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The all-day pollinator visits of sunflower inflorescences in *Helianthus annuus* plantations are independent of head orientation: Testing a widespread hypothesis

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SUMMARY

Mature inflorescences of sunflowers (*Helianthus annuus*) orient constantly on average to the geographical east. According to one of the explanations of this phenomenon, the eastward orientation of sunflower inflorescences increases the number of attracted insect pollinators. We tested this hypothesis in three field experiments performed in flowering sunflower plantations. In experiments 1 and 2 we measured the number of insects trapped by the vertical walls of sticky sunflower models facing north, east, south, and west. In experiment 3 we counted the pollinators' landings on real sunflower inflorescences facing naturally east or turned artificially toward north, south, and west. We found that the all-day number of pollinators (predominantly bees) attracted to model and real sunflowers in *H. annuus* plantations is independent of the azimuth direction of sunflower heads, and after 10 h in the morning, the average number of pollinators counted every 20 min is practically constant in the rest of the day.

Keywords: sunflower, *Helianthus annuus*, pollinating insects, flower azimuth, visual ecology, flower-pollinator interaction.

INTRODUCTION

During the day, the young leaves and the non-flowering head of sunflowers (*Helianthus annuus*, Linnaeus 1753) follow the Sun (Darwin & Darwin, 1897), at sunset they face west, and at night they return to east keeping this direction until sunrise (Leshem, 1977). This occurs by differential growth patterns, with the east sides of stems growing more during the day and the west sides of stems growing more at night (Atamian et al., 2016). Brooks et al. (2023) compared gene expression patterns in sunflowers undergoing phototropism in a controlled environment and sunflowers initiating and maintaining heliotropic growth in the field. They found that the transcriptional regulation of heliotropism is distinct from phototropin-mediated phototropism, and multiple light signaling pathways control solar tracking in sunflowers. This heliotropic biorythmic/circadian oscillation ceases at anthesis, when the mature head begins flowering and the majority of sunflower inflorescences face constantly geographical east (Takács, Kovács, et al., 2022), while they tilt gradually toward the ground due to their increasing weight (Horváth, Slíz-Balogh, Horváth, Egri, et al., 2020; Lang & Begg, 1979; Vandenbrink et al., 2014). There are at least eight explanations of the benefit/function of the eastward orientation of mature sunflower inflorescences:

1. The orientation of sunflower inflorescences toward a particular point of the compass rather than toward the zenith may be advantageous since the seed loss caused by birds can be smaller because the zone on tilted heads is narrower where granivorous birds can cling (Seiler, 1997).
2. According to Leshem (1977) and Lang and Begg (1979), one of the advantages of the eastward orientation of mature sunflower inflorescences can be the decreased heat stress of the head near noon.
3. The east-facing of sunflowers could decrease the heat stress, especially in the early afternoon with strong insolation (Seiler, 1997). Lower inflorescence temperatures can increase the crop yield due to improving viability and fertility of pollens (Ploschuk & Hall, 1995; Seiler, 1997).
4. The eastward orientation of sunflower inflorescences may ensure that the heads absorb much amount of light in the morning hours. After sunrise this could advance

the evaporation of dew condensed on inflorescences, which decreases the risk of fungal diseases (Lang & Begg, 1979).

5 Although a higher head temperature facilitates seed ripening, it reduces the seed weight (Ploschuk & Hall, 1995). Since near noon the temperature of east-facing sunflower inflorescences is smaller by 3–8°C than that of inflorescences turned artificially toward the zenith (Lamprecht et al., 2007; Lang & Begg, 1979), eastward orientation could increase the seed weight.

6 According to Lamprecht et al. (2007), the eastward orientation of sunflower inflorescences could increase the attractiveness to pollinators, since then they absorb much sunlight in the early morning hours which coincide with the pollen occurrence. Field experiments demonstrated that the inflorescence temperature also contributes to the difference in pollinator attractiveness between inflorescences facing east and turned artificially to west (Atamian et al., 2016; Creux et al., 2021).

7 Horváth, Slíz-Balogh, Horváth, Egri, et al. (2020) proposed an environment-optical explanation of the east-facing of sunflower inflorescences: Using astronomical data of the celestial motion of the Sun (Bretagnon & Francou, 1988), meteorological data of diurnal cloudiness (Egri et al., 2010; Dengel et al., 2015; Hersbach & Dee, 2016; Hersbach et al., 2020; Liu et al., 2020) of North-Eastern-American regions from which domesticated sunflowers originate (Blackman et al., 2011), time-dependent elevation angle of mature sunflower heads, and absorption spectra of the inflorescence and the back of heads, they computed the light energy absorbed by the inflorescence between anthesis and senescence. They found that inflorescences facing geographical east absorb maximal light energy, which is advantageous for seed production and maturation. The reason for this is that afternoons are usually cloudier than mornings in the cultivation areas and breeding season of sunflowers. They suggested that the domesticated *H. annuus* developed an easterly orientation of its mature inflorescence because it evolved in a region with cloudier afternoons.

8 Recently, Rajna (2024) tested the hypothesis that the eastward orientation of mature sunflower inflorescences may be caused by the local prevailing wind blowing from west to east because the torque exerted by such a wind on the inflorescence turns the head eastward. Using ERA5 (5th European ReAnalysis) MONTHLY ReAnalysis wind data (Hersbach et al., 2020; Hersbach & Dee, 2016), Rajna (2024) determined those regions in Hungary, Europe, and the USA where the prevailing wind direction averaged for the period 1940–2023 is the geographical east ±15° in the breeding season (May–August) of sunflowers. It was found that eastward (±15°-)-blowing prevailing wind occurs only in ~4, ~17, and ~17% of the area of Hungary, Europe, and the United States of America (USA), respectively. Since mature sunflower inflorescences face practically everywhere east, the wind-torque hypothesis could explain this phenomenon only in a negligible (~4–17%) portion of Europe and the USA.

Using drone photography, Takács, Kovács, et al. (2022) showed that mature sunflower inflorescences indeed face almost exactly geographically east rather than the azimuth of local sunrise, and thus maximize the absorbed light energy. Takács, Slíz-Balogh, et al. (2022) revealed the biological benefit of the eastward orientation of mature sunflower inflorescences: They showed that east-facing *H. annuus* has maximal number and mass of kernel-filled seeds. Thus, explanation 7 is not only theoretically (atmospheric optically) corroborated but also experimentally (biologically/ecologically). Of course, this explanation does not exclude the validity of other explanations. Horváth, Slíz-Balogh, Horváth, Egri, et al. (2020) also gave a critical review of explanations 1–6. They showed that explanations 1, 2, and 3 are physically/meteorologically erroneous, explanation 4 may be correct but is experimentally not tested/validated, and explanation 5 is partly supported by the results of Takács, Slíz-Balogh, et al. (2022).

In this work, we concentrate on and test explanation 6 proposed by Lamprecht et al. (2007), whose proposal is partly supported by the results of Atamian et al. (2016) and Creux et al. (2021). To determine the visual attractiveness of mature sunflower inflorescences to insect pollinators versus head orientation, we performed three field experiments in flowering sunflower plantations. In experiments 1 and 2 we counted the insects trapped by sunflower-inflorescence-imitating sticky vertical test surfaces facing north, east, south, and west. In experiment 3 we counted the pollinators landing on real mature sunflower inflorescences facing naturally east and turned artificially toward north, south, and west. Takács, Slíz-Balogh, et al. (2022) studied the sunflower's seed traits as a function of the head orientation. Although they found that east-facing sunflowers produce the most and the heaviest seeds, the role of pollinator attractiveness (besides the absorbed light energy) of flowering inflorescences remained unclear. The results presented here partly reveal also this role.

