Univerzita Karlova
Přírodovědecká fakulta

Studijní program: Biologie
Studijní obor: BBI

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Ability to Discriminate Floral Morphotypes by Hoverflies

Schopnost diskriminace květních morfotypů u pestřenek

Diplomová práce

Vedoucí diplomové práce: RNDr. Zdeněk Janovský, Ph.D.

Praha 2023

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V Praze dne 10. 8. 2023 Eva Matoušková

Poděkování

Ráda bych na tomto místě poděkovala všem, kteří mě neúnavně podporovali a přispívali dobrou náladou ve chvílích, kdy se mi jí z vlastních zdrojů nedostávalo. Převeliký dík patří mému školiteli, Zdeňku Janovskému, za veškerou trpělivost a inspirativní rady jak v terénu, tak i při analýze dat i psaní práce. Nemenší dík patří Jirkovi, za výdrž všech mých manýrů, zejména při chovu pestřenek, a za neutuchající psychickou a technickou podporu. Obří díky také Kláře D. a Kubovi Š. vlastně za všechno, zejména za posun do finiše. Taťkovi, mamce, Aničce a zbytku rodiny za neutuchající podporu a podněcování mého zájmu už od dětství. Všem dalším kamarádům vedoucím a spoluúčastníkům na Arachne za podnětné diskuse a podporu. Pražskému oddílu Dinosaurus za prostory na pokusy ve složité době covidu. Aničce Větvičkové za klec na pokusy. A v neposlední řadě také grantu Grantové agentury UK č. 842120 za 3D tiskárnu.

Abstrakt

Atraktivita květů pro opylovače je zprostředkována několika květními znaky. Schopnost rozlišovat květiny na základě těchto květních vlastností je velmi důležitá pro reprodukci květin a výživu a následně i reprodukci opylovačů. Na modelovém organismu *Eristalis tenax* jsme v laboratorních podmínkách testovali tři květní znaky – barvu, velikost a tvar a jejich kombinace na umělých květech vytištěných na 3D tiskárně. Zjistili jsme, že nejdůležitějším květním znakem byla barva následovaná velikostí a že efekt barvy byl zesílen efektem velikosti, ale pouze u preferované barvy. To naznačuje, že preference pro květinové vlastnosti jsou nějakým způsobem strukturované. Vliv symetrie jsme nenašli. Následně jsme v terénu pozorovali nenaivní pestřenky a čmeláky na jednodruhové patchi rostliny čertkusu lučního (*Succisa pratensis*). Zajímala nás role ostatních květních znaků v momentě, kdy se barva a velikost neliší. Nejdůležitějšími charakteristikami potom byla výška a efektivní počet kvítků v květenství. Pestřenky měly obecně delší návštěvy než čmeláci a navštěvovaly více květů. Na druhou stranu čmeláci dělali kratší a efektivnější návštěvy, což pravděpodobně souvisí s jejich eusocialitou.

Klíčová slova: Syrphidae, Apidae, Eristalis tenax, Bombus spp., symetrie květu, velikost květu, barva květu, opylování

Abstract

The attractiveness of flowers to pollinators is mediated by several floral traits. The ability to discriminate the flowers based on these floral traits is crucial for the flower reproduction and pollinator nutrition and reproduction. We tested three floral traits – colour, size and shape – along with their combinations using artificially 3D printed flowers on model organism *Eristalis tenax* in laboratory conditions. Our findings revealed that the most important floral trait was the colour followed by size. Additionally, the effect of colour was enhanced by size, but only for the preferred colour. This suggests that preferences for specific floral traits can be structured. The effect of symmetry was not significant. Subsequently, we observed non-naïve hoverflies and bumblebees in the field on flower patch consisting of devil's-bit scabious (*Succisa pratensis*). We were interested in the role of other floral traits when the colour and size were indistinguishable. The most important characteristics were height and effective number of florets in the inflorescence. The hoverflies tend to do longer visits than bumblebees and visited more flowers as well. Conversely, bumblebees did shorter but more efficient visits, likely due to their eusociality.

Keywords: Syrphidae, Apidae, Eristalis tenax, Bombus spp., floral symmetry, flower size, flower colour, pollination

Contents

1. Introduction

1.1 Hoverflies as important flower visitors

When we observe an ordinary meadow we see lots of flowers with a huge variety of its floral visitors, many of whom we may think of as pollinators. Pollination is one of the keystone processes in terrestrial ecosystems as most of the plants (78–94%) are dependent on animal pollination to some extent (Ollerton *et al.*, 2011) from which the insects make the largest portion.

The most common and probably the most effective and definitely the most studied insect pollinators are bees, mainly the honeybee (*Apis melifera*) and bumblebees (*Bombus spp.*). But other pollinators such as other, non-Apis bees (Antophila), flies (Diptera), butterflies (Lepidoptera) and even beetles (Coleoptera) also significantly participate in pollination (e.q. Jauker & Wolters, 2008; Orford *et al.*, 2015; Rader *et al.*, 2009, 2016, 2020) and the hoverflies (Syrphidae) are considered to be the second most important pollinators next to bees.

There are several reasons for their importance. The hoverfly adults are almost exclusively pollinators with very similar ecology but they do posses a wide spectra of larval feeding strategies (Sommaggio, 1999) ranging from carnivory (mainly aphidophagy) larvae in whole subfamily Syrphini, Pipizini and partly in Eristalini (Dunn *et al.*, 2020), through herbivory in Merodontinae (Ricarte *et al.*, 2017) and pollen-feeding in Toxomerini (Dumbardon-Martial, 2016), xylophagy in Xylotini (Krivosheina, 2020), saprophagy in Eristalini (Buckton, 1895) to commensalism and parasitoidism in Microdontinae (Duffield, 1981). These attributes allow them to be widely distributed and also act as replacement for bees in particular situations (Stavert *et al.*, 2018; Doyle *et al.*, 2020). They inhabit all the continents except for Antarctica and range from lowland areas up to mountains. Unlike the bees, the hoverflies are not bound to any nests and therefore they can be much more mobile in the landscape and some of them even migrate to long distances during their life (Wotton *et al.*, 2019). They are considered to be generalist pollinators and even though they are generally thought to be not as effective as bees, they make up for it by their visitation frequency

(Rader *et al.*, 2016). They can carry pollen loads comparable to other non-honeybee pollinators (Campbell *et al.*, 2014; Gómez & Zamora, 1999).

1.2 Flower sensory recognition

During the evolution the flowering plants (Magnoliophyta) developed various floral traits to attract and maintain pollinators. The recognition of these floral traits is done mainly by visual and olfactory senses (Raguso, 2004). There are a lots of floral traits, the most studied are probably the colour of corolla and anthers (eq. Giurfa *et al.*, 1995; Lunau & Maier, 1995; Golding *et al.*, 1999; Campbell *et al.*, 2010; Neimann *et al.*, 2018), colour spots and markings, flower size, corolla shape and arrangement (eq. Gómez & Perfecttiy, 2010), flower height, but also volatiles (eq. Wacht *et al.*, 1996; Wang *et al.*, 2017; Solís-Montero *et al.*, 2018) and in recent years the changes in electric field on the flower (eq. Heuschmann, 1929; Colin *et al.*, 1991; Greggers *et al.*, 2013; Clarke *et al.*, 2017; Khan *et al.*, 2021).

Olfactory cues are very important and detectable by insects in low concentrations (Angioy *et al.*, 2003) and usually do not act alone as single molecules but their signal depends on its' concentration and concentrations of other components (e.q. Zhang, 2018). Their function may vary as they can act both as attractants or as learning enhancers for the pollinators (Wright & Schiestl, 2009). However working with them is challenging from the methodological point of view. There is problem with their spreading in space, when considering olfactory cues. This process depends on many factors such as wind speed and direction, temperature and humidity and the further we are from the source the more complex it is to predict the spread of the volatile. For this reasons we rather focused on the first mentioned floral cues – visual.

1.2.1 Colour perception

The fact that insects posses colour vision is known for a long time, in fact the honeybees were the first insects in which the colour vision was demonstrated (Lubbock, 1888, Chapter IX). The colour detection in insect is mediated by photoreceptors sensitive to particular type of light. Most insects have three types of photoreceptors which are sensitive in UV, blue and green part of the spectrum. The honeybee (*Apis melifera*) is not an exception and has the peaks in 344 nm, 436 nm and 544 nm (Hempel de Ibarra *et al.*, 2014). The situation in Diptera is slightly different as they have four types of phototoreceptors in UV, violet, blue and green (Lunau, 2014). But the colour vision however does not depend only on the photoreceptor peaks but also on the way the information is later processed. Our model of colour coding is based on recognition whether the wavelengths perceived by the ommatidium do differ or not (Backhaus, 1991; Chittka *et al.*, 1992; Chittka, 1992). In insects this is managed by color-oponent and narrowband neurons. In Diptera a special pair of photoreceptors (R7 and R8) are responsible for the excitation or inhibition of the and narrowband neurons by particular wavelengths combinations which can either excite or suppress the neurons. Dipteran ommatidia expressing pR7 and pR8 or yR7 and yR8 photoreceptors are then called "pale" or "yellow" and they encode the colour opponent signals from either short UV/blue (for pale) or long UV/green (for yellow) spectra.

The flowers can be single-coloured or they can have specific pattern or markings on the corolla leaves which serves as navigation to the pollinator towards the generative organs. There are multiple evidence of markings enhancing the centre of actinomorphic flowers in bulls eye pattern.

The hoverflies are considered to be generalist pollinators with innate preference for yellow colour and open flowers with easily accessible anthers and nectaria (Lunau & Maier, 1995). It was shown that their proboscis extension reaction is innate to yellow colour and it’s difficult or merely impossible to change it with learning (Lunau & Wacht, 1994; Lunau & Maier, 1995; An *et al.*, 2018).

1.2.2 Flower size

The minimal size of flower visible from afar is limited by the spatial resolution and the distance from which is the flower observed. There is a good assumption that the larger the flowers are the more easily are they visible and there are evidence for it (eq. Conner & Rush, 1996). The main reason why the floral size can be important is that the insect eyesight is limited by its’ quite low resolution. To understand it we need first understand the structure of the eye and how is the signal gathered.

