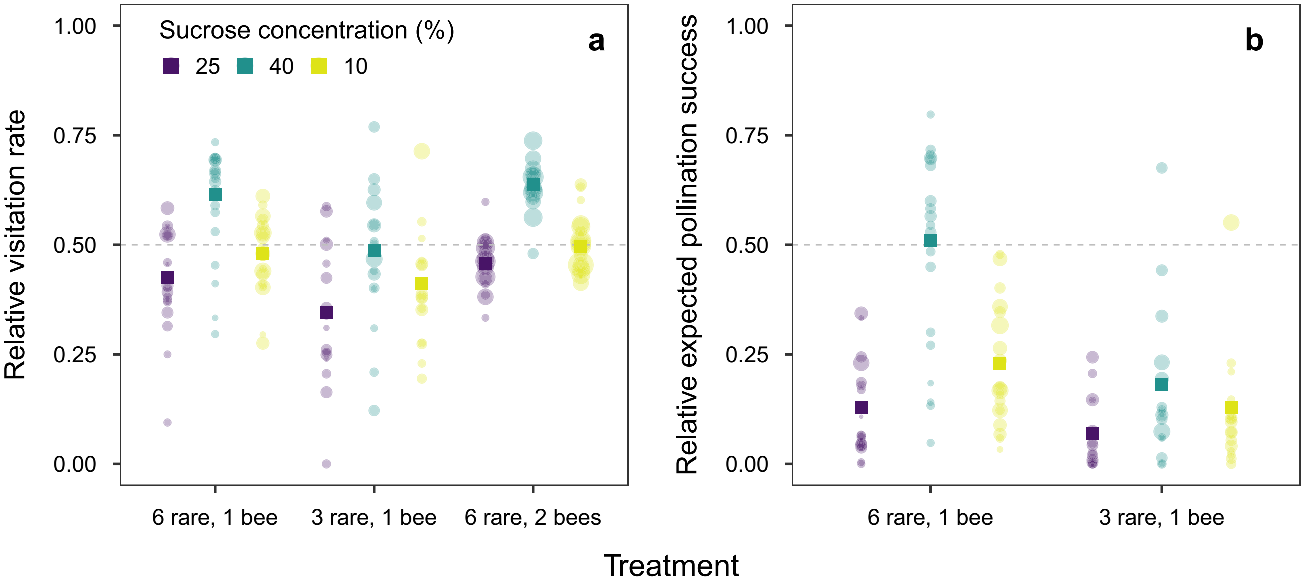

Fig. 1 **a** Relative visitation rate and **b** relative expected pollination success of the rare flower colour for each combination of treatment and sucrose concentration in the rare flowers. A relative visitation rate or expected pollination success of 0.5 indicates that the rare flower colour received the same number of visits or conspecific pollen grains per flower as the abundant flower colour. Values below 0.5 indicate a rare-colour disadvantage, values above 0.5 a rare-colour advantage. Expected pollination success was calculated based on the bumblebee's visitation sequence and a geometric decay model of pollen carryover. Circles are data points with area proportional to the number of flower visits (minimum 43, maximum 433 visits), squares indicate weighted mean values

