



# Local conditions drive quantity-oriented reproductive strategies and pollen diet of a solitary cavity-nesting bee in a Mediterranean peri-urban environment

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## Abstract

Green areas in urban and peri-urban landscapes are increasingly recognized as important habitats for wild bees, but the extent to which species adjust their reproductive behavior to local conditions in these environments remains poorly studied. We studied the reproductive output, offspring's body size, sex allocation, and larval diet (assessed using pollen morphology and DNA metabarcoding) of the solitary bee *Osmia caerulescens* (Linnaeus, 1758) in a Mediterranean peri-urban environment using trap nests and local-scale environmental descriptors. Based on a total of 215 nests and 648 brood cells, females increased their reproductive output with greater floral resource availability and increasing openness of the habitat, but this was accompanied by a reduction in offspring body size (ITD) and a sex allocation skewed toward males. These findings are consistent with a trade-off between offspring number and per-offspring investment and contrary to general expectations that higher resource availability should favor larger and more female-biased offspring. Together, these responses indicate a shift toward quantity-oriented reproductive strategies, in contrast to patterns reported for this species in agricultural systems, where higher resource availability is typically associated with greater per-offspring investment and more female-biased sex ratios. Pronounced among-site variation in pollen diet, reflecting differences in local floral resource composition, further highlights how use of floral resources varies at a fine spatial scale and may shape reproductive strategies and, ultimately, population persistence. Our results show that the ecological value of urban habitats for solitary bees depends not only on the amount of floral resources available, but also on how local conditions influence species-specific reproductive responses. These findings highlight the value of species-specific reproductive analyses in abundant, functionally important solitary bees as a complementary approach to evaluating habitat quality at local scales in urban and peri-urban environments. Understanding how solitary bees adjust reproductive strategies to urban conditions is essential for supporting their conservation and long-term persistence in urban green spaces.

**Keywords** Trap nest · Osmiini · Urban pollinators · Body size · Sex allocation · Solitary bees

## Introduction

Land-use change is a major driver of global biodiversity loss, with strong effects on local terrestrial communities worldwide (Newbold et al. 2015). Urban areas, however, are heterogeneous landscapes that can host relatively high biodiversity when properly managed (Biella et al. 2025a), particularly if compared to highly intensified agricultural

systems (Baldock et al. 2019; Banaszak-Cibicka and Żmihorski 2012; Theodorou et al. 2020). The effects of urbanization on insects depend strongly on local landscape configuration and management (Fenoglio et al. 2020, 2021). In this context, green urban spaces can be characterized by low-intensity, regular disturbance regimes (e.g. mowing) that maintain plant communities rich in floral resources, thereby supporting wild bee populations (Buchholz et al.

2020; Dylewski et al. 2020; Rada et al. 2024). More broadly, these management regimes, together with changes in floral composition and habitat structure, create novel ecological conditions that can shape how bees exploit resources and allocate reproductive effort. As a result, cities may function as refuges for wild bees within landscapes dominated by intensive agriculture, where pollinator habitats are often reduced and homogenized (Hall et al. 2017; Ranalli et al. 2025).

Despite this potential, our understanding of how urban environmental conditions shape pollinator communities and their ecological responses remains incomplete. In response, research has focused on identifying management actions (e.g., sowing pollinator-friendly plants, reducing mowing intensity) capable of enhancing urban habitats for pollinators (Süle et al. 2023; Moldoveanu et al. 2024; Rada et al. 2024; Biella et al. 2025b); while other works have investigated the environmental drivers through which urbanization shapes patterns of pollination, as well as pollinator diversity and abundance (Biella et al. 2022; Wenzel et al. 2020; Graf et al. 2025). Most studies of urban wild bees focus on examining how diversity, assemblage structure, and pollination respond to specific environmental variables at local scales (Makinson et al. 2017; Burdine and McCluney 2019; Graf et al. 2025), or consider urbanization gradients as integrative proxies of multiple environmental change (Birdshire et al. 2020; Splitt et al. 2021).

Species-level responses to urbanization are heterogeneous and mediated by functional traits, including nesting biology, dietary breadth, sociality, body size, wing morphology, and phenology (Fauvieu et al. 2022; Liang et al. 2023). Among these, nesting strategy has been particularly studied, with ground-nesting bees typically showing reductions in urban areas, whereas cavity-nesting solitary bees often remain abundant or even increase (Banaszak-Cibicka and Żmihorski 2012; Ferrari and Polidori 2022). In addition, growing attention has been put towards the reproductive traits (e.g., brood cell number, offspring sex ratio, parasitism, and mortality rate) and nesting strategies of individual solitary cavity-nesting bee species in response to habitat structure and resource availability (Rosas-Ramos et al. 2017; Sexton et al. 2021; Turo and Gardiner 2021; Zaragoza-Trello et al. 2021; Wittmann et al. 2023, 2025; Marrero et al. 2025). To our knowledge, most of these studies have been conducted at landscape-level and mainly in agricultural or semi-natural contexts rather than fine-scale conditions in urban or peri-urban environments. Yet local-scale environmental conditions in cities are expected to exert strong constraints on solitary cavity-nesting bees (e.g., the availability of suitable nesting substrates, access to floral resources, microhabitat structure, and connectivity), shaping their reproductive success, long-term persistence,

and the maintenance of viable populations (Quistberg et al. 2016; Sexton et al. 2021; Graffigna et al. 2024; Polidori et al. 2024).

In this context, we focus our study on *Osmia caerulescens* (Linnaeus 1758), a widespread Palearctic bivoltine solitary cavity-nesting bee (Tasei and Picart 1972; Vicens et al. 1993; Marrero et al. 2025). The species is commonly recorded in trap nest surveys in anthropogenic environments and is a predominant species in Mediterranean agricultural systems (Tobajas et al. 2021; Azevedo et al. 2025). *O. caerulescens* occupies pre-existing cavities, constructing linear series of brood cells separated by chewed plant-based (leaf and petals) partitions (Tasei and Picart 1972), and most commonly uses diameters of 4–6 mm (Satta et al. 2007; Azevedo et al. 2025), although it can exploit a broader range. As in other *Osmia* species, each brood cell is provisioned with a mass of pollen and nectar before egg laying, and females can exert careful control over nesting and offspring characteristics. The number of brood cells produced reflects the actual reproductive output (Kim and Thorp 2001; Bosch and Vicens 2006; Rosas-Ramos et al. 2017); while the body size of the offspring is determined by the mass of the provisioned brood cell (Bosch and Vicens 2002; Kim 1999). As in all Hymenoptera females, offspring sex is facultatively determined at oviposition (Gerber and Klostermeyer 1970), with the sexual allocation of daughters commonly requiring a greater investment of resources than that of sons (Bosch and Vicens 2005; Rehan and Richards 2010).

*O. caerulescens* is highly polylectic, with its pollen diet including Fabaceae, Lamiaceae, Boraginaceae, Asteraceae, and Antirrhineae (Plantaginaceae) (Vicens et al. 1993; Müller 1996, 2025). In agricultural landscapes, provisions are usually dominated by Fabaceae and occasionally co-dominated by Lamiaceae (Satta et al. 2007) or accompanied by Boraginaceae and Campanulaceae (Tobajas et al. 2021), indicating consistent family-level preferences. However, diet composition can vary markedly across landscapes depending on local floral availability. In some cases, this may result in strong dominance of a single-taxon (e.g., *Rosa canina*) (Gresty et al. 2018). However, an apparent specialization, as reported by MacIvor and colleagues (2014) for pollen of *Trifolium repens*, and occasionally, even for wind-pollinated *Quercus* spp., through a study conducted in urban areas outside the species' native range, may in fact reflect the local floral availability. *Quercus* pollen has also been recorded once in agricultural settings (Özök and Güler 2016).

Urbanization can alter plant communities by selectively filtering plant species from local assemblages, thereby changing not only the abundance but also the composition of floral resources available to bees (McKinney 2008; Onandia et al. 2019; Theodorou 2022). For polylectic species like

*O. caerulescens*, altered plant communities may not prevent reproduction, but may influence how females allocate resources among offspring traits. Females may maintain a broad diet by flexibly exploiting available resources, or they may show apparent specialization on dominant local plants, as reported in some anthropogenic contexts (MacIvor et al. 2014; Gresty et al. 2018). *O. caerulescens* is an excellent model species for its prevalence in trap nest studies, generalist diet, and capacity to nest in cavities of varying diameters, to study its key reproductive strategies to varying peri-urban sites (transitional areas at the interface between urban and rural) that differ in local vegetation structure and resource availability.

The aim of this study was to assess whether *O. caerulescens* adjusts key reproductive strategies and pollen use across peri-urban sites differing in local vegetation structure (e.g., grass and tree cover) and floral resource availability. We hypothesized that floral resource availability and vegetation structure influence reproductive strategies by affecting the brood cell production, the foraging and provisioning effort required to supply them, and maternal sex allocation decisions at the local scale. We therefore predicted that (1) reproductive output, measured as the number of brood cells per nest, would increase with greater availability of floral resources, since brood cell production is primarily limited by resource access and provisioning costs (Goodell 2003; Bosch and Vicens 2006; Zurbuchen et al. 2010a, 2010b; Rosas-Ramos et al. 2017). We also expected that (2) offspring body size, measured as intertegular distance (ITD) and used as a proxy for maternal investment, would increase in environments characterized by higher floral resource availability at the local scale, where shorter foraging distances and reduced provisioning costs are expected to allow either greater per-cell investment (larger offspring) or increased cell production, depending on how females allocate resources (Gathmann and Tschardt 2002; Warzecha et al. 2016; Tobajas et al. 2021; Zaragoza-Trello et al. 2021). Furthermore, we predicted that (3) sex allocation would shift toward a higher proportion of female offspring with increasing floral resource availability, as females are the most costly sex to produce, in accordance with conditional sex allocation theory (Charnov 1982; Bosch and Vicens 2005; Wittmann et al. 2023). Finally, we assessed whether (4) local constraints on floral availability would lead to apparent specialization (diet narrowing) or whether the species would maintain a broad diet consistent with its polylectic foraging strategy in agricultural systems.

