Beyond random and forbidden interactions in plant-pollinator networks : how optimizing energy gain results in morphological matching among subalpine Asteraceae and their flower-visitors

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Why do bumblebees prefer deeper flowers? An optimal foraging approach

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Abstract

The proboscis of flower-visitors plays an important role in their flower choice. Often, flower-visitors preferentially visit the deepest flowers on which they can forage, which are the ones of which the nectar tube depth matches the length of their proboscis. This flower preference might be an adaptation for efficient foraging, as optimal foraging theory assumes that animals forage in such a way that maximizes their fitness. In this study we investigated (1) how foraging efficiency of natural foraging bumblebees of *Bombus bifarius* is related to the nectar tube depth of the Asteraceae flowers they forage on, and (2) whether bumblebees visit those species of flowers which produce more nectar or on which they have a higher foraging efficiency more frequently. As an indication of bumblebee foraging efficiency we measured their sugar intake rate per flower, per flower head and per patch. This is the amount of sugar ingested per time unit while extracting nectar from a flower, while foraging on a flower head or while foraging in a patch respectively. In addition we calculated their net energetic gain when foraging within a patch, accounting not only for the amount of sugar bumblebees take in per time unit, but also for the energetic content of the nectar and the energy bumblebees spend while foraging. Bumblebees extracted more nectar per second when foraging on flowers with deeper nectar tubes. Also, the amount of sugar extracted while foraging on a flower head or at a patch increasing nectar tube depth. In contrast, the energy bumblebees spend was not related to the nectar tube depth of the flowers. Consequently, their (rate of) net energy gain increased with increasing nectar tube depth. Further, bumblebees visited the flowers on which they experienced a higher net (rate of) energy gain more frequently. Net energy gain and rate of net energy gain explained respectively 72% and 60% of the variation in visitation rate. Visitation rate was also positively related to the sugar content of the flowers, however, sugar content explained (only) 55% of the variation in visitation rate. Visitation rate was not related to flower head density nor nectar tube depth. Overall, our results show that bumblebees forage more efficiently on flowers with deeper nectar tubes and that they do not visit them at random, but visit those flowers which offer more sugar and provide a higher energy gain more frequently. These results explain why bumblebees prefer visiting flowers with deeper nectar tubes and, because the deepest flowers on which they can forage are the ones that match the length of their proboscis, size-matching in plant-flower-visitor communities.

Key words: Asteraceae, *Bombus bifarius*, flower head density, nectar tube depth, rate of net energy gain, sugar intake rate, visitation rate

Introduction

Morphological traits of animals play an important role in the selection of their diet. For example, among flower-visitors, the length of their proboscis is known to determine the flowers that they visit for nectar. In general, flower-visitors can only visit those flowers of which the nectar tube depth does not exceed the length of their proboscis (Corbet 2000; Stang, Klinkhamer & van der Meijden 2007). Among the flowers which they can potentially visit, they visit flowers with deeper nectar tubes more often, which leads to size-matching between the length of their proboscis and the nectar tube of the flowers they visit (Stang *et al.* 2009). Patterns of size-matching has often been explained by these size-constraints in combination with species abundance (Stang *et al.* 2009) or resource competition (Rodriguez-Girones & Santamaria 2006). However, foraging efficiency, which is determined by both nectar reward of flowers and the energy spent while foraging, might be an important underlying factor influencing flower-visitor flower choice.

Optimal foraging theory assumes that animals forage in a way that maximizes their fitness. Therefore, they should select their diets and structure their foraging activities to maximize their net energy gain per time unit (Schoener 1971; Pyke, Pulliam & Charnov 1977; Pyke 1980; Pyke 1984; Stephens & Krebs 1986; Stephens, Brown & Ydenberg 2007). Consequently, optimal foraging theory predicts that flower-visitors should restrict their foraging efforts to those flowers offering the greatest rates of net energy gain. The net energy gain depends on the nectar reward of flowers and its energetic value, the number of flowers that flower-visitors visit per time unit and the energy they spend while foraging. The number of flowers that flower-visitors visit per time unit depends on the time it takes to (i) handle flowers and ingest the nectar (handling time) and (ii) to fly from flower-to-flower (interfloral flight time). The energetic expenditure depends on whether flower-visitors can walk or need to fly from flower to flower and the time they need for this, which depends on the flower clustering and density. In fact, flight time is the major component of foraging costs, as walking can require about 100 times less energy per second than flying (Heinrich & Raven 1972).

