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Short communication

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Orientation Inside Linear Nests by Male and Female *Osmia bicornis* (Megachilidae)

Justyna Kierat,[1,2] Hajnalka Szentgyörgyi,[3] and Michal Woyciechowski[1]

[1]Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Kraków, Poland (justyna.kierat@gmail.com; michal.woyciechowski@uj.edu.pl), [2]Corresponding author, e-mail: justyna.kierat@gmail.com, and [3]Department of Pomology and Apiculture, University of Agriculture in Kraków, Al. 29 Listopada 54, 31-425 Kraków, Poland (hajnalka.szentgyorgyi@gmail.com)

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Abstract

Numerous species of solitary bees and wasps build linear nests with only one entrance. Developing insects must orient themselves inside their nest to choose the correct direction in which to emerge. Misorientation and chewing towards the dead end of the nest can result in significant mortality. Most insects position themselves towards the nest entrance during cocoon construction; however, some individuals are misoriented. We tested whether imagines can examine and possibly correct their orientation after emerging from their cocoons. Males were usually able to correct their misoriented position based on the shape of the cell wall and emerged through the correct entrance, whereas most females pursued the direction that they faced in their cocoons. We suggest that there can be more than one time point during development when bees can control their position in relation to the nest entrance and that the importance of these time points varies between sexes.

Key words: Apidae, Megachilidae, development, life history, ecology and behavior

A large number of solitary bee and wasp species nest in long and narrow cavities. Their nests consist of a row of linearly arranged cells that are separated by mud walls. Inside each cell, one egg is laid on the provisioned food. The larvae undergo complete development inside their cell, and to emerge from the nest, the imagines have to chew through the cell wall towards the nest entrance. The challenges for insects developing in this type of nest have long been recognized (Cooper 1957). The nest has only one exit, and the emerging bee or wasp must choose the right direction. Misoriented individuals will likely die in their hopeless effort to chew through the blind end that they will eventually reach. Moreover, they may kill or hurt their siblings located deeper inside (Cooper 1957; Tepedino and Frohlich 1984a,b). Within a cell, the majority of larvae orient themselves in their cocoons so that they face the nest entrance (Cooper 1957, Medler 1967, Torchio 1980, Szentgyörgyi and Woyciechowski 2013). Thus, after metamorphosis, these imagines can emerge without needing to turn around in their cell.

In wasps, more than 99% of cocoons are oriented properly (Cooper 1957); however, in the red mason bee, 3–10% of females and as many as 19–29% of males are misoriented in cocoons (Szentgyörgyi and Woyciechowski 2013). Studies suggest that either the location of the provision inside the cell or, more probably, the partition walls are the possible directional cues used for cocoon orientation (Matthews and Kislow 1973, Johnson 1980, Torchio 1980). The location of the provision varies with species (Vicens et al. 1993), but the shape and texture of partition walls are similar in most species, being rough and convex toward the entrance but smooth and concave towards the end.

In our study, we asked whether red mason bee (*Osmia bicornis*) larvae oriented towards the inside of the nest can discover and correct their orientation based on the structure of the partition walls after emerging from their cocoon. Because males are smaller (Seidelmann et al. 2010) and more often misoriented (Szentgyörgyi and Woyciechowski 2013) than larger females, we predicted that they may possess the behavioral ability to discover and correct their mistake after emerging from their cocoon. In contrast, females are rarely misoriented while in a cocoon, and in many cases, they probably would not have enough space in their cell to turn around after emergence; therefore, we predicted that females may have less, if any, ability to check their orientation in relation to the nest entrance after emergence.

Materials and Methods

We studied the behavior of the red mason bees (*Osmia bicornis* L.) inside artificial cells made from plastic tubes with two open ends (8 mm inner diameter) and natural cell walls from red mason bee nests. The cocoons that were used in the experiment were overwintered in a climatic chamber set at +4 °C and were taken from these conditions immediately before use in an experiment. Each cocoon was cut open on top, and the bee inside was sexed based on its morphological characteristics (Seidelmann et al. 2010). Then, the cocoon was placed inside the artificial cell, and both ends of the tube were closed using natural mud cell walls. The two undamaged cell walls were attached to the ends of the tubes with paper tape, and a bee could successfully leave the cell through a wall after chewing through it. One wall was placed with its rough and convex side to the inside of the artificial cell, and the other was placed with its smooth and concave side to the inside of the artificial cell. The convex wall under natural conditions is the one that should be chewed by the bee to emerge from the nest. If a bee were to chew the concave side, it would direct itself towards the inside of the nest. Therefore, bees oriented towards the convex wall are called "correctly oriented", in contrast to those oriented towards the concave wall, which are called "misoriented". We used males and females, and each cocoon was placed either correctly (with the bee's head facing the convex wall) or not (with the bee's head facing the concave wall). Therefore, we had four groups of bees in a crossed arrangement. The artificial cells with bee cocoons were placed inside a cardboard box to ensure darkness. Artificial cells were examined to determine whether a bee emerged through a correct (convex) or incorrect (concave) wall. The frequency of these choices was compared separately for males and females in cocoons that were placed correctly or incorrectly in artificial cells. We used a χ^2 test with Yates's correction. Data analysis was performed using Statistica 10 (StatSoft Inc. 2011).

Results

The emergence of 40 male and 43 female bees from their artificial cells was recorded. All of the 17 males and 18 females that were placed in the artificial cells towards the convex wall (i.e., correctly oriented) emerged through this wall. Of the bees whose cocoons were placed in their cells towards the concave wall (i.e., misoriented), 19 out of 23 males and 2 out of 25 females turned inside their cells and emerged from the correct (convex) wall ($P < 0.001$; Table 1).