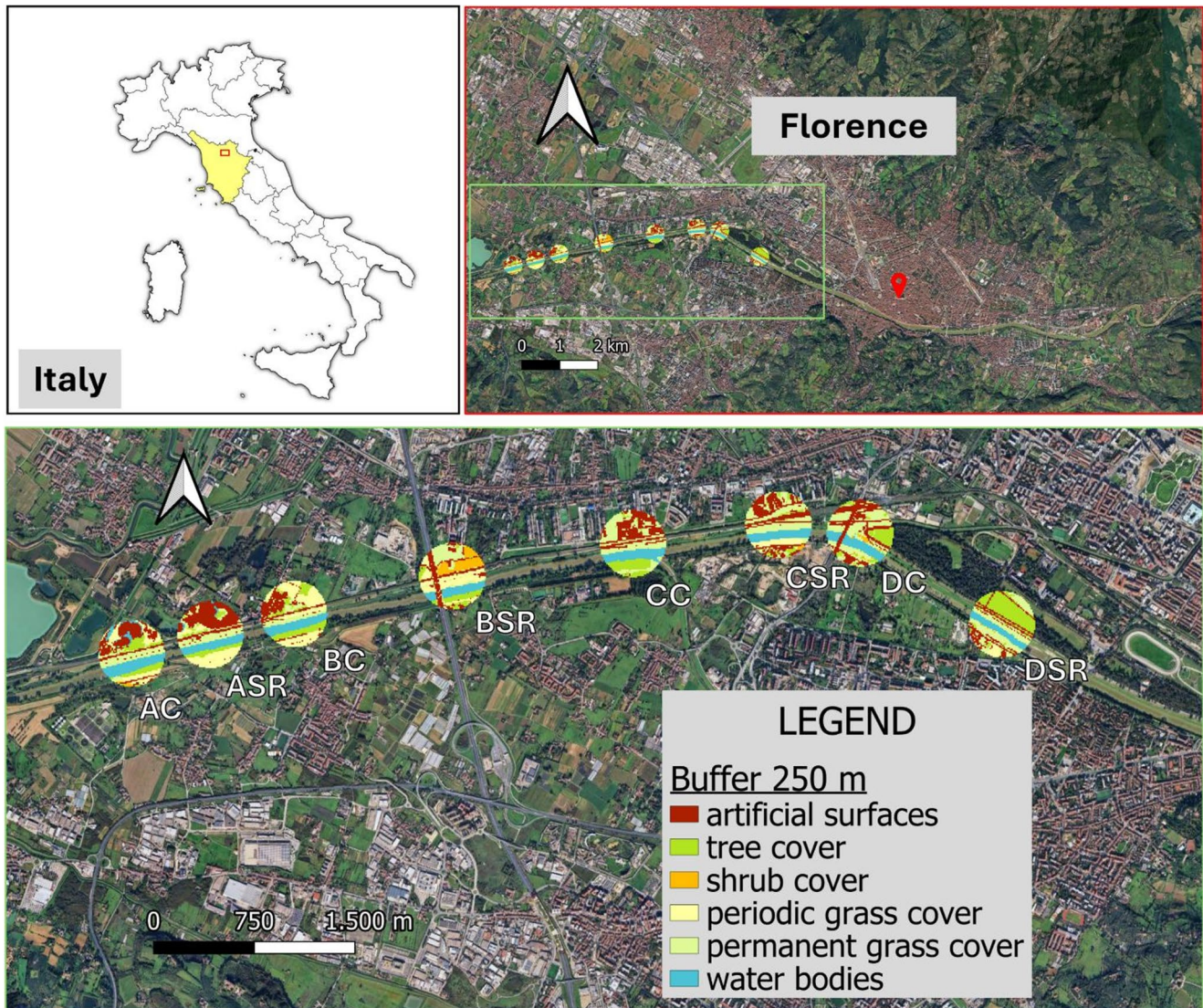
## Materials and methods

### Study area

The study was conducted in the city of Florence, Tuscany (central Italy), along the northern riverside of its main river, the Arno River (Fig. 1). We considered a tract of a linear riverside and narrow green corridor (~50–80 m width) that extends for 8 km from the urban area of Florence to the nearby town of Signa and outside the center of Florence, which is delimited by a railway on its northside. A cycling road widely used for recreational activities runs along the bank. The study area can be classified as peri-urban (urban-adjacent), characterized by a transitional environments that combine some urban features but is not fully embedded within the urban matrix. These areas represent intermediate zones between more densely urbanized and more rural contexts and are characterized by a relatively high percentage of green spaces as well as typical urban features, including car overpasses. More specifically, the study area fits within the “urban riverside grassland” typology proposed by Dylewski et al. (2024), which describes grassland habitats along urban rivers. Green areas consist mainly of spontaneous dry-mesic riparian grasslands with patches of riparian trees and are subject to occasional flooding (e.g., *Populus* spp., *Quercus* spp., *Ulmus* spp., *Juglans* spp., and *Salix* spp.). The invasive giant reed *Arundo donax* L., together with the native *Artemisia vulgaris* L., can locally dominate and partially cover the grassland vegetation in various parts of the study area. However, their occurrence is heterogeneous across the study area and they represent only a limited proportion of the area overall. Nevertheless, the study area hosts a diverse community of spontaneous entomophilous herbaceous plants (Table S1, Supplementary Information, SI\_1). In some sections, such as near an urban park, the tree cover becomes denser, forming locally more structured patches of vegetation. Vegetation management of these areas is charged by the River Authority (Consorzio di Bonifica 3 Medio Valdarno), which mows the meadows consistently across the study sites at least three times per year without the removal of the dead biomass and occasionally trims the trees. According to the Köppen–Geiger climate classification system (Rubel and Kottek 2010), the study area is located in a transitional zone between the Mediterranean (Csa) and humid subtropical (Cfa) climate types, characterized by a moderate maritime influence and warm summers.

### Trap nest sampling

Trap nests are a standardized sampling method that provides direct access to nests of cavity-nesting bees and offer



**Fig. 1** Study area and location of the eight trap nest sampling sites near the city of Florence. Each circle represents a 250 m buffer around the trap nest, within which land-cover composition was extracted from the National Land Cover Map (ISPRA 2023). Land-cover classes include artificial surfaces, tree cover, shrub cover, periodic and permanent grass cover, and water bodies. For all the analyses, periodic

and permanent grass cover and shrub cover were merged into a single grass cover category (see Environmental features section). Distances between consecutive sites ranged from 602 to 1253 m (602, 643, 1096, 1211, 1365, 611, 1253 m; from west to east). Among the eight sites, *O. caerulescens* was not detected at BSR. The basemap is derived from Google Satellite imagery

an effective framework for quantifying key life-history and reproductive traits, including brood-cell number, offspring sex and size, mortality, parasitism, and provisioning patterns (Tschardt et al. 1998; Staab et al. 2018; Dürrbaum et al. 2023; Fornoff et al. 2023; Wittmann et al. 2023). We used this method to sample nests of *O. caerulescens* in eight sites (Tschardt et al. 1998; Staab et al. 2018), defined as spatially distinct sampling locations distributed along the linear riverside corridor and spaced from 600 to 1200 m apart. Site selection was constrained by accessibility and the availability of suitable public areas for trap-nests installation. Each trap nest consisted of a wooden pole with two PVC pipes

(diameter 10 cm, length 23 cm) facing W-E along the river and mounted 1.5 m above the ground (Fig. S1, Supplementary Information, SI\_1). The tubes were filled with internodes of *Arundo donax* and *Phragmites australis* (Cav.) Trin. ex Steud., keeping a consistent range of internode diameters for each sampling site (2–15 mm, covering the range typically used in trap-nest studies to accommodate different cavity-nesting bee species). We left the trap nests in the sites from April to October 2024, allowing females of wild *O. caerulescens* to construct their nests. After the removal of the trap nests from the field, occupied internodes were opened and inspected to record the diameter and

number of brood cells. These were then stored in a cooling chamber at  $\sim 4$  °C for 6 weeks and subsequently kept at room temperature to enable the emergence of adults. We collected all emerging adults of *O. caerulescens* and determined their sex. Voucher specimens are kept in the entomological collection of the University of Florence. Nests of *O. caerulescens* from which adults had already emerged before the removal and inspection of the trap nests were also counted. Empty nests of this species were easily identifiable based on the unique structure and use of chewed plant and leaf material (Lindermann et al. 2023).

### Body size (ITD) measurements and flight distances

Intertegular distances (ITD), a reliable proxy for bee body size (Cane 1987; Kendall et al. 2019), were measured as the shortest distance between the tegulae (Cariveau et al. 2016) on 324 out of the 370 emerged adults (117 females and 207 males from 126 nests). Each specimen was photographed with an Olympus SZ61 TR stereomicroscope equipped with an Olympus EP50 digital camera, and ITD was measured from the photos using the dedicated software EPview 1.4 (Olympus/Evident Technology Center Europe GmbH, 2019–2023). ITD is closely related to body mass, maternal energetic costs, and larval provisioning rates in solitary bees (Bosch and Vicens 2002, 2006). Offspring ITD was used as a proxy for the quality of maternal investment, with mean ITD as per-nest maternal investment, and individual ITD for sex-specific maternal investment. The average ITD of *O. caerulescens* females (2.249 mm) was used to estimate foraging range, following established allometric relationships (Greenleaf et al. 2007). Foraging distances were calculated in R using the ‘foragedist’ function of the “pollimetry” package (Kendall et al. 2022), obtaining average values of 315 m.

