EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **122**: 198–209, 2025
doi: 10.14411/eje.2025.025
ORIGINAL ARTICLE

Exploring behavioural plasticity in the nesting biology of *Megachile sculpturalis* (Hymenoptera: Megachilidae) and its role in invasion success

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Key words. Wild bee, solitary, gregarious, alien, bee hotel, stereotypy

Abstract. The success of animal species is shaped by a combination of ecological conditions and behavioural plasticity, with the latter being particularly crucial for the spread of invasive species. *Megachile sculpturalis* (Apoidea: Megachilidae), an East-Asian solitary bee introduced to France and subsequently spreading across Europe and North America, provides a case study. While its distribution is well-documented, the behavioural traits driving its success remain poorly understood. Our study aimed to explore behavioural patterns associated with its nesting cycle and potential expansion. In 2020, we conducted focal observations of individually marked females nesting in an artificial bee hotel. Daily recordings, based on ethograms, tracked females' activity at the site. We identified key behavioural units related to nesting goals and analysed the frequency and abundance of actions associated with each marked nest. Our results highlighted the significant effort females devote to nest-related actions, with 50-68% of all behaviours focused on nest building, suggesting any strategy of dispersion should be investigated in this context. While a typical nesting sequence was identified, individual variability indicated plastic nesting responses. Notably, females demonstrated a strong tendency to quickly shift their efforts to new nests following closure or abandonment, even provisioning multiple nests simultaneously. This ability to manage several nests at once may be crucial for establishing populations in invaded areas by rapidly expanding nesting efforts across multiple new sites during a single reproductive season. Our findings emphasize the contribution of behavioural studies in understanding reproductive strategies that influence a species' ability to settle in new environments and expand its range.

INTRODUCTION

Animal behaviour emerges from a balance between fixed patterns (stereotypy) and adaptability (plasticity). Evolution contributes a series of behavioural units (stereotypy) necessary for successful animals' reproduction. This series is guided by various critical elements, primarily established at the taxonomic level and repeated by each individual based on the context (e.g., nesting, mating). Notably, solitary bees and wasps are particularly known for exhibiting stereotyped behavioural patterns (Iwata, 1976; Morato & Martins, 2006). Mandujano et al. (2016) identified 11 behavioural units in male *Sphex latreillei* Lepeletier, 1831, a solitary ground-nesting wasp, and statistically assessed their stereotypy. Nonetheless, individuals must adapt their behavioural sequences to unpredictable conditions at the environmental or individual level, employing plasticity when needed to achieve their objectives. Plasticity is crucial in behavioural studies as it contributes significantly to variability (Japassù & Malange, 2014). Behavioural plasticity arises from an animals' ability to adjust behavioural responses to complex environmental conditions, known as "behavioural reaction norms" (Dingemanse & Wolf, 2015). For instance, honeybees foraging for nectar on black locust flowers follow a typical sequence: approaching the flower, positioning on the petals, and sucking nectar. However, this sequence requires adaptation

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to overcome the flower's mechanism, which demands specific strength for nectar access. Some individuals may be too weak to trigger the mechanism, and as a result, a more adaptive decision might be to abandon that flower for another one, thereby disrupting the expected stereotypical sequence (Giovanetti, 2019). Ethograms break down typical behavioural sequences toward ultimate goals, but they also highlight individual variations caused by various factors. Individual differences in nest construction have been detected by recording nest construction traits out of 60 nests of the alfalfa leafcutting bee, *Megachile rotundata* (Royauté et al., 2018), suggesting the importance of nest construction in defining evolutionary traits of a species. For invertebrates, behavioural variability among individuals is sometimes overlooked (Brembs, 2013) or attributed to inefficiency in inexperienced individuals. The sequences typically describe the behaviours of individuals who follow them consistently, often excluding those who deviate.

The nest is a central focal point in the activity and behaviour of bees. While the architecture of wild bee nests can vary significantly, several classifications have been proposed based on the behaviours involved in nest construction. Danforth et al. (2019) proposed four categories: soil excavators, wood excavators, renters, and above-ground builders. However, they also noted that while some bee groups exhibit uniform nesting behaviours, others diversify both the substrates they use and their construction methods. Regardless of the nest structure, females dedicate much of their time to nest building, thereby increasing the chances of survival for their offspring (Michener, 2007; Danforth et al., 2019). Nesting behaviour is often described as a sequence of stereotyped actions. Species-specific traits, innate behaviours, environmental cues, and individual limitations are all thought to be interconnected through an individual's capacity to learn and exhibit some degree of flexibility. It is hypothesized that there exists a threshold beyond which learning is incorporated into evolutionarily programmed behaviours (Mery & Burns, 2010), potentially balancing the costs and benefits of such adaptations.

Megachile (*Callomegachile*) *sculpturalis* (Smith, 1853) belongs to the family Megachilidae (Hymenoptera), a widespread family whose species inhabit diverse environments because of their ability to utilize varying materials and substrates for nest construction (Michener, 2007). The Megachilinae subfamily, which includes *M. sculpturalis* and comprises over 4,000 species, has expanded considerably due to its behaviour of lining brood cells with externally collected materials (Danforth et al., 2019). Originating from the Eastern Palaearctic (Korea, Japan, China, Taiwan), *M. sculpturalis* has been recorded nesting in opportunistic conditions beyond its native range, using pre-existing nests of other large solitary bees and competing for nesting spaces with other cavity-nesting species (Laport & Minckley, 2012), or adopting artificial structures such as bee hotels (Gihr & Westrich, 2013; Quaranta et al., 2014; Geslin et al., 2020). This solitary species constructs brood cells for each individual offspring, with cell walls and plugs (including entrance) sealed with resin; it is reported as a generalist (polylectic) pollinator, while outside its home range bees are reported feeding mainly on Fabaceae (Dubaić & Lanner, 2021). The IUCN (2020) referred to *M. sculpturalis* as invasive, although no control measures have yet been implemented. The rapid expansion has sparked significant interest in USA and Europe, with recent modelling of bioclimatic and anthropogenic variables (Lanner et al., 2022): distance to roads and human population resulted as the most important drivers, while the species seems to prefer moderate precipitation and intermediate temperatures, typical of temperate zone. Understanding the successful behavioural strategies enabling its rapid settlement is crucial for species management.