In some flowers nectar is easy accessible while in other flowers it is hidden in a long nectar tube. Both the amount of nectar that flowers produce and flower handling efficiency is related to the length of this tube. In general, deeper flowers produce more nectar, both in volume and sugar content (Galetto & Bernardello 2004; Kaczorowski, Gardener & Holtsford 2005; Petanidou 2007; Martins & Johnson 2013) and it takes flower-visitors more time to handle these flowers and extract the nectar (Inouye 1980). Yet, it is unknown how the nectar extraction rate and the overall (rate of) net energetic gain of natural foraging bumblebees differs among plant species and whether these aspects are related to nectar tube depth of the flowers they visit. The effect of floral traits, such as nectar tube depth, on nectar extraction rate, have mostly been studied under experimental laboratorial conditions (Hainsworth & Wolf 1976; Harder 1983; Montgomerie 1984; Harder 1986). Comparative studies which have examined the foraging energetics of flower-visitors naturally foraging on a diversity of plant species are rare (but see May 1985 for butterflies).

The present study was designed to get more insight in the foraging efficiency of natural foraging bumblebees and the role this plays in their selection of flowers. Specifically, we asked whether natural foraging bumblebees can forage more efficiently on flowers with deeper nectar tubes and consequently, whether they visit those flowers which provided the largest foraging efficiency more frequently. If so, this offers a possible explanation for bumblebee preference for flowers with deeper nectar tubes, which match their proboscis length (Stang *et al.* 2009). As an indication of bumblebee foraging efficiency we measured their sugar intake rate per flower, flower head and patch. Sugar intake rate is the amount of sugar ingested per time unit while extracting nectar of a single flower, while visiting a flower head or while foraging in a patch respectively. In addition we calculated the net energetic gain of bumblebees while foraging within a patch, accounting not only for the amount of sugar bumblebees take in per time unit, but also for the energetic content of the nectar and the energy bumblebees spend while foraging (energy expenditure). We asked the following questions: (1) is the sugar intake rate of bumblebees, while extracting nectar from a single flower and while foraging on a flower head or in a patch, related to the depth of the flowers they forage on? (2) Is the energetic expenditure of bumblebees related to the depth of the flowers they forage on? (3) Is the (rate of) net energy gain of bumblebees related to the depth of the flowers they forage on? (4) Is the (rate of) net energy gain of bumblebees related to other aspects which determine bumblebee foraging efficiency, including flower head density, sugar content per flower, number of open flowers per head, flight time between heads and the time it takes to visit a flower head? And (5) do bumblebees visit those flowers that have deeper nectar tubes, are more abundant, produce more nectar or provide a larger (rate of) net energy gain more frequently?

Materials and methods

Study site and plant species

Data were collected in the vicinity of the Rocky Mountain Biological Laboratory, Gunnison County, Colorado, USA. In total, seven Asteraceae species were sampled, which belong to the subfamilies Carduoideae and Asteroideae (Table 1). The Asteraceae have tiny flowers (flowers) which are aggregated in flower heads (capitula). Due do their relatively shallow flowers, bumblebees have a proboscis which is longer than the depth of these flowers and therefore, potentially, can visit all plant species.

Nectar tube depth

As nectar tube depth, we measured the length of the upper, wider part of the corolla tube, which roughly begins where the stamens insert and ends at the beginning of the corolla lobes, at the base of the deepest cleft in the corolla. The lower part of the corolla tube of the studied species is almost filled by the style (Graenicher 1909), therefore it is unlikely that flower-visitors can access this part of the corolla tube. We measured the depth of the nectar tube for at least twenty freshly picked flowers, to the nearest 0.01 mm, under a dissecting microscope.

Nectar production

We measured nectar production of disk flowers that were bagged for 24-hours, as an estimate for the nectar production rate (NPR). Flowers were bagged between 8 and 9 AM and collected 24-hours later. We used bags made of fine gauze that do not change the temperature within the bag and thus will not influence the nectar solute concentration (Corbet 2003). For each species, we only measured the nectar production rate of disk flowers as ray flowers are often sterile and do not produce nectar (Mani & Saravanan 1999). We did this for 14-100 flowers per plant species.

Nectar was extracted with microcapillary tubes of 0.25, 0.5 and 1.0 μL. The capillary size depended on the quantity of the nectar produced by the flowers and the nectar tube width. With the microcapillary tubes we probed the base of the nectar tube until no more nectar could be removed and then used digital callipers to measure the distance the nectar had migrated up the microcapillary tubes. Nectar volume was determined by converting the distance measured to volumes (μL). Nectar sugar concentration (expressed in % w/w in a solution) was measured with a hand-held refractometer. When nectar samples were too small for sugar concentration measurements, nectar samples of flowers from the same head were pooled to obtain a single concentration measurement. Sugar content (mg) was quantified as the product of the nectar sugar concentration, which was first converted from wt/wt to wt/vol, multiplied with the nectar volume, as suggested by Bolten *et al.* (1979).

Sugar intake rate per single flower

We calculated the sugar intake rate per flower based on the nectar production of bagged flowers and the handling time of bumblebees when foraging on bagged flowers. As nectar production rate is less variable than nectar standing crop, measuring the nectar production rate and the handling time of insects on bagged flowers gives a more reliable measure of the sugar intake rate per single flower.