RESULTS

Experiment 1: Area proportion *Q* and number of pollinators *N* trapped by 3 sticky sunflower models

In experiment 1 (July 5–September 1, 2021) the west-facing test surface had the largest *Q* and the east-facing one possessed the smallest *Q* (Figure 1a; Table S1), but this difference was statistically not significant (Table S2). Similarly, in experiment 1 the west-facing/east-facing test surface trapped the largest/smallest number *N* of pollinators

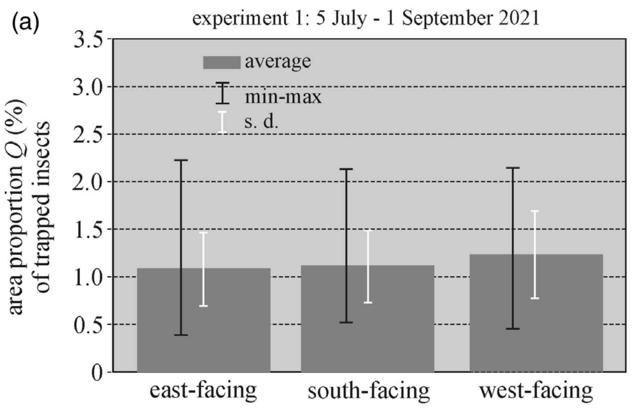

Figure 1. Results of field experiment 1. Average ± standard deviation (SD) as well as minimum–maximum interval of the area proportion Q (a) and number N (b) of insects (=recognized black patches) trapped by the east-, south-, and west-facing sticky test surfaces (vertical walls and the corresponding horizontal ledges beneath them) of the 5 sunflower models in experiment 1 (July 5–September 1, 2021).

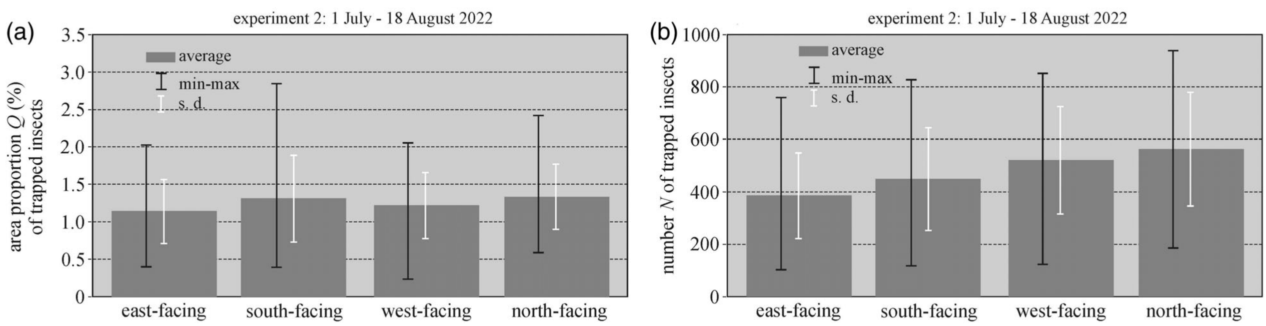

Figure 2. Results of field experiment 2. Average ± standard deviation (SD) as well as minimum–maximum interval of the area proportion Q (a) and number N (b) of insects (=recognized black patches) trapped by the east-, south-, west-, and north-facing sticky test surfaces of the 5 sunflower models in experiment 2 (July 1–August 18, 2022).

(Figure 1b; Table S3), but this difference was not significant (Table S4).

In this work we assume that both the area proportion Q of black pixels and the number N of patches recognized as distinct blobs on the black-white patterns (Figure 6d) derived from the color photographs (Figure 6c) taken about the sticky test surfaces (vertical walls and underlying horizontal ledges) of sunflower-inflorescence-imitating models used in experiments 1 and 2 are proportional to the attractiveness to insect pollinators.

Experiment 2: Area proportion *Q* and number of pollinators *N* trapped by 4 sticky sunflower models

In experiment 2 (July 1–August 18, 2022) the north-facing test surface had the largest Q and the east-facing one possessed the smallest Q (Figure 2a; Table S5), but this difference was not significant (Table S6). On the other hand, in experiment 2 the number N of pollinators trapped by the sticky test surfaces oriented to different azimuth directions decreased in the following order (Figure 2b; Table S7): $N_{north} > N_{west} > N_{south} > N_{east}$. However, only the differences in N between the west- and east-facing ($N_{west} > N_{east}$) as well as the north- and east-facing ($N_{north} > N_{east}$) test surfaces were statistically significant (Tables S8 and S9).

Experiment 3: Number of pollinators *N* attracted to head-manipulated sunflowers

Figure 3 shows the average ± standard deviation of the numbers of insect pollinators counted on the north-, east-, south-, and west-facing real sunflower inflorescences during experiment 3 (Table S10). The observed pollinators were almost exclusively honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*). According to the statistical analyses (Tables S11–S16), there were no significant differences between the average numbers of pollinators counted from 8 to 18 h on the studied 10, 10, 10, and 10 sunflower inflorescences oriented north-, east-, south-, and westward. From this we conclude that the numbers of attracted pollinators (predominantly bees) were independent of the azimuth directions of real sunflower inflorescences.

Figure 4 shows (for numerical values see Table S17) the sum N_{sum}, average N_{ave}, and standard deviation ΔN of

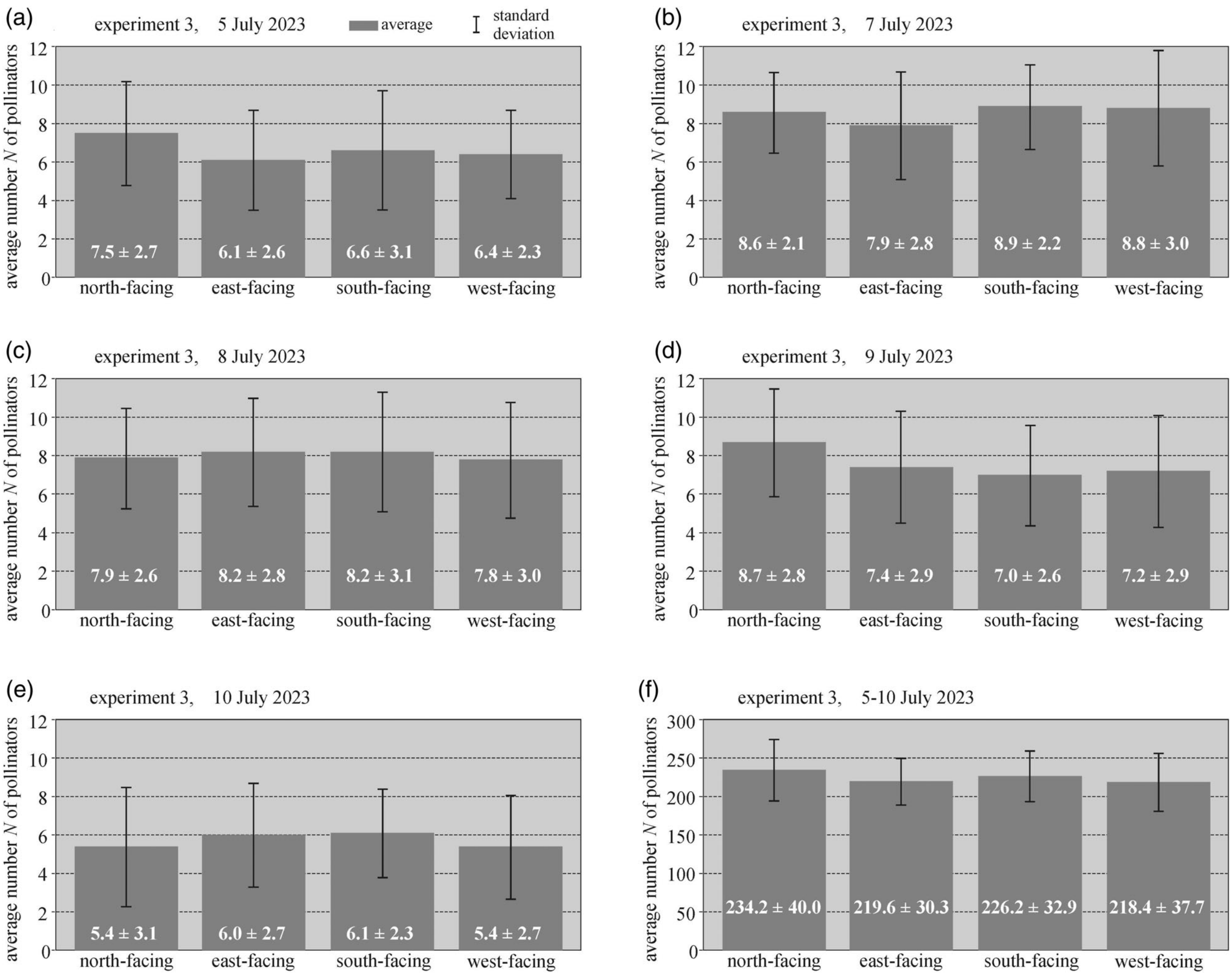

Figure 3. Results of field experiment 3. Average ± standard deviation of the numbers of insect pollinators (predominantly honeybees, *Apis mellifera*, and bumblebees, *Bombus terrestris*) counted on the north-, east-, south-, and west-facing sunflower inflorescences in experiment 3 (July 5–10, 2023).
(a–e) The five sessions.
(f) The whole period of experiment 3.