To advance knowledge of species' behavioural traits possibly connected with reproduction success, we carried out observations focusing on a nesting site and detailing the nesting sequence and flexibility of individually marked females. Our analysis of the records accounted for behavioural flexibility in two ways: (a) by including any record associated with activity directed towards a specific cavity or nest, and (b) by evaluating the nesting strategies of multiple individuals, comparing those that spent more time at the nesting site with those recorded for shorter periods. This approach allowed us to address the issue of variability, which has often been overlooked or misinterpreted in previous studies, and to identify unique strategies that may enhance successful nesting and invasion.

MATERIAL AND METHODS

In the summer of 2020, we conducted daily behavioural observations of marked female bees at a bee hotel located at our institute's premises (CREA Research Centre for Agriculture and Environment, Bologna; coordinates: 44°31′26.9″N, 11°21′05.3″E). A prior study at this same location began after the installation of the artificial structure in 2014, where details on available nesting materials are described by Bogo et al. (2024). This bee hotel housed reeds, drilled wood blocks, or trunk segments. Other species were occasionally seen nesting, including native species such as *Anthidium florentinum* (Fabricius, 1775), *Osmia cornuta* (Latreille, 1805), *Osmia bicornis* (L., 1758), *Heriades* sp., *Ancistrocerus* sp.; another alien species, *Megachile disjunctiformis* Cockerell, 1911. Bogo et al. (2024) observed *M. sculpturalis* nests with an overall average diameter of 0.85 ± 0.01 cm, with the number of nests completed per female varying significantly from year to year (4.51 nests in 2017 and 2.24 in 2018). Highly variable was also the time estimated for nest completion (1–5 days). This variability prompted a renewed recording campaign and a revised data analysis approach.

We carried out focal observations on 58 marked individuals from July 3 to July 31, 2020. Females were caught upon emergence and marked with non-toxic dyes, using a colour combination on their thorax for individual identification. To assess philopatric tendencies, we analysed the data from the first sighting (re-capture) of marked females at the site. Re-captures could occur several days post-marking, and data were grouped by recapture time. Any activity post-recapture was systematically recorded at the bee hotel, and we marked nest entrances upon occupancy. Our study concentrated on nesting activity, encompassing any action near the nesting site, on its surface, or time spent inside

Table 1. The standardized ethogram of *Megachile sculpturalis*, with action titles and descriptions (related to nests*) applied in the study.

Title	Definition
ENTERING	The bee reaches the entrance of a tunnel* by flying or walking and gets inside it. The individual can eventually carry material (pollen, resin, or undefined material) or pollen. Material is recorded separately from the action of entering.
LEAVING	The bee emerges from the entrance of a tunnel* and gets away from it.
QUICK-OUT	The bee performs a sequence of fast leaving/entering from/to the same entrance*, the whole sequence occurring in less than 1 min.
REVERSING	The bee, recently entered a tunnel*, gets out of it and immediately re-enters backwards; the action is associated with the presence of pollen on the scopae (pollen present when first entering and when reversing).
SCANNING	The bee accomplishes various brief actions such as flying in front of an entrance*, laying on the wood blocks or the surface of the reeds, and inspecting entrances* by entering them half-body. These actions can occur in fast sequences.
ATTACKING	The bee interacts with another individual: a bee of the same species or another species nesting in the bee hotel, the interactions being aggressive (mandibles open, biting, or fast moving forward in the direction of the other insect). The behaviour can either start from the bee under observation towards another insect or be the response after being attacked.

*A cavity in a solid wood cube; cut reeds of the species *Arundo donax* Forssk. A detailed description of the bee hotel at the CREA premises can be found in Bogo et al., 2024.

the nest, while other life cycle actions (mating, foraging) were excluded.

Like some other Megachilidae, these nests consist of a linear series of brood cells, separated by various materials already described (Ivanov & Fateryga, 2019; Ivanov et al., 2021; Bogo et al., 2024). Intra-nest activities were not directly observed; the effort dedicated to these activities was estimated out of our behavioural units. Observations were conducted daily for four hours, in the period from 0700 to 1700 DST, totalling 116 h over the entire season. To ensure consistency, the four hours of observation each day were evenly distributed throughout the season. Initial checks of activities confirmed they were concentrated during these hours. We devised a standardized ethogram based on what could be visually observed from a fixed position in front of the nesting site. Records (n = 10,582) detailed actions as per the ethogram, their timing (precision: 1 min), materials carried to the nest, and identities of interacting individuals. The ethogram is detailed in Table 1.

To discern individual nesting strategies, we selected females based on longevity (at least 28 days of observations) and activity records (more than 400 records). This selection aimed to exclude records of transiently visiting individuals and better depict the nesting sequence following a classical approach. Seven females met these requirements. We categorized actions based on identifiable goals into four main contexts: nest-related actions, pollen-related actions, cell/entrance closure actions, and scanning of other entrances or the bee hotel area. Table 2 provides details on how the behavioural units dataset was created and how each action contributed to the respective categories. The seven females selected for the study (hereafter referred to as “long-lived”) spent nearly a month at the nesting site. We also tested our behavioural units on two additional females (referred to as “short-lived”), which spent almost a week at the site.