### Environmental features

To assess the effects of landscape composition on *O. caerulescens*, we used QGIS software “Prizren” v3.34 (QGIS Development Team 2024) to extract land cover data from the National Land Cover and Land Use (LCLU) Map (ISPRA 2023). This map was created at the national level with a spatial resolution of 10 m by integrating data from the Copernicus program (including Urban Atlas, Riparian Zones, CORINE Land Cover/CLC+ Backbone) and the ISPRA national historical series, following the methodological framework described by De Fioravante et al. (2021a, 2021b). We calculated the area (%) occupied by the main land-cover classes within a circular buffer surrounding each sampling site, to describe foraging-scale conditions, we selected a 250 m radius buffer, which corresponds to the

expected foraging distance of *Osmiini* bees of its size (Gathmann and Tschamntke 2002; Zurbuchen et al. 2010b; Hofmann et al. 2020). We selected land cover classes, including artificial surfaces (comprising buildings, roads, parking lots, paved surfaces, and quarries), tree cover, shrub cover, grass cover, and water bodies. Grass and shrub cover were pooled together for analysis, representing open habitats with flowering resources potentially attractive to *O. caerulescens*, in contrast to the closed and shaded conditions associated with tree-covered areas. In addition, shrub cover was negligible across sites, except at BSR (Fig. 1), where *O. caerulescens* was not recorded. Finally, the distance from the city center was computed as the straight-line (Euclidean) distance between each trap nest position and a standard location at the historical center of Florence and used as a proxy of anthropogenic disturbance. All environmental features used in the analyses are reported for each site in Table S2 (Supplementary Information, SI\_1).

### Floral survey and Flower Index

At each site, flowering entomophilous herbaceous plants were surveyed along a 250 × 4 m transect extending from the trap-nest location in a consistent direction across all sites, resulting in a surveyed area of 1,000 m<sup>2</sup>. During each survey all flowering entomophilous herbaceous species within the transect were recorded, and overall floral cover (%) was estimated independently by two observers and then averaged. Vegetation surveys were conducted a total of 10 times throughout the spring and summer season, roughly once every three weeks from March to September 2024, for each sampling site. Plant identification was primarily conducted in the field using a local plant guide (Peruzzi 2021) and confirmed with smartphone-based image recognition apps, such as Flora Incognita (Mäder et al. 2021). When field identification was not possible, samples were collected and subsequently identified in the laboratory at the genus or species level using dichotomous keys (Pignatti 1997). The complete list of plant species recorded at each site is provided in Table S1 (Supplementary Information, SI\_1). This data was then used to calculate a “Flower Index” metric, representing the overall floral resource availability for *O. caerulescens* at each site. For each survey  $v$  in each site  $s$ , we recorded all entomophilous plant species along the transect. The Flower Index  $FI_{s,v}$  per survey ( $v$ ) at each site ( $s$ ) was then calculated as:

$$FI_{s,v} = C_{s,v} \times n_{s,v}$$

where  $C_{s,v}$  is the proportion of area covered by all entomophilous flowering plants (floral cover, expressed as a proportion between 0 and 1) observed during visit  $v$  at site

$s$ , and  $n_{s,v}$  is the total number of entomophilous species recorded during that survey. The annual Flower Index for each site ( $FI_s$ ) was calculated as the mean values between May and August, corresponding to the peak activity period of *O. caerulescens*:

$$FI_s = \frac{1}{V} \sum_{v \in \text{May-Aug}} FI_{s,v}$$

where  $V$  is the number of visits within that period. The index integrates both floral abundance (coverage) and floral diversity. The annual Flower Index calculated for each site is shown in Table S2 (Supplementary Information, SI\_1).

## Pollen diet analysis

### Plant identification through pollen grain morphology

Pollen samples were collected from the brood cells of *O. caerulescens* to assess diet. Sampling instruments were sterilized using alcohol and flame after pollen collection from each brood cell to avoid cross-contamination. Only brood cells containing leftover pollen were sampled, representing either failed egg laying or premature larval death; however, these cells belonged to nests from which adult individuals successfully emerged. Pollen was transferred to a 1.5 mL Eppendorf tube, suspended in a 1:1 ratio with a solution of water and glycerin, and vortexed until completely dispersed. Pollen samples from a total of 18 brood cells were collected. The palynological preparation and morphological identification of pollen grains were performed by the Agriculture and Environment Research Center (CREA-AA, Bologna, Italy). The slides were prepared following the laboratory's protocol: a  $22 \times 22$  mm square was drawn on the slide with indelible ink, the pollen sample in solution was mixed and distributed evenly within the marked area, and the slide was placed on a heating plate at  $\sim 40$  °C until dry. A drop of glycerin gelatin was applied to the cover slip, which was then gently placed on the sample and left on the plate for 5 min to ensure even distribution. Pollen grains were identified and counted with an optical microscope (400-1000X) using reference collections and iconographic keys. For each sample, 500 grains were identified along five equidistant transects on the coverslip. The percentage of each pollen type was calculated as  $\%P = \frac{n_p \times 100}{N}$ , where  $n_p$  is the number of grains of a given pollen type and  $N$  is the total number of pollen grains counted.

### Plant identification by DNA metabarcoding

To complement morphological pollen identification and to increase taxonomic resolution, the same eighteen pollen samples analysed through grain morphology were further analysed using DNA metabarcoding. Samples were processed following standard laboratory protocols (see, e.g. Biella et al. 2022; Tommasi et al. 2023) and post-sequencing bioinformatic recommendations (Tommasi et al. 2021). Details of the protocol and bioinformatic processing are reported in the Supplementary Information (SI\_2).

### Statistical analysis

Statistical analyses were performed in R 4.5.2 (R Core Team 2024). Before regression analyses, we assessed collinearity among the environmental predictors using Pearson correlation matrices. Correlation coefficients  $|r| \geq 0.7$  were considered indicative of strong collinearity. Two matrices were generated: one for the analyses based on seven sites and one for the analyses restricted to six sites (Table S3, Supplementary Information, SI\_1). This distinction reflects the fact that the number of brood cells was quantified across all seven sites, whereas analyses of offspring traits were restricted to the six sites where individuals could be successfully reared from trap nests. Flower Index, grass cover, and distance from the city center showed only weak to moderate correlations and were retained for modelling. Tree cover and artificial surface were strongly negatively collinear with the Flower Index and moderately correlated with other habitat variables, indicating that they represented the same underlying landscape gradient. To avoid multicollinearity, these variables were excluded from all multivariable analyses.

We analysed multiple response variables describing: *i*) number of brood cells per nest (reproductive output, model A); *ii*) the mean offspring ITD per nest (per-nest maternal investment, model B); *iii*) the product between the number of brood cells and the mean offspring ITD per nest (total maternal investment per nest, model C); *iv*) offspring individual ITD (sex-specific maternal investment, model D); *v*) the proportion of female offspring per nest (sex allocation, model E). All models were fitted using the nest as the unit of analysis, except for the analysis of offspring individual ITD, which was conducted using individuals as the unit of analysis. Finally, to jointly describe sex allocation and offspring ITD at the population level, we calculated a population-level female and male investment index per nest as the number of female offspring multiplied by their mean intertegular distance (ITD). This index was used solely for descriptive purposes and was not included as a response variable in the statistical models.

All models were initially fitted using the same set of environmental predictors, including Flower Index, grass cover, and distance from the city center. For model D including individual-level data, sex and its interaction with environmental predictors were additionally considered, while reed diameter was included as an additional predictor in the sex allocation (model E). All predictors were scaled prior to model fitting. Generalized linear models (GLMs) were used for all analyses. Model A was fitted using a negative binomial distribution with a log link, model E using a beta-binomial distribution, and models B, C, and D using Gaussian distributions. We performed stepwise model selection while assessing AIC and log-likelihood improvements with the ‘*stepAIC*’ function from the “MASS” package to find the most parsimonious formulations (Venables and Ripley 2002). The significance of fixed effects was assessed with Anova Type II Wald  $\chi^2$  tests with the “car” package (Fox and Weisberg 2019), except for model D, where fixed-effect significance was assessed using Type III ANOVA by “car” package, appropriate for models including interaction terms. Dispersion and residual structure were evaluated using “DHARMA” package (Hartig 2016), and models’ adequacy was also tested with visual diagnostics using “performance” package (Lüdecke et al. 2021). For graphical presentation, predictions were back-transformed to the