Handling time was recorded with a digital video camera. We analysed these video recordings frame by frame (50 frames/s) with the software Adobe Premiere Pro CC 2014. For each flower head, only the first visit was analyzed. For each plant species, we analyzed 50-201 probes of *B. bifarius*. All handling time measurements were conducted between 8 and 10 am. Sugar intake rate per flower was calculated by dividing the mean sugar content (mg) by the handling time (s). We assume that flower-visitors completely empty the flowers.

Sugar intake rate per flower head and patch

Sugar intake rate per flower head and patch was calculated based on bumblebees foraging on unbagged flowers and the nectar standing crop of these flowers. For these calculations, nectar standing crop (NSC) was estimated, based on the regression analyses between NSC and NPR (Chapter 3 of this thesis). In contrast to NPR, NSC gives a more reliable indication of the foraging energetics of natural foraging bumblebees because NSC is what bumblebees actually

encounter while foraging. We calculated the sugar intake rate per flower head and per patch using the following equations:

$$SIR_{fh} = \frac{nS}{t_h} \quad (1)$$

and

$$SIR_{patch} = \frac{nS}{t_h + t_f} \quad (2)$$

where SIR_{fh}= sugar intake rate per flower head (mg s^{-1}), SIR_{patch}= sugar intake rate per patch (mg s^{-1}), n=mean number of flowers bumblebees probed per flower head, S=average quantity of sugar per flower (mg), t_h=average time spent handling flower heads (s) and t_f=average time spent flying from flower head to flower head (s).

The time bumblebees spend on a flower head and the time it takes bumblebees to fly from flower head to flower head (inter-flower head flight time) within a patch, was measured using a stopwatch.

Energy expenditure

We calculated the energy bumblebees spend while handling a flower head and during inter-flower head flight time using the following equations:

$$H_E = wt_h k_h \quad (3)$$

and

$$F_E = wt_f k_f \quad (4)$$

where H_E=energy spend while handling a flower head, F_E=energy spend during inter-flower head flight time, w=bumblebee mass, t_h=average time spend handling a flower head (s), t_f=average time spend flying from flower head to flower head (s), k_f=bumblebee mass-specific rates of energy expenditure during inter-floral flight ($Jg^{-1}s^{-1}$) and k_h = bumblebee mass-specific rates of energy expenditure while handling a flower head ($Jg^{-1}s^{-1}$). We derived k_f from published values by Heinrich (1975) and k_h from published values by Pyke (1980). Following Pyke (1980), we assumed that all bumblebees had the same body mass of 200 mg and maintained their body temperature at a constant level of 37 °C.

Net energy gain

We calculated the net energy gain (J) using the following equation, modified from Dedej and Delaplane (2005) and Harder and Cruzan (1990):

$$N_E = \frac{I_E - E_E}{t_f + t_h} \quad (5)$$

where N_E= net energy gain, I_E= intake energy, and E_E= energy expenditure (energy spend during both inter-flower head flight and flower head handling activity). Intake energy (J) was calculated as:

$$I_E = nSe \quad (6)$$

where n=mean number of flowers per flower head that bumblebees probe, S=average quantity of sugar per flower (mg), and e=energy content (J) of 1 mg of sucrose (15.48 J) (Heinrich 1972a; Heinrich 1972b). And energy expenditure (J) was calculated as:

$$E_E = F_E + H_E \quad (7)$$

where F_E=energy spend by the bumblebees during inter-flower head flight time and H_E=energy spend while handling a flower. F_E and H_E were calculated following the equations above.

Visitation rate

In plots of two-by-two meter, we observed the number of visits per flower head by *B. bifarius*. Plant were observed during peak flowering time, at sites where the plant species were flowering abundant. Each plant species was observed during twelve intervals of 15 minutes.

Data analyses

Statistical analyses were performed, using R 3.3.2 (R Development Core Team 2014). Prior to all analyses, we tested whether the variables were normally distributed, using Shapiro-Wilk test. To increase normality, all variables were $\log_{10}$, prior to most analyses. We used single ordinary least square (OLS) linear regression analyses to examine whether the sugar intake rate per single flower, flower head and patch and the energetic expenditure of bumblebees was related to the nectar tube depth of the flowers they forage on. OLS regression analyses were also used to test whether the (rate of) net energy gain of bumblebees was related to the nectar tube depth, flower head density, sugar content per flower, number of open flowers per head and/or both the time it takes to fly between flower heads and to visit a flower head. Finally, to test whether flower head visitation rate was related to nectar tube depth, flower

head density, nectar production and/or (rate of) net energy gain, we used OLS linear regression analyses.

Results

Sugar intake rate

The sugar intake rate per single flower and while foraging on a flower head varied fifteen- and twelvefold, while the sugar intake rate while foraging in a patch varied fivefold (Fig. 1). Flowers with deeper nectar tubes, which were bagged for 24-hours, produced more sugar rich nectar (r=0.79, P=0.03). It did not take bumblebees longer to handle flowers with deeper nectar tubes (r=0.52, P=0.23). Consequently, sugar intake rate on a single flower (mg sucrose ingested per second) increased with increasing nectar tube depth (r=0.86, P=0.01; Fig. 1a).