All entrances led to a cavity, favouring twig-nesting species. Repeated activity marked certain entrances as “nests,” identified by letters and numbers for recording purposes. Nests ideally underwent cleaning or debris removal first, followed by pollen provisioning and subsequent cell and nest closure with resin and other materials. Some nests, despite lacking pollen, were still

Table 2. Behavioural units defined according to final goal (nest, pollen, closure, scan).

	Nest-dedicated actions	Pollen-dedicated actions	Closure dedicated actions	Scanning other entrances/ bee hotel area
ENTERING	actions of entering a provisioned nest equally contributed, including those in which some material was recorded*	actions of entering were assigned to this list if pollen was present on the female	actions of entering were assigned to this list if resin or other material was carried by the female	actions of entering a nest were assigned to this category when associated with visited nests
LEAVING	actions of leaving the nest were assigned to this category when occurring in provisioned nests	actions of leaving were assigned to this list if pollen was present on the female	actions of leaving were assigned when following entering with material	actions of leaving a nest were assigned to this category when associated with visited nests
QUICK-OUT	actions of quick-out were assigned to this category when occurring in provisioned nests		actions of quick-out were assigned to this category if the closure of the nest had started	actions of quick-out were assigned to this category when associated with visited nests
REVERSING		all actions of reversing were assigned to this category; occurring usually with pollen still on scopae		
SCANNING				all actions of scanning were assigned to this category
ATTACKING	actions versus other females approaching the provisioned nest		actions versus other females approaching the nest under closure	

* We did also count trips with pollen or other material, since we can not discard the possibility that, more than depositing the pollen or material, the bee would have lined/or adjusted the cell once entered the nest.

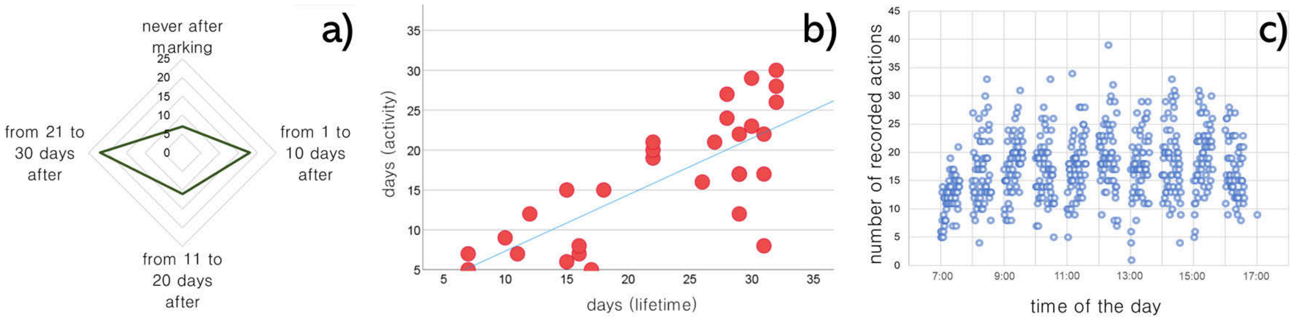

Fig. 1. Recapture results of marked females. a) Highlights 88% recapture rate; b) Activity correlated with potential lifespan (first-last recapture); c) Daily activity constancy during the reproductive season.

considered nests due to observed activity, possibly hinting at nectar provision trips or missed pollen delivery.

To evaluate behaviour consistency among females, we used total actions as the dependent variable, with activity type and monitoring day as independent variables; female identity was treated as a random factor. We applied a generalized linear mixed-effects model (GLMER) with a negative binomial distribution due to overdispersion detected during model selection. After running the model execution, we computed the Intra-Class Correlation (ICC) to examine the variance explained by the grouping structure (Koo & Li, 2016), which is represented in this case by individual females. The selection of the best models was based on the AIC (Akaike Information Criterion). A significance level of 0.05 was employed for hypothesis testing. The study employed R version 4.3.2 with MASS, lme4, and performance packages (Venables et al., 2002; Bates et al., 2015; Lüdecke et al., 2021), and generated visualizations using ggplot2 (Wickham, 2016).

RESULTS

Marked *M. sculpturalis* females demonstrated strong site fidelity to the bee hotel, with 88% recaptured at least once (Fig. 1a). Seven females did not return, likely due to disturbance during marking or immediate dispersal. Twenty others showed sporadic presence (less than 5 days). Recapture often spanned time, with marked instances showing repeated recaptures over weeks: a female was marked on the 30th of June, and recaptured twice, on the 11th and 29th of July. The remaining 31 females were recorded almost constantly, even daily. Calculating the lifespan as first-last recapture and plotting the number of days that each of the 31 females was recorded active, we generally observe a high correspondence (Fig. 1b; $R^2 = 0.567$). These bees did not exhibit a peak in activity at any specific time; instead, their activity was evenly distributed throughout the entire day. (Fig. 1c).

