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Automated 24-h surveys of flower-visiting communities reveal temporal complementarities and overlaps among strawberry pollinators

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ABSTRACT

Differences in flower visitor functional traits, such as time of day of activity or foraging behaviour, allow for complementary contributions to pollination services. These traits vary among flower visitors due both to differing physiological constraints and responses to floral resource diversity and availability. However, little is known about the temporal and behavioural complementarities of flower visitors in terms of their daily activity. We carried out automated 24-h video surveys to track strawberry flower visitors in three study sites in the region of Paris (France) with different surrounding land-use composition. We tested whether different flower visitor groups were active at different times of day (i.e. temporal complementarity vs. overlap), and whether foraging behaviour varied among groups and across the day. We found that most pollinators were active during the day, with ants reported as the main nocturnal flower visitors. Moreover, we found complementarity in the temporal activity of flower visitors in the least urbanised site. In contrast, in the more densely urbanised sites, a single peak of activity occurred during the afternoon, with dominance of honey bees, indicating overlap in temporal niche. We also found that the flower-visit duration varied substantially among pollinator groups, sites, and over the course of the day. These results emphasise how pollinator community functional complementarities can be context dependent. Indeed, current knowledge is based mainly on diurnal observations of pollinator communities, which could bias our understanding of the relations between pollinator community composition and their contributions to pollination services.

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1. Introduction

Animal-mediated pollination is crucial for wild plant reproduction (Ollerton et al., 2011) and the production of over half of crops grown worldwide (Klein et al., 2007). This ecosystem service has been estimated to value between US\$195 billion to US\$387 billion annually (Porto et al., 2020). In addition to its economic value, pollination is important for human health (Ellis et al., 2015; Garibaldi et al., 2022), with many nutritious crops such as apple (Garratt et al., 2023), zucchini (Knapp and Osborne, 2017) or avocado (Sagwe et al., 2021) shown to depend to a degree on pollinators. High quality pollination services require diverse pollinator communities, with pollinator diversity being linked to the reproductive success of many plants (Albrecht et al., 2012; Fründ et al., 2013; Katumo et al., 2022), and to the yield improvement of animal-pollinated crops (Miñarro and García, 2021; Winfree et al., 2018). This is due to the fact that pollinators have differing functional traits, among which behavioural traits such as circadian rhythm, allowing for complementary (Ellis et al., 2017; Fründ et al., 2013; Pisanty et al., 2016) or even synergistic contributions to pollination services (Brittain et al., 2013; Pérez-Méndez et al., 2020). In particular, western honey bees (*Apis mellifera*), which are frequently used in farmlands to pollinate crops, cannot maximise fruit or seed set without the contribution of wild pollinators (Földesi et al., 2021; Garibaldi et al., 2013; Page et al., 2021).

While it is recognized that pollinator diversity is important, current knowledge is largely based on data collection with limited time periods during the day, which may bias our understanding of pollinator complementarity and its role for plant reproduction and crop yield. To date, most data on crop pollinators results from fieldwork focussed on diurnal pollinators (e.g., Deprá et al., 2014; Nicholson et al., 2017; Vergara and Badano, 2009), neglecting the potential role of nocturnal pollinators (Requier et al., 2023), which contribute to production of crops (Buxton et al., 2022), even for some traditionally associated with diurnal pollinators (Buxton et al., 2025; Fijen et al., 2023). Indeed, some pollinators such as Coleoptera can be active throughout the day and night (Genoud et al., 2021; Knop et al., 2018), moths (nocturnal Lepidoptera) are known as efficient pollinators (Buxton et al., 2021; Hahn and Brühl, 2016; Knop et al., 2018; Lu et al., 2021; Walton et al., 2020), and even some bee specie are known to be active at night (Macgregor and Scott-Brown, 2020). Moreover, very little attention is paid to the time of day of flower visitor activity. This points to a potential knowledge gap regarding the importance of complementarities in daily time periods of activity, which differ substantially amongst pollinators (Albrecht et al., 2012; Pisanty et al., 2016; Zaragoza-Trello et al., 2023). For instance, many pollinators, in particular insects from the orders Hymenoptera and Diptera, are known to have overlapping activity periods in the afternoon (Karbassioon and Stanley, 2023; Knop et al., 2018). Conversely, certain pollinators such as bumble bees (genus *Bombus*) can forage earlier in the morning (Peters et al., 2016). Moreover, pollinators have differing foraging behaviours on flowers, with variable flower handling time, which can vary among pollinators but also depending on environmental factors such as vegetation density (Layek et al., 2024). Another example of foraging behaviour which can vary among pollinators is pollen and nectar theft, or pollen removal without pollination, which has been documented in many flower visiting insects, among which honey bees (Hargreaves et al., 2009). The differentiation in the temporal niche occupied by pollinators as well as variations in foraging behaviours are due both to differences in physiological constraints such as thermal balance (Herrera, 1990), and responses to environmental factors such as competition for floral resources and floral resource diversity and availability (Bloch et al., 2017). Despite the knowledge that pollinators differ in their foraging activity periods, full 24-h flower visitor surveys are rarely carried out (but see Alison et al., 2022; Broussard et al., 2022; Knop et al., 2018; Wonderlin, 2023). The common sampling methods used to estimate the abundance and diversity of flower visitors include either active daytime sampling (e.g., focal observations, sweep net or transects), which span only short periods of time across the day, or passive 24 h per day sampling (e.g., pitfall traps, pan traps or bee bowls), which cannot account for time of day of flower visits, or for foraging behaviour (Requier et al., 2023; Westphal et al., 2008). Although some daytime sampling methods allow for the collection of data regarding behaviour on flowers, these are rarely studied throughout the day. Moreover, the traditional methods to sample nocturnal insects, such as moth trapping using light traps (Buxton et al., 2021; Macgregor et al., 2017) do not account for flower visiting behaviour. Thus, little is known on how flower visitor abundances and behaviours differ over the course of the day and night, and whether, at a community level, different pollinator groups show complementarity in their daily temporal occurrences, i.e. different groups are active at different times of day, or conversely show overlap in their time period of activity across the day, i.e. groups are all active in the same daily time frame. Moreover, given this limited understanding, the daily temporal changes in foraging behaviours are mostly unknown.