the number N of pollinators as a function of the time of day t (=local summer time = Universal Time Coordinated + 2 h) counted on the 10, 10, 10, and 10 real sunflower inflorescences facing north (Figure 4a), east (Figure 4b), south (Figure 4c), and west (Figure 4d) in experiment 3. Although the temporal change of N_{sum} is zigzag-like, it is clearly visible that in the morning more pollinators visited the inflorescences than in the afternoon, and after 8 h N_{sum} tendentiously increased until 9–10 h, then it tendentiously decreased. These are true for all four (north, east, south, west) azimuth directions of sunflower heads. In the case of north-facing (Figure 4a) and east-facing (Figure 4b) inflorescences, the average N_{ave} did not change practically during the day, because the small temporal variations of N_{ave} were within the range of the standard deviation ΔN. On the other hand, in the case of south-facing (Figure 4c) and west-facing (Figure 4d) inflorescences, N_{ave} increased until 10 and 9 h, respectively, then it was practically constant in the rest of the day, since the small temporal variations of N_{ave} were again within the range of ΔN.

From Figure 4 (and Table S17) one can see that there are differences between the number of pollinators attracted to north- and east-facing versus south- and west-facing sunflowers at 8 h being the first time point of observation ($P = 0.0008023$ for east vs. west, and $P = 0.03$ for north vs. south by Poisson test for differences in rates). Thus, experiment 3 actually confirmed the similar results of Atamian et al. (2016) and Creux et al. (2021), even in an agricultural setting.

One might wonder why this was only seen at the first time point (8 h) of our observation. On July 5, 2023 (first measurement day) at the field site, sunrise was at 4:50 h. It could have happened that if our pollinator counting had been started earlier, then more timepoints with a

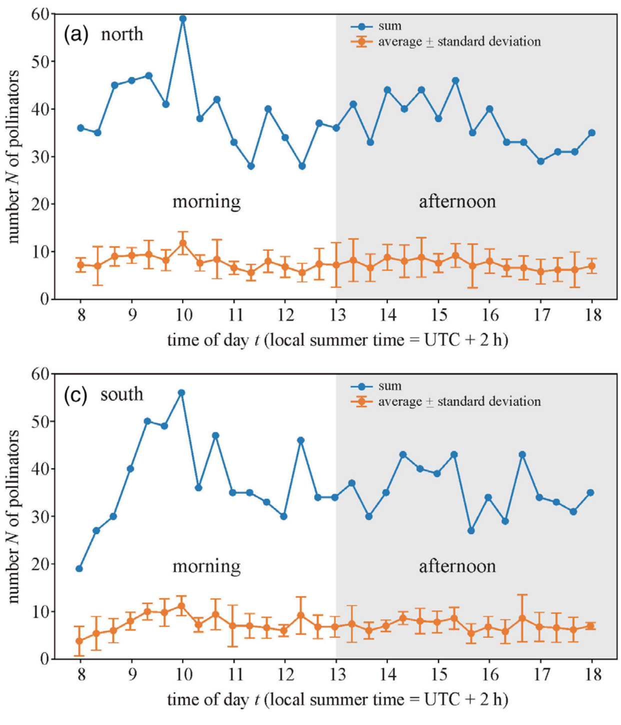

Figure 4. Temporal change of pollinators of sunflower inflorescences in field experiment 3. Sum (blue dots), average (orange dots), and standard deviation (orange vertical I bars) of the number *N* of pollinators versus time of day *t* (=local summer time = Universal Time Coordinated + 2 h) counted on the 10, 10, 10, and 10 real sunflower inflorescences facing north (a), east (b), south (c), and west (d) in experiment 3.

difference between east and west could have been observed. Creux et al. (2021) experienced the largest differences in the first hour after sunrise. However, during our experiment 3, between sunrise and 8 h pollinators did not occur on the studied sunflower inflorescences, mainly due to the low air temperature which hindered the efficient functioning of insects' wing muscles.

According to Figure 4, in the early morning (between 8 and 10 h), there were more insect visitors not only on the east-facing sunflower inflorescences (Figure 4b) but also on north-facing ones (Figure 4a), which seems to be surprising at first. The likely reason for this is that at sunrise at our experimental location and time, the sun azimuth was 55° meaning a northeast direction, from which much direct sunlight illuminated not only the east-facing but also the north-facing inflorescences.

DISCUSSION

Although the majority of mature sunflower inflorescences are oriented to the geographical east (Takács, Kovács, et al., 2022), in sunflower plantations the capitulum of many plants can also face north, south, or upward. Large deviations from the prevailing east direction can decrease the plant's reproductive fitness. Larger mass and number of seeds can guarantee safer seed germination and better early development of more offspring. In a sunflower plantation, Takács, Slíz-Balogh, et al. (2022) compared the number and mass of seeds in plants, the inflorescences of which were naturally or artificially oriented northward, eastward, southward, westward, or upward. They found that the east-facing of sunflower inflorescences ensures a larger seed number and mass compared to disoriented inflorescences. Using radiational computations, they also showed that east-facing ensures more absorbed light energy than other orientations, except upward. This can be one of the reasons for the maximal seed number and mass in east-facing sunflower capitula. Although upward-facing horizontal inflorescences absorbed maximal light energy, they had the fewest and lightest seeds probably because of the larger temperature and humidity as well as the too much sunlight, all three factors impairing normal seed development.

In three field experiments performed in *H. annuus* sunflower plantations, we tested the widespread hypothesis that the constant eastward orientation of mature sunflower inflorescences may increase the number of attracted insect pollinators. Certain aspects of the visual cues, the volatiles that could be released based on differential heating, and the ultraviolet markings of true sunflower heads were missing in our sticky optical sunflower models used in experiments 1 and 2. Even so, the use of these sticky models was important, because they trapped automatically and continuously night and day the insects landed on their sticky test surfaces throughout the flowering season. In our most conclusive and convincing field experiment 3, performed with head-manipulated real sunflowers, the methodological shortcomings of experiments 1 and 2 were eliminated.

We admit that there could be reasons that our sticky model inflorescences might not have represented the same insect response as real sunflowers, including odor (volatile compounds) interacting with color and temperature, for example. Note, however, that our sticky model sunflower inflorescences were odorless, or had always the same odor due to the same (orange, yellow, green) paints and insect monitoring glue. Thus, the (statistically non-significant) differences in the numbers of pollinators trapped by the sticky test surfaces facing north, east, south and west were obviously not affected by the non-existing odor (volatile compounds) differences. Similarly, our model inflorescences had the same color pattern with the same reflection spectra. Consequently, there were no color differences between them that could have influenced their visual attractiveness to pollinators.

Due to the same color pattern, glue cover, and orientations, the temperature of all 5 test surfaces (of the 5 model sunflowers) with the same orientation (north, east, south, west) had the same temperature at any point of time of a given time of day. Consequently, there were no temperature differences between the 5 test surfaces of the same orientation, and therefore the number of trapped pollinators was not influenced by thermal differences. The daily temporal variation of the temperature of the differently oriented test surfaces of our sticky model inflorescences mimicked well the thermal characteristics of real inflorescences facing north, east, south, and west.

