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Relationships between Nest Architecture and Behavior in *Xylocopa virginica* (Hymenoptera: Apidae)

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Abstract The large carpenter bees nest in reeds, stems and wood. Many other Hymenoptera, including many wasps and some bees, have strong associations between the physical elements of their nests and behavior. Nests of the North American carpenter bee, *Xylocopa virginica,* were collected in southern Ontario. Nest architecture elements were examined with respect to their impact on life-history elements. In particular, it was determined that the brood cells are provisioned sequentially both within and among branches. There was also no detectable pattern of sex allocation in broods. Nests with branched architecture contained more foundresses, but these foundresses did not appear to contribute in the construction of larger nests. These findings are discussed with respect to other bees, and to the social structure of *Xylocopa virginica.*

Keywords Nest architecture · carpenter bee · sex allocation · parasitism

Introduction

Nests constitute a large portion of the environment in which social insects spend their life-cycle. Most bees, ants, and wasps lay their eggs within nests and these nests presumably influence reproductive behavior and life-history. Consequently, the influence of nesting biology on aspects of behavior is a common topic in social insect biology. For instance, studies in wasps have considered the role of nest architecture in the evolution of sociality, and a colony's efficiency due to division of behavioral tasks (Jeanne 1975; Karsai and Wenzel 1998). Likewise, studies of bees

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have examined the functional significance of architectural elements as they relate to aspects such as mortality and parasitism (Packer 1991; Packer et al. 1989). These studies note that different nest structures and positions may serve to protect the colonies from parasitism. Finally, nest structure has been investigated with respect to its influence on social evolution in various taxa (Hansell 1993).

The subfamily Xylocopinae consists of four tribes, all of which nest in stems, twigs, or wood (Daly et al. 1987; Maeta et al. 1996; Michener 1974; Michener 1990; Minckley 1998). This includes all members of the genus *Xylocopa* except the ground-nesting subgenus *Proxylocopa* (Hurd 1978). Since these nesting behaviors are characteristic of the genus, descriptive studies of nests have often been a topic of research (Maeta et al. 1996; Steen and Schwarz 2000; Thoenes and Buchmann 1994; Vicidomini 1996). Elements of nest architecture have been linked to numerous life-history elements including: the order of nesting events such as constructing cells and laying brood, brood size, provisioning efficiency, and susceptibility to parasitism (Steen and Schwarz 2000; Velthuis et al. 1984).

Xylocopa virginica, the common eastern North American carpenter bee, constructs nests of two basic shapes, linear and branched, that vary in the number of "tunnels" or "termini" (Gerling et al. 1989). Linear nests have a "T" shape with a single entrance gallery and terminus in each direction, along the grain of the wood (Fig. 1a). Branched nests also have a single entrance gallery, but have additional termini that also follow the grain of the wood (Fig. 1b). As in other Hymenoptera, *Xylocopa* females can choose whether an oocyte is fertilized, giving them control over the sex of oviposited eggs. This control leads to a great deal of speculation about the order and patterns of sex allocation. The linear and fixed nature of brood cells in *X. virginica* nests makes this species well-suited for examining patterns of sex allocation, particularly with respect to nest architecture. Similarly, since the developmental stage of an individual offspring reflects the time since an egg was laid, which occurs immediately after the cell is provisioned (Gerling and Hermann 1976), the developmental stages of brood can be used to infer the order in which brood cells were provisioned.

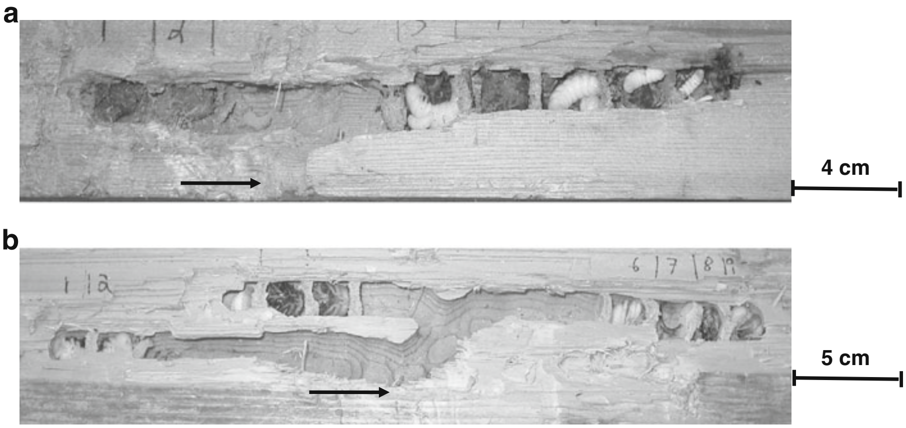

Fig. 1 Typical linear (unbranched) nest (**a**). Typical branched nest (**b**). Arrows indicate nest entrances