In order to assess complementarities or overlaps in pollinator activity periods and foraging behaviour, we used camera traps (Droissart et al., 2021) to monitor the abundance, composition and foraging behaviour of the pollinator communities visiting strawberry flowers across 24-h periods. This community level approach allows for a comprehensive view of pollinator diversity over the course of the day and night. Indeed, automated camera monitoring mimics direct focal observations, an active form of pollinator surveys, without requiring an observer's presence, thus combining the advantages of both active and passive classical surveying methods. We focused our active 24 h per day sampling on strawberries (*Fragaria × ananassa*), a spring flowering crop known to depend to some degree on insect pollinators to produce fruits (Blareau et al., 2023; Gudowska et al., 2024; Klein et al., 2007). James et al. (2024) found that two groups of strawberry pollinators, bumble bees and hoverflies, had different visitation patterns throughout the day. Moreover, a recent study revealed that strawberry crop production requires both diurnal and nocturnal pollinators to maximise fruit quality (Fijen et al., 2023). However, this study did not monitor which pollinators accounted for the diurnal and nocturnal pollination services recorded. Our study took place in urban and residential sites, allowing us to compare timing and behaviour of flower visitor activity in different settings, since fine-scale local factors are known to impact pollinator communities in urban areas (Ayers and Rehan, 2021; Zaninotto et al., 2023). We expect to find some overlap in timing of flower visitor activity with a flower visitor community most active around midday. We also predict that some groups will show complementarities by having different time frames of flower-visiting activity throughout the day. In particular, we expect to observe nocturnal flower visits, additional to diurnal flower visitors. We further predict that foraging behaviours, measured as the part of the flower visited (anther and stigma vs. perianth) and the

Table 1
Average (\pm sd) abundance of different pollinator groups per 24-h cycle in the three sites.

| | Honey bee | | Bumble bee | | Small wild bee | | Large wild bee | | Hoverfly | | Other fly | | Ant | | Butterfly | | Beetle | | Other | |
|------------------|-------------------|-------|-----------------|-------|-----------------|-------|-----------------|-------|-----------------|-------|-----------------|-------|------------------|------------------|-----------------|-------|-----------------|-----------------|-----------------|-----------------|
| | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night |
| Sub-urban garden | 0.57 \pm 0.53 | 0 | 1.43 \pm 2.99 | 0 | 5.71 \pm 9.62 | 0 | 0 | 0 | 0.57 \pm 0.98 | 0 | 0.14 \pm 0.38 | 0 | 9.14 \pm 20.72 | 0.86 \pm 1.84 | 0.43 \pm 0.53 | 0 | 2.00 \pm 1.53 | 0 | 0.29 \pm 0.49 | 0.14 \pm 0.38 |
| Urban park | 10.29 \pm 13.17 | 0 | 1.57 \pm 1.72 | 0 | 1.00 \pm 1.91 | 0 | 0.14 \pm 0.38 | 0 | 1.29 \pm 2.21 | 0 | 0.57 \pm 0.79 | 0 | 2.14 \pm 4.85 | 0.43 \pm 11.13 | 0.29 \pm 0.49 | 0 | 1.71 \pm 2.98 | 0.14 \pm 0.38 | 2.29 \pm 3.30 | 0 |
| Urban rooftop | 1.13 \pm 2.56 | 0 | 1.27 \pm 3.15 | 0 | 0.13 \pm 0.52 | 0 | 0.07 \pm 0.26 | 0 | 0.73 \pm 0.96 | 0 | 0.13 \pm 0.35 | 0 | 0.07 \pm 0.26 | 0 | 0 | 0 | 0 | 0 | 0.20 \pm 0.56 | 0.07 \pm 0.26 |

time spent on flowers will differ among flower visitor groups and time of day.

2. Materials and methods

2.1. Study sites

The study took place in the Île-de-France region (France). Three sites were selected (Supplementary material, Fig. S1A), in different environmental conditions within urban or residential areas. The first site was a suburban garden site within a housing development surrounded mainly by discontinuous urban landscape (41 % within 1.5 km), forested area (32 % within 1.5 km), and agricultural landscape (24 % within 1.5 km) (Itsap, 2023). This site was located in the town of Chevreuse (48°42'42.4"N 2°03'47.7"E, approximately 20 km south west of Paris) (Supplementary material, Fig. S1B), and had some ornamental and crop floral resources available in the surrounding gardens and allotments. The second site was an urban park (27 ha) surrounded mainly by continuous urban landscape (89 % within 1.5 km including roads and rail), with other land use types being waterways (7 % within 1.5 km, i.e. the Seine river), and urban green space (4 % within 1.5 km) (Itsap, 2023). This site was located within the city centre of Paris (Jardin des plantes, 48°50'38.0"N 2°21'41.0"E) (Supplementary material, Fig. S1C), with mainly ornamental and a few native floral resources available within the park. The third site was an urban rooftop site located on the rooftop of a 30 m high building (8 stories) within the city centre of Paris (48°51'00.1"N 2°21'47.6"E), and surrounded mainly by continuous urban landscape (90 % within 1.5 km including roads and rail), with other land use types being waterways (6 % within 1.5 km, i.e. the Seine river), and urban green space (4 % within 1.5 km) (Itsap, 2023) (Supplementary material, Fig. S1D). This site offered few floral resources from small plants grown in pockets in vertical planting walls. The urban park site and the urban rooftop site were approximately 600 m from each other, thus the surrounding landscapes overlap.