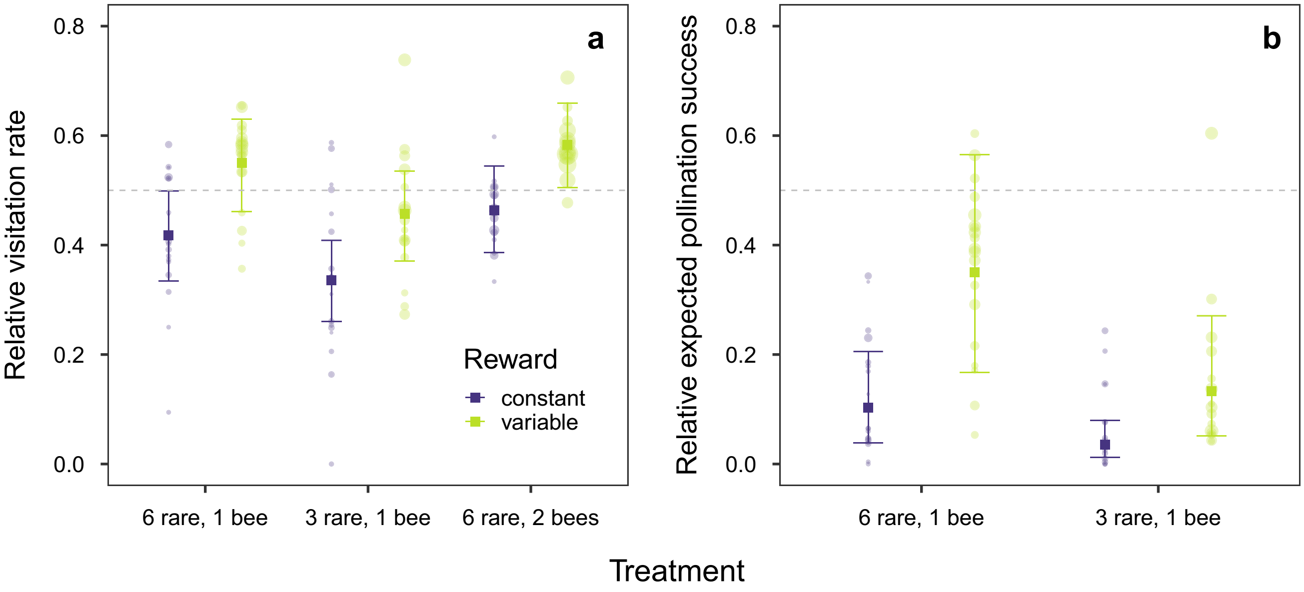

Fig. 2 **a** Relative visitation rate and **b** relative expected pollination success of the rare flower colour as a function of reward scenario and treatment. In the "constant" reward scenario, both flower colours contained 25% sucrose solution, while in the "variable" reward scenario, the rare flower colour's sucrose concentration was first increased to 40%, then decreased to 10% (see Fig. 1). Squares and error bars show the mean and 95% credible interval of the expected value of the posterior predictive distribution, calculated from 100 samples. Circles are data points with area proportional to the number of flower visits (minimum 43, maximum 781 visits)

(Fig. 1), this relationship was reversed in the last part of the visitation sequences (Fig. S2). However, when combining the data from the periods with 40% and 10% sucrose into one “variable reward" scenario, the values were quite similar to the data of all flower visits (Fig. S3). Consequently, the estimated effects of treatment and reward scenario were also similar to those of the full data set (Tables S1 and S2). The effects of rare colour and colony were no longer significant when considering only the last 1/3 of visits. In the models of this last part of the visitation sequence, the zero-inflation parameter (probability of an observation being exactly zero) was significantly lower in the variable reward scenario, but this effect decreased with three rare flowers compared to six rare flowers.

In the additional analysis of the proportion of visits to empty rare flowers during the period with 40% sucrose concentration in the rare flowers, neither treatment, nor rare colour or colony had a significant effect (Table S3). Thus, we found no evidence that two simultaneously foraging bumblebees or single bees foraging on three rare flowers encountered empty rare flowers more frequently than single bees foraging on six rare flowers.

Discussion

In this experiment, bumblebees indeed foraged in a way which resulted in a lower quantity and quality of visits to the rarer flower type when both flower types were equally rewarding, but differed in abundance. While the per-flower visitation rate of the rare colour was on average only slightly lower than that of the abundant colour (relative visitation rate close to 0.5), the rare colour’s expected pollination success was strongly limited by the fact that bumblebees often visited several flowers of the abundant colour between two visits to the rare colour, and so would have lost most of the rare colour’s conspecific pollen according to the model of pollen carryover. Temporal variation of the rare colour’s sucrose concentration (specifically, an increase followed by a decrease in concentration) considerably increased both the proportion of visits it received per flower and its expected pollination success. This effect is likely due to the fact that during the period with 40% sucrose, bumblebees concentrated their foraging effort on the few available highly rewarding flowers, which each received so many visits that this more than compensated for their low visitation rate during the period with 10% sucrose (see Benadi and Gegear 2018, for a similar effect in a simulation model). In addition, during the period with low reward, the rare colour benefitted from the bumblebees’ memory of the previous high-reward period. Most bees decreased the proportion of visits they made to the rare colour only gradually and continued to make a few visits to the rare colour even in their last foraging bout (see Fig. S4 for an example), presumably to check whether the high sucrose concentration had returned. Thus, the order of rewards (first high, then low) is probably critical for the positive effect of reward variation observed here. Despite these positive effects of temporal reward variation, the rarity disadvantage with respect to expected pollination success was only reduced, but not completely eliminated.

