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Original article

The function of the vestibulum in nests of a solitary stem-nesting bee, *Osmia rufa* (L.)

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Abstract – Nests of the stem- or hole-nesting megachilid bee, *Osmia rufa*, were analysed to help clarify the function of the outermost empty chamber of the nest, the vestibulum. Only nests in an exposed nesting environment had a long vestibulum, whereas nests protected from sun and temperature fluctuations (within a honey bee hive body) had short vestibuli or none at all. The rate of parasitism of the first cell from nests with a vestibulum did not differ from nests without a vestibulum in both nesting environments. The short vestibulum built by *O. rufa* in protected nests probably represents the remaining space of a nest hole that is too short for an additional cell. Nests in exposed environments suffered much higher mortality in all brood cells owing to parasites attacking open cells during nest construction. Additionally, mortality caused by the cleptoparasitic drosophilid, *Cacoxenus indagator*, one of the main parasites of the Red Mason bee, increased greatly from the rear to the entrance of nests. When nesting bees detect the cleptoparasitic fly, they do not provision the outermost space of nesting holes, thus constructing a vestibulum, to avoid misinvestment due to the high risk of parasitism. In nests exposed to normal weather factors, vestibular cells probably shelter the brood also from high fluctuating temperatures. © Inra/DIB/AGIB/Elsevier, Paris

Osmia rufa / **vestibulum / nest architecture / avoidance of parasitism**

1. INTRODUCTION

Nests of many Aculeata have empty cells in variable numbers and positions [9, 10, 19]. To date, the function of empty cells has remained unclear. Usually it is thought that the nest structures are a defence against parasites, predators and nest destroyers. By probability models Tepedino et al. [21] were able to demonstrate that empty, yet sealed cells can reduce the success of parasites of mud-nesting Hymenoptera. These species

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attach several cells on a surface or construct subterranean nests with cells branching off from a main tunnel in the soil.

Empty cells are also found in twig- or hole-nesting, xylophilous Aculeata, especially megachilid bees that construct their brood cells in a linear order one behind the other. In such linear nests an empty cell is usually found between the final provisioned cell and the nest plug. These so called vestibular cells are believed to be a protection against parasitism of the nest [7, 11, 12, 22]. Krombein [9] assumed that the parasites that inserted their ovipositor through the nest plug no longer exist. Therefore the vestibulum has become a behavioural relict without current adaptive value.

According to Rust [15], a vestibulum is typical for all *Osmia* species. However, during the analysis of *Osmia rufa* nests around Halle, Germany, vestibuli were observed to be facultative structures. This was not to be expected under their assumed function in parasite defense. Furthermore, the lack of a vestibulum did not result in a marked increase in parasitism of outermost brood cells, although all major parasites of *O. rufa* were present. The vestibulum could therefore represent remaining space which is too small to construct an additional brood cell. To test these hypotheses, and thus to clarify the function of a vestibulum, its frequency and length were recorded in nests of *O. rufa* from different nesting environments, and the outermost provisioned cells were examined for parasites. To identify possible influences of the construction of a vestibulum on parasitism of inner brood cells, the total nest contents of random samples were examined.

2. MATERIALS AND METHODS

The study was carried out on nests of *Osmia rufa* from the Botanical Garden of the University of Halle (Germany). In 1992 and 1993, females of this species were offered wooden nest blocks with 100 nesting holes (8 mm in diameter × 160 mm in length) in each block. To test for possible influences of the nesting environment on the production of a vestibulum, these nesting blocks were placed either in an intact ('protected environment') or dismantled ('exposed environment') honey bee hive body (box with no combs or bees). The protected nest blocks could be reached only via the regular flight entrance of the hive. Thus, nests in the intact hive were protected from direct weather influences. In the exposed environment, the entire front side of the hive box was removed. Nesting blocks in such dismantled hives were sheltered from rain but exposed to normal temperature fluctuations.

A total of 1 712 complete nests of *Osmia rufa* from within 22 nest blocks were evaluated. A nest was considered complete when the nesting tube contained several brood cells, had a regular nest plug, and, in cases where the nest had a vestibulum, if the outermost brood cell was completely sealed off by a cell partition. These restrictions were necessary because at the end of the flight season old females also seal incomplete nests [18]. In this case, it is difficult to interpret the empty space between the nest plug and the first provisioned cell.