2.2. Study plants

Strawberry plants (*Fragaria x ananassa*) of the variety "Charlotte" (cross of the varieties "Mara des bois" and Cal 19, (Gasic et al., 2016)) were bought from a plant nursery in March 2023. They were brought to the experimental sites in April, and were kept in 5 L pots throughout the experiment, except on the urban rooftop, where they were planted in 2.5 L soil pockets on vertical planting walls. The soil in which the plants were potted came from the plant nursery, and was thus standardised for all plants. This limits impacts of local soil on plant growth and flowering (Ariza et al., 2021). The suburban garden and the urban park had 16 potted plants set up, whereas 40 were installed on the urban rooftop. Automated irrigation systems were set up to ensure that all plants were watered sufficiently (Orbit 24600 programmer with a 4 L per hour dripper in each pot for the urban park and the suburban garden). Plants were watered daily using these automated irrigation systems, which removes any potential bias from water stress on plant development (Klamkowski and Treder, 2006), although differing temperatures among sites in different urban configurations, due to the urban heat island, could have affected plants' water requirements (Zipper et al., 2017).

2.3. Automated 24-h surveys of flower visitors

We used PICT (Plant-insect Interaction Camera Traps) technology (Droissart et al., 2021) to film plant-pollinator interactions. The equipment to build these cameras was purchased in 2021 and comprised of a Raspberry Pi A+ computer linked to a camera lens (NoIR, Waweshare) and a large battery (power: 24000 mAh, Ansmann) (Supplementary material, Fig. S2). The cameras were equipped with an infrared light, making nocturnal monitoring possible (Droissart et al., 2021). Videos were stored on a micro-SD card (128 GB storage space, SanDisk). These cameras were set up to follow visitors over 24 h cycles to single, or maximum two, strawberry flowers from the 16th of May to the 9th of June 2023. The lens was placed at approximately 30 cm from the flowers (Supplementary material, Fig. S2). In total, 29 cycles of 24 h (i.e. a total of 695 h of video, where one session in the suburban garden was missing one hour of footage) were recorded: 7 cycles in the suburban garden site, 7 cycles in the urban park site, and 15 cycles on the urban rooftop site. Overall, we

Table 2

Results from the GAMM testing the effect of time of day on the activity of different flower visitor groups, in the three study sites. Effective Degrees of Freedom (EDF) indicate the degree of linearity of the relationship between abundance of each group and time of day, with increasing values indicating the relationship is more complex, with more cycles of increase and decrease (i.e. more oscillatory). Groups within sites that showed significant change in activity pattern across the day, with $p < 0.05$, are indicated in bold.

| | Suburban garden | | | Urban park | | | Urban rooftop | | |
|----------------|-----------------|---------|---------------------|-------------|---------|---------------------|---------------|---------|---------------------|
| | EDF | F-value | P-value | EDF | F-value | P-value | EDF | F-value | P-value |
| Honey bee | 1.431 | 0.674 | 0.046 | 3.612 | 121.311 | p < 0.001 | 2.852 | 10.493 | p < 0.001 |
| Bumble bee | 2.882 | 4.782 | p < 0.001 | 2.540 | 7.884 | p < 0.001 | 3.076 | 11.044 | p < 0.001 |
| Small wild bee | 3.961 | 51.283 | p < 0.001 | 2.193 | 3.213 | p < 0.001 | 5.700e - 05 | 0 | 0.492 |
| Hoverfly | 4.599e - 05 | 0 | 0.439 | 2.038 | 1.788 | 0.002 | 2.265 | 3.496 | p < 0.001 |
| Other fly | 4.925e - 07 | 0 | 0.843 | 1.478 | 0.730 | 0.039 | 8.783e - 06 | 0 | 0.624 |
| Ant | 5.285 | 36.896 | p < 0.001 | 4.084 | 9.107 | p < 0.001 | 1.458e - 06 | 0 | 0.888 |
| Butterfly | 1.092 | 0.357 | 0.126 | 5.377e - 07 | 0 | 0.825 | 7.577e - 07 | 0 | 1 |
| Beetle | 3.878 | 7.520 | p < 0.001 | 3.292 | 11.437 | p < 0.001 | 7.532e - 07 | 0 | 1 |

monitored plant-pollinator interactions on 40 flowers (10 in the suburban garden site, 8 in the urban park site and 22 on the urban rooftop site) since several flowers could be filmed at once. Cycles within each site were distributed evenly across the 25-day timespan of the experiment.

2.4. Identification of flower visitors and their behaviour

For each flower visit, we aimed to record the identity of the flower visitor, the time at which it took place, as well as foraging behaviour data such as the part of the flower visited (anthers and stigmas vs. perianth), and the duration of the flower visit. Having accumulated 695 h of footage, we opted for a sampling method that allowed us to reduce the observation time while maintaining a representative flower visitor community. Although this reduced the overall observation time, the sampling effort was consistent throughout the 24-h time series, where the same amount of time was viewed for each hour of recorded footage. Along similar lines, Fijen and Kleijn (2017) show that after a certain threshold of observation time, increasing observation time did not increase the accuracy of visitation rate predictions. For each hour of footage, we viewed 5 randomly selected slots of 5 min, amounting to 25 min viewed per hour of footage. This method mimics 5 min field observations traditionally used (e.g. Castle et al., 2019; Griffiths-Lee et al., 2020 on strawberry), but with greater replication. According to a prior analysis, this choice was robust since at least 50 % of total diversity per hour was accounted for (Supplementary material: Fig. S3).