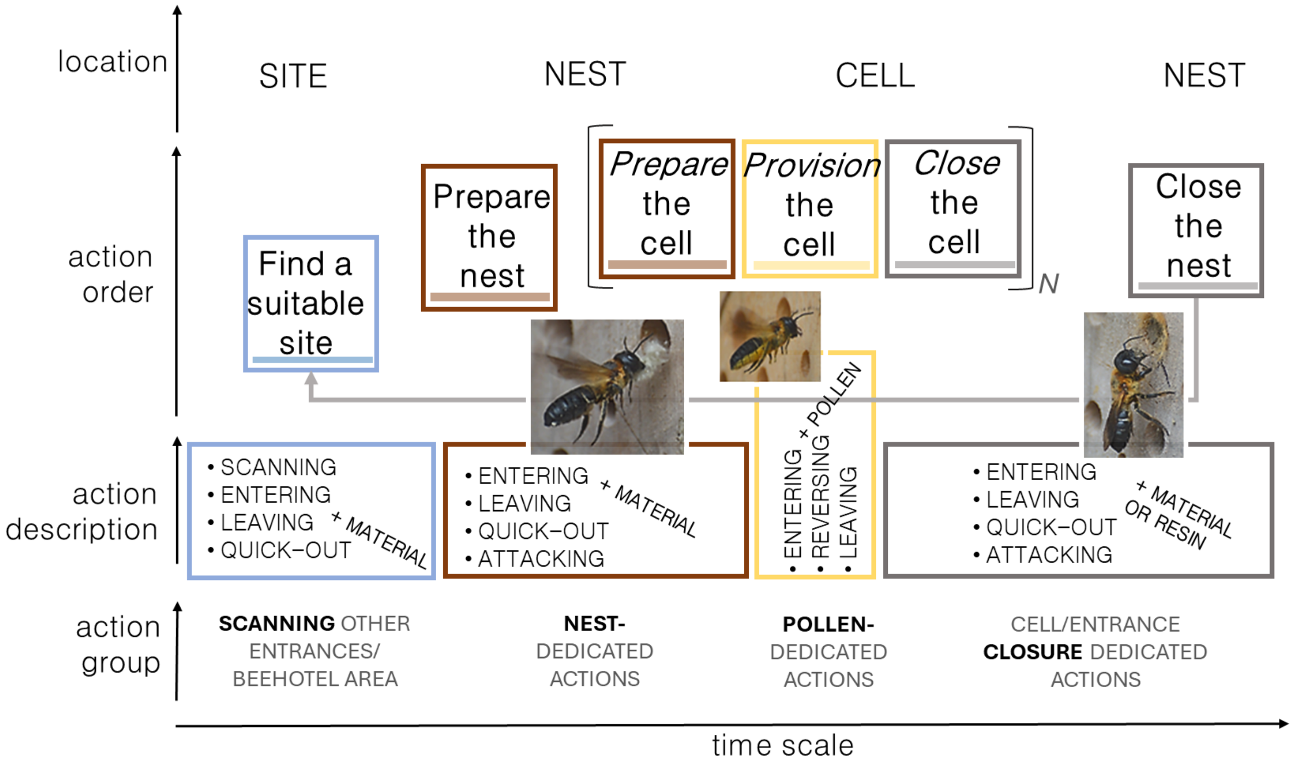

Fig. 2. Ethogram. Graphical representation of record attribution, their occurrence and grouping according to goals.

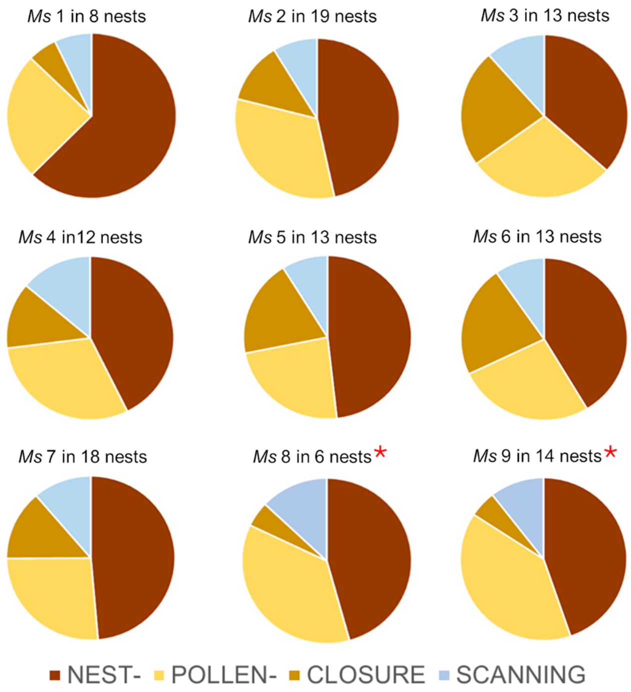

Fig. 3. Long-lived female activity pie charts. Ms 1–7 (long-lived) and Ms 8–9 (short-lived (*)) females' behavioural units represented.

From our observations, we were able to map out the actions and their sequence in the nesting activity of females. We also realized that each action must be considered within the context of different scales at which it occurs. Nesting is a process that unfolds over time (Fig. 2), and can be broken down according to location, action sequence, description, and grouping into behavioural units. "Find a Suitable Site" (Fig. 2, blue box) clearly represents the first step. During this phase, several actions indicate that the female is patrolling the area. Females searching for a suitable nest site often perform frequent, short flights with no clear direction, flying to and from the bee hotel and landing on the available surfaces, sometimes disturbing other females while inspecting occupied entrances. Once a suitable entrance and cavity are identified, the *M. sculpturalis* female initiates a series of behaviours that contribute to "Prepare the Nest and the Cell" (or multiple cells; Fig. 2, brown boxes). Several actions signal this phase: the female may remove material from the nest (such as detritus from previous nesting activity or cellulose fibers from reeds), spend long periods inside the nest, or engage in a quick series of entering and leaving. At a certain point, the nest seems ready, and the female begins provisioning the cell (Fig. 2, yellow box). This phase is characterized by a sequence of flights to collect and return with pollen, visibly carried under the bee's abdomen. Not all females, however, brought pollen into the nests; some were observed entering and leaving the same nest entrance regularly but without performing pollen provisioning. Finally, "Cell and Nest Closure" (Fig. 2, boxes on the right) is marked by trips to collect and deposit resin and other materials either inside the nest or at the entrance.