In all complete nests, the thickness of the nest plug (except protected environment in 1992) and vestibulum length were measured. The contents of the outermost cell (= first brood cell behind the vestibulum) was recorded for 1 413 nests, and for 1 073 of these, the length and contents of all brood cells were also recorded. From the length of the provisioned cells of each nest, the mean length for male and female cells were calculated. In *O. rufa* nests, sons occupy smaller cells than daughters, and they are located towards the entrance [14, 16, 17]. Therefore, the space which would have been needed for an additional male cell in that particular nest was compared to the length of the vestibulum, if it existed. To compute mean vestibulum length for nest blocks, vestibulum length was assumed as zero for nests lacking this empty space.

To ascertain the distribution of parasites within nests, every nest was equally divided into 300 sections by length and the contents of each section registered. A distribution curve of parasites could be constructed by totalling the number of parasitized cells in every section over all nests [17].

Differences in vestibulum length and entrance plug thickness between exposed and protected nesting environments were statistically analysed by a two-way model I ANOVA with year and nest environment as fixed effects followed by a Scheffé test for a posteriori comparison of means. The existence of a vestibulum and the parasitism of the outermost cell were added as fixed effects in a model I ANOVA to analyse influences of nest parasitism rate on outermost cell parasitism. Parasitism rate (PR) was computed as number of cells parasitized per provisioned cells. A log-linear analysis according to Warnstorff and Dörfel [23] of a four-dimensional contingency table was used to detect influences on the occurrence of a vestibulum and a dependence of the outermost cell's contents on the existence of a vestibulum. In the contingency table, year (Y), nesting environment (NE), and existence of a vestibulum (V) were considered design variables, and the content of outermost brood cell (BC) was the response variable. All calculations were computed with the Statistica® package (StatSoft Inc.).

3. RESULTS

3.1. Frequency and length of the vestibulum

The occurrence of a vestibulum was related to the type of nesting environment: (NE × V 2I = 274.04, $P < 0.001$). A vestibulum was found in only half of the protected nests compared to ca. 90 % of exposed nests (*table I*). Also the mean vestibulum length differed between the types of nesting environments. In both years, vestibuli from exposed nests were twice as long as vestibuli from protected nests (*table I*; Scheffé-Test, all $P < 0.001$). Most of the variance in vestibulum length was associated with the factor NE ($F = 413.62$, $P < 0.001$). In 1993, the vestibuli were slightly shorter than in 1992.

Only 15 % (1992) and 5 % (1993) of vestibuli in protected nests were large enough to accommodate an average-sized male cell. In exposed nests, 63 % (1992) and 50 % (1993) of vestibuli would have been large enough to accommodate another male cell (*figure 1*).

3.2. Thickness of the nest plug

Osmia rufa nests had nest plugs from 1.3 to 14.5 mm in thickness (*table II*). The thickness of the plug depended mainly on the occurrence of a vestibulum ($F = 149.71$, $P < 0.001$), but was not correlated with the vestibulum length (all $R^2 < 0.01$). In nests without a vestibulum, the plug was significantly thicker than in nests with one (*table II*, all $P < 0.001$). An influence of the nest environment on plug thickness was not found ($F = 0.64$, n.s.).

3.3. Contents of the outermost brood cell

Parasites found in the outermost brood cells were *Cacoxenus indagator* (Diptera: Drosophilidae) in 10.4 % of nests, *Anthrax anthrax* (Diptera: Bombyliidae) in 4.6 % of nests, and *Chaetodactylus osmiae* (Acari:

Table I. Frequency and length of vestibuli in *Osmia rufa* nests.

Year	Nest	n	Frequency of vestibuli (%)	Length of vestibuli (mm)			
					sd	Min	Max
1992	exposed	196	85.6	12.92	5.64	3	29
	protected	307	57.4	6.86[a]	3.83	2	29
1993	exposed	378	92.2	11.55	5.76	2	34
	protected	242	45.0	5.79[a]	2.49	2	12

[a] Means are not different.

Table II. Thickness (mm) of nest plugs of *Osmia rufa* nests.