In sum, the same optical and thermal characteristics of our sticky model sunflower inflorescences imitated physically well the same characteristics of real sunflowers, and the lack of odor cues did not influence the differences in the numbers of trapped pollinators.

In experiments 1 and 2 the sticky sunflower models were odorless being a relevant difference compared to the head-manipulated real sunflower inflorescences used in experiment 3 in which odor, color, and temperature might interact in a key fashion to attract pollinators. In experiments 1 and 2 we followed a standard method of insect choice experiments when we used odorless sticky models imitating optically sunflower inflorescences. The lack of odors was not a serious problem, because in a flowering sunflower plantation the odor concentration is practically homogeneous due to the simultaneous flowering of several thousand sunflowers. In such a direction- and site-invariant odor field the detection, recognition and finding of a given sunflower inflorescence can happen almost exclusively by optical cues, rather than by odors. Consequently, our main finding, that the number of pollinators of mature sunflower inflorescences in *H. annuus* plantations is independent of the azimuth orientation of sunflower heads, is not invalidated by the fact that in our experiments 1 and 2 the sticky test surfaces did not have odor cues. This assumption is strongly supported by the same result of experiment 3 using head-manipulated real sunflower inflorescences.

We emphasize that in choice experiments investigating the attractiveness of various targets to insects, the use of odorless test surfaces with only optical cues is a quite widespread standard method. We mention here, for example, only the experiment series in which it was shown that horseflies (Tabanidae) prefer dark and strongly polarizing host animals against bright and weakly polarizing hosts and are repelled by hosts possessing striped or spotted furs (Blahó et al., 2012, 2013; Egri, Blahó, Kriska, et al., 2012; Egri, Blahó, Sándor, et al., 2012; Horváth et al., 2010; Horváth, Pereszlényi, Åkesson, & Kriska, 2019; Horváth, Pereszlényi, Egri, Fritz, et al., 2020; Horváth, Pereszlényi, Egri, Tóth, & Jánosi, 2020; Horváth, Pereszlényi, Tóth, et al., 2019; Száz et al., 2023; Takács, Száz, et al., 2022). These findings were obtained in field experiments in which the horseflies landed on odorless sticky or dry (non-sticky) test targets with different colors, polarization, and temperature were counted. In these experiments olfactorial cues were purposely omitted, because the researchers concentrated only on optical signals attracting or repelling horseflies, which are also lured by host-specific odors (e.g., urin and exhaled CO_2).

Atamian et al. (2016) studied, among others, the possible ecological advantage of the eastward orientation of mature sunflower inflorescences. Since the flower temperature of high-altitude (e.g., alpine) plants enhanced by heliotropism increases the frequency of visits of insect pollinators, following hypothesis 6 proposed by Lamprecht et al. (2007) and mentioned in the Introduction, Atamian et al. (2016) also assumed that the east-facing of sunflower inflorescences could increase their attractiveness to pollinators due to the stronger morning insolation, which coincides with the daily timing of the emergence of anthers and stigmas.

Atamian et al. (2016) conducted two experiments in August and September 2014 in Davis (USA, California), furthermore three others in the summer of 2013 and 2014 in Morven (USA, Virginia). They raised sunflowers in buckets outdoors. Prior to anthesis, the head of half of the sunflowers was turned to the geographical west, while that of the other half remained naturally to face the geographical east (5 + 5 plants in 2013 and 8 + 8 plants in 2014 in Morven, while 4 + 4 plants in Davis). The mature inflorescences were videofilmed for 45 min at 8, 12, and 16 h in Morven, and for 30 min at 9, 13, and 17 h in Davis. Using these videos, the insect pollinators visiting the inflorescences were counted frame by frame, independently of their species.

In the morning, sunlit east-facing inflorescences were warmer than shady west-facing ones, which was the opposite in the afternoon (Atamian et al., 2016). Of course, from a simple physical point of view, all these were expected. In the morning hours, pollinators visited the sunlit east-facing inflorescences 5-times more often than the shady west-facing ones. However, this difference occurred predominantly only if the sunlit east-facing inflorescences were warmer than the shady west-facing ones. When shady west-facing inflorescences were warmed up by an electric heater to the temperature of sunlit east-facing inflorescences, the heated west-facing inflorescences attracted significantly more pollinators than the unheated west-facing ones, but still less than sunlit east-facing ones. From their field experiments Atamian et al. (2016) concluded that the flower temperature directly contributes to, but not exclusively determines, the pollinator attractiveness of east- or west-facing sunflower inflorescences. These temperature characteristics of the heads may partly be an explanation for the east-facing of mature sunflower inflorescences.

As a first approximation, for sunflower inflorescences the most important is the total number of pollinators landing on them during the whole flowering season. Insect visits can happen all day: from sunrise to sunset day-active insects and between sunset and sunrise night-active insects can pollinate. As a more sophisticated approximation, not only these total pollinator visits but visits based on time of day also matter, because not all pollinator visits are equally productive. The reason for the latter is that pollen release occurs in the morning, and west-facing shady sunflowers have reduced siring success compared to sunlit east-facing sunflowers (Creux et al., 2021).

For a thorough investigation of sunflower-visiting pollinators, it would be ideal if these pollinators could be counted continuously on numerous inflorescences for 24 h in all days of the flowering period. However, in the field it is practically impossible to automatically or personally monitor many inflorescences with weather-proof cameras or with the naked eye for 2–3 weeks and for 24 h every day. As a substitution approach, in field experiments 1 and 2 we trapped the pollinators continuously for several weeks by sticky colored sunflower-inflorescence-imitating test surfaces, the vertical side walls of which faced north, east, south, and west. Since the main sunflower pollinators are usually day-active insects, in experiment 3 our alternative method was to count every 20 min from sunrise to sunset the insects landing on real sunflower inflorescences, the azimuth direction of which was naturally east and artificially turned toward north, south, and west on cloudless, warm days.

Under sunny conditions, in the morning obviously the east-facing sunflower inflorescences are sunlit (receiving both direct sunlight and scattered skylight) and the west-facing ones are shady (receiving only skylight), while in the afternoon *vice versa*: east-facing inflorescences are shady and west-facing ones are sunlit. Under totally overcast skies, sunflower inflorescences receive practically the same intensity of skylight, independent of their azimuth orientation, while under partly cloudy skies they are sunlit or shady, depending on the spatiotemporally changing cloud pattern. Under cloudy and cool weather too, certain pollinators, bumblebees, for example, are almost continuously flying and searching for flowers to collect pollen and nectar. Other pollinator species prefer either the morning or the afternoon hours for their flower visits. Since it is not known which pollinator species of sunflowers, at which time of day, and under which weather conditions visit sunflower inflorescences, it is pertinent to count them in the whole flowering period in all 24 h of the day, or at least from sunrise to sunset for several cloudless, warm days.

Atamian et al. (2016) found that at 16 h/17 h within 30/45 min the number of pollinators of west-facing sunflower inflorescences was (i) not significantly smaller, or (ii) not significantly larger, or (iii) significantly larger than that of east-facing inflorescences, depending on the site and/or time of their field experiments. From these results it is not quite clear whether west-facing inflorescences are less or more attractive to pollinators than east-facing ones. On the other hand, we performed three field experiments, in which the automatic mechanical sampling of insects landing on north-, east-, south-, and west-facing sticky test surfaces happened for 24 h every day for 6–9 weeks including the whole flowering period (experiments 1 and 2), or the visual sampling of pollinators of north-, east-, south-, and west-facing real inflorescences happened for the whole flowering period between 8 and 18 h every day (experiment 3).