Table 3. Negative Binomial GLMER Summary, with estimate, Standard Error (SE), z-value and p-values. ICC = 0.07; Marginal R2 / Conditional R2 = 0.31 / 0.36, AIC= 2326.07.

Fixed effects:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept (closure)	1.25	0.25	5.11	0.00
Nesting	1.65	0.32	5.22	0.00
Pollen	1.11	0.32	3.49	0.00
Scanning	–0.10	0.33	–0.31	0.76
Days	0.03	0.02	1.76	0.08
Nesting x Days	–0.04	0.02	–1.70	0.09
Pollen x Days	–0.03	0.02	–1.58	0.11
Scanning x Days	–0.02	0.02	–1.01	0.31

The analyses of long-lived females highlighted the percentage of work dedicated to each group of actions. In Fig. 3, each pie represents a single female, according to the number of records for each of the four groups of actions (scanning, nest-, pollen, closure-dedicated actions): we report the female code and the number of nests. The seven long-lived females occupied from 8 to 19 nests in almost a month of activity (average ± SD: 13.7 ± 3.7); the short-lived ones occupied 4 to 6 nests, in barely a week of activity. Four of the long-lived females were never observed provisioning with pollen, notwithstanding they performed other nest-dedicated actions, in two cases including the final closure of the nest. Six out of the seven long-lived females provisioned with pollen in two nests simultaneously; five of them were even observed performing the multi-nest provisioning more than once during their activity. Nest-related actions frequently surpassed others, contributing half or more to total activities (range: 50–68%). Pollen-related actions typically amounted to a third of all actions (23.6–39.5%), and scanning, the least frequent (7.1–12.9%), remained consistent.

The percentage of actions dedicated to nest-cell activities, pollen provisioning, nest closure or scanning showed some variation for each female but were regularly distributed as overall activity for each one. The model confirmed that the total number of actions performed by each female is influenced by the behavioural unit (Table 3).

Activity consistency remained stable throughout monitoring. A low ICC (0.07) indicated low reliability (Koo & Li, 2016) and suggested greater within-female than between-female variability, revealing individual plasticity amidst overall species behavioural uniformity. Short-lived females' activity patterns corresponded with model predictions for individual plasticity in the corresponding pies of Fig. 3 and the predicted number of actions per day obtained from the model in Fig. 4.

DISCUSSION

Several findings from this study suggest that the nesting strategy plays a crucial role in the rapid spread of this species in invaded areas. Our hypothesis is that individuals may divide their reproductive efforts between their original (philopatric) site and a new (expansion) site, nesting partly in the familiar location and partly in a new one. If this behaviour is consistent across all females (at the species level), dispersal could occur more quickly. Many in-

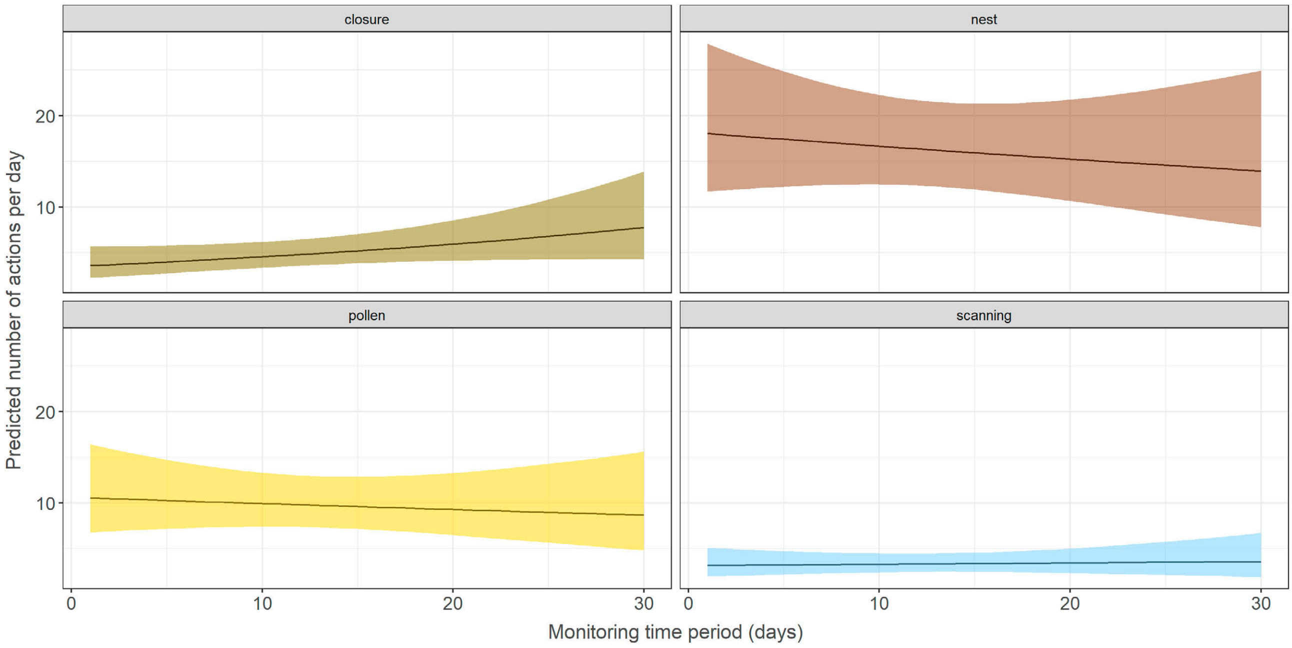

Fig. 4. Model predictions. Daily actions of long- and short-lived females maintained consistency.

dividuals would then (a) ensure reproductive success by splitting their efforts across multiple sites, and (b) colonize new areas more efficiently.