We focused on 10 flower visitor groups acknowledged as crop pollinators and easily identifiable (Rader et al., 2020; Requier et al., 2023; Rader et al., 2016): honey bees (*Apis mellifera*), bumble bees (genus *Bombus*), small wild bees (i.e. body length shorter than 1 cm), large wild bees (i.e. body length longer than 1 cm), hoverflies (flies from the Syrphidea family), non-hoverfly Diptera, butterflies (diurnal Lepidoptera), moths (nocturnal Lepidoptera), beetles (Coleoptera) and ants (family Formicidae). Any other flower visitor was assigned to the “other flower visitor” category. For each flower visit, we recorded the part of the flower that was visited (i.e. the reproductive parts of the flower such as pistils and stamens, or non-reproductive parts such as sepals and petals), and the total duration of each visit, from the first contact with either reproductive or non-reproductive parts of the flower to the moment the insect left the flower, in order to assess pollinator behaviour.

2.5. Statistical analysis

All statistical analysis was carried out in R 4.3.2 (R Core Team, 2024). In all models, we considered each 24-h cycle of a single flower within each site as a unique monitoring session. In order to understand how the abundance of different pollinator groups changed across the day, we first calculated, for each monitoring session, the number of visits per flower visitor group per hour, using the “dplyr” R-package (Wickham et al., 2023). We then ran a Generalised Additive Mixed Model (GAMM) using the “mgcv” R-package (Wood, 2011) to explore whether the abundance of flower visitors (response variable with Poisson distribution of errors) varied with time of day (considered as a smooth term, with $k = 8$, where k is the number of basis functions used to model the data) and potentially depended on pollinator group and study site. The value of k was chosen to be high enough to account for complex patterns in flower visitor abundance across the day without overfitting. We considered cyclic cubic splines in the GAMM to account for the cyclic nature of time over 24-hs, and the monitoring session nested within the site as random variables. We removed the “other flower visitor” and “large wild bee” categories for which too few data points were available.

In order to assess how flower visitor behaviour differed over the course of the day, we fitted a GAMM to explore whether the duration of flower visitor visit (response variable with Poisson error distribution) varied over the course of the day (considered as a smooth term, with $k = 4$) and potentially depended on pollinator group. Here the value of k is lower than for the previous model since we expect less complex variation of visit duration than visitor abundance over the course of the day. Moreover, the dataset for this

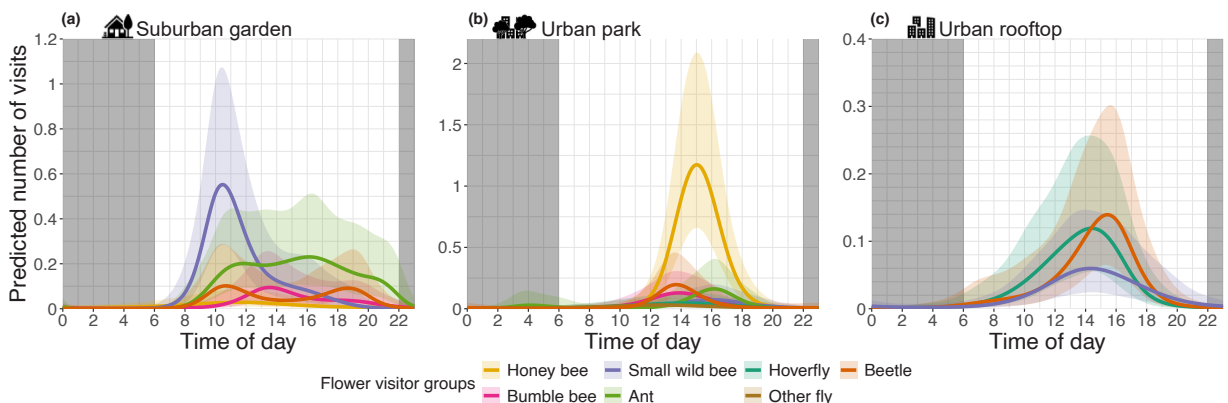


Fig. 1. Predicted number of visits (\pm standard error) of different flower visitor groups over the course of the day in (a) the suburban garden, (b) the urban park, and (c) the urban rooftop. Only groups which showed significant change in activity across the day are represented. Areas shaded in grey represent the night time.

Table 3

Results from the GAMM testing the changes in visit duration depending on flower visitor group, the part of the flower visited, their interaction, and study site, as well as whether visit duration changes across the day for each flower visitor group. Effective Degrees of Freedom (EDF) indicate the degree of linearity of the relationship between abundance of each group and time of day, with increasing values indicating the relationship is more complex, with more cycles of increase and decrease (i.e. more oscillatory). Variables that had a significant effect on visit duration, and groups which showed significant variation in visit duration across the day ($p < 0.05$) are indicated in bold.

| Parametric terms | F | p-value | Time of day for each group (smooth terms) | | | |
|--|---------------|---------------------|---|--------------|---------------|---------------------|
| | | | EDF | F | p-value | |
| Flower visitor group | 635.84 | p < 0.001 | Honey bee | 1 | 0.537 | 0.46 |
| Flower part visited | 1.191 | 0.276 | Bumble bee | 2.03 | 2.34 | 0.10 |
| Site | 16.82 | p < 0.001 | Small wild bee | 2.824 | 22.02 | p < 0.001 |
| Flower visitor group: Flower part visited | 34.681 | p < 0.001 | Ant | 2.94 | 58.37 | p < 0.001 |
| | | | Hoverfly | 2.97 | 48.50 | p < 0.001 |
| | | | Beetle | 2.96 | 309.35 | p < 0.001 |