The number of flowers that bumblebees probed when visiting a flower head was not related to the depth of the flowers of those flower heads (r=0.26, P=0.57). Consequently, bumblebees did not spend more time on flower heads of flowers with deeper nectar tubes (r=0.36, P=0.42). As a result of these relationships, sugar intake rate when visiting a flower head increased with increasing nectar tube depth (r=0.83, P=0.02; Fig. 1b).

The time it took bumblebees to fly from flower head-to-flower head was not related to the nectar tube depth (r=0.61, P=0.15). Consequently, also the sugar intake rate while foraging in a patch increased with increasing nectar tube depth (r=0.79, P=0.03; Fig. 1c).

Energetic expenditure and net energetic gain

When foraging, bumblebees spend between 2.08 to 15.62 seconds visiting a flower head, and between 0.72 to 2.47 seconds flying from flower head-to-flower head, depending on the plant species they visited (Table 1). Thus, they spend most of their time (between 72% to 87%) visiting a flower head when foraging in a patch. As bumblebees spend more energy during flight, the energetic expenditure while visiting a flower head and during flight were comparable (Fig. 2). Neither the amount of energy spent while visiting a flower head (Fig. 2a) nor when flying from flower head-to-flower head (Fig. 2b) was related to nectar tube depth of the flowers.

The rate of net energy gain was strongly positively correlated with nectar tube depth (Fig. 3a), sugar content per flower (Fig. 3c) and both time spent flying between flower heads (Fig. 3e) and visiting a flower head (Fig. 3f). In contrast, the rate of net energy gain decreased with increasing flower head density (Fig. 3b), most likely because flower head density is strongly negative correlated with sugar content (r= -0.73, P=0.003), and was unrelated to the number of open flowers per flower head (Fig. 3d).

Table 1. Sugar production, number of flowers probed, handling time and interflower head flight time of *B. bifarius* while foraging on the different plant species studied. The table gives mean ± s.e.m. and sample size (n).

Plant species	Sugar production bagged flowers (mg)	Number of flowers probed of a flower head	Handling time of a single flower (s)	Handling time of a flower head (s)	Inter flower head flight time (s)
Cirsium sp.	0.26 ± 0.026 (14)	12.0 ± 1.5 (91)	1.85 ± 0.10 (88)	15.62 ± 1.51 (91)	1.94 ± 0.15 (91)
Helianthella quinquenervis	0.10 ± 0.010 (100)	14.2 ± 1.0 (131)	1.37 ± 0.11 (71)	8.07 ± 0.48 (201)	2.06 ± 0.47 (188)
Heliomeris multiflora	0.01 ± 0.001 (33)	7.6 ± 0.6 (86)	0.95 ± 0.05 (166)	4.80 ± 0.34 (108)	1.06 ± 0.07 (110)
Heterotheca villosa	0.02 ± 0.002 (34)	4.5 ± 0.3 (104)	0.63 ± 0.10 (50)	2.08 ± 0.10 (167)	0.72 ± 0.04 (173)
Hymenoxys hoopesii	0.06 ± 0.005 (77)	9.7 ± 0.6 (129)	1.11 ± 0.04 (201)	8.44 ± 0.55 (198)	1.21 ± 0.07 (215)
Pyrrocoma crocea	0.11 ± 0.011 (24)	8.5 ± 0.5 (139)	1.42 ± 0.09 (93)	8.12 ± 0.53 (214)	1.52 ± 0.08 (224)
Senecio bigelovii	0.11 ± 0.014 (45)	8.5 ± 0.6 (92)	1.20 ± 0.08 (88)	6.23 ± 0.54 (183)	2.47 ± 0.17 (181)