The differences between the results of Atamian et al. (2016) and our findings presented in this work might be explained by the different experimental methods and environmental conditions. (i) While Atamian et al. (2016) conducted a 2-location and 2–3-season study by sunflowers grown in isolated and widely spaced large pots or buckets, a half of which were turned artificially toward west, our field studies were performed in three different sunflower plantations where plants were grown directly on the soil in a standard agricultural setting following agronomic practices (e.g., high-density and row-cropping). (ii) While Atamian et al. (2016) counted flower-visiting pollinators on 3–4 days at 8/9 h, 12/13 h, and 16/17 h, for 30/45 min periods in east and west azimuth directions of 4–8 real sunflower inflorescences, in our experiments 1 and 2 the pollinators trapped by sunflower-imitating sticky test surfaces were counted all day long for several weeks, and in experiment 3 we counted every 20 min the pollinators landed on real sunflower inflorescences from 8 to 18 h on 5 days. These differences could lead to variances in the number of pollinators attracted to the differently studied sunflower inflorescences facing various points of the compass. Since the field experiments of Atamian et al. (2016) and ours were conducted under different growing conditions and/or environments, a direct comparison between them cannot be done. Another likely difference between these studies may be the different pollinating insect fauna of the American (Davis, California; Morven, Virginia) and Hungarian (Csörög, Sződ) experimental sites.

Our main finding is that in *H. annuus* plantations the pollinator attractiveness of sunflower inflorescences (the quantitative measures of which were the area proportion Q and number N of insects trapped by sticky sunflower-imitating test surfaces, as well as the number N of pollinators attracted to real sunflower inflorescences) is practically independent of their azimuth orientation. This can be explained as follows: As Takács, Slíz-Balogh, et al. (2022) have emphasized, sunflower inflorescences facing different points of the compass are differently illuminated by direct sunlight, thus they have different appearances to pollinators (e.g., due to the UV markings of the yellow coronal petals). This can significantly influence the visual attractiveness of inflorescences to pollinators. Instead of speculating about the possible consequences of this effect on the number of flower-visiting insects, we accentuate that on every day of our three field experiments pollinators had the chance to visit the sunflower inflorescences at any time, during all 24 h of the day (experiments 1 and 2) or from 8 to 18 h (experiment 3). Therefore, during the day, an inflorescence with any azimuth direction was confronted with the same or similar illumination conditions as any other one with another orientation. Consequently, on a given day, differently oriented inflorescences had the same or similar series of visual appearances and attractiveness to pollinators. The only difference was the temporal subalternation of appearances. For instance, a sunlit west-facing inflorescence has the same appearance at 2 h after noon as a sunlit east-facing inflorescence at 2 h before noon. On the other hand, north-facing inflorescences are sunlit for shorter periods than east-, south-, or west-facing ones. When a pollinator lands on a naturally east-facing sunflower inflorescence dominating a plantation, it can see well the neighboring inflorescences, practically independent of their orientation. Thus, after its pollen/nectar collection on the selected east-facing inflorescence it can fly to any neighboring inflorescence with any orientation and continue its pollinating task. Consequently, it can visit further on not only the east-facing inflorescences but also inflorescences facing north, south, west, or any other points of the compass.

On the one hand, if an insect pollinator is flying above a sunflower plantation with differently oriented inflorescences, during its flight its compound eyes composed of omnidirectional (practically from 0° to 360°) ommatidia can detect any sunflower head with any azimuth direction (Figure 5). On the other hand, if this pollinator lands on any inflorescence and during pollen/nectar collection it looks around, its compound eyes can always see the yellow coronal petals of all neighboring heads with any orientation (Figure 5). Thus, a preference of a particular (e.g., eastern) azimuth direction of sunflower inflorescences by insect pollinators is not expected, as we indeed found in our three field experiments.

We emphasize that our experiments were performed at agricultural planting densities of sunflowers, unlike the experiments of Atamian et al. (2016) and Creux et al. (2021). Although agricultural densities are most relevant if the question is about the impact of sunflower orientation on agricultural yield, these conditions are not necessarily relevant for determining the possible evolutionary pressures that led to east-facing of mature sunflower inflorescences in the first place. The head fixation of solitary wild sunflowers occurs at anthesis (Darwin & Darwin, 1897; Lang & Begg, 1979; Vandenbrink et al., 2014), so agricultural planting densities may not be more relevant for addressing this question.

Finally, the question arises whether the pollinator visits lead to differences in sunflower yield/fitness. This question was studied by the field experiment of Takács, Slíz-Balogh, et al. (2022), who showed that compared to north-, south-, and west-facing sunflowers, east-facing sunflowers have maximal number and mass of kernel-filled seeds, that is maximal yield/fitness. The reasons for this can be at least twofold: (i) the enhanced pollinator visits early morning (as shown by Atamian et al., 2016; Creux et al., 2021 and the present work), furthermore (ii) the maximal light energy absorbed by east-facing sunflower inflorescences compared to flowers with other azimuth directions, if afternoons are cloudier than mornings (as shown by Horváth, Slíz-Balogh, Horváth, Egri, et al., 2020).

CONCLUSIONS

In experiment 1, there were no statistically significant differences between the area proportion Q and number N of insects trapped by the east-, south-, and west-facing sticky test surfaces (vertical side walls and underlying horizontal ledges) of the sunflower-inflorescence-imitating models.

In experiment 2, there were no statistically significant differences between the area proportion Q of insects trapped by the east-, south-, west-, and north-facing sticky test surfaces of sunflower models. However, the numbers N of pollinators trapped by the north- and west-facing sticky test surfaces were significantly larger than that of the east-facing test surface ($N_{west} > N_{east}$, $N_{north} > N_{east}$).

Conclusion 1: From experiments 1 and 2 we conclude that in sunflower plantations pollinators were not differentially attracted to optically and thermally sunflower-inflorescence-mimicking sticky vertical test surfaces facing north, east, south, and west.

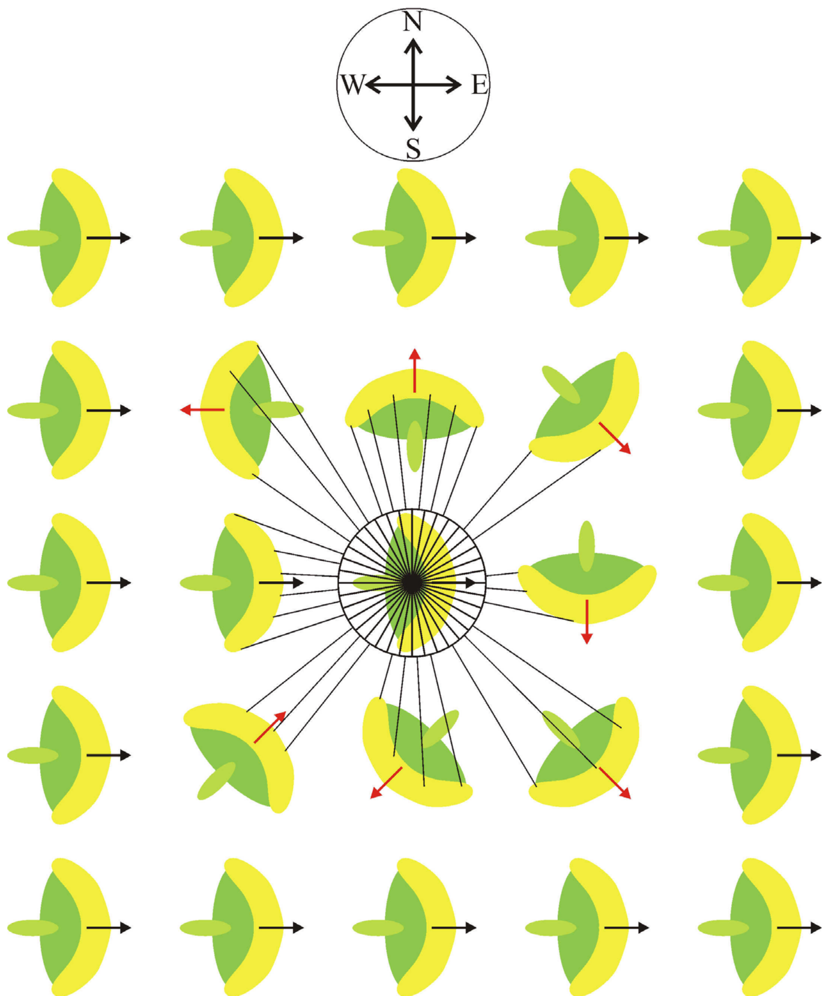

Figure 5. Visual field of a pollinator's compound eye in a sunflower plantation. At least one ommatidium of the omnidirectional compound eyes (black rosette) of an insect pollinator flying above a sunflower plantation with predominantly east-facing inflorescences (sunflower heads with black arrows) can detect the yellow coronal petals of the heads oriented toward any points of the compass (red and black arrows).