The signal from image seen by individual ommatidia is gathered by photoreceptor cells (rhabdomeres) and then later processed in the ganglia. Each ommatidium can gather light signal only from small part of the space surrounding the insect and the size of the part is limited by the diameter of the ommatidium which is approximately 0.025 mm. This is described by the acceptance angle and the wider the angle is the more light enters the ommatidium. For the resolution is essential the size of the angle between ommatidia. If the interommatidial angle is small it results in higher resolution (Land, 1997). Each ommatidium consists of 6-8 rhabdomeres and therefore acts similar to one pixel so the compound eye resolution is proportional to the number of ommatidia which is at least in bees proportional to the square root of body size (Jander & Jander, 2002). The number of ommatidia in bees scales with the relative body size and although no works are counting the number of ommatidia of hoverflies it is safe to assume that they have at a maximum smaller tens of thousands as the known number of ommatidia for similar sized insects with daily activity ranges from 6 000 up to 30 000 for honeybee and dragonfly, respectively (Jander & Jander, 2002). These numbers give not much high resolution even at the top estimate.

Therefore the size of the flower could be very important for the pollinators because it could increase the probability of detecting the other floral traits.

1.2.3 Flower symmetry

The likely ancestral flowers were symmetrical, and asymmetrical flowers subsequently evolved from them on multiple occasions. This phenomenon is believed to have been driven by more specialised plant-pollinator relationships (Cubas, 2004) which led to more targeted attraction. But even more specialised flowers can benefit from more generalist pollinators and even more generalist pollinators can have preferences (Gómez *et al.*, 2008). The effect of symmetry on hoverflies was by far less studied in comparison to the colour and size but there are some evidence describing that the trait of symmetry is important for bees and their flower selection (Rodríguez *et al.*, 2004). Symmetry can select the angle from which are the pollinators approaching the flower and therefore direct them to particular parts of the flower, such as anthers or nectaria (Culbert & Forrest, 2016).

1.3 Spatial arrangement

Most flowers do not grow and flower evenly in space but form flowering patches separated from each other by different vegetation. To efficiently use the resources present in the floral patch the pollinator has to make decisions based not only on the attractiveness of individual flowers but also on the distribution of flowers within the patch (Barley *et al.*, 2021). The specific floral traits makes the flowers attractive to the pollinators but the visibility and accessibility of the flowers depends on their position in space relatively to other flowers (Klecka *et al.*, 2018).

1.4 Questions

This leads us to several questions which we asked ourselves in this work:

1. How do the different floral traits affect flower attractiveness for the hoverflies and bumblebees?
2. Which of the studied floral traits carries the most important signal for the pollinators?
3. Do the different floral traits interact? And if yes, then what is the relation between different floral traits?
4. How do hoverfly pollinators select the flowers when the most attractive traits are closely similar, and how does it differ from bees?

2. Material and methods

2.1 Model organism

The hoverflies come in various sizes and shapes but most of the past studies worked with only a few species from mainly *Eristalis* and *Syrphus* genera. *Eristalis tenax* is a worldwide distributed (all continents inhabiting) and most studied syrphid pollinator. It is commonly used as model organism for syrphids in experiments mostly due its' mimicry of honeybee (*Apis melifera*) (Lunau *et al.*, 2018). *Eristalis* individuals are also relatively easy to breed and kept in large quantities (Nicholas *et al.*, 2018). We managed to establish breeding in the last few years. Moreover, *Eristalis tenax* are the most abundant floral visitors of devils' bit scabious (*Succisa pratensis*) which was our model flower in the field experiments.

2.2 Laboratory setup

2.2.1 *Eristalis tenax* rearing

We used two clutches of *E. tenax* which yielded sufficient number of adults for the experiment (135 and 140) to control possible effect of the clutch. For acquisition of the study organisms, we used a protocol adapted from Nicholas *et al.* (2018). We acquired overwintering gravid females of *E. tenax* in Alkazar quarry near Beroun, Central Bohemia, Czech republic (N 49°57.03762', E 14°7.43738'). Then the females *E. tenax* were placed into plastic cage and provided with water, sugar and pollen ad libitum to stimulate oviposition. If this treatment was not successful the females were placed into the refrigerator for 2-3 days to stimulate hibernation and then the treatment was repeated. Laid eggs were transferred into a small bowl of water to prevent drying out and destruction by the adults. The larvae emerged usually after 2 days. When the larvae emerged, they were transferred into a bucket of rabbit manure with water (3:1) obtained from rabbits kept at Toulcův dvůr enviroment educational facility (Kubatova 32/1, 102 00 Praha 10). The larvae took typically between 10 to 12 days to pupate, then the pupae were transferred into a cage to hatch. Newly emerged adults were kept in the same conditions as their parents, adults from each clutch were kept in separate cages.

For the illumination of the rearing cage as well as the experimental cage we used UV-vis lamp SunLux UV 150W PAR38 (SunLux, Brno, Czech Republic) with the distance from cages 1.3 m. The boxes for keeping were made from $40 \times 40 \times 50\ cm$ plastic boxes obtained in a local hobby market, the pollen was bought in a local bio shop.

2.2.2 Artificial flowers design

We decided to produce our own artificial flowers which would resemble the look of real flowers and would be still easy to control its' reward amounts. The artificial flowers were designed in two morphs - zygomorphic (Z) and actinomorphic (A) and each morph was designed in two sizes - small (A) and large (L) (Fig. 1). Both zygomorphic and actinomorphic flowers had 5 petals and did not differ significantly in their surface area in their size category. The larger variant has 25 mm radius and 10 cm^2 surface area while the small variant has 15 mm radius and 4.5 cm^2 surface area. Due to rendering constrains, small flowers differ slightly in their diameter in the drawing but it is under the print resolution. For printing we used the Prusa i3 MK3S+ printer and white PLA filament (FLM-PLA-175-WHT, Prusa Research, a.s., Prague, Czech republic).

After the flowers were printed they were painted with acrylic paint and let dry. We used standard red, lemon yellow and purple for the blossoms and green for the stands which attached the flowers to wooden tripods. We measured the colour spectra of the acrylic colours on spectrometer AvaSpec-ULS2048CL-EVO-RS. The yellow colour rises steeply from 508 nm, the purple has maximum in 444 nm (Table 1). Although the absolute values of reflectance vary between the measurements the yellow has always higher reflectance than the other colours. We also checked the colours in the model of colour vision of blowfly *Lucilia sp.* (Troje, 1993) using the pavo library in R, the results are shown in Fig 3.

The 3D flowers were designed with a hole in the middle where a small vial is inserted and then covered by a cap so the pollinators do not have direct access to the nectar. The flowers were filled with 30% sucrose solution and replenished every day or more

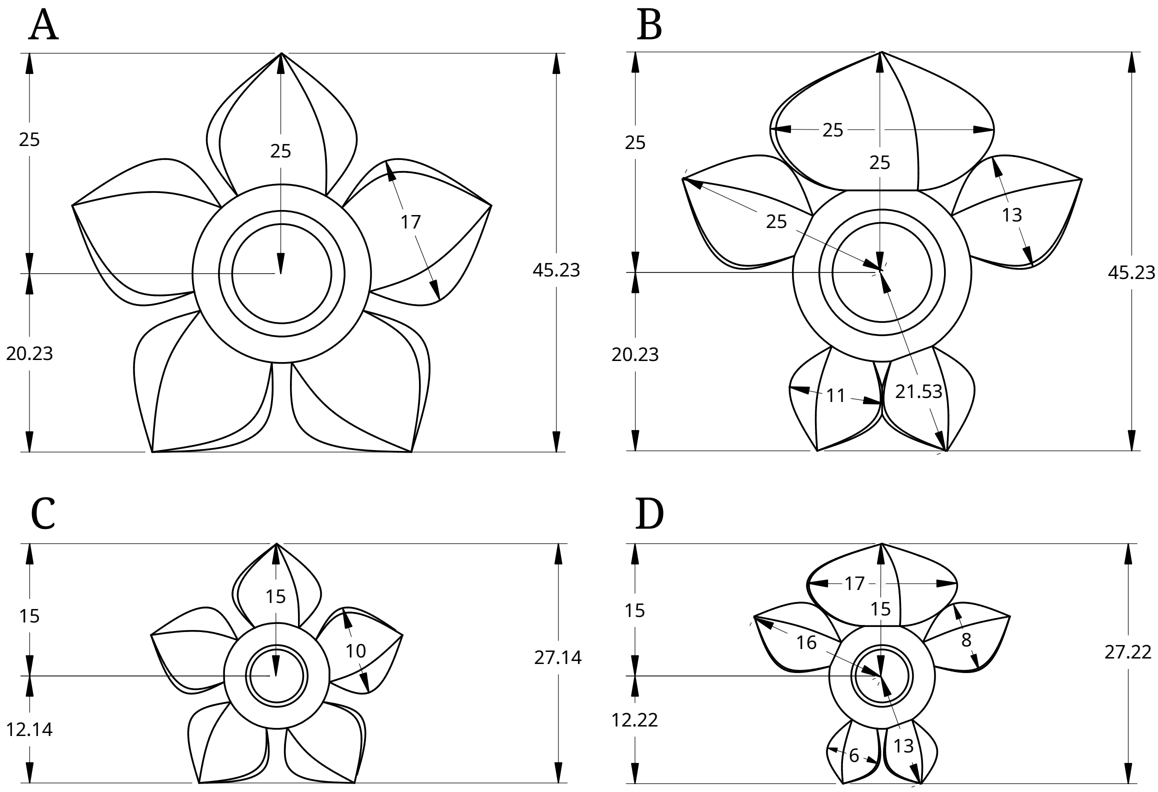

Figure 1: Designs of artificial blossoms: A - large zygomorphic blossom, B - large actinomorphic blossom, C - small zygomorphic blossom, D - small actinomorphic blossom. All dimensions are in millimetres.

often if necessary. Simultaneously no sugar was provided to them and pollen was very limited.

For the suction mechanism we used an approach similar to the one done in Ishii & Masuda (2014). The nectar supply is provided by a small thread which leads through the cap and works like a wick. The advantage of this approach is that it limits the amount of nectar available on the flower per one visit and allows the nectar source to be temporally depleted. This serves as a very important motivation for the animals to leave the blossom and move to the next one. We made the wick from a polyester thread with diameter 0.5 mm pierced through the cap with 3 knots on the upper side and a lead sink on the bottom side. In the earlier versions we also tried to make the wick from a silk thread as in Ishii & Masuda (2014) but the knots did not held together and also did not appeared to be depletable.

We used online software OnShape v 1.105 for the design of the 3D models of flowers and caps which we then printed on 3D printer Original Pusa i3 MK3S+.

Table 1: Filament, acrylic coulours painted filament and green background peaks measured for each colour.