Year	Nest	Vestibulum	n		sd	Min	Max
1992	exposed	existent	181	5.15	1.1	2	10.5
		absent	30	6.9	2.08	3.5	12.2
1993	exposed	existent	345	6.15[a]	1.23	3.6	9.8
		absent	29	8.1	2.02	3.5	11.4
	protected	existent	229	6.16[a]	1.2	2.9	11.3
		absent	286	7.18	1.55	1.3	14.5

[a] Means are not different.

Table III. Content of the outermost brood cell in relation to the occurrence of a vestibulum (dead = dead larva or pupa).

Year	Nest	Vestibulum	n	Contents of outermost cell (%)		
				Bee	Dead	Parasite
1992	exposed	existent	144	71.9	7.3	20.8
		absent	18	55.6	11.1	33.3
	protected	existent	305	89.2	7.5	3.3
		absent	216	81.9	14.4	3.7
1993	exposed	existent	369	70.2	11.9	17.9
		absent	23	60.9	17.4	21.7
	protected	existent	145	89.0	9.7	1.4
		absent	154	85.7	7.8	6.5

Chaetodactylidae) in 0.3 % of nests. These species attack open cells during provisioning. In none of the 1 712 investigated nests had a parasite broken through an intact nest plug and parasitized the first cell after the nest was sealed. Parasitism by *Monodontomerus obscurus* (Hymenoptera: Pteromalidae) was rare. It occurred in less than 0.6 % of all nests and could always be attributed to a defective nest plug or a damaged nest block.

The lack of a vestibulum had no significant influence on the mortality of the outermost brood cell (*table III*, [V × BC]/Y NE: 2I = 15.014, n.s.). Only in one trial (1992, protected nests) was the mortality in nests without a vestibulum higher than in nests with one ($[V \times BC]/Y_1$ NE_2: 2I = 6.387, $P = 0.041$). This was caused by increased larval mortality apparently due to reasons other than parasitism (contrast: bee + parasite against dead, 2I = 6.206, $P = 0.012$) and not by parasitism itself (contrast: bee + dead against parasite, 2I = 0.068, n.s.).

The length of the vestibulum clearly had no influence on the mortality of the outermost brood cell (*table IV*). A multiple comparison of means did not show significant differences between vestibulum lengths in nests with different outermost brood cell

Table IV. Mean vestibulum length (mm) in nests with different contents of first brood cell (dead = dead larva or pupa).

Nest	Contents	n		sd
Exposed	bee	387	11.61	5.54
	dead	57	13.46	6.75
	parasite	103	12.26	5.57
Protected	bee	401	6.46	3.49
	dead	38	7.04	4.24
	parasite	12	6.46	3.38

contents in one nesting environment over the other (*table IV*, all $P > 0.206$).

3.4. Parasitism of nests and nest blocks

The same parasites found in the outermost cells were also present in the inner cells of *Osmia rufa* nests. However, parasitism by *Cacoxenus indagator* decreased from 10.4 to 5.5 % from outer to inner cells, respectively, whereas mortality caused by *Anthrax anthrax* increased from 4.6 to 9.1 %. Mean parasitism of exposed nests (PR = 0.287) was much higher than in protected nests (PR = 0.081, $P < 0.001$). No differences were found in the mean parasitism of nests without a vestibulum (PR = 0.184) compared to nests with a vestibulum (PR = 0.193, $P = 0.495$). The amount of parasitism of the outermost cell corresponded to the parasitism rate of the remaining cells of the nest (F = 14.641, $P < 0.001$). Nests with a parasitized outermost cell were twice as parasitized (PR = 0.304) in the other brood cells compared to nests with an unparasitized outermost cell (PR = 0.155, $P < 0.001$).

There was also variation in parasitism between nest blocks pooled for both nest environments and years. The parasitism rate of a nest block (total cells parasitized per total provisioned cells) was correlated with the frequency of vestibulum occurrence ($R^2 = 0.465$, $P < 0.001$) and mean vestibulum length ($R^2 = 0.809$, $P < 0.001$) of all