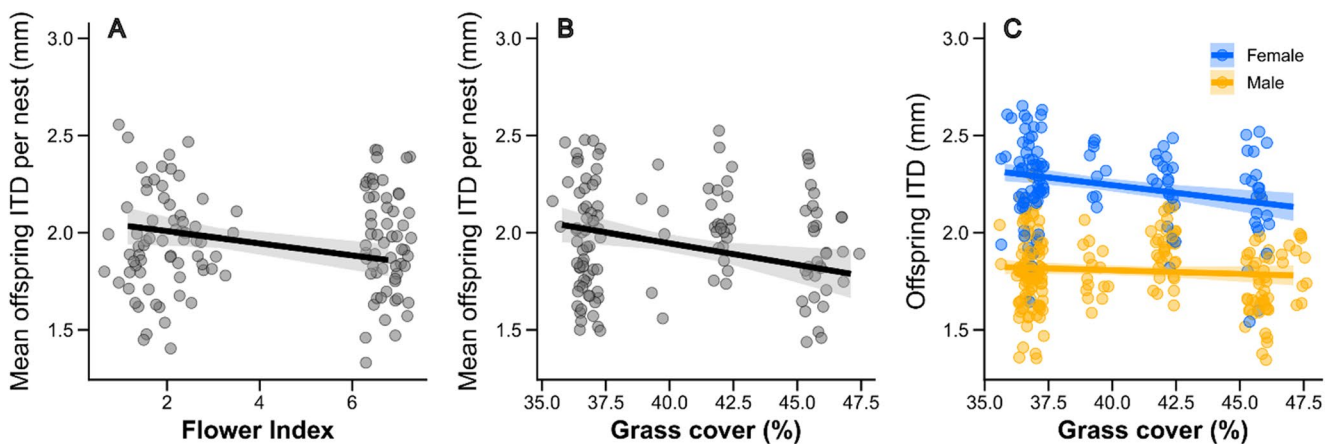
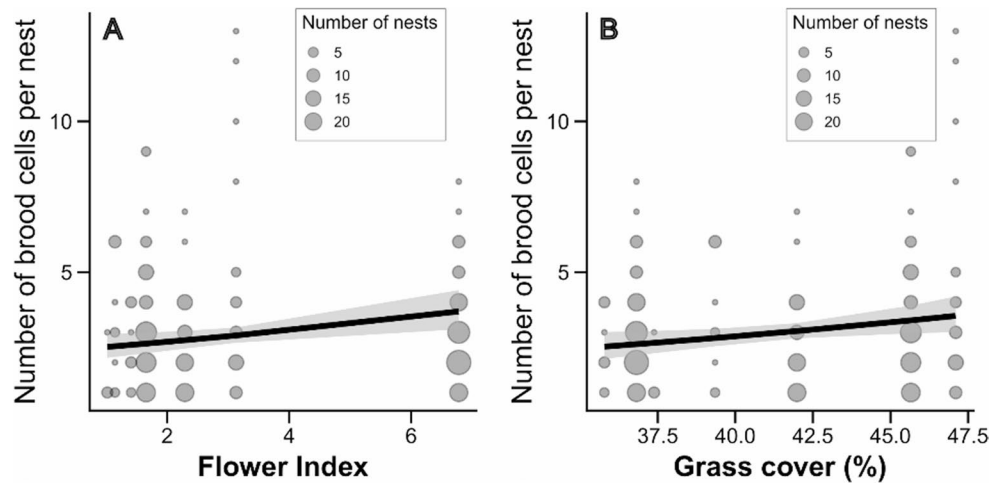
original scale. All model’s prediction curves and associated 95% confidence intervals were generated using “ggeffects” package (Lüdecke 2018). A summary of all model results, structures, families, estimates, and significance tests is presented in Table 1.

To examine variation in pollen composition among sites, we used non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities calculated from Hellinger-transformed pollen abundance data by using the “vegan” package (Oksanen et al. 2001). Differences in pollen composition among sites were tested using a permutational multivariate analysis of variance (PERMANOVA; 999 permutations). We additionally assessed multivariate dispersion among sites followed by permutation tests. To identify plant taxa associated with gradients in pollen composition, we fitted species vectors to the NMDS ordination using ‘*envfit()*’ with 999 permutations, retaining only taxa with  $p \leq 0.05$  for visual interpretation. To summarize pollen diet across sites, pollen counts from each brood-cell sample were converted to relative abundances and then averaged across the three samples per site. The resulting site-level mean proportions were visualized in a bubble plot using *ggplot2*, with taxa assigned to plant families for clarity.

**Table 1** Summary of all statistical models on the selected response variables at 250 m radius buffer landscape. For each model, we report the response variable, level of analysis (nest-level or individual-level, number of sites), model family, fixed effects (estimate  $\pm$  SE), test statistics (z/t), and p-values derived from Type II or Type III ANOVA depending on model structure. Model C is the null Gaussian model (log-transformed total maternal investment) selected as the best-supported model based on AIC and is reported with intercept only. Predictor sets reflect collinearity-based separation and best AIC selection

Model	Response variable	Level of analysis	Model family	Predictor	Estimate $\pm$ SE	z/t	p value
A	Number of brood cells	Nest level (215 nests), 7 sites	Negative binomial GLM (log link)	Flower Index	0.1547 $\pm$ 0.0668	2.318	0.0205*
				Grass cover (%)	0.1262 $\pm$ 0.0569	2.217	0.0266*
				Distance from the city center	0.1179 $\pm$ 0.0520	2.266	0.0235*
B	Per-nest maternal investment (mean offspring ITD per nest)	Nest level (126 nests), 6 sites	Gaussian	Flower Index	-0.0760 $\pm$ 0.0343	-2.213	0.0269*
C	log(Total maternal investment) - (number of brood cells x mean ITD per nest)	Nest level (126 nests), 6 sites	Gaussian	Intercept (null model)	1.675 $\pm$ 0.050	33.64	<0.0001***
				Grass cover (%)	-0.0870 $\pm$ 0.0343	-2.535	0.0112*
D	Sex-specific maternal investment (offspring ITD)	Individual level (324 individuals), 6 sites	Gaussian	Sex (F)	-0.4371 $\pm$ 0.0197	-4.250	<0.0001***
				Grass cover (%)	-0.0597 $\pm$ 0.0169	-3.542	0.0004***
				Sex x Grass cover (%)	0.0454 $\pm$ 0.0204	2.222	0.0263*
				Distance from the city center	0.0189 $\pm$ 0.0105	1.806	0.0709
E	Sex allocation (proportion of females)	Nest level (130 nests), 6 sites	Beta-binomial GLM (logit link)	Reed diameter (mm)	1.2595 $\pm$ 0.1450	8.684	<0.0001***
				Flower Index	-0.5352 $\pm$ 0.2163	-2.474	0.0125*
				Grass cover (%)	-0.6824 $\pm$ 0.2389	-2.856	0.0032**

**Fig. 2** The number of brood cells per nest in *O. caerulescens* increased with increasing Flower Index (A) and grass cover (B). Points represent observed nest-level values, with point size indicating the number of overlapping observations, and solid lines show negative binomial GLM predictions of marginal effects with 95% confidence intervals (shaded bands)



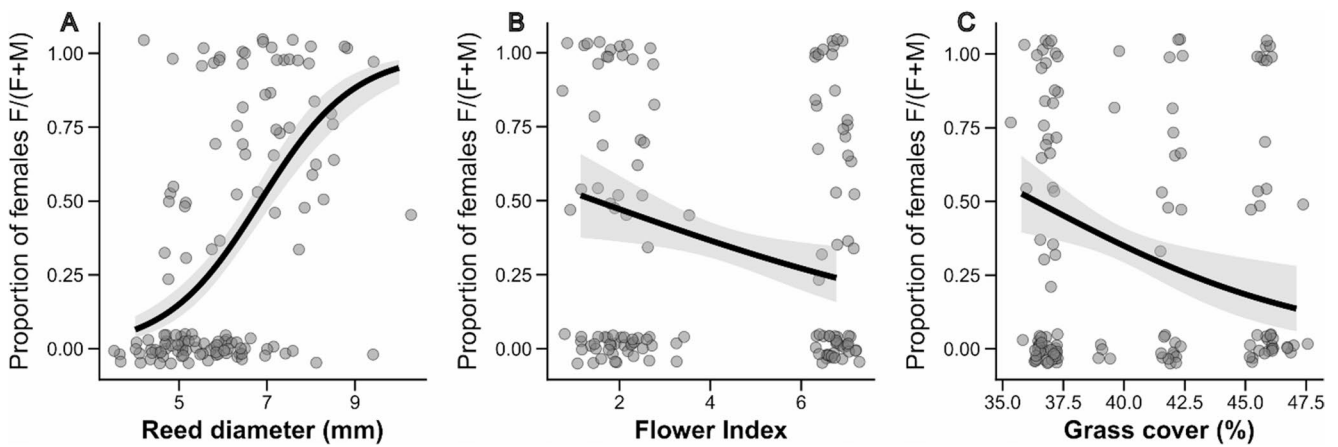
**Fig. 3** *O. caerulescens* maternal investment declined with (A) increasing Flower Index and (B) increasing grass cover. (C) sex-specific maternal investment declined with increasing grass cover for females

and was constant for males. Points represent nest-level values and solid lines Gaussian GLM predictions of marginal effects with 95% confidence intervals (shaded bands)

## Results

*O. caerulescens* represented by far the most abundant cavity-nesting bee species in the study area (77.5% of all occupied nests), with individuals recorded from seven of the eight sampling sites. Here, each nest corresponds to a single reed stick used as a nesting cavity. A total of 215 nests of *O. caerulescens* were sampled, corresponding to 648 brood cells. Of these, 130 nests provided adult individuals, while in the 85 remaining nests, individuals had already emerged before collection. The number of brood cells per nest (reproductive output) increased with increasing Flower Index (A,  $z=2.39$ ,  $p=0.0205$ ; Table 1; Fig. 2), grass cover ( $z=2.22$ ,  $p=0.0266$ ), and distance from the city center ( $z=2.27$ ,  $p=0.0235$ ). Inter-tegular distance differed considerably between sexes (Wilcoxon rank-sum:  $p<0.001$ ), confirming the expected sexual size dimorphism in *O. caerulescens*. Individuals also exhibited a high within-sex size variation, especially in females (Fig. S2A). The mean offspring ITD