Colour	Reflectance	Hue	FWHM*	HWHM.l	HWHM.r
Yellow	104.29365	700	NA	192	NA
Red	42.82336	631	NA	43	NA
Purple	19.42868	444	94	50	44
Green	24.01720	543	94	40	54
Filament	107.25420	556	NA	153	NA

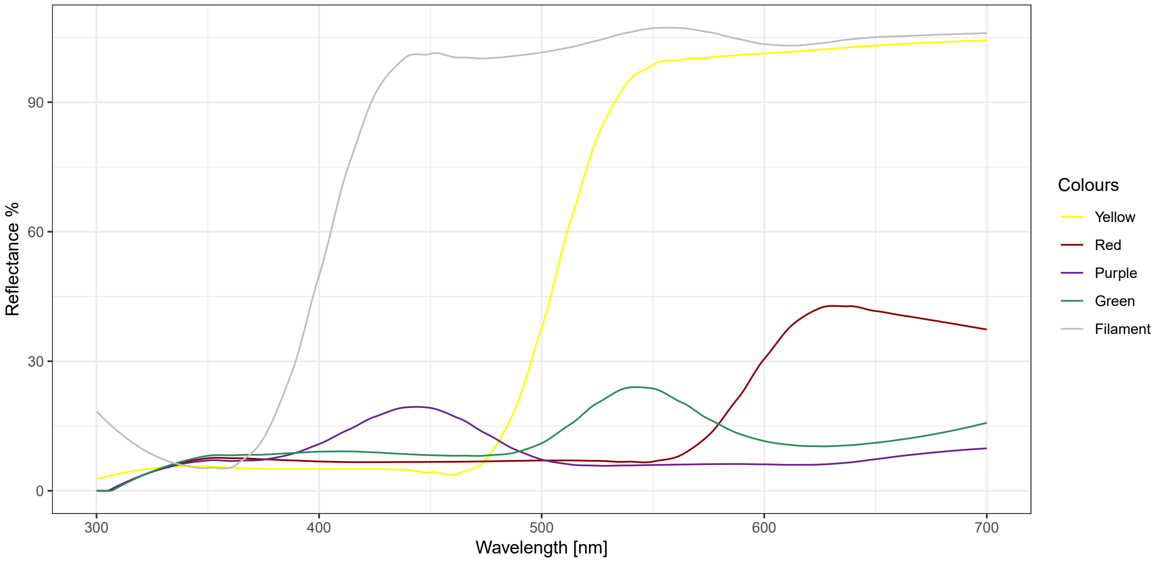

Figure 2: Wavelengths spectra for the filament, yellow, red and purple acrylic colour and for the green non-woven cloth used as background in the experiments.

2.2.3 Experiment setup

The main aim of the observation experiment was to determine the preferences of *Eristalis tenax* for three floral traits – colour (yellow × purple), size (small × large) and shape (actinomorphic × zygomorphic) and their respective combinations as displayed in fig 4 B. We set up a patch of artificial flowers which differed in at least one trait and then recorded how many individuals would choose the first one and how many would choose the other one. This was done for all the possible combination except for those combinations which did not differ in any trait. Due to the experimental setup it would be quite complicated to record visitations from a patch with one type of flower and therefore we did not tested the flower combinations where the flowers did not differ in any traits. We deal with it furthermore in the analysis section.

Prior the start of the experiment, young naïve adults of *Eristalis tenax* had to be

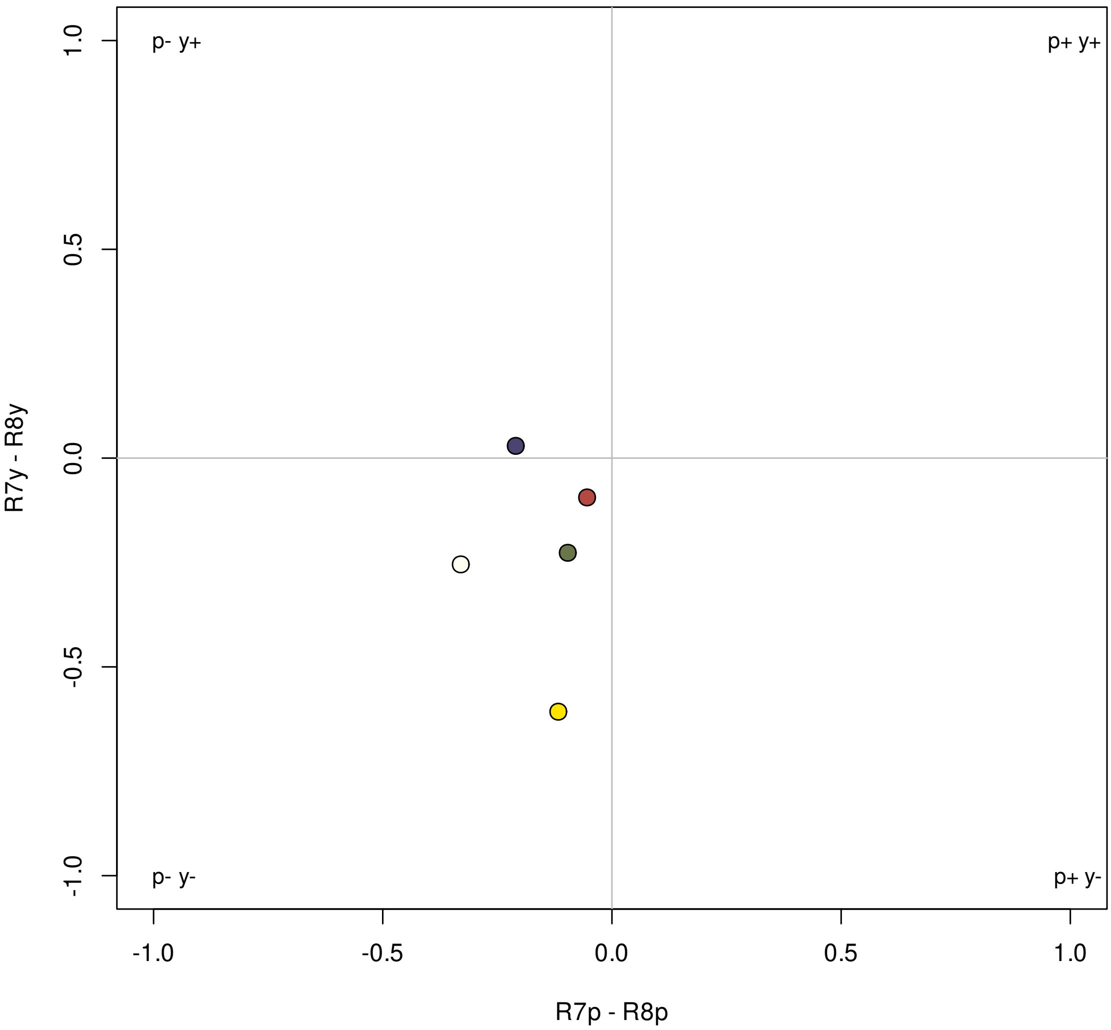

Figure 3: The filament, acrylic

preconditioned to recognise the artificial flowers as relevant food source but at the same time minimize the effect of preconditioning on their innate preferences. This was achieved by providing them with red coloured flowers from all four morphs into their home cage close after hatching. This procedure took 5 days and it was maintained in the home cage throughout the experiment. At first, we tried to conduct preconditioning without any pollen provided but this turned out to be impossible due to experiment length. Therefore our experiment entered individuals which were fed on sugar water and pollen.

The tests were carried out in an observation cage made of a thin transparent net fixed in a wooden frame, with dimensions 80 × 80 × 80 cm. In the bottom of the cage was a green nonwoven fabric cloth simulating green background. The experimental room had overshadowed windows to diffuse the direct sunlight so the main light source was the UV-vis lamp. We tested both clutches simultaneously and switched between the observation cages to minimise the influence of time variation and observing cage.

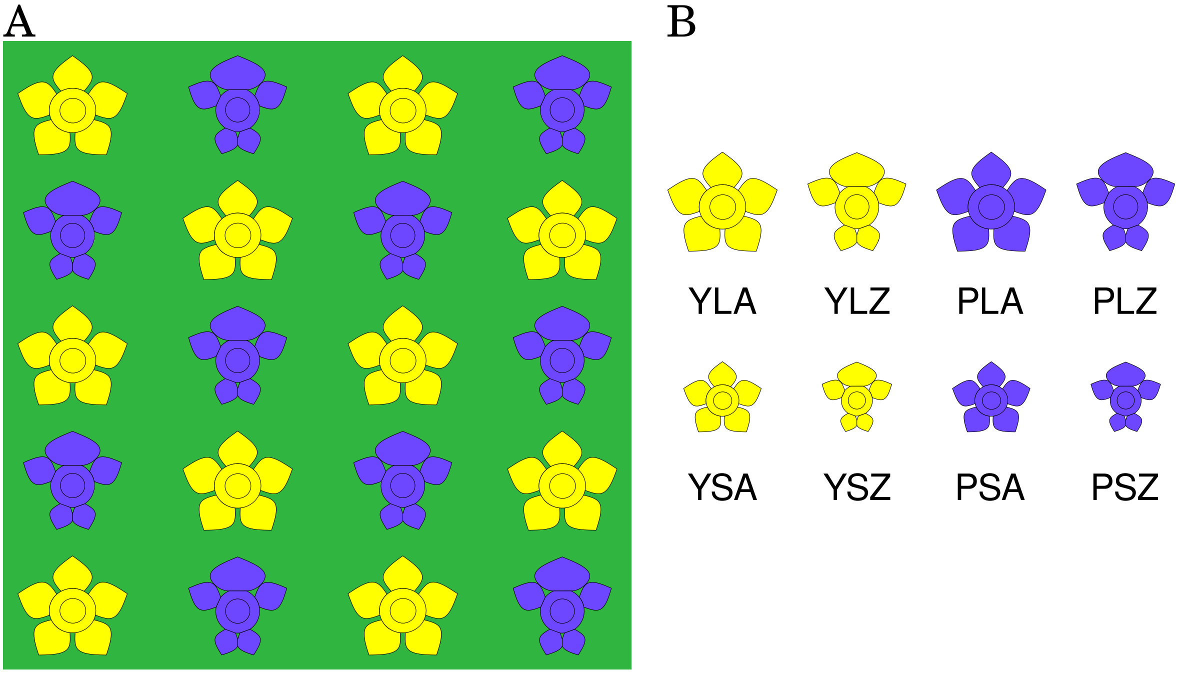

Figure 4: A: Typical patch set-up here for morphs YLA × PLZ (yellow large actinomorphic × purple large zygomorphic) with green background. B: All possible flower morphs with their code names.