Conclusion 2: From the results of experiment 3 we conclude that there were no significant differences between the average numbers of pollinators counted from 8 to 18 h on 10, 10, 10, 10 real sunflower inflorescences facing north, east, south, and west in sunflower plantations. Furthermore, in the morning more pollinators visited the inflorescences than in the afternoon, independently of the azimuth directions (north, east, south, west) of sunflower heads. In the case of north- and east-facing inflorescences, the average number of pollinators N_{ave} counted every 20 min practically did not change during the day, while in the case of south- and west-facing inflorescences, N_{ave} increased until 9–10 h, then it remained practically constant in the rest of the day.

Conclusion 3: The morning differences in pollinator visitation rates depending on the orientation of sunflower inflorescences observed by Atamian et al. (2016) and Creux et al. (2021) were observed by us even in an agricultural setting (i.e., sunflower plantation), confirming the earlier similar results.

Conclusion 4: Our final conclusion is that in spite of the differences in morning visitation rates, the total number of pollinators (predominantly bees) across an entire day attracted to mature sunflower inflorescences in *H. annuus* plantations does not depend on the azimuth direction of sunflower heads.

MATERIALS AND METHODS

Field experiments 1 and 2 with sticky models imitating sunflower inflorescences

Field experiment 1 was dedicated to measure the attractiveness of sunflower-inflorescence-imitating vertical sticky test surfaces with three different azimuth directions (geographical east, south, west) to insect pollinators as a function of time, including the 4-week blooming period (Dárdai, 2022). The experiment was conducted between July 5 and September 1, 2021, in a sunflower plantation (hybrid type Corteva P64LE25, *H. annuus*) at the Hungarian village Csörög (47°43′53″ N, 19°12′10″ E), where 5 uniform sunflower-inflorescence-imitating models were set up (Figure 6a). The cubiform models (30 cm × 30 cm × 30 cm) were composed of

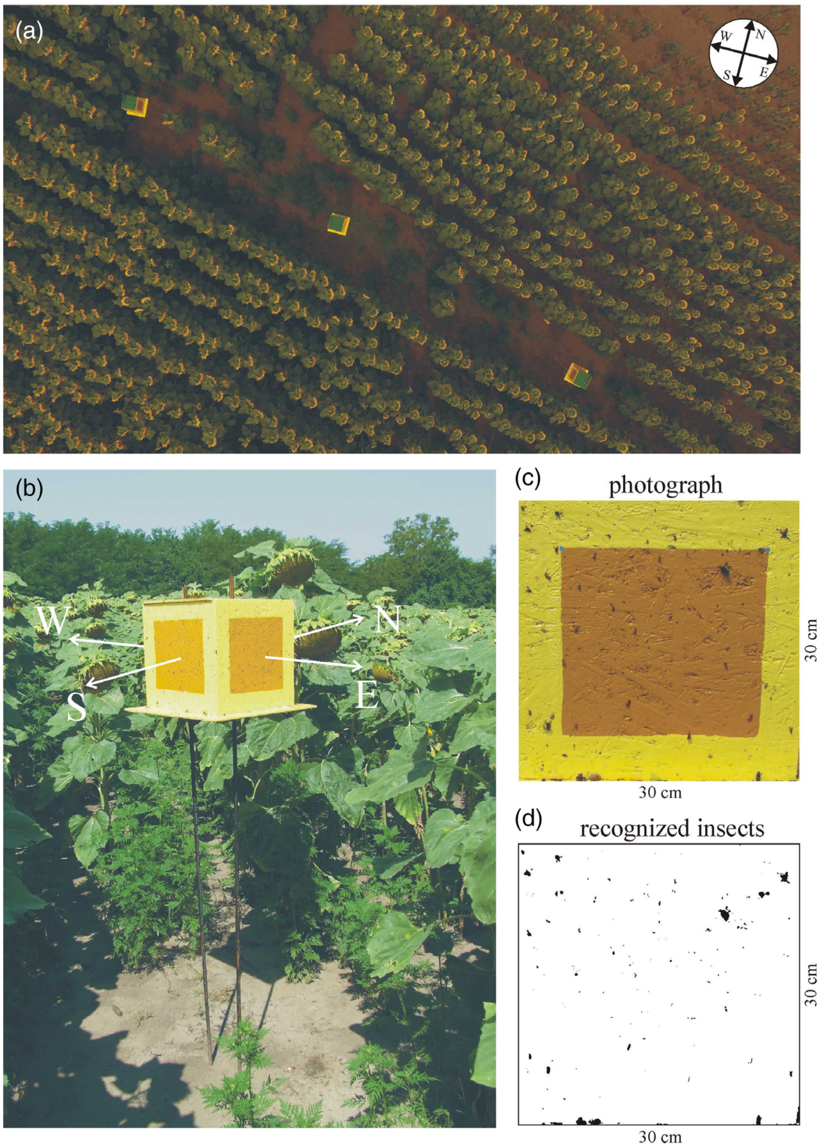

Figure 6. Drone photography of sunflower plantations and evaluation of photos taken about the sticky test surfaces. (a) Drone photograph of three sticky models imitating sunflower inflorescences in a sunflower plantation at Csörög (47°43′ N, 19°12′ E) taken from a height of 80 m. The other two models are not visible here.
(b) A sunlit sunflower model photographed from south-east direction of view.
(c) Photograph of one of the vertical sticky test surfaces of the sunflower model with the trapped insects (dark patches).
(d) Trapped insects (black patches) are recognized computationally in photograph c.

chipboards. The top horizontal green chipboard (30 cm × 30 cm) imitated a leaf or the back of a sunflower head. The three orthogonal vertical chipboards (30 cm × 30 cm) were yellow with an orange square (16 cm × 16 cm) in the middle (Figure 6b,c) and imitated mature sunflower inflorescences. The horizontal bottom of the model (40 cm × 40 cm) had a 5 cm wide horizontal yellow ledge (Figure 6b). Each model was fixed at a height of 150 cm to two vertical iron rods stuck into the ground in the average level of sunflower inflorescences. The models stood 10 m apart from each other. The normal vector of the three yellow-orange vertical side walls of the models oriented to geographical east, south, and west (Figure 6b). These walls were covered with a colorless, transparent, odorless, weather-proof insect-monitoring glue (BabolnaBio® mouse trap) in order to trap insects landing on them. Figure 7(a) shows the reflectance spectra of the green, yellow, and orange model's walls, while Figure 7(b) displays the reflectance spectra of yellow coronal petals, an orange central inflorescence, and a green leaf of a sunflower measured with a spectrometer (Ocean Optics STS-VIS, Ocean Insight, Largo, USA).

The five sticky models were installed on July 5, 2021 (start of blooming) in the sunflower plantation, then they were visited nine times, depending on the weather: (1) July 12 (blooming), (2) July 15 (blooming), (3) July 24 (blooming), (4) July 28 (end of blooming), (5) August 4, (6) August 11, (7) August 18, (8) August 26, (9) September 1. During every visit, we photographed the sticky model's vertical walls and the four sticky horizontal ledges below them containing the trapped insects (Figure 6c), then insect carcasses not smaller than 1 mm were removed with a nipper, and finally the insect-monitoring glue was refreshed. During photography, the sticky vertical walls of the models were shadowed by a black umbrella in order to eliminate the shadows of insect carcasses. In direct sunlight these carcasses casted shadows which would have made very difficult the computer recognition of insects in the photographs. Note that the glue-trapped insects would have been pollinators, if they had landed on real sunflower inflorescences.