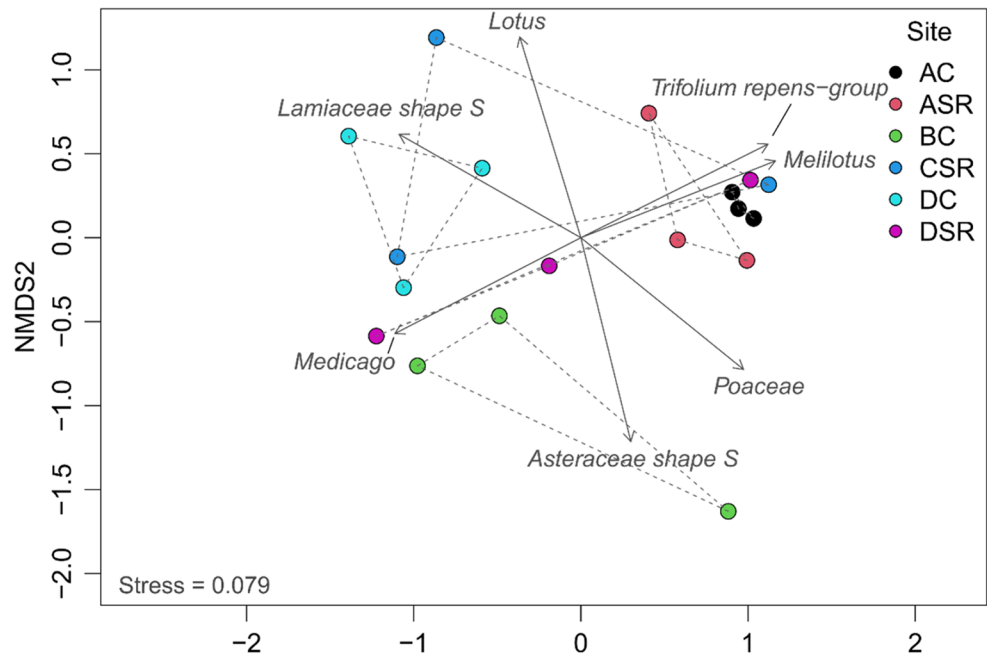
per nest (per-nest maternal investment) decreased with both increasing Flower Index and grass cover (B,  $t = -2.21$ ,  $p=0.0269$  and  $t = -2.54$ ,  $p=0.0112$ , respectively; Table 1; Fig. 3). The product between the number of brood cells and the mean offspring ITD per nest (total maternal investment per nest) did not vary with any environmental predictor (C; Table 1). Offspring individual ITD (sex-specific maternal investment) showed a negative association with increasing grass cover in females (D;  $t=-3.54$ ,  $p<0.001$ ; Table 1; Fig. 3), whereas this relationship was significantly weaker in males, as indicated by the positive sex  $\times$  grass cover interaction ( $t=2.22$ ,  $p=0.0263$ ). The overall population sex ratio across all sites was male-biased 1.6/1. The proportion of female offspring per nest (sex allocation) and reed diameter had a strong positive relationship (E,  $z=8.68$ ,  $p<0.001$ , Table 1; Fig. 4), with wider reeds containing a higher proportion of female offspring, while Flower Index ( $z = -2.47$ ,  $p=0.0125$ ) and grass cover ( $z = -2.86$ ,  $p=0.0032$ ) showed a negative relationship, resulting in a shift toward male-biased proportion in sites with higher Flower Index and



**Fig. 4** The predicted proportion of female offspring in *O. caerulescens* increased with reed diameter (A), but declined with increasing Flower Index (B) and grass cover (C). Points represent observed nest-level

proportions of females (jittered to reduce overlap), and solid lines show beta-binomial GLM predictions of marginal effects with 95% confidence intervals (shaded bands)

**Fig. 5** NMDS ordination (Bray–Curtis distance, stress=0.079) of pollen composition collected by *O. caerulescens* across six study sites. Points represent individual brood-cell pollen samples, colored by site. Dashed hulls outline the multivariate extent of each site. Significant plant taxa (envfit,  $p \leq 0.05$ ) are shown as vectors, scaled for clarity, indicating their contribution to major compositional gradients. The ordination highlights clear site-level differences in pollen use, driven primarily by Fabaceae, Astera-ceae, and Lamiaceae taxa



grass cover. The population-level female and male investment index per nest was highly skewed toward zero, reflecting the frequent absence of female offspring across nests, whereas male investment showed a more continuous distribution (Fig. S2B, Supplementary Information, SI\_1).

**Pollen diet**

The NMDS ordination revealed site-level differences in pollen composition (PERMANOVA:  $R^2 = 0.47$ ,  $F_{5,12} = 2.10$ ,  $p=0.025$ ; Fig. 5). Multivariate dispersion did not differ among sites ( $F_{5,12} = 0.93$ ,  $p=0.49$ ), indicating homogeneous within-site variability. We identified that several taxa were significantly associated with the main NMDS axes ( $p \leq 0.05$ ), including Fabaceae, Asteraceae, and Lamiaceae

among the significant taxa. The bubble plot (Fig. S3, Supplementary Information, SI\_1) illustrated clear among-site differences in the diet, with some morphotypes widespread and others restricted to certain sites, summarizing the structure of *O. caerulescens* pollen use across sites. DNA metabarcoding analyses largely confirmed the patterns observed through pollen grain morphology, identifying a polylectic diet dominated by Fabaceae (Table S4, Supplementary Information, SI\_1). While the two approaches were broadly consistent, metabarcoding allowed finer taxonomic resolution and revealed some additional taxa not distinguishable through morphology, whereas some pollen types identified morphologically, were not detected by metabarcoding. Both approaches revealed among-site variation in

pollen composition, with some taxa widespread and others restricted to specific locations.

## Discussion

In the Mediterranean peri-urban study sites, *O. caerulescens* was the dominant species among the cavity-nesting community, although we provided nest cavity diameters extending far beyond the species' expected usage and body size, but suitable for other species. This result confirms findings from Mediterranean regions' agricultural landscapes (Satta et al. 2007; Baños-Picón et al. 2013; Tobajas et al. 2021; Marrero et al. 2025; Azevedo et al. 2025), highlighting the dominance of the species across Mediterranean systems. These findings demonstrate its suitability as a model species and how well the species is adapted to a Mediterranean environment, potentially benefiting from its polylectic flower usage.

Our results show that the number of brood cells increased with the Flower Index, which represents a proxy of the availability of floral resources for *O. caerulescens* throughout the season. The polylectic foraging of *O. caerulescens* likely explains this result, as access to a wide range of floral resources can sustain brood cell production over time. In solitary cavity-nesting bees, the number of brood cells is a direct indicator of reproductive output and is mainly limited by access to resources and provisioning costs (Goodell 2003; Bosch and Vicens 2006; Zurbuchen et al. 2010). For *O. caerulescens*, field studies show that brood cell production increases in the presence of more favorable foraging conditions and greater availability of floral resources (Baños-Picón et al. 2013; Rosas-Ramos et al. 2017; Marrero et al. 2025). A similar link between resources and reproduction has also been documented for other *Osmia* species, in which offspring production increases with flower abundance and decreases when resources are limited (Goodell 2003; Palladini and Maron 2014; Zaragoza-Trello et al. 2021); although these studies were conducted under different spatial contexts, ranging from experimental manipulations to broader landscape-scale observations, whereas our results reflect patterns operating at a finer spatial scale around nesting sites. However, we also found a positive effect of grass cover, which may reflect more open and sun-exposed conditions associated with a microclimate more favorable to foraging activity (Tobajas et al. 2021; Polidori et al. 2024), or a reduction in foraging costs in more open habitats, consistent with experimental evidence showing that increased foraging distance reduces brood cell production in solitary bees (Zurbuchen et al. 2010a). Alternatively, grass cover may also be associated with the availability of small-flowered forbs, which are commonly exploited by polylectic species such as *O. caerulescens*. In addition, we found that brood cell

number also increased with distance from the city center, which may reflect a general decrease in anthropogenic disturbance (e.g., traffic, human presence and activity, noise, and pollution) away from the urban core. However, distance from the city center is a coarse proxy that could likely capture multiple, unmeasured environmental gradients. Taken together, these findings indicate that brood cell production in *O. caerulescens* is shaped by both floral resource availability, habitat structure and spatial position along the peri-urban corridor.

In solitary cavity-nesting bees, body size is related to provisioning costs and foraging distance, as larger individuals are able to cover greater distances and sustain higher movement costs (Gathmann and Tscharnke 2002). In our study, the wide variability in body size observed within each sex indicates marked plasticity in maternal investment, suggesting that females finely modulate the provisioning rate of individual brood cells (Radmacher and Strohm 2010). Previous studies on *Megachile* and *Osmia* species, including *O. caerulescens*, have shown that offspring size can increase with higher floral resources and availability, higher pollen diversity and favorable microclimatic settings, including sunnier and more open habitats. (Kim 1999; Tobajas et al. 2021, 2024; Zaragoza-Trello et al. 2021). Moreover, response to habitat gradients has been shown to differ between sexes of the same species (Zaragoza-Trello et al. 2021). More generally, larger body size has been shown to be favored under increased spatial constraints, such as habitat fragmentation, because of its association with enhanced dispersal capacity and the ability to sustain higher foraging costs (Warzecha et al. 2016). In line with decreased foraging constraints, we found that average ITD per nest decreased with increasing floral resource availability and in more open habitats, indicating that under favorable conditions, maternal investment in *O. caerulescens* is redistributed following a quantity–quality trade-off toward a greater number of brood cells rather than toward larger offspring. This is also emphasized by considering that the total maternal investment per nest remained constant and did not vary depending on environmental conditions, which could be consistent with the evidence of a limit on overall reproductive investment, suggesting that females may adjust allocation strategies rather than increasing the overall reproductive effort. However, this pattern should be interpreted with caution given the limited number of sites. These results closely parallel the findings of Rosas-Ramos et al. (2017), who showed that in relatively less favorable agricultural contexts (vineyard and cereal monoculture), which were associated with lower floral resources availability and higher foraging costs, larger individuals were selected whereas more resource-rich contexts (mixed vegetable crops), where foraging cost are reduced, smaller offspring were selected, consistent with

relaxed selection on body size. In our system, this contrast is captured by vegetation structure: open, grass-dominated habitats (and conversely lower forest cover) are associated with reduced average ITD, consistent with lower foraging constraints and a shift toward quantity-biased reproductive strategies, in line with the relationship between landscape structure, foraging costs, and body size (Gathmann and Tschamtké 2002; Warzecha et al. 2016).