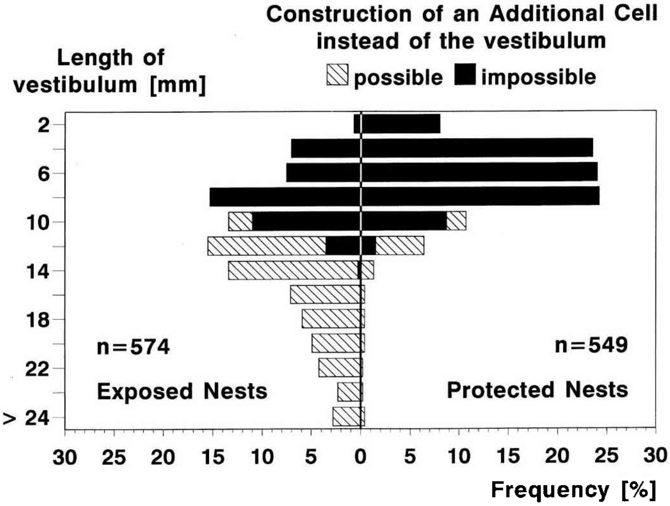

Figure 1. Histogram of the vestibulum length of nests from different types of nesting environments. Striped portion of column: vestibulum large enough to accommodate an additional average-sized male cell of the particular nest.

nests in this particular block. However, a better correlation of vestibulum frequency was achieved by regarding only parasitism by *Cacoxenus indagator* ($R^2 = 0.687$, $P < 0.001$).

3.5. Distribution of parasites within nests

The main parasites *Cacoxenus indagator* and *Anthrax anthrax* were not equally distributed throughout the nests (*figure 2*). Parasitism by *Anthrax anthrax* increased with distance from the nest entrance, whereas *Cacoxenus indagator* caused highest mortality in the outermost brood cells. The sections near the entrance and the rear of nests lacked provisioned cells (owing to the presence of the nest plug, vestibulum and empty space); therefore, a curve for parasitism rate could not be drawn for these sections.

4. DISCUSSION

Many stem-, twig- or hole-nesting xylophilous Aculeata such as *O. rufa* are not able to excavate cavities to form their nests by themselves. They depend on finding a suitable hollow twig or a bore hole of a beetle in dead wood. The nesting place is a rare resource for these species [4, 5, 21]. Under such conditions it would be expected that once a hole is found, its space would be completely used. If a certain part of the nesting hole usually remains vacant, an adaptive function would be expected to explain this space. The vestibulum represents such a regular structure.

The frequency of occurrence and mean length of vestibuli may give an important indication of their purpose. If it is assumed that the vestibulum plays a protective role against parasites, then it would be expected to have a regular occurrence as well as a minimal length. If on the other hand a vestibulum represents only the space remaining after completion of as many cells as possible in the cavity, it should be shorter than a mean male cell of a given nest.

Only 51 % of *O. rufa* nests in protected environments had a vestibulum, and in 90 % of these nests it was smaller than a male cell. For these protected nests, it may be concluded that the vestibulum represents remaining space which was too short to con-

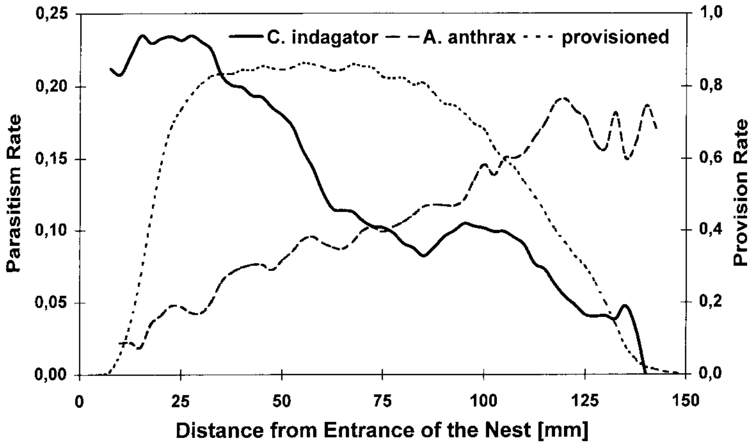

Figure 2. Distribution of parasites in nests from exposed environments (543 nests). Parasitism rate and provision rate refer to 0.5 mm segments of nests. The portion of provisioned cells for each segment, whether cells were parasitized or not, is given as a provision curve.

struct an additional brood cell. In contrast, almost every nest in exposed environments had a vestibulum twice as long as those of protected nests. Vestibuli with a mean length of 20–30 mm occurred also in more than 80 % of *O. rufa* nests in trap nest studies [1–3, 8]. Therefore, vestibuli in exposed environments seem to have a functional advantage.