2.2.4 Experiment procedure

We tested both clutches simultaneously for two different combinations in separate cages in 30 minute rounds. We alternated the clutches between the rounds. Every testing cage contained 20 individuals with a sex ratio of 1:1 per round. The individuals were left in the observation cage for five minutes to become accustomed to the environment. After that their numbers on respective flower variants were censused every 3 minutes each sex separately for 30 minutes yielding 11 censuses in total per round. Every tested flower combination had 4 rounds at a minimum but if the number of visits in total was below 150 we added more rounds. The overall numbers for every combination are shown in table 2. The individuals used in the round were placed into separate storage box. We endeavour not to use the same individuals multiple times to avoid pseudoreplications. We reuse the individuals only if there was no other option, mainly in the final rounds to even the sex ratio.

Table 2: The table displays the number of observations and the number of rounds per combination. The first number is the overall number of observations the number after the slash is the overall number of rounds per combination. The minimum number of rounds per combination was 4 and we aimed to have at least 120 visits.

	LYA	**LYZ**	**SYA**	**SYZ**	**LPA**	**LPZ**	**SPA**	**SPZ**
LYA	210 / 6							
LYZ	334 / 4	210 / 6						
SYA	189 / 4	160 / 6	210 / 6					
SYZ	270 / 4	311 / 4	390 / 11	210 / 6				
LPA	186 / 6	241 / 6	217 / 4	219 / 8	210 / 6			
LPZ	334 / 6	244 / 10	197 / 8	168 / 8	178 / 4	210 / 6		
SPA	292 / 4	281 / 8	255 / 7	150 / 6	220 / 6	228 / 8	210 / 6	
SPZ	247 / 6	133 / 4	220 / 6	168 / 4	239 / 11	154 / 7	239 / 9	210 / 6

2.2.5 Analyses

As stated above, the main aim was to determine the effect of flower colour, size and shape on naïve *E. tenax* prefferences towards different flower morphs. For that reason we recorded the number of visitors on first and second flower for each flower combination. To find out how the flower colour, size and shape affects the number of visits on each flower not only by itself but also with regard to the respective neighbour flower we then defined variables coding colour, size and shape differences for every combination. The defined variables which then entered the model are in table 3.

Table 3: The description of the variables entering the quasi-binomial GLM.

Variable name	Variable type	Range/Levels	Description
count1	numeric discrete	0 – 69	The sum of visits on both flowers for the overall run
sum_total	numeric discrete	1 – 125	The number of visits on flower1 for the overall run
col1	categorical	Y / P	The colour of flower1
size1	categorical	L / S	The size of flower1
sym1	categorical	A / Z	The symmetry of flower1
col_diff	categorical/binomial	0 / 1	The difference in colour between the two flowers
size_diff	categorical/binomial	0 / 1	The difference in size between the two flowers
sym_diff	categorical/binomial	0 / 1	The difference in symmetry between the two flowers

The data are by its nature binomial therefore we wanted to use binomial generalised linear models. But due to overdispersion in data we needed to use quasi-binomial generalised linear models (GLM) instead of binomial. We needed to test for every flower for every combination and we wanted to evaluate the effect of the levels of every floral trait. Therefore we knew the analysis would strongly depend on the decision which flower would be the first flower (`flower_1` and which would be the second flower (`flower_2`. Therefore we divided every flower combination rounds into two – one where the first flower was noted as `flower_1` and one where the second flower was noted as `flower_1`. Then we derive our model. The equation is:

```
(count1,sum_total-count1)~col1*size1*sym1*(col_diff+size_diff+sym_diff)
```

The collected data were analysed in software R version 4.0.4 in IDE RStudio.

2.3 Field setup

2.3.1 Meadow conditions

We conducted a field experiment in a small meadow near village Krsovice in the Central Bohemian Region in Czech republic (N 49°50.81397', E 15°8.96943'). Its' area is approximately 3.7 ha and it is surrounded by a pond on the northern side, a forest on the south-western side and a field on the eastern side. On the meadow there is a gradient of abiotic conditions and so the meadow can host various plant communities and attract a large spectrum of different pollinators. Our experiment was conducted in the wet part of the meadow where devil's-bit scabious (*Succisa pratensis*) grows and is the most abundant plant there. Apart from devil's-bit scabious lesser spearwort (*Ranunculus flamula*) and meadow buttercup (*Ranunculus acris*) were present in greater numbers. Most of pollinators present in this part of the meadow were hoverflies (Syrphidae) from the genus *Eristalis* of which the most abundant was *Eristalis tenax*, the other *Eristalis* species were relatively minor. The second most abundant were bumblebees (*Bombus spp.*) mainly *Bombus pascuorum* and *Bombus lapidarius*. There were other insect pollinator groups present such as butterflies (Lepidoptera) mainly green-veined white (*Pieris napi*) and small tortoiseshell (*Aglais urticae*) and other circular-seamed flies (Diptera: Cyclorrhapha) mainly blowflies (Calliphoridae), flesh flies (Sarcophagidae) and tachinid flies (Tachinidae). But their numbers were negligible in comparison to the hoverflies and bumblebees. Honeybees presence in this meadow varies among the years and the year in which we conducted this experiment (2017) was its presence in the field insignificant.

2.3.2 Observation arena setup

We did outline two square arenas with the dimensions of 1x1 m and at the distance of 1 m from each other. We trimmed all the flowers in the patch which were not from devils'-bit scabious and all the flowers within close surroundings including devils'-bit scabious to create monospecific flower patch. We marked and numbered all the devils'-bit scabious blooming inflorescences within each patch. Each patch consisted of approximately 30 inflorescences (Fig.: 5). This steps were repeated every morning if necessary.

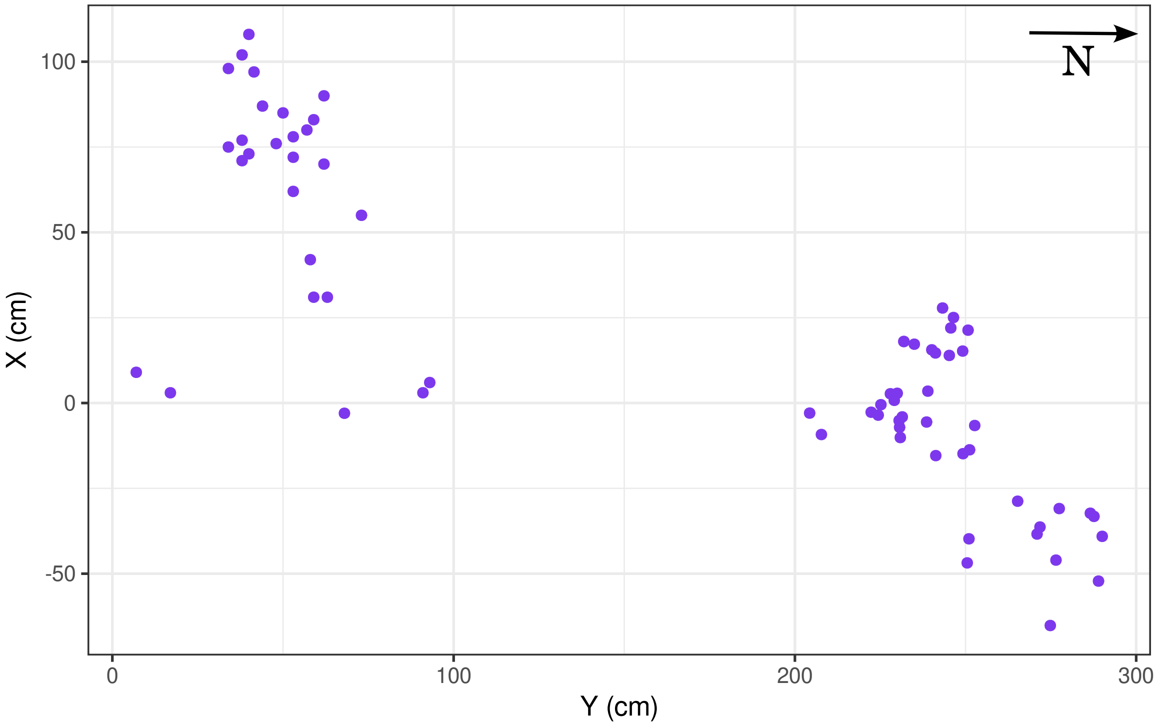

Figure 5: The position of individual inflorescences of devils'-bit scabious within the two patches. The axis dimensions are in centimetres. North is indicated by the black arrow in the upper right corner.

We recorded the path of the pollinator from the point of entering the patch to the point of leaving the patch. We did not have any specified time frame and we did not interfere with the pollinator. The length of the sequence therefore varies from 1 up to 74 flowers and the spent time from 1 second up to 40 and half minutes. We recorded which flower the pollinator visited and the amount of time it spent on the inflorescence. The pollinators' species and sex was determined by observation. We never observed more than one individual at a time. As the patch was isolated in both by its' position in the meadow and by the trimming of other flowers the number of pollinator encounters on the flower was minimal.

For every inflorescence we measured its' coordinates (`x`, `y` and `height`) to determine its' position within the patch. We also estimated the percentage of flowering, faded and not yet opened flowers within each inflorescence. We estimated these percentages each evening and used them later when estimating the inflorescence size for each day. After the experiment ended the inflorescences were collected, dried and later the number of flowers were summed up. The defined variables are in the table 4 below.

2.3.3 Analyses

For our analyses, we defined variables describing the floral traits and variables describing the characteristics of the path. We did not catch the individuals therefore we have only their group, species and sex identity. All of the variables are summarised in table 4.