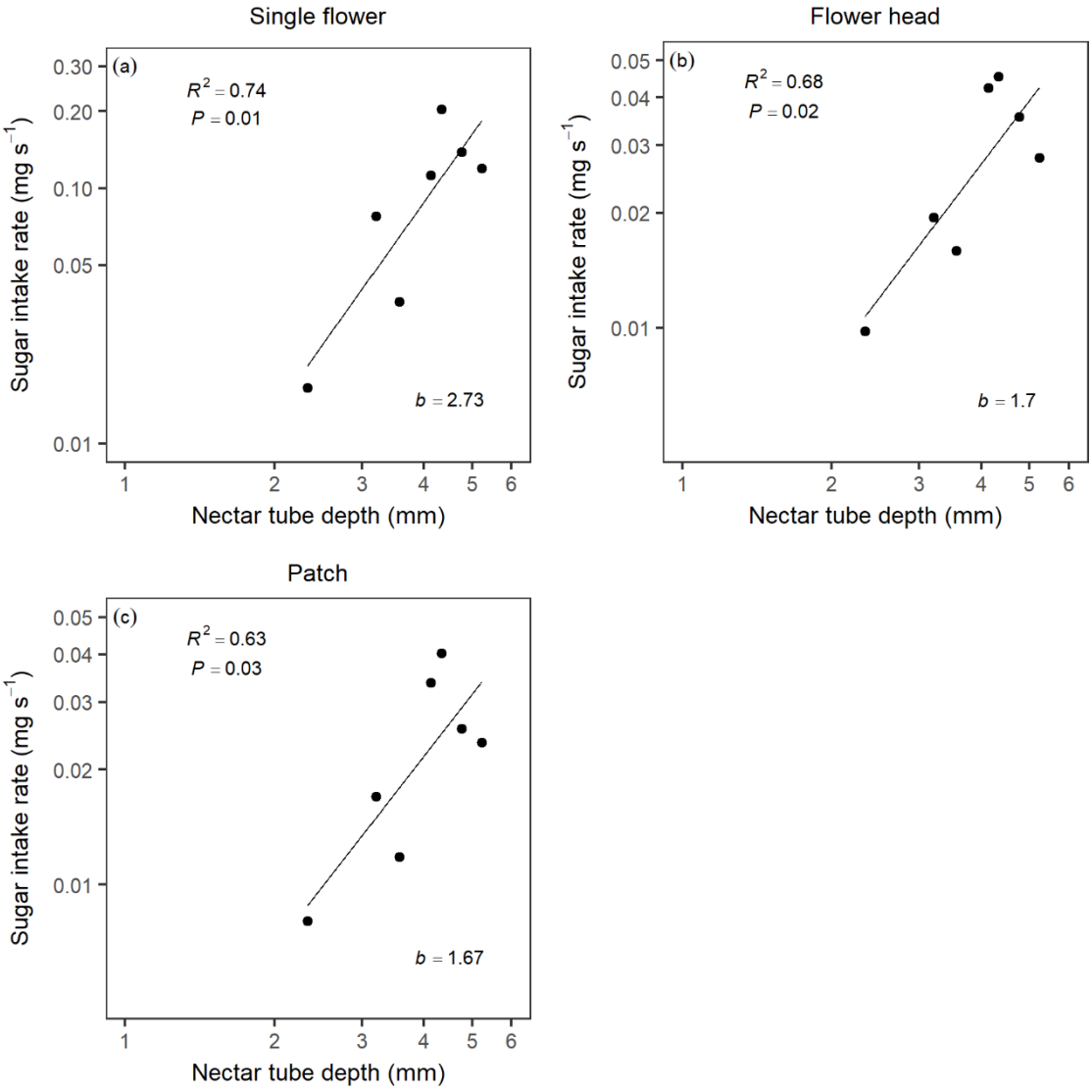

Fig. 1. Sugar intake rate while (a) extracting nectar from a single flower, (b) visiting a flower head and (c) foraging in a patch of *B. bifarius* individuals in relation to the nectar tube depth of the flowers. The sugar intake rate while extracting nectar from a single flower was based on nectar production rate measurements. Both the sugar intake rate while visiting a flower head and foraging in a patch were based on nectar standing crop measurements. Each dot represents a plant species (n=7).

Visitation rate

How often flower heads were visited by *B. bifarius* was not related to their nectar tube depth (Fig. 4a) nor flower head density (Fig. 4b). Flower heads of plant species which produced more nectar per flower (Fig. 4c) and which offered a higher net energy gain (Fig 4d) and rate of net energy gain (Fig. 4e) were more frequently visited by *B. bifarius*. Net energy gain explained 72% of the variation in visitation rate while rate of net energy gain and sugar per flower explained 60% and 55% of this variation respectively.