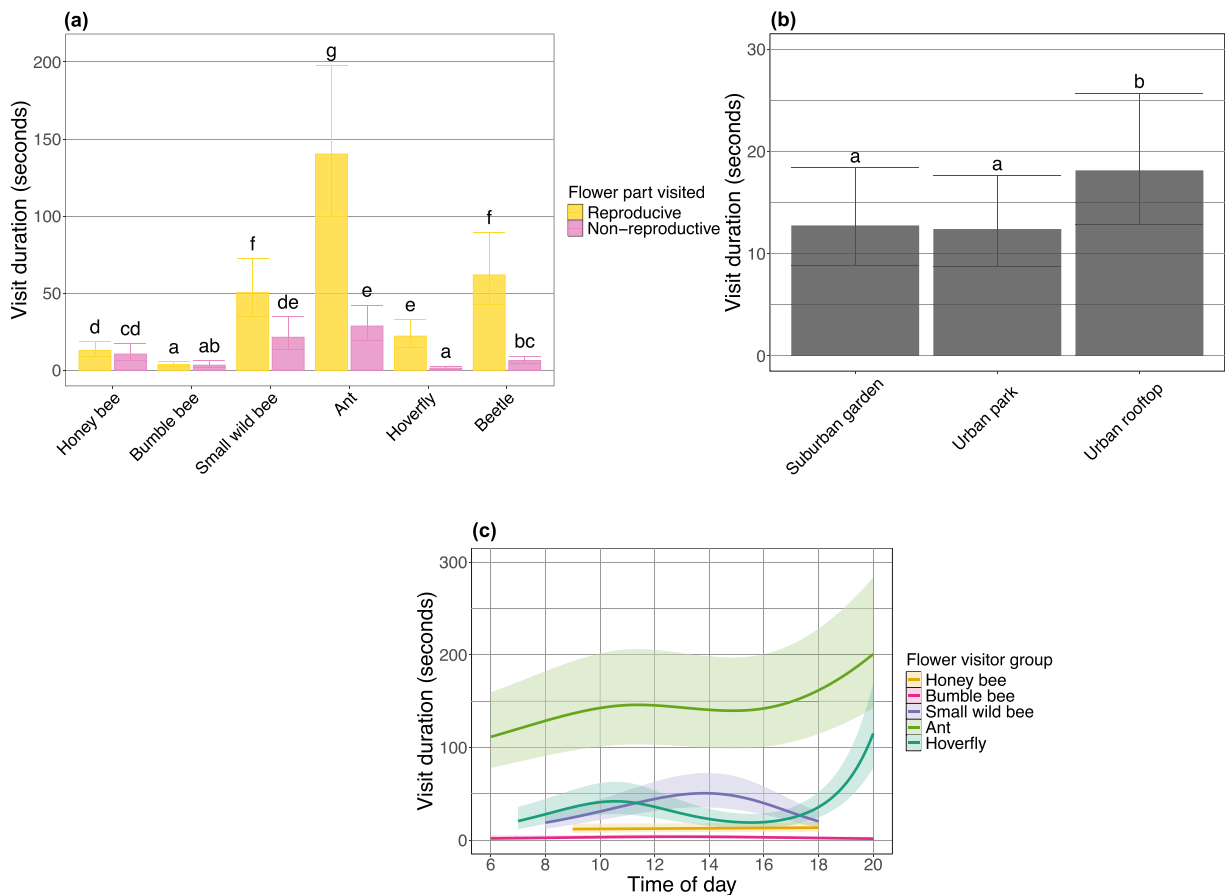


Fig. 2. (a) Visit duration to flower reproductive and non-reproductive parts for different flower visitor groups. Bar height represents the predicted values with standard errors shown as error bars. Different letters indicate a significant difference in visit duration. (b) Visit duration across sites. Bar height represents the predicted values with standard errors shown as error bars. Different letters indicate a significant difference in visit duration. (c) Visit duration (\pm standard error) to flowers throughout the day for different flower visitor groups. Plotted predictions are restricted to the hours of the day for which each group is active.

analysis being smaller, there is a risk of overfitting for high values of k . Due to the large majority (96.38 %) of visits taking place during the daytime (from 6:00 to 22:00), we only considered this time span in this GAMM. This avoided overfitting during hours where very few visits were recorded. This time span was not cyclic, thus we considered non-cyclic cubic regression splines in this GAMM. Flower visitor group and the part of the flower visited, as well as their interaction, and study site, were set as fixed factors. Monitoring session nested within the site was set as a random variable.

Regarding flower visitor groups, we excluded pollinator groups that had less than 10 occurrences. This removed the following

categories: large wild bees, butterflies, moths and non-hoverfly Diptera. We also removed the “other flower visitor” category since having insects on a wide functional scale within it, it would not be informative to test the differences in visit duration compared to other groups. We also excluded outliers with visit durations that exceeded 1000 s (over 15 min).

For both GAMMs, we checked the significance of the variables using the “car” R-package (Fox and Weisberg, 2019), and we used the “ggeffects” R-package (Lüdtke, 2018) to generate predictions, which we plotted using the “ggplot2” R-package (Wickham, 2016). We used the “emmeans” R-package (Lenth, 2024) to generate pairwise comparisons of visit duration among pollinator groups for the different parts of the flower visited, and for the different study sites.