As expected, temporal reward variation had a weaker positive effect when there were only three rare flowers or when two bumblebees foraged simultaneously. In both cases, this reduction was likely caused by a higher frequency of encounters with depleted flowers of the rare colour during the period with increased sucrose concentration, which prompted bees to switch back to the abundant flower colour with lower sucrose concentration. While we did not detect a difference in the proportion of visits to empty rare flowers between treatments, that may be because bumblebees quickly responded to such unrewarding visits by increasing their visitation rate to the abundant flower type, thereby allowing the rare type’s flowers to refill before the next visit. This is in line with previous studies which showed that bees are more likely to switch to a different flower type after encountering flowers with zero or low nectar (Goulson 1999, and references there in; Austin et al. 2019), and can even adjust their visitation patterns to intra- and interspecific differences in nectar replenishment rates (Klinkhamer et al. 2001; Stout and Goulson 2002).

The finding of a lower average visitation rate to the rarer flower type when both types were equally rewarding is consistent with several previous laboratory studies which found that bumblebees preferred an abundant flower colour over a rarer one, i.e. they showed positive frequency dependence of colour choice (reviewed by Smithson 2001). Such positive frequency dependence is supposed to occur whenever it increases the flower visitors’ foraging efficiency by reducing the cognitive costs of switching between flowers with different traits (Smithson 2001, and references therein). Thus, positive frequency dependency of flower choice is a special case of flower constancy, the temporary specialization of flower visitors on one flower type (e.g. Goulson 1999; Gegear and Thomson 2004; Amaya-Marquez 2009; Grüter and Ratnieks 2011).

Compared to a previous laboratory experiment with *B. terrestris* foraging on blue and yellow artificial flowers (Smithson and Macnair 1996), the frequency effect in our study was relatively small. Moreover, while in the present study bees on average showed a slight frequency-independent preference for yellow flowers, in the experiment of Smithson and Macnair (1996), bumblebees avoided yellow and preferred blue flowers. In that study, at 10% and 20% yellow flowers, nearly all bees tested made less than 5% of their visits to yellow flowers. By contrast, in our experiment, the average proportion of visits to yellow flowers was 6% when there were ca. 8% yellow flowers (3 of 36) and 17% when there were ca. 17% yellow flowers (6 of 36). This difference between studies may be due to a difference in methodology. Specifically, the difference in frequency-independent colour preferences could be caused by the fact that we trained bumblebees on each colour separately, while Smithson and Macnair trained bees on mixed arrays of both colours. Therefore, in their study innate colour preferences may have had a greater influence on bumblebee behaviour. The stronger rare-colour avoidance reported by Smithson and Macnair could be due to the very short inter-flower distances in their experimental array compared to ours. Whereas in the present study neighbouring artificial flowers were spaced 0.5 m apart, Smithson and Macnair used an array with 150 flowers on an area of 0.8 × 0.8 m. According to foraging theory (Stephens and Krebs 1986, and references therein), a high density of floral resources should favour greater specialization of foragers due to the lower energetic cost of bypassing a rewarding flower. While Gegear and Thomson (2004) indeed found a positive effect of artificial flower density on individual specialization of bumblebees, in a follow-up study on their previous experiment, Smithson and Macnair (1997) did not find an effect of flower density on the strength of rare-colour avoidance. However, the lowest flower density they tested was still much higher (248 flowers per m^2) than the density of flowers in our study (9 per m^2).

Whereas the evidence for a rarity disadvantage under laboratory settings with a single flower visitor is relatively clear, it is much less certain how important this disadvantage is under natural conditions. If the reproductive success of flowering plants generally increased with relative abundance, rare plant species (Levin and Anderson 1970; Benadi et al. 2012) and rare flower morphs (Smithson 2001) might become locally extinct (but diversity could still be maintained at a regional scale: Greenspoon and M'Gonigle 2013). However, while some studies of natural plant communities have found positive frequency dependence of flower visitation rates, conspecific pollen receipt or seed set (Kunin 1993; Runquist and Stanton 2013; Schmid et al. 2016), others reported no such frequency dependence (Eckhart et al. 2006) or a hump-shaped (Benadi and Pauw 2018) or negative relationship (Bergamo et al. 2020). This inconsistency could be due to variation in frequency effects across spatial scales and in relation to plant and pollinator traits (e.g. Benadi and Pauw 2018; Bergamo et al. 2020). In addition, exploitation competition between foraging pollinators (within and between species) could lead to a more even distribution of foragers among floral resources, thereby reducing the positive frequency dependence of flower visitation rates (Eckhart et al. 2006; Schmid et al. 2016). Our finding that the rare colour's average relative visitation rate was closer to 0.5 when two bumblebees foraged simultaneously is consistent with this expectation.