The large fluctuations in the occurrence and length of a vestibulum argues against the parasite defense function of the vestibulum. Parasites are able to locate and attack *O. rufa* nests in both nest environments. Thus, the bees should not make a difference in their nest architecture between environments. Additionally, a vestibulum may defend only against enemies that attack a sealed nest by drilling through the nest wall or plug. Among the major parasites of *O. rufa*, only *M. obscurus* shows this behaviour [16]. Due to its sting length, this species is hardly able to penetrate structures thicker than 4 mm [17]. An ordinary nest plug offers enough defence, especially since bee cocoons lie at the rear partition of the cell, and therefore at the greatest distance from the nest plug. However, the observed strengthening of the nest plug if a vestibulum is lacking indicates a possible defence role of the vestibulum against parasitic wasps. If both alternative strategies – the construction of a vestibulum, and strengthening of the nest plug – have the same effect, the little extra cost required to build a thicker nest plug could be easily used by the bees to better exploit rare nesting holes.

Parasitism in the first brood cells is slightly but not significantly increased in nests without a vestibulum compared to nests with a vestibulum. In addition, nests with parasites in the first cell do not have shorter vestibuli than others. Nevertheless, the occurrence and mean length of a vestibulum is related to parasitism. Exposed nests suffered higher mortality due to parasites attacking cells during provisioning. These nests had more and longer vestibuli than protected nests. The construction of a vestibulum is not correlated with the parasitism rate of the particular nest. It depends on parasitism of the whole nest block by species attacking cells under construction. In Halle, main parasites of this group are *Anthrax anthrax* and *Cacoxenus indagator*. The bomylid, *A. anthrax*, is a rare enemy of *Osmia rufa*, but in the botanical garden of Halle it causes regular mortality [16]. *A. anthrax* females hover in front of the nest blocks and throw their eggs in the nest entrances, obviously unnoticed by the bees. *Cacoxenus indagator* is a widespread parasite of *Osmia rufa* causing high mortality regularly [3, 6, 14, 16, 17]. This drosophilid sits on the surface of the nest block waiting for its chance to parasitize. Occasionally it walks into nesting holes to lay eggs on the provision mass. The parasite can be easily detected by the nesting females and is sometimes attacked. If the bees detect *C. indagator* on their nest (or nest block) during construction they should let the outermost space of the nesting hole remain empty to avoid the risk of high parasitism. Due to the increasing probability of parasitism by *C. indagator* closer to the nest entrance, the outermost space suffers highest parasitism. Provisioning of a cell next to the nest entrance would lead to very high parasitism because the parasite would not have to enter the nest and risk being caught by the bee. Therefore, leaving the outermost cell empty by constructing a vestibulum might be a strategy to avoid misinvestment in a brood cell which has an unacceptably high risk of being parasitized.

Under such circumstances, a higher parasitism of the outermost cells would be expected in exposed nests without a vestibulum. However, mortality of the outermost cell caused by parasitism is not independent of the rate of parasitism in the remaining cells of the nest. This suggests that particular nests face different risks of parasitism depending on their location within the nest block [17]. Part of the nests without vestibuli were probably exposed to less parasitism resulting in the observed reduction of expected mortality. In addition, this effect is probably responsible for the stopped increase of parasitism by *C. indagator* near the nest entrance (*figure 2*). The curve represents there only nests without a vestibulum.

The construction of a large vestibulum instead of an additional brood cell in most of the nests in exposed environments may also suggest a possible thermoregulatory function of the vestibulum. Immature stages of *O. rufa* are relatively temperature sensitive. Already at 32 °C the mortality of larvae and pupae increases precipitously [13]. In a hole drilled by a beetle in dead wood, a vestibulum may be able to protect the outermost cells from excessive warming in sunshine and to buffer temperature variations. Therefore, larvae in exposed nests without a vestibulum should suffer higher mortality in the outermost cell due to reasons other than parasitism compared to nests with a vestibulum. This effect could not be demonstrated. The only difference was found in the protected environment where it was not expected. But because of the low number of nests without a vestibulum in exposed environments, the data base of this study is too small to accept or reject a thermoregulatory function of the vestibulum. Precise temperature measurements within nests to test this hypothesis have yet to be performed. As *O. rufa* nests also have vestibuli in twigs or stems where temperature regulation effects should be negligible, this effect can not be regarded as its main function.