In the first step, we focused on analysing the characteristics of the entire path and the differences between hoverflies and bumblebees. We were interested in the means, medians and distributions of the overall time spent and flowers visited. Due to some very long sequences, the distribution of the variable `sequence_length` was skewed. Therefore we decided to have this predictor under logarithmic transformation to lessen the effect of the tail of very long sequences. We tested the sequence length by the Analysis of variance with the following formula:

```
ln(seq_length) ~ group
```

We also wanted to know whether the two groups differ in the time spent on the inflorescence and whether they tend to leave the patch after fully fed (in which case we expected for them to do long visits in the end) or after unlucky visits (in which case we expect for them to do shorter visits in the end). To test that and to take into account the individuality of the pats we used Linear Mixed model with the following formula:

```
ln(time_spent+1) ~ group*rev_rank + group*ef_no_flowers + (1|id_seq)
```

In the next step we focused on the start of the path. We were again interested whether there were any differences between the hoverflies and the bumblebees and if the first flower characteristics can somehow predict the subsequent behaviour of the animal. We were interested in height, the number of active florets within inflorescence and the position of the flower within patch. For the initial height by the rank and the group. Again to take into account the individuality of the paths we used Linear Mised model with the following formula:

```
height ~ ef_no_flowers*rank + group*rank  + (1|id_seq)
```

We also focused on the end of the sequence and if we could see any floral traits that managed to repel the pollinators or if there is no evidence at all for it. We fitted flight distance between the flowers (`dist_3D`) by the reverse rank (`rev_rank`, lenght of the previous visist (`prev_time_spent`) and the group identity (`group`) by the following formula:

```
ln(dist_3D) ~ group*(rev_rank + rev_rank^2) +
             + ln(prev_time_spent) + (1|id_seq)
```

Table 4: Variables used in the models

Variable name	**Description**
x	x coordinate of the inflorescence
y	y coordinate of the inflorescence
height	z coordinate of the inflorescence
group	group identity: bumblebee or hoverfly
time_spent	time spent on the actual inflorescence
prev_time_spent	time spent on the previous inflorescence
dist_3D	3D distance travelled between two inflorescences
ef_no_flowers	effective number of flowers within the inflorescence
rank	Position in the flight sequence
rev_rank	Reverse position in the flight sequence
id_seq	flight sequence identifier

3. Results

3.1 Laboratory experiment

3.1.1 Choices of the flower morphs

To see the overall preferences towards individual floral morphs we computed binomial tests for every combination of flower morphs we tested in the experiments. The flower morphs are coded as follows: S/L – small/large, P/Y – purple/yellow and A/Z – actinomorphic/zygomorphic. The largest discrepancy between the flower morphs was between yellow large zygomorphic (YLZ) and purple large zygomorphic (PLZ) flowers where 93 % of the visits were made on the YLZ morph. On the other hand, there were only small differences in visitations of both small and large purple flower morphs. Table 5 shows the percentages of visits on each flower morph and the table [reference] shows the actual numbers of visits. The complete results of binomial tests are in the Table 6.

Table 5: The numbers in the cells represent the overall percentages of the visits on the flower morph in the row when it was tested against the flower morph in the column. The colour gradient ranges from the most visited morphs (green) through the moderately visited morphs (yellow) to the least visited morphs (red). Significant differences in visitations tested by bionminal test are bold.

	YLA	**YLZ**	**YSA**	**YSZ**	**PLA**	**PLZ**	**PSA**	**PSZ**
YLA		**63%***	**79%***	**79%***	**84%***	**82%***	**71%***	**74%***
YLZ	**37%***		**83%***	**72%***	**79%***	**93%***	**81%***	**77%***
YSA	**13%***	**17%***		47%	**68%***	**61%***	**66%***	**65%***
YSZ	**21%***	**28%***	53%		**65%***	**63%***	**69%***	**74%***
PLA	**16%***	**21%***	**32%***	**35%***		54%	52%	**60%***
PLZ	**18%***	**7%***	**39%***	**38%***	46%		53%	55%
PSA	**29%***	**19%***	**34%***	**31%***	48%	47%		54%
PSZ	**26%***	**23%***	**35%***	**26%***	**40%***	45%	46%	

Table 6: Binomial tests for every combination. The green cells are significant with p<0.05, the red cells are not significant. Every combination had at least 150 observations.

	YLA	**YLZ**	**YSA**	**YSZ**	**PLA**	**PLZ**	**PSA**	**PSZ**
YLA		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
YLZ	<0.001		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
YSA	<0.001	<0.001		3.360	<0.001	0.003	<0.001	<0.001
YSZ	<0.001	<0.001	3.360		<0.001	0.002	<0.001	<0.001
PLA	<0.001	<0.001	<0.001	<0.001		0.261	0.544	0.003
PLZ	<0.001	<0.001	0.003	0.002	0.261		0.466	0.227
PSA	<0.001	<0.001	<0.001	<0.001	0.544	0.466		0.244
PSZ	<0.001	<0.001	<0.001	<0.001	0.003	0.227	0.244	

3.1.2 Interaction among floral traits

To test the effects of particular floral traits and also the interaction between them we used Generalised linear model (GLM). We decided to use the model with quasi-binomial distribution due to overdipersion. The visitation was significantly affected by colour (p = 1.367e-15, deviance = 285.64, df = 1), size (p = 7.569e-07, deviance = 98.60, df = 1) but the effect of symmetry not the difference in symmetry was not significant. The significant interactions were colour×colour difference (p = < 2.2e-16, deviance = 539.27, df = 1), colour×size (p = 3.291e-05, deviance = 68.19, df = 1), size×size difference (p = 8.893e-09, deviance = 136.33, df = 1), size×size difference (p = 8.893e-09, deviance = 136.33, df = 1), and interaction between colour. In brief *Eristalis* prefer flowers which are yellow to purple flowers and large flowers to small flowers. The predictions of visitations of different floral morphs from the model are in fig 6. The complete results of the analysis are in Table 7.

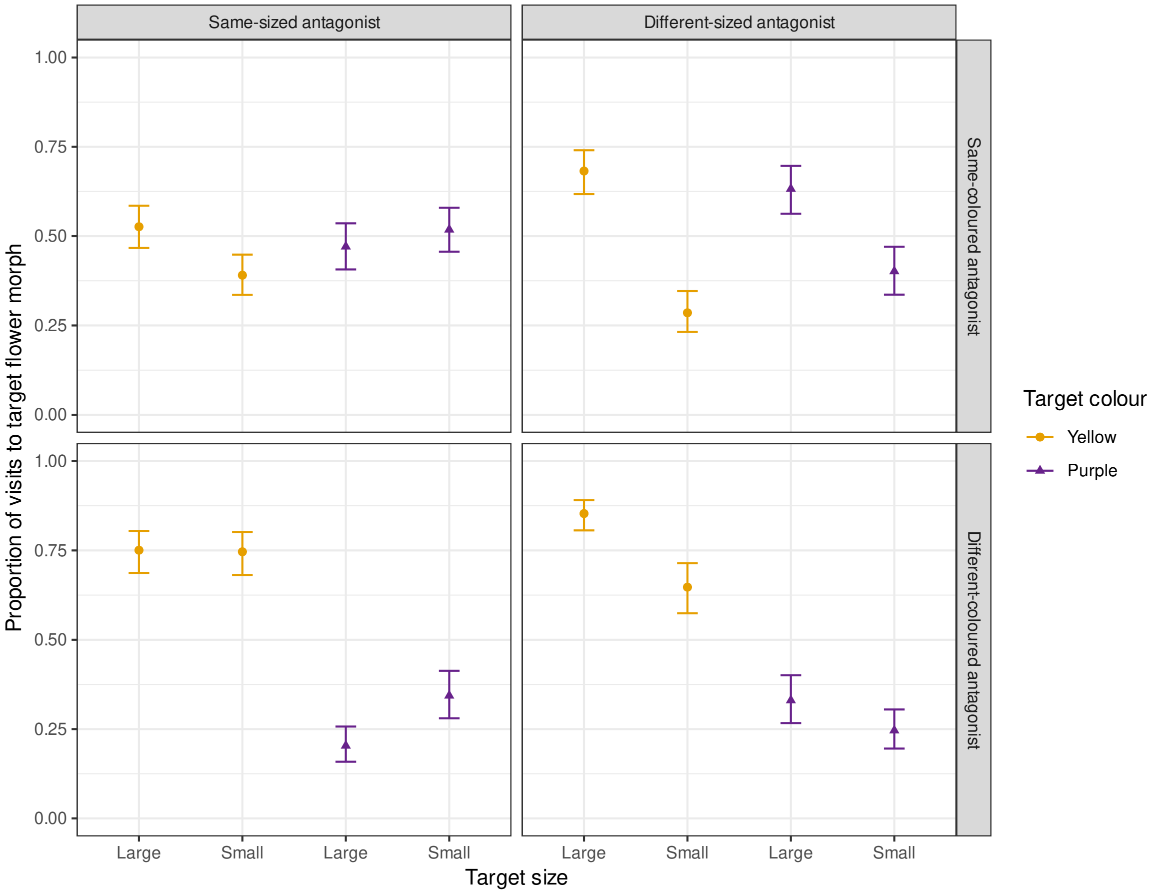

Figure 6: The graph shows the proportions of visitation of particular target flower morphs in relation to the other floral morph present in the patch. It is divided into four parts by the difference of the target and antagonist flower morph in size (in the first column the morphs differ in size, in the second they do not) and colour (in the first row the morphs differ in size, in the second they do not). The actual target colours are yellow (yellow dot) and purple (purple triangle). The symmetry was not significant and therefore we do not show its effect in the graph.

Table 7: The results for all the predictors used for Generalised linear model with quasi-binomial distribution, the significant predictors are bold. Predictors col1, size1, sym1 stand for colour, size, symmetry of flower one and diff_col, diff_size and diff_sym stand for difference in colour, size and symmetry between the flowers within the combination. Link function: logit, NULL deviance = 2062.33, Df = 226, residual deviance = 783.34, Dispersion parameter = 3.772546.

Predictor	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev**	**Pr(>F)**
col1	**1**	**285.64**	**225**	**1776.69**	**<0.001**
size1	**1**	**98.60**	**224**	**1678.09**	**<0.001**
sym1	1	13.84	223	1664.26	0.057
diff_col	1	5.62	222	1658.64	0.224
diff_size	1	6.34	221	1652.29	0.196
diff_sym	1	12.54	220	1639.75	0.070
col1:size1	**1**	**68.19**	**219**	**1571.56**	**<0.001**
col1:sym1	1	0.16	218	1571.40	0.839
size1:sym1	1	1.62	217	1569.78	0.513
col1:diff_col	**1**	**539.27**	**216**	**1030.51**	**<0.001**
col1:diff_size	1	10.69	215	1019.82	0.094
col1:diff_sym	1	3.20	214	1016.63	0.359
size1:diff_col	**1**	**15.39**	**213**	**1001.24**	**0.045**
size1:diff_size	**1**	**136.33**	**212**	**864.91**	**<0.001**
size1:diff_sym	1	10.65	211	854.26	0.095
sym1:diff_col	1	6.87	210	847.39	0.179
sym1:diff_size	1	0.95	209	846.44	0.616
sym1:diff_sym	1	1.14	208	845.30	0.583
col1:size1:sym1	1	4.89	207	840.41	0.256
col1:size1:diff_col	1	0.92	206	839.49	0.622
col1:size1:diff_size	**1**	**15.19**	**205**	**824.30**	**0.046**
col1:size1:diff_sym	1	0.20	204	824.10	0.817
col1:sym1:diff_col	1	12.03	203	812.07	0.076
col1:sym1:diff_size	1	0.00	202	812.07	0.972
col1:sym1:diff_sym	1	0.05	201	812.02	0.908
size1:sym1:diff_col	1	1.10	200	810.91	0.589
size1:sym1:diff_size	1	1.02	199	809.89	0.603
size1:sym1:diff_sym	1	8.73	198	801.16	0.130
col1:size1:sym1:diff_col	1	7.61	197	793.55	0.157
col1:size1:sym1:diff_size	1	0.49	196	793.06	0.718
col1:size1:sym1:diff_sym	1	9.72	195	783.34	0.110

3.2 Field experiment

3.2.1 Basic characteristics of the transfers

We observed 141 flights of hoverflies and bumblebees between 21st and 26th August 2017 of which 114 contained at least one transfer between the flowers, the rest being single flower visits. The mean length of the sequence was slightly longer for the hoverflies than for the bumblebees (10.75 for hoverflies and 7.88 for bumblebees) but the analysis of variance showed that the groups did not differ significantly in the length of the sequence (p = 0.227, F-value = 1.4725, Df = 1, Sum Sq = 263.8, Residual Sq = 24902.5, Residual Df = 139, full results are in Table). However the hoverflies were prone to do very long visits. The ratio of sequences longer or equal to 10 for hoverflies and bumblebees was 17:9 and for the sequences longer than 20 was 11:2. The longest sequence consisted of 74 transfers. The overall lengths of sequences are in Table 8.