3. Results

3.1. Flower visitor diversity and circadian rhythms

After having reviewed 290 h of video data from the 695 h of footage, we recorded a total of 359 visits to strawberry flowers across all sites. Different flower visitor groups had varying abundances overall. Honey bees were the most abundant group with 93 observations (25.9 % of total visits), followed by ants with 89 observations (24.8 % of total visits), then small wild bees with 49 observations (13.6 % of total visits), bumble bees with 40 observations (11.1 % of total visits), beetles with 27 observations (7.5 % of total visits), hoverflies with 24 observations (6.7 % of total visits), non-hoverfly Diptera with 7 observations (1.9 % of total visits), butterflies with 4 observations (1.1 % of total visits) and large wild bees with 2 observations (0.6 % of total visits). Other flower visitors accounted for 24 observations, and included 3 arachnids (0.8 % of total visits), 2 caterpillars (0.6 % of total visits), 1 aphid (0.3 % of total visits), and 18 flower visitors which we were not able to assign to a category (5 % of total visits). Visits were not homogeneously distributed among sites (Supplementary material: Fig S4), with an average of 21.9 visits per monitoring session in the urban park, 21.3 visits per monitoring session in the suburban garden and 3.8 visits per monitoring session on the urban rooftop. The dominant flower visitor in the suburban garden were ants, whereas in the urban park visits were dominated by honey bees (Table 1). On the urban rooftop, bumble bees were the most abundant group (Table 1). Nocturnal flower visits represented 3.3 % of total visits. These nocturnal flower visitors included mainly ants, with 10 observations, across two sites: the suburban garden and the urban park. The remaining nocturnal visits were by a beetle in the urban park, a caterpillar on the urban rooftop and an arachnid in the suburban garden.

Regarding time of day of flower visitor activity, the GAMM shows that most groups within the different sites had variation in their activity period across the day (Table 2). Some groups within certain sites had constant levels of activity across the day, i.e. no significant variation in activity levels. These were butterflies in all three sites, non-hoverfly Diptera in the suburban garden and on the urban rooftop, hoverflies in the suburban garden, small wild bees, ants and beetles on the urban rooftop (Table 2).

For groups that showed variation in activity over the course of the day, there were differences in timing and spread of activity. Indeed, in the suburban garden, overall activity of flower visitors was spread across the day, between 7:00 and 23:00. Small wild bees showed a unimodal peak in activity at 10:30. Ants were active from 8:00–23:00 with two peaks at 11:48 and 16:06. Beetles showed two peaks in activity at 10:42 and 18:42, and bumble bees showed a unique activity peak at 13:30. Honey bees had low levels of activity throughout the day in this site, with a unique peak in activity at 11:36 (Fig. 1a). In the urban park, most flower visitor activity was concentrated between 11:00 and 20:00. All groups in this site showed unimodal patterns of activity. There was a high peak in honey bee visits at 15:00, with lower peaks of activity for bumble bees at 13:54, beetles at 13:42, ants at 16:12, small wild bees at 16:00, hoverflies at 14:12 and non-hoverfly Diptera at 12:48 (Fig. 1b). On the urban rooftop, flower visitor activity took place between 7:00 and 20:00. There was also a unique peak in activity for the three groups that showed temporal activity variation. Activity peaks were at 14:24 for honey bees, 15:24 for bumble bees, and 14:18 for hoverflies (Fig. 1c).

3.2. Flower visitor behaviour

After having filtered the data according to the method described previously (i.e. removing nocturnal visits, removing groups with too few observations etc.), of the 359 flower visits observed, we took visit duration into account for 306 insect visits (i.e. 85.2 % of all observed visits). According to the GAMM, visit duration to flowers differed significantly among pollinator groups ($p < 0.001$) and among sites ($p < 0.001$) (Table 3). Ants were the group that spent the longest time on flowers, with a visit duration significantly greater than all other groups ($p < 0.001$ for each pairwise comparison involving ants, Table S1, Fig. 2a). Bumble bees showed shorter visits than all groups except for hoverflies, from which visit duration did not differ significantly ($p = 0.245$, Table S1, Fig. 2a). Although overall visit duration did not differ between the parts of the flower that were visited, the interaction between the flower visitor group and the part of the flower visited was significant (Table 3). For all groups, time spent on non-reproductive parts of the flower was either equal to or shorter than time spent on reproductive parts of the flower (Fig. 2a). Groups that showed shorter visits to non-reproductive parts were small wild bees, ants, hoverflies and beetles (Fig. 2a, $p < 0.001$ for each). Visit duration was significantly lower on the urban rooftop compared to the suburban garden ($p < 0.001$) and to the urban park ($p < 0.001$) (Fig. 2b). There was no difference in visit duration between the suburban garden and the urban park ($p = 0.881$, Fig. 2b). Of the six flower visitor groups tested, only 4 showed variations in flower visit duration across the day. These were small wild bees, ants, hoverflies and beetles (Table 3). Ants show a general increase of their visit duration over the course of the day, with an increase between 06:00 and 11:24, a slight decrease until 14:54 followed by another increase until 20:00 (Fig. 2c). Hoverflies show a similar pattern of visit duration across the day, with an increase from 07:00–10:36, then a decrease until 15:30, and a final sharp increase until 20:00 (Fig. 2c). Small wild bees show a unimodal pattern of flower visit duration, with a peak at 13:48 (Fig. 2c). Beetles show a decrease in visit duration to flowers from 10:00–13:36, and then a sharp increase until 20:00 (Supplementary material: Fig. S5).