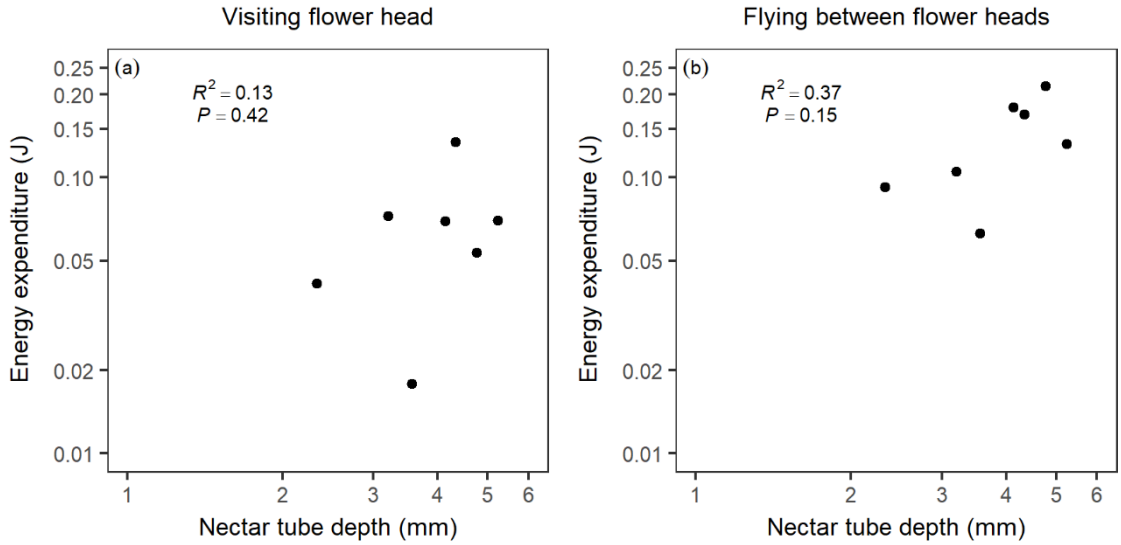

Fig. 2. Energy expenditure of *B. bifarius* individuals when (a) visiting a flower head and (b) when flying from flower head-to-flower head, in relation to the nectar tube depth of the flowers. Energy expenditure calculations were based on nectar standing crop measurements. Each dot represents a plant species (n=7).

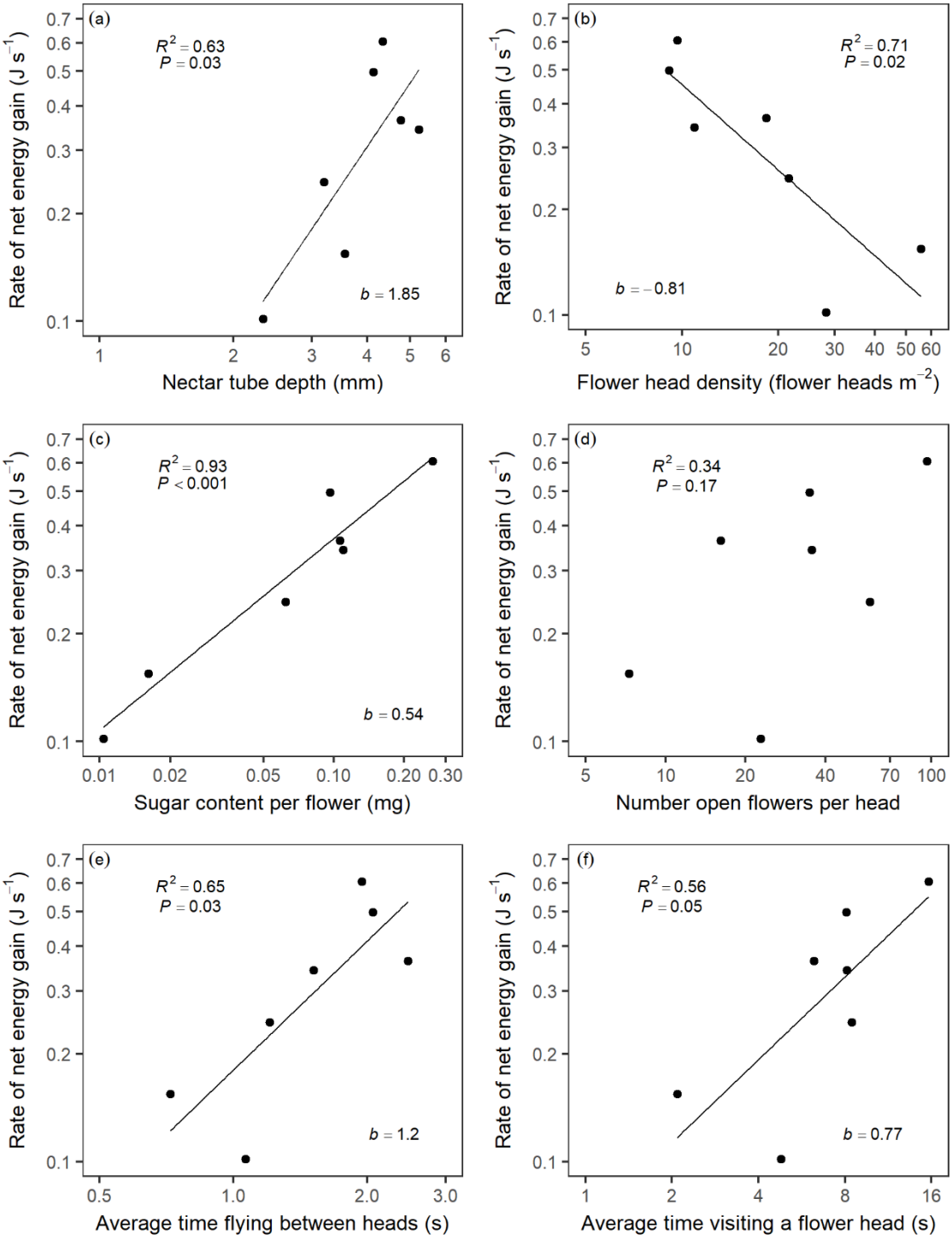

Fig. 3. Rate of net energy gain of *B. bifarius* individuals when foraging in a patch, in relation to (a) the nectar tube depth of the flowers, (b) flower head density, (c) sugar content per flower (NPR), (d) number of open flowers per flower head, and both (e) time spend flying between heads, and (f) time spend visiting a flower head. Rate of net energy gain was based on nectar standing crop measurements. Each dot represents a plant species (n=7).