Even if flower visitation rates are relatively independent of plant species abundance, our results suggest that rare flowering plants may experience a strong disadvantage with respect to the quality of flower visits, since most of their conspecific pollen is lost in visits to more abundant flowering species. While factors such as spatial aggregation of conspecific plants (Campbell 1986; de Waal et al. 2015), morphological complexity of flowers (Gurevich and Hadany 2021) and differentiated pollen placement on pollinators' bodies (Morales and Traveset 2008) may limit the loss of conspecific pollen, several field studies found that rare plant species indeed received smaller amounts of conspecific pollen than more abundant species (e.g. de Waal et al. 2015; Bergamo et al. 2020). Our experiment suggests that this rarity disadvantage could be alleviated through a synchronous increase in nectar sugar concentration, even if the increase is temporary and followed by a period with low sugar concentration. Whether this is a feasible strategy depends on the flexibility of resource allocation to nectar production, which has rarely been studied until now. Previous studies of floral nectar production found that the volume and concentration of nectar can vary substantially both between and within plant species. While interspecific differences may be adaptations to different groups of pollinators (Fenster et al. 2004), intraspecific variation in nectar amount and composition is partly heritable, but also related to environmental conditions (e.g. Boose 1997; Parachnowitsch et al. 2019, and references therein), time of day and flower age (e.g. Devlin et al. 1987; Witt et al. 1999). In some plant species, nectar sugar (either sucrose or hexose) is directly produced in the nectaries through photosynthesis, while other plants produce these sugars through hydrolysis of starch stored in the parenchyma (Pacini et al. 2003). The latter are more flexible in their nectar production patterns, since the stored starch allows them to produce larger quantities of sugars independent of the current rate of carbon assimilation through photosynthesis. In general, the nectar sugar concentration of plant species is often considerably lower than the preferred concentration of their flower visitors (e.g. Nicolson 2002) and the concentration which would maximize the visitors' energy intake rate (Kim et al. 2011). The reason for this discrepancy is not entirely clear, but it has been suggested that a low concentration prevents the nectar from becoming too viscous over time through evaporation (McCallum et al. 2013) or that high costs of nectar sugar production prevent most plants from investing more resources into this floral reward (Parachnowitsch et al. 2019, and references therein). In summary, the evidence so far suggests that there is some flexibility in resource allocation to nectar, but that nectar production is also constrained by various factors which could prevent some rare plant species from increasing their floral reward. Even in our experimental "variable reward" scenario, where the average sugar concentration over the two periods was the same for the rare and abundant plant species, the average cost of a flower visit in terms of nectar sugar was greater for the rare flower type because it received most of its visits during the period with 40% sucrose and very few visits in the period with 10% sucrose. Therefore, this scenario is only realistic if rare plant species are able to invest a higher amount of resources into floral rewards than abundant plant species. In addition, to achieve maximum benefit from a temporary increase of nectar sugar, the increase needs to occur synchronously in all plant individuals. Such a synchronous change could be genetically determined or triggered by an environmental cue. However, the effect of a synchronous increase in nectar sugar production might be weakened by other factors which cause additional variation in the quality and quantity of nectar, for example, nectar robbery (e.g. Irwin et al. 2010) and the presence of nectar microorganisms (e.g. Canto and Herrera 2012). Moreover, since bees also forage for pollen (and in some cases floral oil) to provision their larvae, the quantity and quality of these other rewards may be as important or even more important in determining their foraging behaviour (but see Konzmann and Lunau 2014).

Conclusions

Overall, the results of this experiment suggest that rare plant species pollinated by *B. terrestris* experience a slight disadvantage with respect to the quantity of flower visits, coupled with a strong disadvantage regarding the quality of pollination. Offering a higher nectar sugar concentration, even if only temporarily, would be a way to alleviate this rarity disadvantage, but only if flower visitors forage primarily for nectar and if nectar production is the primary determinant of nectar availability. Moreover, rare plant species need to invest additional resources into nectar production, which may not be possible under all circumstances. Future studies should therefore aim to understand how the costs and benefits of floral reward production vary depending on environmental conditions. This knowledge will also help to preserve plant populations that are experiencing strong shifts in relative abundance as a result of global change.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11829-023-10007-8.

Acknowledgements We thank Jo Hoeser, Robert Dietrich, Felix Lindicke, Severin Hauenstein and Matthias Jäger for their help in assembling the artificial flowers and setting up the flight cage. Erno Kuusela and Andreas Gimbel provided technical support in configuring the artificial flower system. The Chair of Ecosystem Physiology at the University of Freiburg kindly hosted the experiment in their laboratory. This study was funded by Deutsche Forschungsgemeinschaft Grant No. 6231/1 to GB.

Author contributions GB, RJG and JL designed the experiment. RK and GB performed the experiment and analysed the data. GB wrote the first draft of the manuscript. All authors contributed critically to the revisions and approved the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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