4. Discussion

In this study we used automated 24-h camera monitoring to explore patterns of complementarity or overlap in strawberry flower visitor activity and behaviour. We found distinct patterns in flower visitor activity among groups, but these varied among sites. Indeed, we show that complementarity or overlap in flower visitor activity is context dependent, with more complementarity in the suburban site compared to the urban sites. We observed very few nocturnal flower visitors, which were mainly ants. Moreover, we found that time spent on flowers differed among groups, with non-winged insects such as ants showing longer visits, and pollinators such as bumble bees showing longer visits. Overall, visits were longer on the urban rooftop. Certain groups showed varying visit duration over the course of the day, with mainly increases throughout the day, except for small wild bees. These results emphasise the need to take different times of day into account when surveying pollinator communities, and how environmental conditions such as different urban configurations could change timing and behaviour of insect pollinators, since local scale characteristics in cities are strong drivers of pollinator abundance and diversity (Zaninotto et al., 2023). Considering temporal and environmental elements may reduce risks of missing key pollinators active only at specific times of day or in specific environmental settings.

4.1. Timing of flower visitor activity across sites

We found a wide window of activity with several peaks of activity of the flower visitor community across the day in the least urbanised site, and unimodal peaks in activity in the afternoon in the two most urbanised sites. This points to a potentially different split in the temporal niche of flower visitors depending on environmental conditions. Indeed, in the suburban garden, small wild bees dominated flower visits in the morning, after which the activity peaks of certain groups coincide with dips in activity of others, suggesting complementarity in flower visits, i.e. the temporal niche is split between different flower visitors. This is in accordance with results from previous research which found that solitary bees were mainly active in the morning, whereas social bees preferred the afternoon (Albrecht et al., 2012; Pisanty et al., 2016). This could indicate an avoidance of competition for floral resources (Bloch et al., 2017; Santos et al., 2013). However, this complementarity was not consistent among sites. Indeed, the urban park was characterised by more overlapping flower visitor activity, with a very large dominance of honey bees, showing a peak in activity in the mid-afternoon, at 15:00. This result could be linked to the recent development of urban beekeeping, leading to an overrepresentation of managed honey bees in cities (Alton and Ratnieks, 2016; Ropars et al., 2019). Interestingly, other flower visitor groups were also only active in the afternoon in this site, with bumble bees and beetles showing activity peaks slightly earlier than honey bees (around 14:00), and small wild bees and ants slightly later (around 16:00), indicating somewhat of a split in the temporal niche. This site, which was within a large park offering diverse floral and nesting resources, showed a much higher abundance of pollinators compared to the urban rooftop, which was less than 1 km away, highlighting the importance of urban greenspaces to promote pollinators (Anderson et al., 2023a; Daniels et al., 2020; Normandin et al., 2017). Indeed, the urban rooftop received the fewest visits overall, with overlapping flower visitor activity, i.e. all groups were active at the same time. This lack of visits to the urban rooftop could be explained by its difficulty to access for insects due to its height and wind exposure, as well as the lack of floral resources in rooftop habitats (Rajbhandari et al., 2023; Tonietto et al., 2011). Thus, the competitive pressure from other flower visitors could have been weaker, allowing them to visit flowers at the same time of day. It is surprising that there were few visits in the morning in the two most urbanised sites, since higher temperatures in the morning due to the urban heat island should allow flower visitors to be active earlier (Zeballos et al., 2022). These patterns could be explained by other disturbances that occur in urban environments, such as the high proportion of impervious surfaces, which prevents the presence of ground-nesting bees in urban environments (Geslin et al., 2016; Pfeiffer et al., 2023). In particular, it is surprising that small wild bees were active mainly in the morning in the suburban garden, whereas they were active mainly in the afternoon in the two most urbanised sites. This could be due to the categorisation of flower visitors into groups, which pool a high number of species together. Thus, urban environments may filter out certain species of small wild bees, namely those most active in the morning.

4.2. Nocturnal pollinators' response to urban environments

As predicted, most of the flower-visiting activity took place during the day. We observed very few nocturnal flower visitors, of which ants were the most abundant. This is consistent with results from Wonderlin (2023), who found that ants dominated nocturnal flower visits in urban gardens. Contrary to our expectation, we did not observe any moths visiting strawberry flowers at night. Although strawberry flower morphology is not typically associated with moth pollination, crops with similar floral morphologies such as apple (Robertson et al., 2021) or kiwifruit (Broussard et al., 2022), are visited by moths. Moreover, Buxton et al., (2024) showed that, contrary to expectations, moths visit flowers with open morphology as frequently as those with tubular morphology. Moreover, nocturnal pollinators have been found to contribute to pollination services on this crop (Fijen et al., 2023). In the context of our study, a potential reason for the lack of moths is that Lepidoptera are very sensitive to land use change, and are particularly impacted by urbanisation (Desaegher et al., 2023; Wonderlin, 2023). An additional factor explaining the lack of moths is that nocturnal temperatures remain low in spring in the study area, potentially too low for moths to be active. Indeed, Anderson et al. (2023b) recorded numerous nocturnal visits of moths to brambles but they limited their sampling to nights with temperature above 12°C. Furthermore, Artificial Light At Night (ALAN) could be detrimental to nocturnal pollinators in urbanised areas, through direct flight-to-light effects (Macgregor et al., 2017), increasing mortality and vulnerability to predation, as well as indirect effects to reproductive success (Macgregor et al., 2015). Detrimental effects of ALAN on nocturnal pollinators could in turn disrupt pollen transfer (Macgregor et al., 2017), thus potentially impacting pollination services. The three sites in our study could have been impacted by ALAN since they are all

in densely urbanised or residential areas. This could further explain why there were so few nocturnal flower visits across all sites. It has even been suggested that lower plant reproduction as a result of negative impacts of ALAN on nocturnal pollinators could subsequently decrease floral resources for diurnal pollinators (Knop et al., 2017). This could add to the factors disturbing the whole diurnal and nocturnal pollinator communities in urban habitats.