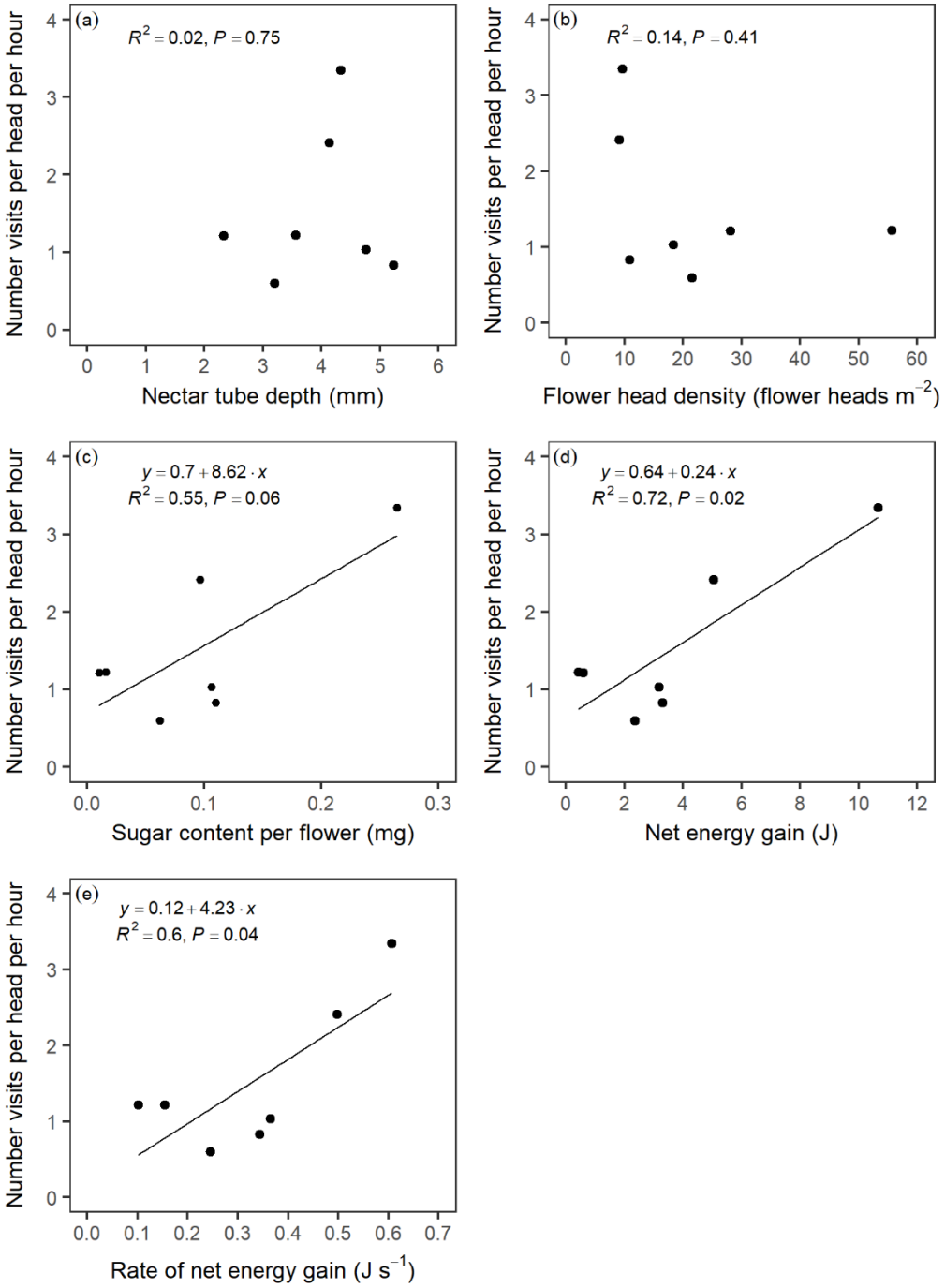

Fig. 4. Visitation rate of *B. bifarius* individuals, in relation to (a) nectar tube depth, (b) flower head density, (c) sugar content per flower (NPR) and both (d) net energy gain and (e) rate of net energy gain that *B. bifarius* individuals experience while foraging in a patch. Both net energy gain and rate of net energy gain were based on nectar standing crop measurements. Each dot represents a plant species (n=7).

Discussion

This study shows that the foraging efficiency of bumblebees is related to the nectar tube depth of the flowers on which they forage. Not only did the sugar intake rate when extracting nectar from a flower increase with increasing nectar tube depth, but also while visiting a flower head and foraging in a patch. Sugar intake rate while visiting a flower head and foraging in a patch varied less among plant species, compared to the sugar intake rate when extracting nectar from a single flower. This is most likely due to differences is number of open flowers per flower head and flower head density, which affect the time bumblebees spend visiting a flower head and flying between heads. Apparently, by clustering their flowers, plants species with flowers that produce less nectar become more profitable for bumblebees.