Table 8: The table shows the numbers of sequnces for particular sequence lengths shown separately for hoverflies and bumblebees. We do not show sequence lengths where there are no records for either bumblebees or hoverflies. It's worth the notice that there are far fewer very long sequences made by the bumblebees unlike the hoverflies.

Length	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Bumblebee	10	5	5	2	1	3	3	0	4	2	1	3	0	2	2
Hoverfly	17	9	7	10	7	4	4	3	3	3	2	0	2	4	2
Length	**16**	**17**	**20**	**22**	**24**	**27**	**28**	**39**	**45**	**54**	**57**	**59**	**67**	**74**	
Bumblebee	2	2	0	0	0	1	0	0	1	0	0	0	0	0	
Hoverfly	3	0	1	1	1	0	1	1	1	2	1	1	1	1	

3.2.2 Time spent on the inflorescence

The mean time spent on the inflorescence was longer for the hoverflies than for the bumblebees, 26.28 seconds and 10.49 seconds respectively, which is also shown as boxplot in Fig. 8. We tested the end of the sequence and whether the time spent on the inflorescence differed between bumblebees and hoverflies (hoverflies spent overall more time on the inflorescence) and depended positively on the reverse rank of the position within sequence, the effective number of florets within the inflorescence and the interaction of the group identity and effective number of florets within the inflorescence. The results are in Table 9 and the visualisation of the predictions are in Fig 7, the boxplot in Fig 8 shows the differences in spent time on the inforescence on the real data not the predictions from the more complex model.

Table 9: The results of linear mixed model fitted by REML algorithm. The standard deviation of random effect id_seq was 0.3098, residual standard error was 0.81600. Response variable (time_spent) was under log transformation. The reverse rank was log-transformed.

Predictor	**Estimate**	**Df**	**Den.df**	**F-value**	**p-value**
Bumblebee (Intercept)	2.16	1			
Hoverfly (diff. from Bumblebee)	0.69	1	78.13	51.7	<0.001
Reverse rank	0.23	1	823.69	18.0	<0.001
Eff. no. of flowers	0.29	1	1358.98	58.6	<0.001
Hoverfly × Reverse rank	-0.13	1	823.69	2.8	0.093
Hoverfly × Eff. no. of flowers	-0.14	1	1358.98	6.2	0.013

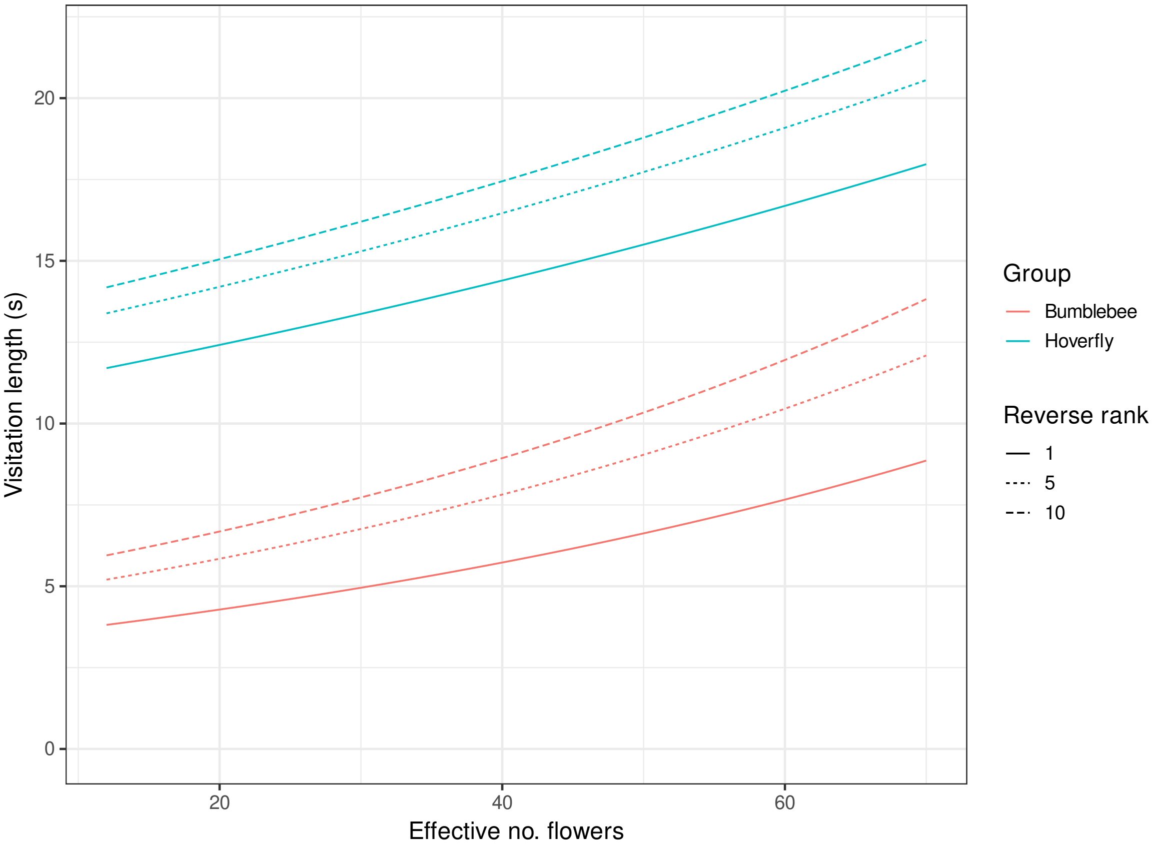

Figure 7: The boxplot shows the predictions from the linear mixed model summarised in table 9. The lines shows the predictions of time spent on the inflorescence for the last flower, the 5th and 10th flower from the end.

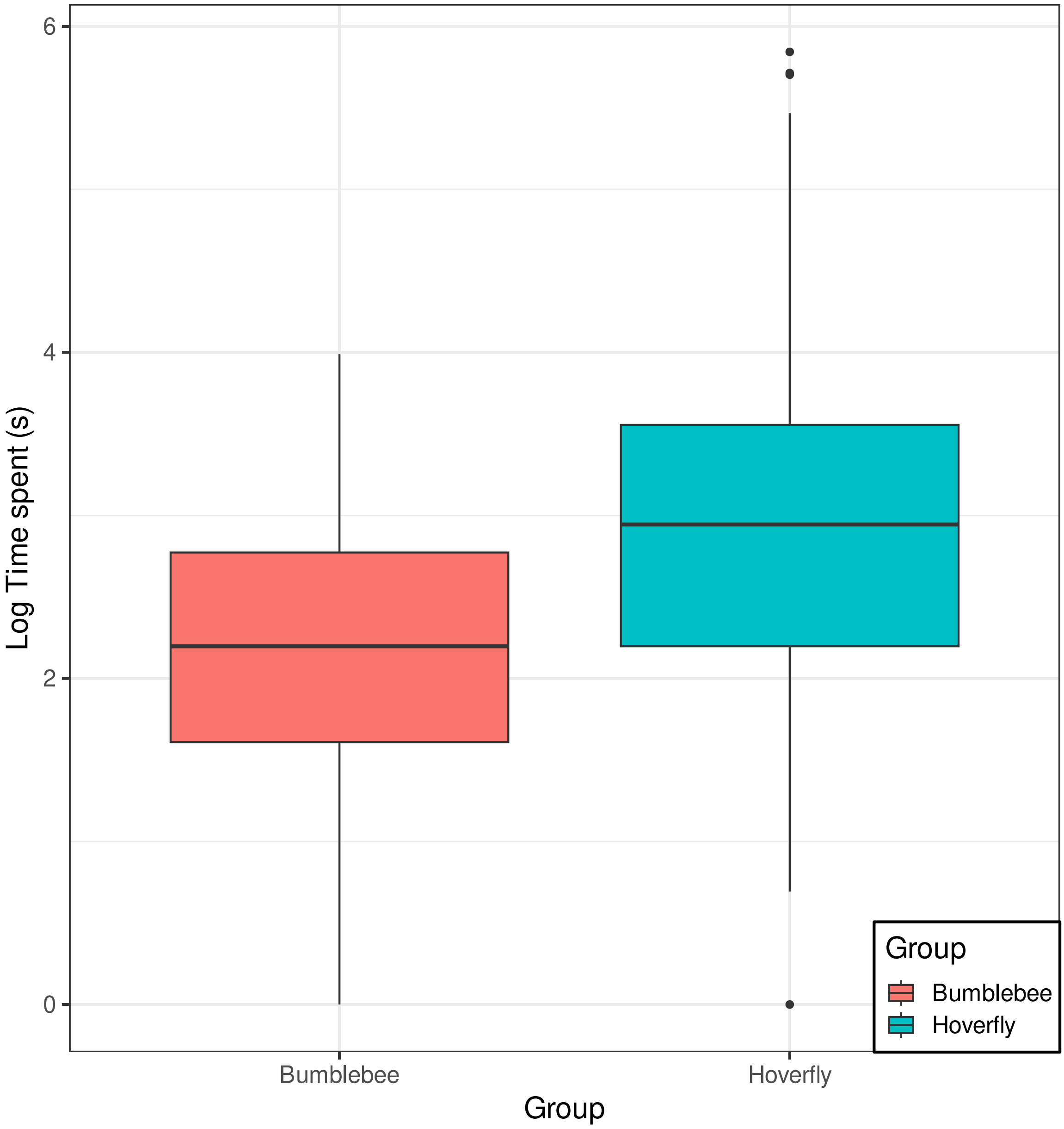

Figure 8: Plotted time spent on the inflorescence for the two groups of pollinators. The y-axis is in log scale.