Sex allocation in *O. caerulescens* was strongly related by reed diameter, with larger cavities containing a higher probability for female offspring. Overall, our results are consistent with Conditional Sex Allocation Theory (Charnov 1982) in showing that *O. caerulescens* adjusts offspring number, size, and sex in response to environmental conditions. Specifically, we found that the proportion of females decreased with increasing Flower Index and grass cover, indicating a shift toward the less costly sex under resource-rich conditions. This contrasts with previous studies on *O. caerulescens* and also with evidence from other *Osmia* species, where environments rich in foraging resources are generally associated with a higher probability towards females (Bosch and Vicens 2005; Zaragoza-Trello et al. 2021; Marrero et al. 2025; Wittmann et al. 2025). The mechanisms underlying this pattern remain unclear. One possible explanation is that sex allocation is linked to variation in offspring body size. Previous studies have shown that smaller females tend to produce offspring that are more biased towards males (Bosch and Vicens 2006; Rehan and Richards 2010). In our system, resource-rich and open habitats were associated with the production of a greater number of smaller brood cells, which may lead to smaller mothers and consequently to a shift toward male-biased sex allocation as part of a quantity-quality trade-off. This pattern may be further reinforced by seasonal effects and bivoltinism, as sex allocation decisions are known to vary throughout the season in *O. caerulescens* and related species, with later reproductive periods often more male-biased (Wittmann et al. 2023). In this context, our Flower Index, cumulative for the entire season, may obscure the timing of resource availability at the time of sex determination. *O. caerulescens* reproduction could also be influenced by the balance between external resource availability and internal constraints on reproduction, in line with multidimensional models of parental investment that incorporate limits on provisioning rate and egg maturation (Rosenheim et al. 1996; Rosas-Ramos et al. 2017; Wittmann et al. 2025). However, alternative explanations, such as body size carry-over effect, internal constraints, or local adaptation, cannot be excluded and should be explicitly tested in future studies conducted over multiple years, across a wider study area and encompassing different habitat types. Finally, looking at the population level, we found that the overall sex ratio was

skewed towards males, and considering the sexual dimorphism of *O. caerulescens*, it was expected to be 1.25/1 in favor of males; this therefore slightly deviates from Fisher's theory (Fisher 1930). This is in contrast with another species of *Osmia*, in which the investment is kept equal for both sexes, considering the difference in cost due to sexual dimorphism (Bosch and Vicens 2005). Moreover, this deviation at the population level becomes clearer when female offspring number and size are considered jointly, reinforcing the conclusion that male-biased sex ratios in our system reflect a broader shift in reproductive allocation rather than sex ratio adjustment alone.

The diet of *O. caerulescens* in the Mediterranean peri-urban environment confirms its polylectic diet with a marked preference for Fabaceae, followed by Lamiaceae, Papaveraceae, and Boraginaceae, and it is consistent with patterns documented in Mediterranean agricultural systems (Satta et al. 2007; Özkök and Güler 2016; Tobajas et al. 2024). At the same time, the composition of pollen from brood cells differed significantly between sites, with almost half of the diet varying locally, indicating the great adaptability of this species and also that the small scale in the immediate vicinity of nesting sites is a determining factor in the choice of resources. However, this result should be interpreted with caution, as the pollen analysis was based on a limited number of brood cells per site, which may reduce the power to detect within-site variability and potentially emphasize among-site differences. Although *O. caerulescens* has been shown to exhibit trophic specialization in some anthropized contexts, both within and outside its native range, our results indicate that within its native range, and at least in the studied area, the species maintains a broad diet, similar to agricultural environments, rather than specializing on a narrow set of dominant resources (MacIvor et al. 2014; Gresty et al. 2018). The persistence of a broad, non-specialized diet suggests that the studied urban riverside grassland habitats provide a sufficiently diverse and continuous floral resource base, allowing *O. caerulescens* to express its generalist diet rather than a forced specialization driven by resource limitations. Consistent with evidence that urban riverside grasslands can function as high-quality habitats for pollinators (Dylewski et al. 2024). Finally, the frequent occurrence of pollen types that were not detected during floristic surveys suggests that local foraging decisions are only partially captured by field-based assessments of floral availability (MacIvor et al. 2014; Splitt et al. 2021).

Together, these evidence on *O. caerulescens* suggest that open habitats with high floral availability promoted more "opportunistic" quantity-oriented strategies that are characterized by increased brood production, reduced per-cell investment, and male-biased sex allocation, while structurally more complex habitats may promote opposite

conservative strategies. This shift in reproductive strategies was not accompanied by a reduction in diet breadth, indicating that changes in reproductive allocation occurred independently of trophic narrowing. Moreover, the variation among sites in pollen composition indicates that females strongly rely on locally available plant species, highlighting that the immediate surroundings of the nest are critical for resource acquisition and therefore for overall reproduction (Zurbuchen et al. 2010b). This pronounced variability between sites within a relatively small spatial extent reflects the mosaic nature of urban environments, where fine-scale differences in habitat structure and resource distribution can generate markedly different ecological conditions for reproduction (Moretti et al. 2021; Graffigna et al. 2024). Our results may further suggest that, more generally, urban environments could shape solitary bees' reproduction by modifying the balance between habitat structure and the resources accessible around nesting sites. Rather than acting as uniformly favorable or unfavorable habitats, urban systems appear to reorganize the processes underlying reproductive success by altering how different components of reproduction are prioritized and combined, so that overall reproductive output emerges from compromises among key traits such as offspring number, size, and sex allocation (Moretti et al. 2021).

## Conclusion

This study demonstrates that *O. caerulea* responds to the studied peri-urban conditions by adjusting reproductive strategies toward quantity-oriented allocation that differ from those reported in agricultural systems (Rosas-Ramos et al. 2017; Wittmann et al. 2023), while maintaining a broad polylectic diet. By revealing strong effects of fine-scale habitat structure and local resource availability on reproduction and resource use, this work highlights that the value of a linear peri-urban green corridor for solitary bees depends critically on fine-scale conditions around nesting sites. Whether these quantity-oriented reproductive shifts represent short-term responses to local conditions or involve longer-term consequences for population persistence through carry-over effects across generations remains to be evaluated (Rosas-Ramos et al. 2017; Wittmann et al. 2023). Addressing this question will require future studies explicitly linking reproductive strategies to fitness outcomes across successive generations and consecutive years. More broadly, our results emphasize that reproductive traits represent key life-history properties through which solitary bees respond to environmental variation. Understanding how these traits are adjusted across heterogeneous environments may provide mechanistic insight into how species

face, from a wider perspective, urban conditions (Fitch et al. 2019; Moretti et al. 2021). Such species-specific approaches are essential for evaluating how peri-urban and urban linear green spaces support the persistence and long-term conservation of solitary bees.

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**Author contributions** MarM conceived and designed the study. MarM and OCM conducted field sampling. MarM, OCM, FF and MatM performed laboratory work and data acquisition. MarM, MasM, and FF performed data and statistical analyses. PB and AG carried out DNA metabarcoding and bioinformatic analyses. MarM, GG, GA, and MarMo carried out GIS and spatial analyses. MarM wrote the original draft of the manuscript. FRD supervised the research and acquired funding. All authors contributed to data interpretation and manuscript revision. All authors read and approved the final manuscript.

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**Data availability** The data analysed for this paper are available in the Supplementary Information and additional data on request.

## Declarations

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** All authors have contributed to and approved the manuscript's content. The materials within this manuscript are neither published nor being considered for publication elsewhere.