4.3. Flower visitor behaviour across sites and times of day

Our results suggest that the flower visitor groups recorded in this study are all potential pollinators, since they spend more or equal amounts of time on reproductive parts of the flowers than on non-reproductive parts. This shows that they feed on floral resources and can potentially transfer pollen from flower to flower. This constitutes one of the conditions for an effective pollinator, the other conditions being the transport and deposition of compatible pollen. Indeed, feeding on floral resources and duration of flower visits is not necessarily an indicator of pollination efficiency (Broussard et al., 2022; Sakamoto et al., 2012). On one hand, we found that ants, the only non-winged insect considered, spent considerably more time on flowers than the other flower visitor groups. The role of ants in pollination remains ambiguous, with evidence that antibiotic secretions kill pollen grains (Beattie et al., 1984), but recent studies emphasise their potentially neglected role in pollination (Das and Das, 2023). On another hand, bumble bees and honey bees had shorter visits than other wild pollinators. However, single-visit pollen deposition studies have shown that wild pollinators have equal (Broussard et al., 2022; Page et al., 2021; Reilly et al., 2024) if not greater (Földesi et al., 2021; Garibaldi et al., 2013) pollination efficiency than honey bees. Here we found that flower visitors on the urban rooftop, the least visited site, showed longer visits than their counterparts in the two other sites. This could reflect how competition for floral resources pushes pollinators to shorten their flower visits, as shown for honey bees in competition with bumble bees (Balfour et al., 2015). This is particularly relevant in the urban context, since studies show that the increase in abundance of managed honey bees in cities creates strong competition for floral resources with wild pollinators (Ropars et al., 2019). In addition, the urban park and suburban garden had more abundant floral resources available in the immediate surroundings, thus attracting more pollinators, increasing competition and thus decreasing time spent on flowers (Layek et al., 2024). The lack of floral resources on the urban rooftop could also potentially have led pollinators to spend more time on the few that were available. We found that ants and hoverflies show a general increase in visit duration over the course of the day, with slightly shorter visits in the mid-afternoon. This matches the peak in activity in the more urbanised sites, in particular of honey bees. This further points to a potential effect of competition on the duration of flower visits. However, this dip in visit duration could also be attributed to increasing temperature in the afternoon (Steen, 2017), which allows insects to move faster. Interestingly, small wild bees showed a pattern with longest visits in the early afternoon. This could be due to fluctuations in nectar production, with evidence from certain plants that peak secretion is timed with the period of peak pollinator activity (Bloch et al., 2017; Edge et al., 2012). Pollinators would thus spend more time on flowers at the peak times of nectar secretion since there are more resources to collect (Jones et al., 1998; Manetas, Petropoulou 2000). Thus, patterns in visit duration throughout the day vary between flower visitor groups, which potentially respond differently to drivers such as temperature, competition or nectar secretion. For honey bees and bumble bees, which show the shortest visits of all groups, we found no temporal variation in visit durations. This does not mean there were no differences, only that our time scale, which does not go below one second, was too coarse to detect any. Indeed, Sakamoto et al. (2012) underline that pollinators show varying behaviours on flowers at a very fine time scale.

4.4. Research perspectives in 24-h pollinator monitoring

Our results show how flower visitor community activity and foraging behaviour can vary over the course of the day and depending on environmental conditions. However, exhaustive data collection on timing of flower visitor activity is challenging to set up. Although we were able to maintain full 24-h cycles of monitoring, we were not able to get a comprehensive view of all flower visitors, due to time constraints. With the rise of automated video (Pegoraro et al., 2020) and audio (Folliot et al., 2022) monitoring, as well as artificial intelligence tools such as deep learning, automatic insect detection can be developed, thus reducing the observation time and allowing for exhaustive surveys of flower visitors over 24-h periods. This kind of tool could allow to detect less frequent flower visitors. These methods have the additional advantage of offering a non-lethal approach to pollinator monitoring, since debates have recently emerged on the ethics of traditional insect sampling methods (Barrett and Fischer, 2024; Lövei and Ferrante, 2024).

5. Conclusion

Using automated 24-h camera monitoring, we report varying patterns of flower visitor activity and behaviour throughout the day. In the context of this study, we found that complementarity or overlap in flower visitor activity was context dependent, with more complementarity in the suburban site compared to the urban sites. We also report that time spent on flowers varies among flower visitor groups and over the course of the day. Pollinator communities are known to be sensitive to local landscape characteristics, which can vary between urban sites (Bennett and Lovell, 2019; Birdshire et al., 2020; Quistberg et al., 2016). Thus, we call for future research to perform similar analyses in more sites in various landscapes, in order to understand how these different landscapes affect flower visitor activity. For instance, nocturnal pollinators are often neglected (Requier et al., 2023), but are subject to ALAN in urbanised areas (Macgregor et al., 2015), or night-time pesticide applications in agricultural landscapes, which are recommended to mitigate impacts on diurnal pollinators (Decourtye et al., 2016; Karbassioon and Stanley, 2023). We highlight the importance of taking different times of day and environmental conditions into account when evaluating pollinator abundance and diversity, since different groups are not active at the same times of day. Indeed, complementarities in pollinator communities require round the clock surveys to

be detected, and these complementarities may be disrupted in highly disturbed environments, leading to overlapping patterns of activity among pollinator groups.

CRedit authorship contribution statement

Elsa Blareau: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Clarisse Gabard:** Methodology, Investigation, Formal analysis, Data curation. **Clémence Riva:** Resources, Methodology. **Isabelle Dajoz:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization. **Fabrice Requier:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

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Data statement

All data is available on the open repository Zenodo, within the iEES-Paris community: <https://doi.org/10.5281/zenodo.15772826>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03727](https://doi.org/10.1016/j.gecco.2025.e03727).

Data availability

Data will be made available when paper is accepted for publication.

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