Discussion

The results of our experiment show that shape and/or texture of the cell walls can be used by emerging adult bees as a cue indicating the direction of the nest entrance and allow them to correct their wrong orientation. Whereas most males that we examined used the information provided by the cell walls to emerge through the correct side of the artificial cell, females did not follow this cue and simply headed in the direction in which they had been positioned in their cocoons. Females are larger than males, which makes it more difficult for them to turn inside the narrow space of a cell. Under natural conditions, it is possible that females in narrower nests are only able to proceed straight ahead. However, the tendency not to turn arises from more than physical inability. When placed in an artificial cell with both ends closed without the ability to chew their way outside, ca. 45% of females (and not only the smallest ones) turned around in their artificial cells (unpublished data). A similar observation was made in solitary wasps, where insects that were experimentally tuned around as pupae tried to emerge towards the blind end of the nests, although in many cases they probably had enough space to turn around (Cooper 1957).

Differences in the strategies of males and females are logical in light of previous studies on cocoon orientation in the nest. Females are positioned with their heads towards the inside of the nest much less frequently than are males (Torchio 1980; Szentgyörgyi and Woyciechowski 2013). This difference is explained by the relatively decreased ability of females to turn around inside their cells because of their size. However, this difference does not mean that proper orientation in the nest is not necessary for males. Our experiment shows that the decision of from where to emerge may be postponed in males compared to females, who orient themselves correctly as cocooned larvae and, thus, do not verify their decision as eclosed adults. In contrast, males follow directional cues less strictly as larvae and tend to choose to chew through the correct wall regardless of their position in their cocoons.

Males can chew through both convex and concave cell walls (unpublished data). However, the concave side of the wall may be more difficult to chew for a male than for a female. Males have weaker mandibles than females, and chewing through the smooth surfaces of the concave wall can be a challenge. In contrast, the convex wall is rough, with many small bulges and cracks that allow mandibles to get a good grip. Difficulty chewing can be a directional cue informing a male red mason bee that he is chewing the wrong wall for emergence. However, it is also possible that bees carefully examine the walls using their antennae or legs before they start to attack the wall.

Our experiment on the red mason bee shows that the regulation of behavior inside the nest may be more complicated than previously thought. There seems to be more than one time point during development when bees can control their position in relation to the nest entrance. The time points differ in their relative importance between the two sexes, and this behavioral difference is likely related to their sexual size dimorphism.

Sexual dimorphism in solitary bees most likely evolved because of the different fitness of males and females in relation to their body mass. Larger females are more effective in collecting food for offspring which increases their reproductive success, e.g., by reducing risk of nest parasitism (Seidelmann et al. 2010). In contrast, effect of body size on reproductive success has not been shown in males, because their competition for mates does not involve fights between males (Seidelmann 1999). Our study shows that this dimorphism can result in evolving further differences between sexes, even in behavioral traits.

Table 1. Number of red mason bees that chewed through the convex (correct) or concave (incorrect) mud wall of their artificial nest after emerging from their cocoon, stratified by sex and initial position

Initial position	Sex	Which exit did they take?	
		Correct	Incorrect
Correct	Male	17	0
Correct	Female	18	0
Incorrect	Male	19	4
Incorrect	Female	2	23

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References Cited

Cooper, K. W. 1957. Biology of eumenine wasp. V. Digital communication in wasps. J. Exp. Zool. 134: 469–513.

Johnson, M. D. 1980. Observations on cocoon orientation in *Osmia (Osmia) lignaria lignaria* Say (Hymenoptera: Megachilidae). J. Kans. Entomol. Soc. 53: 581–586.

Matthews, R. W., and C. J. Kislow. 1973. Cocoon orientation in a megachilid bee: larval response to pollen placement. Environ. Entomol. 2: 157–158.

Medler, J. T. 1967. Biology of *Trypoxylon* in trap nests in Wisconsin (Hymenoptera: Sphecidae). Am. Midl. Nat. 78: 344–358.

Seidelmann, K. 1999. The race for females: the mating system of the red mason bee, *Osmia rufa* (L.) (Hymenoptera: Megachilidae). J. Ins. Beh. 12: 13–25.

Seidelmann, K., K. Ulbrich, and N. Mielenz. 2010. Conditional sex allocation in the Red Mason bee, *Osmia rufa*. Behav. Ecol. Sociobiol. 64: 337–347.

StatSoft Inc. 2011. STATISTICA (data analysis software system, version 10). (www.statsoft.com).

Szentgyörgyi, H., and M. Woyciechowski. 2013. Cocoon orientation in the nests of red mason bees (*Osmia bicornis*) is affected by cocoon size and available space. Apidologie. 44: 334–341.

Tepedino, V. J., and D. R. Frohlich. 1984a. Fratricide in *Megachile rotundata*, a non-social megachilid bee: impartial treatment of sibs and non-sibs. Behav. Ecol. Sociobiol. 15: 19–23.

Tepedino, V. J., and D. R. Frohlich. 1984b. Fratricide in a Parsivoltine bee (*Osmia texana*). Anim. Behav. 32: 1265–1266.

Torchio, P. F. 1980. Factors affecting cocoon orientation in *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). J. Kans. Entomol. Soc. 53: 386–400.

Vicens, N., J. Bosch, and M. Blas. 1993. Análisis de 10s nidos de algunas *Osmia* (Hymenoptera, Megachilidae) nidificantes en cavidades preestablecidas. Orsis. 8: 41–52.