3.2.3 Characteristics of the start and the end of the sequence

In the next step we were interested whether the floral traits of the first and last flower in the sequence differ from the other flowers and if the pollinators choose differently. We found that there was significant difference between the two groups in the starting flower height ($p < 0.01$, F-value = 8.0483, Df = 1, Sum Sq = 946, Residual Sq = 16338, Residual Df = 139), this was tested by the analysis of variance.

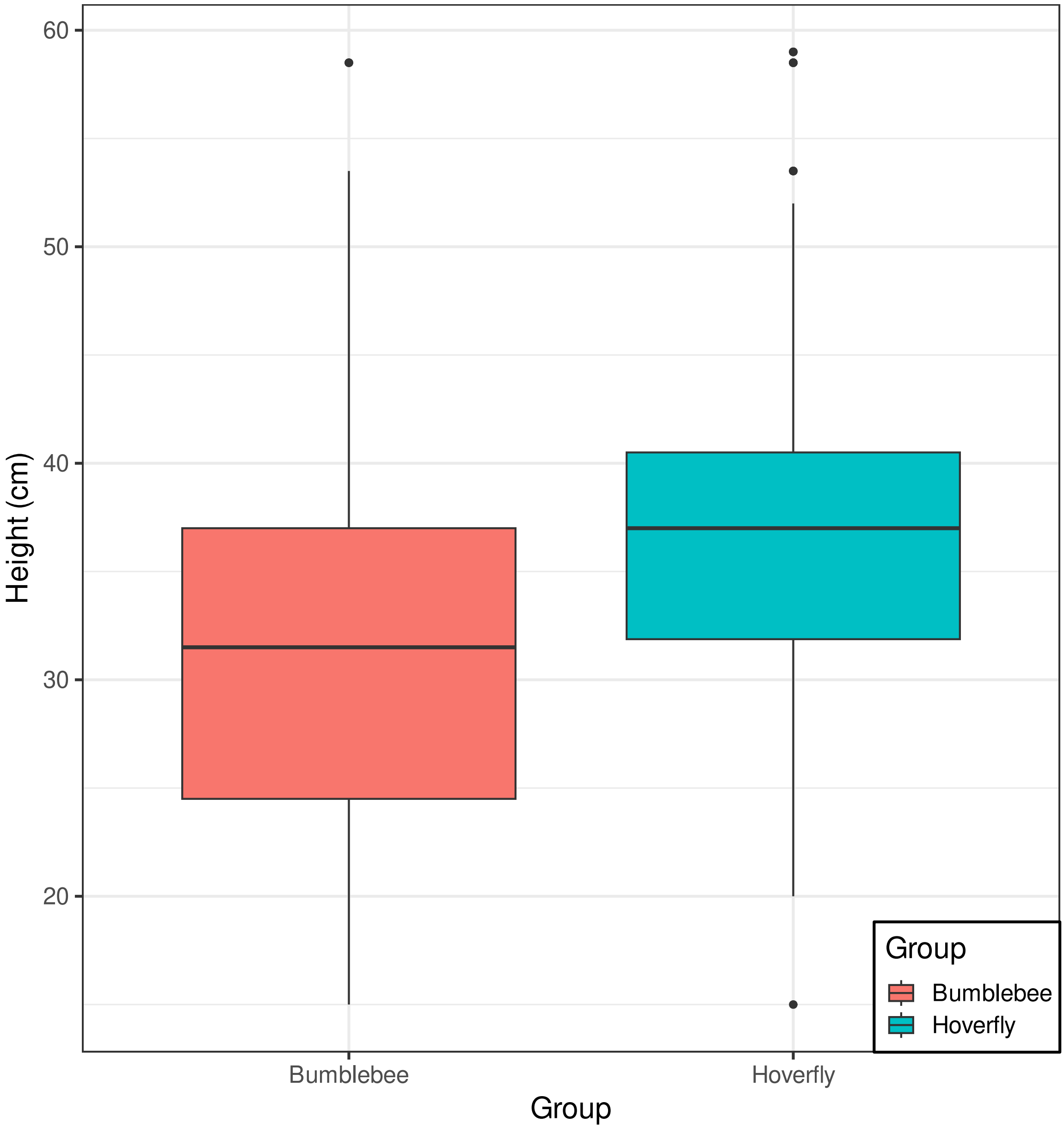

Figure 9: The boxplot shows the difference in starting flower height between hoverflies and bumblebees.

We also found that the flower height was declining with the rank in the sequence. The results are summarised in table 10.

Table 10: The results of linear mixed model fitted by REML algorithm, t-tests use Satterthwaite's method. The standard deviation of random effect id_seq was 4.346, residual standard deviation of the random effect was 8.643. Response variable (rank) was scaled and under log transformation. The rank was scaled and log-transformed. The lower table shows the effect size for each predictor.

Predictor	**Estimate**	**Df**	**Den.df**	**F-value**	**p-value**
Bumblebee (Intercept)	32.63	1			
Hoverfly (diff. from Bumblebee)	3.73	1	92.74	11.21	<0.005
Eff. no. of flowers	-0.03	1	1352.2	8.16	<0.05
Rank	-0.88	1	1364.97	4.27	<0.005
Eff. no. of flowers × Rank	0.01	1	1342.32	0.75	0.387
Hoverfly × Rank	-0.82	1	1358.98	1.26	0.262

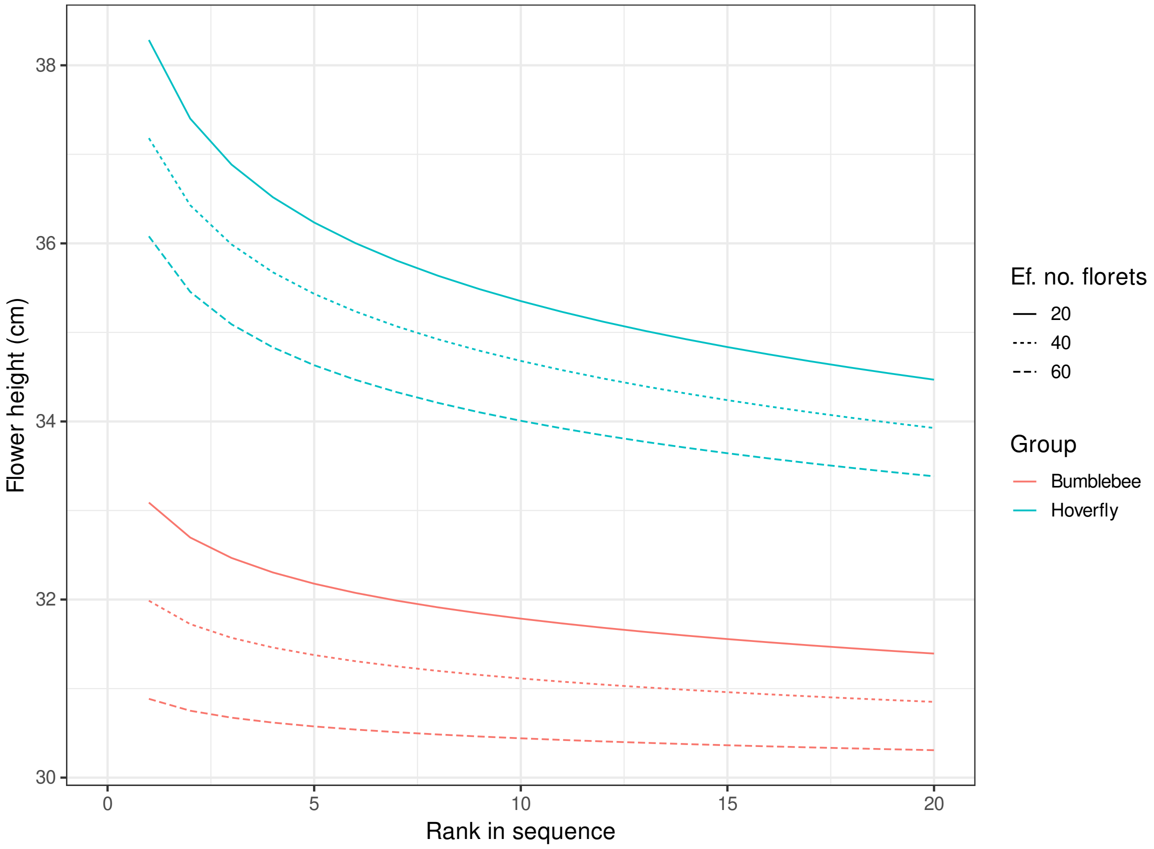

Figure 10: The plot shows the predicted declining flower height from model shown in Tab. 10 which significantly differ for hoverflies and bumblebees.

3.2.4 Travel distance

Later we were interested in the overall distance travelled in the patch. The reasoning for this is that the bumblebees should be more performance oriented to sustain their colony while hoverflies need to sustain only themselves. We used linear mixed models again due to sequence individuality. The results are in table 11 and the visualisation of the model is in the Fig. 11.

Table 11: The results of linear mixed model fitted by REML algorithm. The standard deviation of random effect id_seq was 0.3032, residual standard deviation for random effect was 0.8807. Response variable (travel_dist) was under log transformation. The reverse rank and prev visit length was log-transformed.