In experiment 1, we did not use a sticky vertical test surface facing north, because we assumed (erroneously) that sunflower heads never orient northward. However, a field experiment

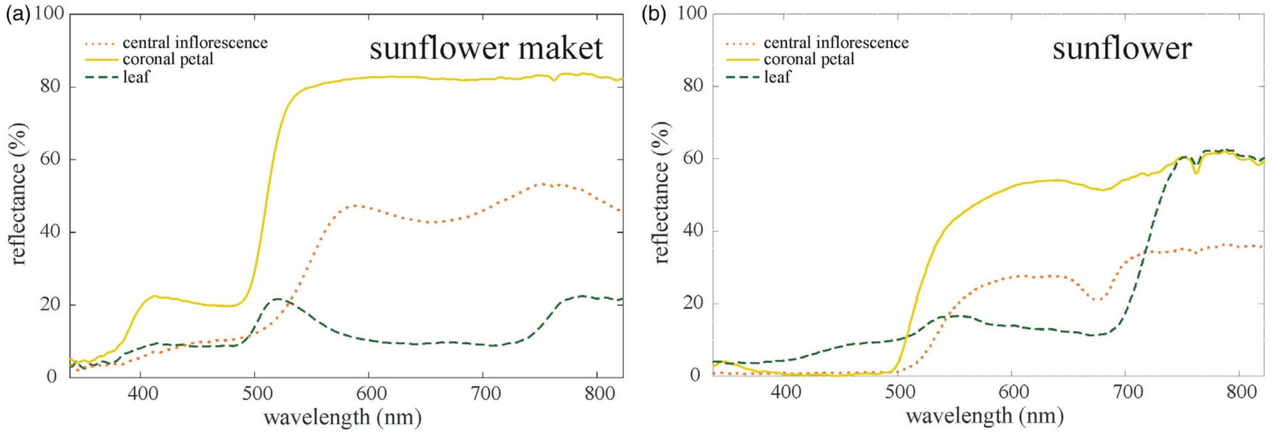

Figure 7. Spectra of sunflowers and sticky test surfaces. Reflectance spectra of the green, yellow, and orange sides of the sunflower-inflorescence-imitating models used in field experiments 1 and 2 (a), and of a green leaf, yellow coronal petals, and the orange central inflorescence of a sunflower (b).

(Takács, Kovács, et al., 2022) showed that in sunflower plantations there can also be a few north-facing sunflower inflorescences. Therefore, in the summer of 2022 we performed experiment 2 using also a north-facing test surface.

Field experiment 2 was the same as experiment 1 with the only modification that the sunflower-imitating models had four vertical sticky side walls facing geographical north, east, south, and west. This experiment happened between July 1 and August 18, 2022, in a sunflower plantation (hybrid type Corteva P64LE25, *H. annuus*) at the Hungarian village Sződ (47°43′00″ N, 19°12′00″ E), where 5 uniform sunflower-inflorescence-imitating models were set up (Figure 6b). The five sticky models were installed on July 1, 2022 (start of blooming) in the sunflower plantation, then they were visited six times: (1) July 7 (blooming), (2) July 14 (blooming), (3) July 21 (blooming), (4) July 28 (end of blooming), (5) August 9, (6) August 18. During every visit, we photographed the four sticky vertical side walls and the four sticky horizontal ledges below them containing trapped insects, then insect carcasses not smaller than 1 mm were removed, and the insect-monitoring glue was refreshed. Other details were the same as in experiment 1.

Evaluation of photographs taken about trapped insects

The photographs taken about the sticky vertical side walls and the sticky horizontal ledge below them trapping insect pollinators were evaluated by the software written by Dárdai (2022) in Python programming language using GNU (Gnu's Not Unix) Image Manipulation Program. This software recognized the insect carcasses trapped by the sticky test surfaces. Using appropriate threshold values of color and intensity, the software could distinguish the insect carcasses from the yellow-orange background (sticky substrate). Finally, the color photographs (Figure 6c) were transformed to black-and-white binary maps, in which the insect carcasses occurred as black patches on the white background (Figure 6d).

In the black-and-white maps, the numbers N_{black} and N_{white} of black-and-white pixels were determined, and then the area proportion $Q = N_{black}/(N_{black} + N_{white})$ of the black pixels was calculated. In this work, Q is one of the quantitative measures of the pollinator attractiveness of the sunflower-inflorescence-imitating sticky vertical side walls of our models.

Another measure of pollinator attractiveness is the number N of black patches counted in the black-and-white maps (Figure 6d). This patch-recognizing software (AlgoNet, http://www.estrato.hu/algonet) was written by one of the authors (András Barta), and its algorithm was described by Száz et al. (2015). Every recognized black patch was considered as an individual insect carcass, thus N was assumed to coincide with the number of pollinators trapped by the sticky test surfaces. This software was validated in such a way that its output values (N) were compared with those obtained by visual-manual evaluation of the same color photographs of the sticky test surfaces containing the carcasses of trapped insects. This software can determine the N-value with an error smaller than 1%. It was also used successfully in two earlier studies in which the number of mayflies (*Ephron virgo*) was determined on photos taken about lamplit swarming mayflies (Farkas et al., 2016; Száz et al., 2015).

Field experiment 3 with head-manipulated sunflowers

In the summer of 2023 we performed field experiment 3 under more naturalistic conditions than in experiments 1 and 2. It served to count the numbers of insect pollinators landed on real sunflower inflorescences facing geographical north, east, south, or west. This experiment happened from 5 to July 10, 2023, on cloudless and warm days, when all the 40 selected sunflowers bloomed simultaneously in a sunflower plantation (hybrid type Corteva P64LE25, *H. annuus*) at the Hungarian village Sződ (47°43′00″ N, 19°12′00″ E).

Sunflowers in the plantation were monitored for the cessation of heliotropism before the onset of anthesis (first week of July), and at this time we selected four rows in the middle of the plantation, where the developmental condition of plants was the same. Using green lightweight metal tubes (mass = 35 g, length = 20 cm, diameter = 2 cm) in three selected rows, we forced 10-10-10 immature (non-flowering) sunflower heads to turn north, south, and west (±5°). The artificial turn of a given head was ensured with this tube fixed by two black plastic bonds to the sunflower stem so that they did not hinder the normal development of the plant (Figure 8). In the fourth sunflower row, we selected 10 heads facing geographical east (±5°), and for them we also applied the tube treatment, but without turning them from their natural eastward orientation. The reliability of this tube treatment was demonstrated in an earlier field experiment with sunflowers (Takács, Slíz-Balogh, et al., 2022). Between the four selected rows with tube-treated sunflowers there were 2-2-2 rows with intact (non-treated) sunflowers.

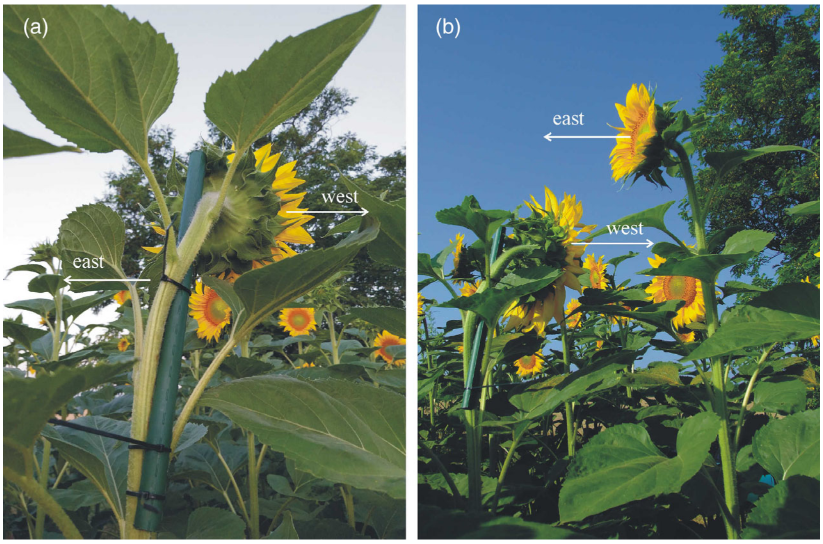

Figure 8. Sunflower inflorescences turned artificially westward. Photographs (A: close-up, B: remote) of sunflower inflorescences forced to turn westward by green lightweight metal tubes (mass = 35 g, length = 20 cm, diameter = 2 cm) fixed to the stems by two black plastic bonds among naturally east-facing sunflowers in experiment 3.