While foraging, bumblebees spend about 90% of their energy during flight (Heinrich & Raven 1972). Therefore, minimizing flight time, and thus choosing flowers which are more abundant, would be expected to be an effective means to increase the rate of net energy gain. Surprisingly, our result show that the rate of net energy gain actually decreased when bumblebees foraged on plant species of which the flower heads were more abundant. Consequently the rate of net energy gain increased when bumblebees foraged on plant species on which they experienced longer flight times. This can be explained by the fact that flower heads which were less abundant actually produced more nectar. Therefore, bumblebees experience longer flight times on more rewarding flowers. Apparently, flowers of less abundant plant species offer much more energy than the extra energy bumblebees spend due to increased flight times. Furthermore, although bumblebees spend most energy in flight, when they are in a patch, they spend on average 80% of their time on a flower head and only 20% flying from flower head-to-flower head. Consequently, when foraging within a patch, their energetic expenditure while visiting a flower head and during flight was comparable. However, we only observed bumblebee foraging behavior and -energetics within a meadow. Flower abundance and the distance of meadows from the nest might still be important cues for bumblebees when choosing meadows.

Although the energy expenditure of bumblebees tended to increase with increasing nectar tube depth, bumblebees which foraged on flowers with deeper nectar tubes experienced also a higher rate of net energy gain. Rate of net energy gain was also positively correlated with sugar content of bagged flowers. Therefore, both nectar tube depth and sugar content are potential cues for flower selection. This is in accordance with the results of May (1988), who found that nectar volume and nectar tube depth were strongly correlated with the foraging profit that two butterfly species experienced when foraging on a diversity of plant species.

Many network studies assume that flower-visitors distribute themselves randomly among flowers, proportional to flower abundance (Bascompte *et al.* 2003; Jordano, Bascompte & Olesen 2003; Vazquez 2005). If flower-visitors indeed forage randomly, than the number of visits per flower head should not differ among plant species. In contrast, we found that plant species of which the flowers produced more nectar and on which bumblebees experienced a higher (rate of) net energy gain were more frequently visited by bumblebees.

Net energy gain and rate of net energy gain explained 72% and 60% of the variation in visitation rate respectively and sugar content of bagged flowers explained 55% of this variation. In contrast, we did not find a relationship between visitation rate and flower head density. This indicates that bumblebees do not choose flowers based on their abundance, but on the nectar reward or the (rate of) net energy gain they provide, as assumed by theoretical models on optimal foraging (Pyke 1984). Surprisingly only few previous studies have empirically tested this optimal foraging approach and only for flower-visitors foraging behaviour when foraging on a single plant species (Whitham 1977; Pyke 1981; Pyke & Waser 1981; but see Schaffer & Schaffer 1979).

If bumblebees indeed select flowers in order to optimize their rate of net energy gain, based on floral cues such as nectar tube depth and the amount of nectar that flowers produce, the nectar production rate of flowers might be the results of this selective pressure by flower-visitors. If plant reproduction is pollen limited, than selection would favour an increase in nectar sugar content in order to attract bumblebees. Then why do not all plant species produce more nectar in order to ensure many bumblebee visits? First of all, shallow flowers might not have a strong incentive to produce more nectar, compared to deeper flowers. In contrast to shallow flowers, deeper flowers can only be visited by flower-visitors with a long proboscis (Corbet 2000; Stang *et al.* 2009), which can (potentially) visit a wide diversity of flowers (Borrell 2005). As bumblebee handling time, and thus their foraging costs, increases with increasing nectar tube depth (Inouye 1980; Harder 1983; Harder 1986), in order to attract flower-visitors, flowers with a deeper nectar tube might need to produce more nectar than shallow tubed flowers. Further, plants should not produce too much nectar, either to ensure outcrossing or to reduce geitonogamy (Klinkhamer & de Jong 1993). Finally, in our study, we did not include other flower-visitors than *B. bifarius*. Nevertheless, most of the studied plant species are visited by a variety of other insect species, mostly other bumblebees and solitary bees, butterflies and flies (Chapter 2 of this thesis). Therefore, a higher visitation rate by *B. bifarius* does not necessarily imply a higher visitation rate in general.

Overall our study shows that bumblebees experience a higher foraging efficiency when foraging on flowers with deeper nectar tubes and that flowers of plant species on which bumblebees experience a higher net energy gain are visited more frequently by these bumblebees. This indicates that bumblebees do no forage randomly, but optimally. These results may explain why bumblebees preferentially visit flowers with deeper nectar tubes and, because these flowers are the ones of which the nectar tube depth matches the length of their proboscis, why size-matching between flower- and flower-visitor morphology occurs in plant-flower-visitor communities.

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