Predictor	**Estimate**	**Df**	**Den.df**	**F-value**	**P-value**
Bumblebee (Intercept)	3.0860	1			
Hoverfly (diff. from Bumblebee)	-0.2486	1	126.64	4.7	0.032
Reverse rank	-0.6219	1	1199.48	18.3	<0.001
Rev rank^2	0.7575	1	1140.76	12.2	<0.001
prev_time_spent	-0.0035	1	1203.09	0.8	0.371
G. hoverfly * rev_rank	0.2745	1	1199.48	1.5	0.226
G. hoverfly * rev_rank^2	-0.5550	1	1140.76	4.1	0.044
G. hoverfly * prev_visit_length	0.0693	1	1203.09	1.0	0.320

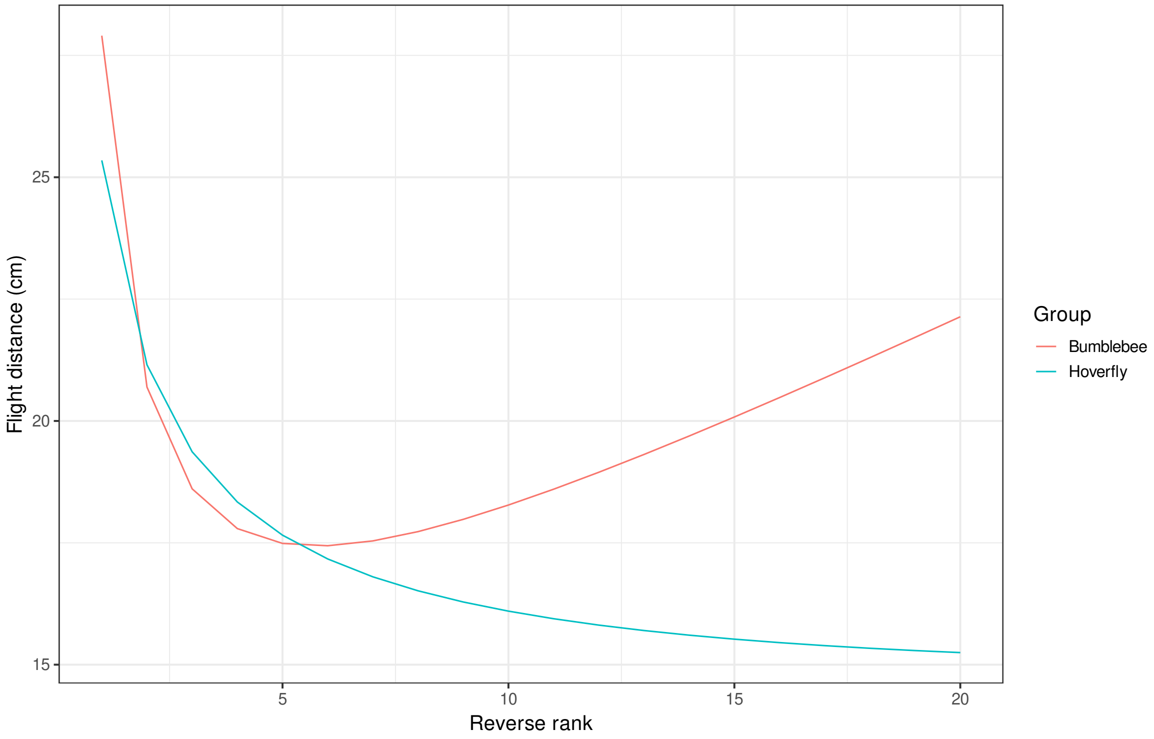

Figure 11: The plot shows the predicted curves for flight distance for the model shown in Tab. 11 which significantly differ for hoverflies and bumblebees and was dependent on the rank in the sequence.

4. Discussion

Our results of the laboratory experiments show that the colour was the most defining floral trait for *E. tenax* flower choice in our lab setup which is in agreement with previous findings such as the landing behaviour (An *et al.*, 2018) or proboscis extension (Lunau & Wacht, 1994). When the colours within the combination differed, the yellow colour was significantly more preferred than the purple colour. The second most important floral trait was the size of the flower which showed us the large flowers to be significantly more preferred than the small flowers. Additionally, if the focal and antagonist flower forms differed both in colour and size, the effect of the difference in colour largely overrode the effect of the difference in flower size 6. The detected interaction of the effects of flower colour and flower size seems consistent with the concept that flower colour is the main attractant causing pollinator preference, while a larger flower size primarily increases the perception intensity of the preferred colour (Ishii & Masuda, 2014). Since we did not observe any effect of flower size when the focal flower was of the non-preferred purple colour (comparison of yellow and small flowers versus purple and large), it is possible that flower size increased flower detectability for *E. tenax* rather than actively stimulated preference for size itself. But it is also possible that the flower size does not acts only as enhancer to colour but that in more general terms it enhances other factors of the flower resulting for the flower to be found by wider spectra of pollinators.

We did not find significant effect of the symmetry on *E. tenax* preference when the flowers differed only in the symmetry or more traits. This can be because the naive hoverflies actually do not perceive symmetry as relevant floral trait at all and the observed preferences in nature are learned due to association with rewards (Gómez & Perfecttiy, 2010). However, to our knowledge, there is no direct evidence supporting the ability of hoverflies to recognise and form learned preferences based on flower symmetry. Furthermore, various experiments on bees found mixed evidence preferences towards flower symmetry, resulting only in moderate preferences for both radial (Free, 2008; Wignall *et al.*, 2006; Culbert & Forrest, 2016) and bilateral (West & Laverty, 1998; Rodríguez *et al.*, 2004; Naghiloo *et al.*, 2019) flower symmetry. This can mean that the hoverflies are generally less selective when searching for food but also that symmetry is less important in overall pollinator visitation decisions, despite being considered an important visual cue (Giurfa *et al.*, 1999).

The other possible explanation is that symmetry is relevant even for hoverflies but almost never acts alone but coupled with other factors such as the angle in which the flower is tilt relative to the ground (Fenster *et al.*, 2009). Our both actinomorphic and zygomorphic flowers were oriented vertically and therefore we do not have enough evidence to support this tilt hypothesis. However the combination of symmetry and flower tilt is topic which should be studied further.

The floral symmetry can be also coupled with the complex colour markings on the petals or the difficulty of access to the nectar within the flowers. And even though the hoverflies may not have naïve preferences towards symmetry they may posses the ability to learn to distinguish flowers by symmetry based on the amount of reward present within the flowers. There is no evidence for this ability in hoverflies but there are studies which found the ability to develop preferences towards floral symmetry in bees (Plowright *et al.*, 2017).

In the field experiments we had two connected patches of one flower species – devils' bit scabious (*Succisa pratensis*). We could thus assume that the flowers did not differ significantly in colour and we also had their size represented by the amount of flowering florets. Therefore we could focus more on the impact of other flower characteristics on the behaviour of the pollinators. We had two groups of pollinators. The first group were hoverflies which were mainly represented by the species *Eristalis tenax* and in minority by other *Eristalis* species. The second group were bumblebees represented by *Bombus terrestris*, *Bombus pascuorum* and *Bombus lucorum.* We found out that both of the groups spent longer time on the inflorescences with more active florets. The hoverflies were more prone to stay longer in the patch in general and do overall longer visits in both time spent on the inflorescence and the number of visited flowers in the patch (Tab. 8, Tab. 9). On the contrary the bumblebees tended to make shorter visits. This could be explained by the need of the bumblebees to be more efficient while foraging to take care not only for themselves but also for their siblings in the nest. Indeed the larvae of bumblebees are dependent on the richness of the nutriment they get from their sisters foraging outside the nest (Moerman *et al.*, 2015). It is also known that the bees can memorise their foraging trips and visit specific flowers in non-random pattern. This phenomenon is called traplining and it was widely described on various bees including bumblebees (Heinrich, 1976; Ackerman *et al.*, 1982; Thomson, 1996; Thomson *et al.*, 1997; Ohashi & Thomson, 2012). The bumblebees are also capable optimise their learned pathways to get better rewards when new rich resource is added (Lihoreau *et al.*, 2010). There are no evidence of this behaviour in hoverflies and we think it is probably due their lack of need to take care of their offspring or make supplies to overwinter.

Even though our main aim was not to test the differences between sexes and also due to complicated identification of bumblebee individuals it would be very interesting to further study how big portion of the noise in the data was caused by the differences between sexes. The hoverfly females devote more of their time to foraging than males (Sánchez *et al.*, 2021) who often spent time hovering over the foraging females and protecting their territory (Wellington & Fitzpatrick, 1981), so the females could probably be responsible for the longest visits.

Interesting role played the floral height. There was tendency to visit high flowers and then decline in hoverflies but the effect was not strong and for the bumblebees the effect was non existent (Tab. 10). This is consistent with previous findings in which the bees tended to stay in the same height (Klecka *et al.*, 2018; Faulkner, 1976). It is speculated that the constant height is beneficial due to minimised energy losses spent on flying up and down (Klecka *et al.*, 2018). Hoverflies started relatively higher than the bumblebees. But surprisingly we have not found the starting flowers to be significantly higher or more flowering than the other flowers in the sequence. This was probably due to the fact that often the flower were visited multiple times during one flight sequence especially by hoverflies.

We were also interested in the pollinators' decision to leave the patch, and in the factors which drives the pollinator to go search and move to a new patch of flowers. We expected to find relation with the time spent on previous inflorescence, which we meant as proxy to pollinators' satisfaction with previous visit. Interestingly, this relationship was not significant in our analyses (Tab. 11). Nevertheless we found out that in the end of the sequence both of the groups made a few longer transfers and it declined rapidly around five visits before the end of the sequence. We also found, that the visitation length was significantly shorter on inflorescences which bloomed in the same amount in the end of the sequence (Tab. 9). In our opinion, after the slight decline, where the pollinator visited nearby flowers, was the point where the pollinator started to be disgusted by the lack of rewards in the inflorescences, and the end was the point where the pollinator already searched for better resources but only in smaller scales.

5. Conclusion

We tested how three floral traits – colour, size and shape affect floral preferences of the dronefly *Eristalis tenax* on the artificial flowers. We found out that the most important visual trait was colour followed by height. We found out that our traits do not act alone and their perception by pollinators could be structured. In our case the flower colour was enhanced by flower height but only for the preferred yellow colour. This could mean that the evolution of different floral traits is under different evolutionary pressures.

We were the first to test the effect of flower symmetry on hoverflies. Even though the effect of symmetry was not significant, it is possible that it usually acts in interaction with other floral traits, such as the angle of tilt of the flower or more complex floral markings.

In the field conditions we observed the response of non-naïve hoverflies and bumblebees on floral traits of devils'-bit scabious (*Succisa pratensis*). We found out significant differences between these two groups and their response to the floral traits. There was significant difference in time spent on the inflorescence and the number of visited flowers. Both groups tend to do a few long transfers and relatively shorter visits before the end of the flight sequence. Hoverflies spent relatively longer time on the inflorescences and were prone to do very long sequence. They also started on higher flowers and went lower in the patch, however the bumblebees started little bit lower and tend to stay in the same height.

Overall our findings suggest that there are more complex interactions between particular floral traits. Moreover, response to these floral traits varies between pollinator groups. Such diversity in plant pollinator interactions can result into diverse selection pressures and can have influence floral ecology and morphology. This is something which should be studied more in the future.

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