**Competing interests** The authors declare no competing interests.

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## References











- Azevedo M, Figueiredo E, Carvalho R, Rebelo MT (2025) Supporting wild *Osmia* populations in Mediterranean orchards: nesting success across different substrates and landscapes. *J Insect Conserv* 29:51. <https://doi.org/10.1007/s10841-025-00690-8>
- Baldock KCR, Goddard MA, Hicks DM et al (2019) A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nat Ecol Evol* 3:363–373. <https://doi.org/10.1038/s41559-018-0769-y>
- Banaszak-Cibicka W, Żmihorski M (2012) Wild bees along an urban gradient: winners and losers. *J Insect Conserv* 16:331–343. <https://doi.org/10.1007/s10841-011-9419-2>
- Baños-Picón L, Torres F, Tormos J et al (2013) Comparison of two Mediterranean crop systems: Polycrop favours trap-nesting solitary bees over monocrop. *Basic Appl Ecol* 14:255–262. <https://doi.org/10.1016/j.baae.2012.12.008>
- Biella P, Bani L, Caprio E et al (2025a) Biodiversity-friendly practices to support urban nature across ecosystem levels in green areas at different scales. *Urban Forestry Urban Green* 105:128682. <https://doi.org/10.1016/j.ufug.2025.128682>
- Biella P, Borghesan S, Colombo B et al (2025b) Lawn management promoting tall herbs, flowering species and urban park attributes enhance insect biodiversity in urban green areas. *Urban Forestry Urban Green* 104:128650. <https://doi.org/10.1016/j.ufug.2024.12.8650>
- Biella P, Tommasi N, Guzzetti L et al (2022) City climate and landscape structure shape pollinators, nectar and transported pollen along a gradient of urbanization. *J Appl Ecol* 59:1586–1595. <https://doi.org/10.1111/1365-2664.14168>
- Birdshire KR, Carper AL, Briles CE (2020) Bee community response to local and landscape factors along an urban-rural gradient. *Urban Ecosyst* 23:689–702. <https://doi.org/10.1007/s11252-020-00956-w>
- Bosch J, Vicens N (2002) Body size as an estimator of production costs in a solitary bee. *Ecol Entomol* 27:129–137. <https://doi.org/10.1046/j.1365-2311.2002.00406.x>
- Bosch J, Vicens N (2005) Sex allocation in the solitary bee *Osmia cornuta*: do females behave in agreement with Fisher's theory? *Behav Ecol Sociobiol* 59:124–132. <https://doi.org/10.1007/s00265-005-0017-8>
- Bosch J, Vicens N (2006) Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee *Osmia cornuta*. *Behav Ecol Sociobiol* 60:26–33. <https://doi.org/10.1007/s00265-005-0134-4>
- Buchholz S, Gathof AK, Grossmann AJ et al (2020) Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. *Landsc Urban Plan* 196:103731. <https://doi.org/10.1016/j.landurbplan.2019.103731>
- Burdine JD, McCluney KE (2019) Interactive effects of urbanization and local habitat characteristics influence bee communities and flower visitation rates. *Oecologia* 190:715–723. <https://doi.org/10.1007/s00442-019-04416-x>
- Cane JH (1987) Estimation of bee size using intertegular span (Apidae). *J Kans Entomol Soc* 61:145–147
- Cariveau DP, Nayak GK, Bartomeus I et al (2016) The allometry of bee proboscis length and its uses in ecology. *PLoS ONE* 11:e0151482. <https://doi.org/10.1371/journal.pone.0151482>
- Charnov EL (1982) *The Theory of Sex Allocation*. Princeton University Press, Princeton, NJ
- De Fioravante P, Luti T, Cavalli A et al (2021a) Multispectral Sentinel-2 and SAR Sentinel-1 Integration for Automatic Land Cover Classification. *Land* 10:611. <https://doi.org/10.3390/land10060611>
- De Fioravante P, Strollo A, Assennato F et al (2021b) High Resolution Land Cover Integrating Copernicus Products: A 2012–2020 Map of Italy. *Land* 11:35. <https://doi.org/10.3390/land11010035>
- Dürbaum E, Fornoff F, Scherber C et al (2023) Metabarcoding of trap nests reveals differential impact of urbanization on cavity-nesting bee and wasp communities. *Mol Ecol* 32:16818. <https://doi.org/10.1111/mec.16818>
- Dylewski Ł, Białas JT, Szymysł A, Banaszak-Cibicka W (2024) Pollinator assemblages in grasslands along river valleys depend on the urban matrix and local habitat scale variables. *Ecol Indic* 159:111687. <https://doi.org/10.1016/j.ecolind.2024.111687>
- Dylewski Ł, Maćkowiak Ł, Banaszak-Cibicka W (2020) Linking pollinators and city flora: How vegetation composition and environmental features shapes pollinators composition in urban environment. *Urban Urban Green* 56:126795. <https://doi.org/10.1016/j.ufug.2020.126795>
- Fauviau A, Baude M, Bazin N et al (2022) A large-scale dataset reveals taxonomic and functional specificities of wild bee communities in urban habitats of Western Europe. *Sci Rep* 12:18866. <https://doi.org/10.1038/s41598-022-21512-w>
- Fenoglio MS, Calviño A, González E et al (2021) Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. *Ecol Entomol* 46:757–771. <https://doi.org/10.1111/een.13041>
- Fenoglio MS, Rossetti MR, Videla M (2020) Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Glob Ecol Biogeogr* 29:1412–1424. <https://doi.org/10.1111/geb.13107>
- Ferrari A, Polidori C (2022) How city traits affect taxonomic and functional diversity of urban wild bee communities: insights from a worldwide analysis. *Apidologie* 53:46. <https://doi.org/10.1007/s13592-022-00950-5>
- Fisher RA (1930) *The Genetical Theory of Natural Selection*. Clarendon, Oxford
- Fitch G, Glaum P, Simao MC et al (2019) Changes in adult sex ratio in wild bee communities are linked to urbanization. *Sci Rep* 9:3767. <https://doi.org/10.1038/s41598-019-39601-8>
- Fornoff F, Halla W, Geiger S et al (2023) DNA barcoding resolves quantitative multi-trophic interaction networks and reveals pest species in trap nests. *Insect Conserv Divers* 16:725–731. <https://doi.org/10.1111/icad.12664>
- Fox J, Weisberg S (2019) *An R Companion to Applied Regression*, 3rd edn. Sage, Thousand Oaks, CA
- Gathmann A, Tschantke T (2002) Foraging ranges of solitary bees. *J Anim Ecol* 71:757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>
- Gerber HS, Klostermeyer EC (1970) Sex Control by Bees: A Voluntary Act of Egg Fertilization during Oviposition. *Science* 167:82–84. <https://doi.org/10.1126/science.167.3914.82>
- Goodell K (2003) Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia* 134:518–527. <https://doi.org/10.1007/s00442-002-1159-2>

- Graffigna S, González-Vaquero RA, Torretta JP, Marrero HJ (2024) Importance of urban green areas' connectivity for the conservation of pollinators. *Urban Ecosyst* 27:417–426. <https://doi.org/10.1007/s11252-023-01457-2>
- Graf LV, Meyer FS, Jeronimo FF, Gonçalves RB (2025) Urbanization as a driver of changes in mutualistic networks between bees and plants. *Urban Ecosyst* 28:30. <https://doi.org/10.1007/s11252-024-01639-6>
- Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596. <https://doi.org/10.1007/s00442-007-0752-9>
- Gresty CEA, Clare E, Devey DS et al (2018) Flower preferences and pollen transport networks for cavity-nesting solitary bees. *Ecol Evol* 8:7574–7587. <https://doi.org/10.1002/ece3.4234>
- Hall DM, Camilo GR, Toniello RK et al (2017) The city as a refuge for insect pollinators. *Conserv Biol* 31:24–29. <https://doi.org/10.1111/cobi.12840>
- Hartig F (2016) DHARMA: residual diagnostics for hierarchical (Multi-Level / Mixed) regression models. 0.4.7
- Hofmann MM, Fleischmann A, Renner SS (2020) Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. *J Hymenopt Res* 77:105–117. <https://doi.org/10.3897/jhr.77.51182>
- ISPRA (2023) Carta Nazionale di Copertura del Suolo. <https://www.isprambiente.gov.it/it/attivita/suolo-e-territorio/suolo/copertura-dei-suolo/carta-nazionale-di-copertura-del-suolo>
- Kendall LK, Mola JM, Portman ZM et al (2022) The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology* 103:e3809. <https://doi.org/10.1002/ecy.3809>
- Kendall LK, Rader R, Gagic V et al (2019) Pollinator size and its consequences: Robust estimates of body size in pollinating insects. *Ecol Evol* 9:1702–1714. <https://doi.org/10.1002/ece3.4835>
- Kim J (1999) Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). *Behav Ecol* 10:552–556. <https://doi.org/10.1093/beheco/10.5.552>
- Kim J, Thorp RW (2001) Maternal investment and size-number trade-off in a bee, *Megachile apicalis*, in seasonal environments. *Oecologia* 126:451–456. <https://doi.org/10.1007/s004420000540>
- Lüdecke D (2018) ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *JOSS* 3:772. <https://doi.org/10.21105/joss.00772>
- Lüdecke D, Ben-Shachar M, Patil I et al (2021) performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *JOSS* 6:3139. <https://doi.org/10.21105/joss.03139>
- Liang H, He Y-D, Theodorou P, Yang C-F (2023) The effects of urbanization on pollinators and pollination: A meta-analysis. *Ecol Lett* 26:1629–1642. <https://doi.org/10.1111/ele.14277>
- Lindermann L, Grabener S, Fornoff F et al (2023) Wildbienen und Wespen in Nisthilfen bestimmen. <https://doi.org/10.3220/MX1685523077000>
- MacIvor JS, Cabral JM, Packer L (2014) Pollen specialization by solitary bees in an urban landscape. *Urban Ecosyst* 17:139–147. <https://doi.org/10.1007/s11252-013-0321-4>
- Makinson JC, Threlfall CG, Latty T (2017) Bee-friendly community gardens: Impact of environmental variables on the richness and abundance of exotic and native bees. *Urban Ecosyst* 20:463–476. <https://doi.org/10.1007/s11252-016-0607-4>
- Marrero HJ, Gómez-Martínez C, Allasino ML et al (2025) Local and landscape effects on the reproduction of wild bees and wasps in Mediterranean communities along a gradient of land-use. *Ecol Entomol* 50:399–410. <https://doi.org/10.1111/een.13417>
- McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst* 11:161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Mäder P, Boho D, Rzanny M et al (2021) The Flora Incognita app – Interactive plant species identification. *Methods Ecol Evol* 12:1335–1342. <https://doi.org/10.1111/2041-210X.13611>
- Müller A (1996) Convergent evolution of morphological specializations in Central European bee and honey wasp species as an adaptation to the uptake of pollen from nototribic flowers (Hymenoptera, Apoidea and Masaridae). *Biol J Linn Soc* 57:235–252. <https://doi.org/10.1006/bijl.1996.0013>
- Müller A (2025) Palaeartic osmiine bees: systematics and biology of a fascinating group of solitary bees. <https://blogs.ethz.ch/osmiini/>
- Moldoveanu OC, Maggioni M, Dani FR (2024) Environmental ameliorations and politics in support of pollinators. Experiences from Europe: A review. *J Environ Manag* 362:121219. <https://doi.org/10.1016/j.jenvman.2024.121219>
- Moretti M, Fontana S, Carscadden KA, MacIvor JS (2021) Reproductive trait differences drive offspring production in urban cavity-nesting bees and wasps. *Ecol Evol* 11:9932–9948. <https://doi.org/10.1002/ece3.7537>
- Newbold T, Hudson LN, Hill SLL et al (2015) Global effects of land use on local terrestrial biodiversity. *Nature* 520:45–50. <https://doi.org/10.1038/nature14324>
- Oksanen J, Kindt R, Legendre P et al (2001) vegan: Community Ecology Package. R package.
- Onandia G, Schittko C, Ryo M et al (2019) Ecosystem functioning in urban grasslands: The role of biodiversity, plant invasions and urbanization. *PLoS ONE* 14:e0225438. <https://doi.org/10.1371/journal.pone.0225438>
- Palladini JD, Maron JL (2014) Reproduction and survival of a solitary bee along native and exotic floral resource gradients. *Oecologia* 176:789–798. <https://doi.org/10.1007/s00442-014-3028-1>
- Peruzzi L (2021) Flora empoiese: elenco della flora vascolare della terra d'Empoli. ETS, Pisa
- Pignatti S (1997) Flora d'Italia. Edagricole, Bologna
- Polidori C, Rodrigo-Gómez S, Ronchetti F et al (2024) Sunny, hot and humid nesting locations with diverse vegetation benefit *Osmia* bees nearby almond orchards in a mediterranean area. *J Insect Conserv* 28:57–73. <https://doi.org/10.1007/s10841-023-00523-6>
- Portal to the Flora of Italy (2025) Portale della flora d'Italia - Portal to the flora of Italy. <http://dryades.units.it/floritaly>
- QGIS Development Team (2024) QGIS Geographic Information System. QGIS Association
- Quistberg RD, Bichier P, Philpott SM (2016) Landscape and local correlates of bee abundance and species richness in urban gardens. *Environ Entomol* 45:592–601. <https://doi.org/10.1093/ee/nvw025>
- Rada P, Bogusch P, Rom J, Horák J (2024) Adding a mosaic mowing regime to urban lawns is the key to city biodiversity management for pollinators. *Urban For Urban Green* 128452. <https://doi.org/10.1016/j.ufug.2024.128452>
- Radmacher S, Strohm E (2010) Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). *Apidologie* 41:169–177. <https://doi.org/10.1051/apido/2009064>
- Ranalli R, Borghesan S, Labra M, Biella P (2025) From cities to refuges for pollinators: Urban practices for enhancing pollinator habitats in changing landscapes. *J Appl Ecol* 62:2874–2881. <https://doi.org/10.1111/1365-2664.70005>
- R Core Team (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Rehan SM, Richards MH (2010) The Influence of Maternal Quality on Brood Sex Allocation in the Small Carpenter Bee, *Ceratina calcarata*. *Ethology* 116:876–887. <https://doi.org/10.1111/j.1439-0310.2010.01804.x>
- Rosas-Ramos N, Baños-Picón L, Tobajas E et al (2017) Both landscape and local scale factors matter for the parental investment