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Résumé – La fonction du vestibule dans les nids de l'abeille solitaire *Osmia rufa* (L.), qui nidifie dans des tiges. Les nids de nombreux apoïdes solitaires et xylophiles comprennent entre le bouchon qui ferme le nid et la première cellule approvisionnée un espace vide dénommé vestibule. Afin d'expliquer la fonction de cette cellule vide à l'entrée du nid, 1 712 nids d'*Osmia rufa* ont été ouverts et analysés. Les nids provenaient de 22 blocs nichoirs démontables qui avaient été placés soit dans une ruche intacte (« nids protégés »), soit dans une ruche dont on avait ôté le panneau frontal (« nids exposés »).

La fréquence et la taille des vestibules est indépendante du lieu. Les nids exposés possédaient un vestibule à 90 % (*tableau I*). Dans 55 % des cas les vestibules étaient suffisamment grands pour qu'une cellule à couvain supplémentaire soit construite. En revanche, 51 % seulement des nids protégés avaient un vestibule et 10 % seulement de ces vestibules auraient pu contenir une cellule à couvain supplémentaire (*figure 1*). Là où manquait le vestibule, la fermeture du nid était renforcée (*tableau II*). L'existence du vestibule n'a pas eu d'influence sur le contenu de la première cellule à couvain. Les nids sans vestibule n'étaient pas plus parasités que les nids avec vestibule (*tableau III*). De même, on n'a pas trouvé de différence dans la longueur du vestibule entre les nids parasités et les nids non parasités (*tableau IV*). On n'a pas trouvé un seul nid où un parasite ait réussi à pénétrer dans un nid obturé.

La fonction du vestibule ne peut donc pas résider dans la défense contre les parasites, qui attaquent le nid après sa finition. Une fermeture moyenne suffit à empêcher les ichneumons comme *Monodontomerus obscurus* de pénétrer dans le nid. En outre, les parasites peuvent localiser et envahir les nids cachés, de sorte qu'il ne faut pas s'attendre à des différences dans la position du vestibule en fonction du lieu de nidification.

Les vestibules courts et rares des nids protégés représentent donc certainement l'espace restant, insuffisamment grand pour construire une autre cellule. En revanche il

faut reconnaître une fonction adaptative aux vestibules des nids exposés, puisque presque tous ces nids possèdent un vestibule.
La construction d'un vestibule dépend de l'attaque des blocs nichoirs par les parasites, qui déposent leurs œufs dès la phase d'approvisionnement dans les cellules à couvain encore ouvertes.
La fréquence de la construction d'un vestibule et de sa longueur moyenne a été corrélée avec le parasitisme de l'ensemble du bloc nichoir par *Cacoxenus indagator* et *Anthrax anthrax*. Alors que *A. anthrax* compte parmi les parasites peu fréquents d'*O. rufa*, *C. indagator* est un parasite important qui cause régulièrement une forte mortalité. Ce drosophilidé ne parasite pas toutes les cellules du nid hôte avec la même probabilité (*figure 2*): le taux de parasitisme des cellules augmente fortement quand on se rapproche de l'entrée du nid. Puisque les femelles d'*O. rufa* peuvent détecter la présence de *C. indagator*, elles évitent le risque de parasitisme très élevé des cellules extérieures en laissant celles-ci vides. Le vestibule qui en résulte semble représenter le résultat pour éviter un investissement mal placé, ou une stratégie de réduction du risque. Pour un insecte tel que *O. rufa*, qui niche dans du bois mort, le vestibule pourrait avoir aussi une autre fonction : celle d'améliorer le microclimat du nid, puisque l'espace rempli d'air peut atténuer les fortes variations extérieures de températures, lorsqu'il y a par exemple ensoleillement.