Philopatry, or the tendency of bees to nest near their emergence site, is common in Hymenoptera. The reasons behind this behaviour often involve a combination of factors. The selection of a site with favourable local ecological conditions (such as available nesting and feeding options) can lead to reduced dispersal and a more sedentary lifestyle (Franzén et al., 2009). The presence of conspecifics may serve as a cue indicating the suitability of the site (Yanega, 1990). More generally, the costs and benefits of dispersal at the individual level can be influenced by the local landscape, including factors such as habitat size, spacing, and the quantity and quality of available habitats (Thomas, 2000). *Megachile sculpturalis* has been recorded nesting at the same study sites in successive years (Bogo et al., 2024); however, previous records did not specifically investigate whether the nesting females born at the site were the same individuals marked and observed later. In this study, we assessed philopatry using recapture data from marked females born at the site, revealing a high rate of philopatry, with 88% of them returning. While some of these females maintained almost continuous nesting activity, others showed a more intermittent pattern. The discrepancies between estimated longevity and observed activity seem to support our hypothesis. Females that were recaptured weeks after emergence but showed little activity at the site likely dispersed to other locations for nesting, although they occasionally returned nesting to their original site. Individual size may have influenced the strategy adopted by each female. Unfortunately, we did not measure head width during our study, even though it is a reliable proxy for individual size differences. Size is influenced by nest conditions and the diet provided to the larvae, but it can also, in turn, affect foraging, flower handling, conflict resolution, and division of labour in social species (Chole et al., 2019). Given our observations of direct conflicts over nest ownership, it is plausible that size plays a role in determining the outcome, potentially forcing smaller individuals to disperse.

Ethograms are valuable tools for identifying demanding actions, both in terms of the complexity of behavioural units and the effort dedicated to them, helping to better understand potential evolutionary pathways. For example, they have been used to identify how honeybees adopt alternative strategies to overcome barriers (Giovanetti, 2019), to describe the behavioural patterns – climbing, questing, and posturing – employed by ticks to follow the sit-and-wait strategy for finding a host (Vargová et al., 2022), and to standardize the highly frequent and similar behaviours of different cat species, despite differences in study goals and species (Stanton et al., 2015). Nesting activity can be analysed in various ways. Our results indicate that the behavioural units were not uniform in terms of action frequency; nest care was significantly more demanding than food provisioning. While this is typical among solitary bees (Danforth et al., 2019), it may have driven females to seek new nesting sites and sources of nesting material, preferably those that are already "prepared" by conspecifics. This may have contributed to a back-and-forth nesting strategy, where females either nest at multiple sites or simultaneously care for several nests.

We are still puzzled by the unexpectedly low records on pollen carried at the nest. We cannot completely rule out the possibility of missing some data, given the inherent challenges of conducting field observations. However, given the high frequency of non-foraging females, it seems unlikely that a significant amount of data was overlooked. Another possible explanation is that failures (e.g., not provisioning the nest) or the construction of fake nests may be more common than initially expected. Variability in resource acquisition agrees with previous Bogo et al. (2024) findings of "anomalies", as nests with no or a single cell, absence of pollen provision, and the presence of an antechamber and other empty chambers. In the solitary bee genus *Andrena*, fake nests are frequently reported in the literature, with detailed records of the time and effort invested in their construction (Osgood, 1989; Schönitzer & Klinksik, 1990; Rezkova et al., 2012). Some authors suggest that empty nests may reduce the likelihood of parasitism by deterring parasites: in the case of *M. sculpturalis* we never observed parasites at the site, or emerging from the nests at the beginning of the season. Regardless of the underlying reason for constructing these chamber-like nests, the process requires considerable effort, potentially reducing the overall time spent on pollen collection. Additionally, nest construction in the genus *Megachile* also involves the gathering of materials. Similar observations have been made in *Megachile cephalotes* (Smith, 1853), where some foraging trips were dedicated to collecting resin or other materials used to seal brood cells and block the nest entrance with a plug (Akram et al., 2022). Resins may play a pivotal role in nest construction, serving as intermediate cell layers, inner cell linings, or adhesives for camouflaging materials, and helping to regulate nest humidity, reduce infestations, and inhibit the growth of microbial antagonists (Chui et al., 2022). Resin collection is an additional effort associated with nest construction, and it may be a common behaviour at the genus level. In our study, we recorded 449 actions related to the manipulation of nesting materials, 40% of which were clearly dedicated to resin. The bees were observed carefully manipulating resin drops in front of nest entrances and applying them to the surface using their mandibles and first pair of legs. We also recorded four females collecting resin from adjacent nests – either from inactive nests of the previous season or by robbing resin from nests where other females were in the process of closing their nests. These observations seem to support our hypothesis by confirming that the collection of nesting material may occur transversally across sites and nests.

By marking females and their nests, our ethograms enabled us to investigate the spatial aspects of nesting activity. Assigning specific nests to females allowed us to estimate that each female completed 0.5 ± 0.1 nests per day, with those observed for nearly a month caring for 13.7 ± 3.7 nests. A key finding was the frequent absence of nest closure, even in nests with deposited pollen, challenging the common assumption that nests are "complete" only when closed. While Bogo et al. (2024) reported fewer closed nests per female, counting nests regardless of closure suggests a higher nesting success rate. They also noted annual fluctuations in completed nests due to variations in nesting resources and intraspecific interactions, a point we expand on by suggesting that differences may also stem from varying amounts of time spent on nest closures, a task not performed by all females.