When sunflower blooming began on July 5, 2023, every 20 min we counted the insect pollinators landed on the tube-treated 40 sunflower inflorescences from 8:00 h to 18:00 h (=local summer time = Universal Time Coordinated + 2 h). Before 8 h and after 18 h, pollinators practically did not occur on sunflower inflorescences because the air temperature was not high enough for the functioning of pollinators' wing muscles. Walking along the four selected rows, we registered the numbers of pollinators on the 10-10-10-10 tube-treated inflorescences. After such a counting (lasting about 5 min) we rested 15 min among the sunflowers, then repeated the counting until sunset. We registered only the numbers of pollinators because *in situ* we could not identify them at species level. However, we took several photographs of the flower-visiting pollinators in order to determine later their taxa at least in the genus level.

Statistical analyses

Using one-way ANOVA (ANalysis Of VAriance), we compared the data groups of the area proportion Q and the patch number N_{patch} of pollinators recognized on the photographs taken of the north-, east-, south-, and west-facing vertical sticky side walls and of the sunflower-inflorescence-imitating models and the sticky horizontal ledge below them. Hence, different data groups belonged to different azimuths (north, east, south, west) of the test surfaces. Fisher's F-test was applied to determine, whether the variability between the group averages is or is not larger than the variability within the groups. When comparing several groups, ANOVA can detect only the existence/absence of a significant difference between group averages, but cannot determine the significantly different groups. To determine the latter groups, we used Tukey–Kramer post-hoc test when ANOVA detected a statistically significant between-group difference. The critical significance value was $P^* = 0.05$.

AUTHOR CONTRIBUTIONS

Substantial contributions to conception and design: GH, JS-B, MB. Software development: BD, AB, ÁE. Performing experiments and measurements: GH, BD, JS-B, MB, ÁE. Data visualization: GH, BD, DS, ÁE. Data analysis and interpretation: GH, BD, DS, AB, MB. Drafting the article and revising it critically: GH, DS.

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CONFLICT OF INTEREST STATEMENT

The authors have no competing interests.

DATA AVAILABILITY STATEMENT

The data underlying this article are available in the article and in its online Supporting material.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Table S1. Average ± standard deviation of the area proportion Q of insects trapped by the south-, east-, and west-facing sticky vertical surfaces of the 5 sunflower models in the whole period of experiment 1 (July 5–September 1, 2021). In sessions 3 and 4, some photos of models 1–2 and 5, respectively, were non-evaluable, therefore data on these models are lacking.

Table S2. Statistical ANOVA analysis of the data in Table S1 for the whole period of experiment 1 (July 5–September 1, 2021). The critical significance value is $P^* = 0.05$, meaning that if $P > P^*$, then there are no significant differences between the Q-values of the south-, east-, and west-facing test surfaces.

Table S3. Average ± standard deviation of the number N of insects (=recognized black patches) trapped by the south-, east-, and west-facing sticky test surfaces of the 5 sunflower models in the whole period of experiment 1 (July 5–September 1, 2021). In sessions 3 and 4, some photos of models 1–2 and 5, respectively, were non-evaluable, therefore data on these models are lacking.

Table S4. Statistical ANOVA analysis of the data in Table S3 for the whole period of experiment 1 (July 5–September 1, 2021) with

$P^* = 0.05$. Since $P > 0.05$, the statistical differences between the groups are not significant, and thus there is no need for Tukey–Kramer post hoc test.

Table S5. Average ± standard deviation of the area proportion Q of insects trapped by the east-, south-, west-, and north-facing sticky test surfaces of the 5 sunflower models in experiment 2 (July 1–August 18, 2022).

Table S6. Statistical ANOVA analysis of the data in Table S5 for experiment 2 (July 1–August 18, 2022) with $P^* = 0.05$. Since $P > 0.05$, the statistical differences between the groups are not significant, and thus there is no need for Tukey–Kramer post hoc test.

Table S7. Average ± standard deviation of the number N of insects (=recognized black patches) trapped by the east-, south-, west-, and north-facing sticky vertical surfaces of the 5 sunflower models in experiment 2 (July 1–August 18, 2022).

Table S8. Statistical ANOVA analysis of the data in Table S7 for experiment 2 (July 1–August 18, 2022). Since $P < 0.05$, there are statistical differences between certain groups, and thus an additional Tukey–Kramer post-hoc test is necessary.

Table S9. Tukey–Kramer post-hoc test of the data in Table S7. If $D > C$, then there is a statistically significant difference between the two test surface groups compared.

Table S10. Average ± standard deviation (SD) of the numbers of insect pollinators (predominantly honeybees, *Apis mellifera*, and bumblebees, *Bombus terrestris*) counted on the north-, east-, south-, and west-facing sunflower inflorescences during experiment 3 (July 5–10, 2023).

Table S11. Statistical ANOVA analysis of the numbers of insect pollinators counted between sunrise and sunset on the 10 north-facing, 10 east-facing, 10 south-facing, and 10 west-facing sunflower inflorescences on July 5, 2023, in experiment 3 (Table S10; Figure 3). Result: differences are not significant. df, degree of freedom; F, F-value of Fisher's test; F-crit, critical value of Fisher's test; MS, mean square; P, significance value (significant if $P < 0.05$); SS, sum of squares.

Table S12. Statistical ANOVA analysis of the numbers of insect pollinators counted between sunrise and sunset on the 10 north-facing, 10 east-facing, 10 south-facing, and 10 west-facing sunflower inflorescences on July 7, 2023, in experiment 3 (Table S10; Figure 3). Result: differences are not significant. df, degree of freedom; F, F-value of Fisher's test; F-crit, critical value of Fisher's test; MS, mean square; P, significance value (significant if $P < 0.05$); SS, sum of squares.

Table S13. Statistical ANOVA analysis of the numbers of insect pollinators counted between sunrise and sunset on the 10 north-facing, 10 east-facing, 10 south-facing, and 10 west-facing sunflower inflorescences on July 8, 2023, in experiment 3 (Table S10; Figure 3). Result: differences are not significant. df, degree of freedom; F, F-value of Fisher's test; F-crit, critical value of Fisher's test; MS, mean square; SS, sum of squares; P, significance value (significant if $P < 0.05$).

Table S14. Statistical ANOVA analysis of the numbers of insect pollinators counted between sunrise and sunset on the 10 north-facing, 10 east-facing, 10 south-facing, and 10 west-facing sunflower inflorescences on July 9, 2023, in experiment 3 (Table S10; Figure 3). Result: differences are not significant. df, degree of freedom; F, F-value of Fisher's test; F-crit, critical value of Fisher's test; MS, mean square; P, significance value (significant if $P < 0.05$); SS, sum of squares.

Table S15. Statistical ANOVA analysis of the numbers of insect pollinators counted between sunrise and sunset on the 10 north-facing, 10 east-facing, 10 south-facing, and 10 west-facing sunflower inflorescences on July 10, 2023, in experiment 3 (Table S10; Figure 3). Result: differences are not significant. df, degree of freedom; F, F-value of Fisher's test; F-crit, critical value of Fisher's test; MS, mean square; P, significance value (significant if $P < 0.05$); SS, sum of squares.

Table S16. Statistical ANOVA analysis of the total numbers of insect pollinators counted between sunrise and sunset on the 10 north-facing, 10 east-facing, 10 south-facing, and 10 west-facing sunflower inflorescences on July 5, 7, 8, 9, and 10, 2023, in experiment 3 (Table S10; Figure 3). Result: differences are not significant. df, degree of freedom; F, F-value of Fisher's test; F-crit, critical value of Fisher's test; MS, mean square; P, significance value (significant if $P < 0.05$); SS, sum of squares.

Table S17. Sum (Σ), average ($\langle\rangle$), and standard deviation ($\pm$) of the number N of pollinators versus time of day t (=local summer time = Universal Time Coordinated + 2 h) counted on the 10, 10, 10, and 10 real sunflower inflorescences facing north, east, south, and west in experiment 3. (1) July 5, 2023, (2) July 7, 2023, (3) July 8, 2023, (4) July 9, 2023, (5) July 10, 2023.

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