***Osmia rufa* / vestibule / nid / parasitisme**

Zusammenfassung – Die Bedeutung der Vorzelle in Nestern der solitären, röhrenbewohnenden Biene *Osmia rufa* (L.). Die Nester vieler solitärer, xylophiler Apoidea enthalten zwischen dem Nestverschluβ und der ersten verproviantierten Zelle einen leeren Raum, das Vestibulum. Um die Bedeutung dieser leeren Zelle am Eingang der Niströhre zu klären, wurden 1 712 Nester von *Osmia rufa* geöffnet und analysiert. Die Nester stammen aus 22 zerlegbaren Holz-Nistblöcken, welche entweder in einer normalen Bienenbeute ('geschützte Nester') oder in einer Beute, deren Vorderfront entfernt worden war ('ungeschützte Nester'), untergebracht waren.
Die Häufigkeit und Gröβe des Vestibulums war vom Standort abhängig. Ungeschützte Nester enthielten zu 90 % ein Vestibulum (*Tabelle I*). Bei 55 % dieser Vestibuli hätte der Raum für die Anlage einer weiteren Brutzelle ausgereicht. Demgegenüber besaβen nur 51 % der geschützten Nester ein Vestibulum und nur 10 % dieser Vestibuli waren groβ genug für eine weitere Brutzelle (*Abb. 1*). Fehlte das Vestibulum, so wurde der Nestverschluβ verstärkt (*Tabelle II*). Die Existenz eines Vestibulums beeinfluβte den Inhalt der ersten Brutzelle nicht. Nester ohne Vestibulum waren in diesem Bereich nicht stärker parasitiert als Nester mit Vestibulum (*Tabelle III*). Auch die mittlere Länge des Vestibulums unterschied sich nicht zwischen parasitierten und unparasitierten Nestern (*Tabelle IV*). Es konnte kein einziges Nest gefunden werden, in dem ein Parasit den intakten Nestverschluβ überwunden hatte.
Die Bedeutung des Vestibulums kann daher nicht in einer Abwehr von Parasiten liegen, welche das Nest nach seiner Fertigstellung angreifen. Schlupfwespen wie *Monodontomerus obscurus* werden bereits von einem durchschnittlichen Nestverschluβ abgewehrt. Auβerdem können Parasiten auch verdeckte Nester lokalisieren und befallen, so daβ keine Unterschiede in der Anlage eines Vestibulums in Abhängigkeit vom Nistort zu erwarten wären.
Die kurzen und seltenen Vestibuli der geschützten Nester stellen daher sicherlich den Restraum der Niströhre dar, welcher zur Anlage einer weiteren Zelle nicht mehr ausreichte. Demgegenüber muβ den Vestibuli der ungeschützten Nester eine adaptive Funktion zukommen, da fast alle Nester ein

Vestibulum enthalten, für dessen Anlage auf die Verproviantierung einer weiteren Brutzelle verzichtet wurde.

Die Anlage eines Vestibulums erwies sich vom Befall der Nestblöcke durch Parasiten abhängig, welche ihre Eier bereits in der Phase der Verproviantierung in die noch offenen Brutzellen legen. Bei einer zusammenfassenden Analyse aller Nester ohne Diskriminierung des Neststandortes war die Häufigkeit der Anlage eines Vestibulums und dessen mittlere Länge mit der Parasitierung des gesamten Nistblockes durch *Cacoxenus indagator* und *Anthrax anthrax* korrelliert. Während *A. anthrax* zu den seltenen Parasiten von *O. rufa* zählt, ist *C. indagator* ein Kardinalparasit, welcher regelmäßig eine hohe Mortalität verursacht. Die Drosophilide parasitiert dabei nicht alle Zellen des Wirtsnestes mit gleicher Wahrscheinlichkeit (*Abb. 2*): die Parasitierungsrate der Zellen steigt zum Nesteingang hin stark an. Da *O. rufa*-Weibchen die Anwesenheit von *C. indagator* feststellen können, vermeiden sie ein unakzeptabel hohes Parasitierungs-Risiko der äußersten Brutzelle und lassen diesen Bereich leer. Das resultierende Vestibulum scheint somit das Ergebnis der Vermeidung einer Fehlinvestition bzw. eine Risiko-Minderungs-Strategie darzustellen. Eine weitere Funktion des Vestibulums könnte bei einem typischen Totholzbewohner wie *O. rufa* in der Verbesserung des Mikroklimas im Nest liegen, da dieser luftgefüllte Raum starke äußere Temperaturschwankungen z.B. bei Besonnung abmindern kann.

***Osmia rufa* / Vestibulum / Nestarchitektur / Vermeidung von Parasitierung**

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