All females exhibited a behaviour we termed "scanning", which involved surveying the area, searching for new nests or material, and checking previous nests. This behaviour sometimes included cleaning activities in cavities, rapidly interrupted. Scanning could serve multiple purposes: assessing nesting conditions, preparing for future nest construction, or acting as a territorial behaviour, potentially deterring other species and expanding nesting opportunities (Geslin et al., 2020). While aggression was observed, it was unclear whether it stemmed from nest proximity or a strategy of usurpation. Although primarily recorded at the bee hotel, some females left the site for short periods, suggesting scanning may also occur at nearby, unidentified sites. These findings support the hypothesis that identifying new nesting options is integral to a fixed nesting strategy.

Finally, our analysis of behavioural units in relation to the longevity of females, supported by the model, aligns with recent literature emphasizing the need to distinguish between stereotypical behaviours and individual plasticity (Brembs, 2013; Lehtonen et al., 2023). In some cases, this could even demonstrate problem-solving innovation, as observed in Collado et al. (2021) study on solitary bees. The main sequence of nesting actions observed closely matched the expected progression toward successful nest completion and reproduction, validating stereotypical behaviours commonly seen in solitary nesting hymenopterans. However, the model also revealed significant individual variation: some females provisioned multiple nests simultaneously, while others focused on just one at a time. Plasticity in behaviour arises from responses to complex environmental conditions throughout an individual's lifespan. However, for this flexibility to exist, it must be an option from the outset – without it, only stereotypical responses would be possible, limiting adaptability to environmental variability. It would be valuable to compare the nesting sequence of *M. sculpturalis* in its native range to determine whether the behaviours we observed are intrinsic to the species – stereotypical behaviours that coincidentally align with similar conditions in the new environment – or whether they reflect an adaptive evolution driven by individual plasticity and cognitive abilities.

FUNDING. This research was conducted as part of the BeeNet project (2019–2025), funded through the FEASR 2014–2020 program (European Agricultural Fund for Rural Development), and overseen by RRN (Rete Rurale Nazionale) and MASAF (Ministry of Agriculture, Food Sovereignty, and Forestry).

ACKNOWLEDGEMENTS. We are indebted to G. Bogo for brainstorming during the preparation of this manuscript.

COMPETING INTERESTS. Authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS. M. Giovanetti: conceptualization, investigation, data curation, formal analysis, writing original draft, writing review & editing; L. Zavatta: investigation, data curation, formal analysis, writing review & editing; S. Albertazzi: investigation, data curation; S. Flaminio: investigation, data curation, writing review & editing; R. Ranalli: investigation, data curation, writing review & editing; L. Bortolotti: conceptualization, methodology, writing review & editing, supervision.

ETHICAL NOTE. We adhered to the ASAB/ABS Guidelines for the use of animals in research. Individuals were collected by insect net and manipulation was reduced to the minimum required to mark and release them, alive; after release, they were free to fly away. No institutional approval was required for this study.

DATA AVAILABILITY. Data are available as supplementary material (Tables S1–S9).

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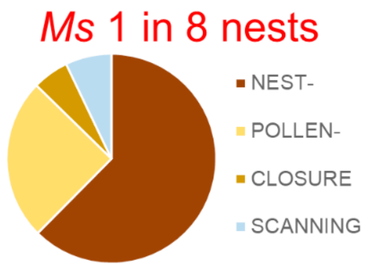
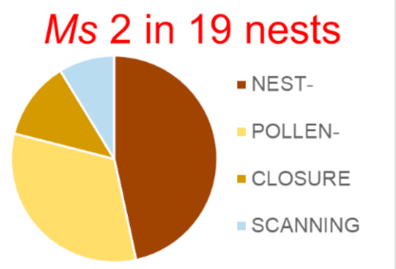
Received April 7, 2025; revised and accepted July 9, 2025

Tables S1–S9. Individual ethograms with number of actions.



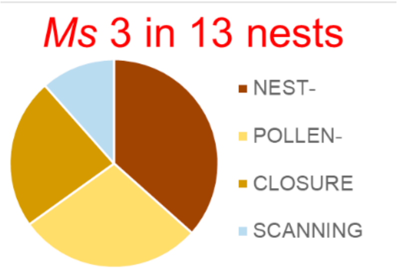
Bee *Ms*1 Life history traits

	NEST	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity	B3	79	40	9	7
09/07/2020	A11	36	1	0	5
11/07/2020	B14	33	11	4	4
14/07/2020	P1	20	8	0	1
15/07/2020	P2	30	20	9	1
19/07/2020	C22	7	2	0	0
20/07/2020	A26	30	12	0	9
27/07/2020	A1	21	4	0	1
29/07/2020 end of activity		246	98	22	28



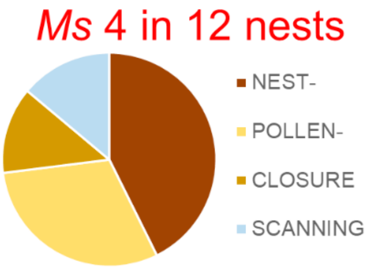
Bee *Ms2* Life history traits

	NEST	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity	I2/A3	16	9	0	2
03/07/2020	H3	6	1	0	0
04/07/2020	B3	1	3	0	0
05/07/2020	H5/H8	15	1	0	0
06/07/2020	A9/H12	19	14	3	6
07/07/2020	I12	24	13	11	0
12/07/2021	L14	2	5	1	3
13/07/2021	X3	2	10	0	0
14/07/2021	L17	9	7	6	0
15/07/2021	L19	9	0	0	3
17/07/2021	L23	13	7	1	6
20/07/2021	L25	2	7	0	0
21/07/2021	H19/L11	5	9	13	1
23/07/2021	Y4	2	8	0	1
27/07/2021	CANES	19	6	3	5
31/07/2020 end of activity		144	100	38	27