- strategies of the pollinator *Osmia caerulescens*. *J Apic Res* 56:1–12. <https://doi.org/10.1080/00218839.2017.1282079>
- Rosenheim JA, Nonacs P, Mangel M (1996) Sex Ratios and Multifaceted Parental Investment. *Am Nat* 148:501–535. <https://doi.org/10.1086/285937>
- Rubel F, Kottek M (2010) Observed and projected climate shifts 1901–2100 depicted by world maps of the Köppen–Geiger climate classification. *Meteorol Z* 19:135–141. <https://doi.org/10.1127/0941-2948/2010/0430>
- Satta A, Floris I, Ruiu L, Palmieri N (2007) Trap-nesting of some Megachilidae bees (Hymenoptera Apoidea) in the north west of Sardinia (Italy). *Redia XC* :131–134
- Sexton AN, Benton S, Browning AC, Emery SM (2021) Reproductive patterns of solitary cavity-nesting bees responsive to both local and landscape factors. *Urban Ecosyst* 24:1271–1280. <https://doi.org/10.1007/s11252-021-01116-4>
- Süle G, Kovács-Hostyánszki A, Sárospataki M et al (2023) First steps of pollinator-promoting interventions in Eastern European urban areas – positive outcomes, challenges, and recommendations. *Urban Ecosyst* 26:1783–1797. <https://doi.org/10.1007/s11252-023-01420-1>
- Spittl A, Skórka P, Strachecka A et al (2021) Keep trees for bees: Pollen collection by *Osmia bicornis* along the urbanization gradient. *Urban For Urban Green*. 64. <https://doi.org/10.1016/j.ufug.2021.127250>
- Staab M, Pufal G, Tscharnkte T, Klein A (2018) Trap nests for bees and wasps to analyse trophic interactions in changing environments—A systematic overview and user guide. *Methods Ecol Evol* 9:2226–2239. <https://doi.org/10.1111/2041-210X.13070>
- Tasei J-N, Picart M (1972) Observations préliminaires sur la biologie d'*Osmia* (*Chalcosmia*) *caerulescens* L., (Hymenoptera: Megachilidae), pollinisatrice de la luzerne (*Medicago sativa* L). *Apidologie* 3:149–165. <https://doi.org/10.1051/apido:19720203>
- Theodorou P (2022) The effects of urbanisation on ecological interactions. *Curr Opin Insect Sci* 52:100922. <https://doi.org/10.1016/j.cois.2022.100922>
- Theodorou P, Radzevičiūtė R, Lentendu G et al (2020) Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat Commun* 11:576. <https://doi.org/10.1038/s41467-020-1449-6-6>
- Tobajas E, De Paz V, Rosas-Ramos N et al (2024) Pollen use by the solitary bee *Osmia caerulescens* in cherry orchard agroecosystems in Spain. *J Apic Res* 63:1126–1135. <https://doi.org/10.1080/00218839.2022.2080952>
- Tobajas E, Rosas-Ramos N, Asís JD et al (2021) Effects of hillside aspect, landscape features, and kleptoparasitism on the reproductive success of the solitary bee *Osmia caerulescens*. *Ecol Entomol* 46:541–551. <https://doi.org/10.1111/een.13000>
- Tommasi N, Biella P, Maggioni D et al (2023) DNA metabarcoding unveils the effects of habitat fragmentation on pollinator diversity, plant–pollinator interactions, and pollination efficiency in Maldivian islands. *Mol Ecol* 32:6394–6404. <https://doi.org/10.1111/mec.16537>
- Tommasi N, Ferrari A, Labra M et al (2021) Harnessing the power of metabarcoding in the ecological interpretation of plant–pollinator DNA data: strategies and consequences of filtering approaches. *Diversity* 13:437. <https://doi.org/10.3390/d13090437>
- Tscharnkte T, Gathmann A, Steffan-Dewenter I (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *J Appl Ecol* 35:708–719. <https://doi.org/10.1046/j.1365-2664.1998.355343.x>
- Turo KJ, Gardiner MM (2021) Effects of urban greenspace configuration and native vegetation on bee and wasp reproduction. *Conserv Biol* 35:1755–1765. <https://doi.org/10.1111/cobi.13753>
- Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*, Fourth. Springer, New York
- Vicens N, Bosch J, Blas M (1993) Análisis de 10s nidos de algunas *Osmia* (Hymenoptera, Megachilidae) nidificantes en cavidades preestablecidas. *Orsis* 8:41–52
- Warzecha D, Diekötter T, Wolters V, Jauker F (2016) Intraspecific body size increases with habitat fragmentation in wild bee pollinators. *Landsc Ecol* 31:1449–1455. <https://doi.org/10.1007/s10980-016-0349-y>
- Wenzel A, Grass I, Belavadi VV, Tscharnkte T (2020) How urbanization is driving pollinator diversity and pollination – A systematic review. *Biol Conserv* 241:108321. <https://doi.org/10.1016/j.biocon.2019.108321>
- Wittmann K, Klein A-M, Staab M (2023) The influence of habitat properties on sex determination in cavity-nesting Hymenoptera. *Basic Appl Ecol* 70:1–11. <https://doi.org/10.1016/j.baee.2023.04.001>
- Wittmann K, Klein A, Pichler M, Staab M (2025) Disentangling the influence of environmental conditions on sex determination in haplodiploid organisms. *J Anim Ecol* 1365-2656.70153 <https://doi.org/10.1111/1365-2656.70153>
- Zaragoza-Trello C, Vilà M, Bartomeus I (2021) Interaction between warming and landscape foraging resource availability on solitary bee reproduction. *J Anim Ecol* 90:2536–2546. <https://doi.org/10.1111/1365-2656.13559>
- Özök A, Güler Y (2016) Encountered Pollen in Nests Two *Osmia* Species (Hym.:Megachilidae) from Sweet Cherry Orchards in Sultandağı Town (Afyonkarahisar, Turkey). *Hacettepe J Biol Chem* 1:15–15. <https://doi.org/10.15671/HJBC.20164417561>
- Zurbuchen A, Cheesman S, Klaiber J et al (2010a) Long foraging distances impose high costs on offspring production in solitary bees. *J Anim Ecol* 79:674–681. <https://doi.org/10.1111/j.1365-2656.2010.01675.x>
- Zurbuchen A, Landert L, Klaiber J et al (2010b) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol Conserv* 143:669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>

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