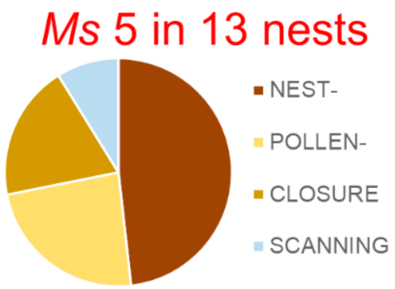
Bee *Ms3* Life history traits

	NEST	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity	B4/G5	10	3	0	1
04/07/2020	H3	3	2	0	8
05/07/2020	H11	5	8	0	0
06/07/2020	F3	10	0	14	2
08/07/2021	G10	2	11	12	1
10/07/2021	H16	7	0	0	0
11/07/2021	L16	25	21	14	4
17/07/2021	L19	15	9	7	5
19/07/2021	I20B	9	10	6	1
23/07/2021	CANE8/H24	16	12	16	10
24/07/2021	CANE9	6	8	0	0
29/07/2020 end of activity		108	84	69	34



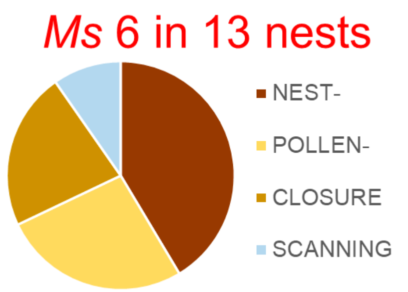
Bee *Ms4* Life history traits

	NEST	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity					2
04/07/2020	C11	16	21	2	2
07/07/2020	V1	18	6	3	9
08/07/2020	A12	27	9	0	0
09/07/2020	A16	11	7	1	0
12/07/2020	A21	38	30	1	3
14/07/2020	A24/A22	14	31	1	5
18/07/2020	A25	4	3	0	8
21/07/2020	H17/H22	20	4	0	1
23/07/2020	H24	11	0	37	8
27/07/2020	CANE	7	7	6	12
31/07/2020 end of activity		166	118	51	54



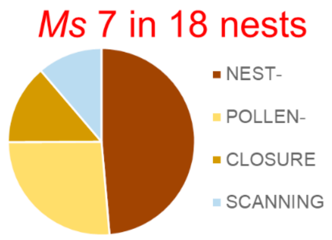
Bee *Ms5* Life history traits

	NEST	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity	I3	60	14	9	0
06/07/2020	I10	11	2	0	10
07/07/2020	T1/T2	24	5	5	0
09/07/2020	X1	8	10	1	0
10/07/2020	X4	23	11	41	0
14/07/2020	X6	14	10	1	3
15/07/2020	X8	15	0	5	2
17/07/2020	X2	3	1	2	2
18/07/2020	X10	16	13	2	0
21/07/2020	L22/X3	58	38	30	0
27/07/2020	X12	13	16	2	22
29/07/2020 end of activity		245	120	98	45



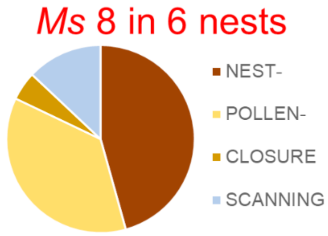
Bee *Ms6* Life history traits

	NEST	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity	L2/I6	47	12	3	2
05/07/2020	I10	10	3	0	13
06/07/2020	H10	13	4	4	4
08/07/2020	V2	1	3	0	5
09/07/2020	L12	3	23	9	2
10/07/2020	X5	20	6	26	2
13/07/2020	X6	7	8	0	7
14/07/2020	I19	27	9	3	0
17/07/2020	L24	19	20	7	6
21/07/2020	I8	46	32	36	0
27/07/2020	L25	17	12	7	8
29/07/2020	CANE	16	13	27	1
31/07/2020 end of activity		226	145	122	53



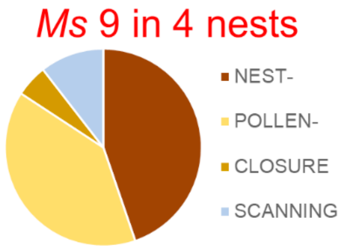
Bee *Ms7* Life history traits

	NEST (18)	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity	I4/B5	13	6	0	4
03/07/2020	L4/L3	35	4	0	0
05/07/2020	L7/XF12	33	8	17	9
07/07/2020	L5	12	9	22	15
09/07/2020	L13	11	11	0	0
11/07/2020	I15	16	6	4	0
13/07/2020	I18	38	29	4	11
16/07/2020	C17	55	25	1	8
17/07/2020	C19	16	14	0	14
18/07/2020	L21	15	12	10	0
21/07/2020	I22	9	11	0	0
22/07/2020	L26	33	5	0	1
27/07/2020	C29	3	4	0	10
28/07/2020	C27	15	19	29	0
30/07/2020	N1	16	10	4	2
31/07/2020 end of activity		320	173	91	74



Bee *Ms8* Life history traits

	NEST (18)	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Scanning other entrances/ beehotel area
02/07/2020 start of activity	A3	22	4	1	2
05/07/2020	A6	9	8	0	0
06/07/2020	B9	0	5	0	0
07/07/2020	B8	4	20	1	0
09/07/2020	B10	30	18	0	0
11/07/2020	L13	9	4	6	16
13/07/2020 end of activity		74	59	8	21



Bee *Ms9* Life history traits

	NEST (18)	Nest-dedicated actions	Pollen-dedicated actions	Cell/entrance closure dedicated actions	Ccanning other entrances/ beehotel area
02/07/2020 start of activity					
04/07/2020	H8	19	4	0	0
07/07/2020	A9	11	14	0	9
09/07/2020	A14	14	15	6	0
10/07/2020	A17	7	12	0	0
11/07/2020 end of activity		51	45	6	12