Nest architecture of *X. virginica* has been studied twice previously, by Rau (1933) in Missouri, and later by Gerling and Hermann in Georgia (1976). These studies both concentrated on description of the nest architecture. Here we extend the studies of *X. virginica* nesting behavior. Specifically, we examine the relationships among nest architecture and the order of laying, brood sizes, parasitism and foundress number of a southern Ontario population of *X. virginica*.

Methods

Study Sites

Nests used in this study were collected at two sites in St. Catharines, Ontario (43°07'21", 79°14'37"). Between 13 July and 26 August, 2003 nests were collected at a site on the campus of Brock University. Nests were contained in cedar benches located in a dirt courtyard situated in front of an old farmhouse, a tree lot, and grass fields. Benches were constructed of 12 individual planks and cement legs. In 2006, an additional five nests were obtained from the rafters of a 'picnic pavilion' in Burgoyne Woods, a public park 2 km from the Brock University campus.

Nest Collection and Excavation

All nests were 'excavated' using a similar process. On the night prior to collection, the entrances to every nest in a bench were stuffed with non-sterile cotton secured with duct tape; this prevented bees from leaving the nest prior to collection. The following morning, the wooden planks containing nests were brought to the lab and a hand plane was used to remove layers of wood until the nest was exposed. Once nests were exposed, adults were removed, stored at -80°C, and later scored for wing and mandible wear for use in other analyses. At the time of nest opening, we recorded the contents of each brood cell (Table 1) and the developmental stage of all brood (very small, small, medium, large, or fully-grown larvae; white, pink, red, brown, or black-eyed pupae; 1/4, 1/2, 3/4, or fully pigmented pupae; adult); the use of developmental stage gives more gradation than instars. Larvae and pupae were left *in situ* and raised to adulthood. When brood reached the adult stage or died, their brood cell position and final development stage was recorded and they were stored at -80°C or in 95% ethanol. The majority of nests collected on the Brock University campus contained broods in advanced stages, suggesting that females had finished laying, and broods were complete at the time of nest collection.

Nest Architecture as It Relates to Laying Order and Size

The number of brood cells in a nest may be constrained by nest architecture. To determine if constraints existed, we counted the number of brood cells in each terminus and compared this to the length of termini and the total length of nests using linear regression. In order to test the hypotheses that eggs are laid starting from the end of a terminus, and one branch at a time, a rank that reflected developmental stage (pollen ball, larva, unpigmented pupa, pigmented pupa, adult) was assigned to

Table 1 The developmental stage and sex of brood relative to its position within the nest. Cells are given as the number of cells between a between a given cell and the branch in which it is located. Lower numbers are farther from the nest entrance gallery, while larger numbers are closer to the gallery. Developmental stages are given as: pollen ball (PB), larva, unpigmented pupa (UP), pigmented pupa (PP), and adult. Individuals that developed into females are indicated by F, those that developed into males are indicated as M, U indicates an individual of unknown sex. Parasitized cells could not be sexed and are not assigned a developmental stage. Empty cells contained no pollen or offspring

Nest	Branch	Cell 0	Cell 1	Cell 2	Cell 3	Cell 4	Cell 5	Cell 6	Cell 7	Cell 8	Cell 9
A	A	Larva-M	Larva-U	Larva-M	Larva-U	Larva-U	Larva-U	Larva-U			
	B	Larva-U	Larva-U								
B	A	PB-U	PB-U	PB-U							
BB	A	Parasitized	UP-U								
	B	Adult-F	Adult-F	PP-F	Parasitized	UP-M	UP-U	UP-U			
C	A	Larva-U									
CC	A	PP-M	PP-M	PP-U	PP-U						
	B	UP-M	UP-M	UP-M	UP-F	UP-M					
	C	PP-M	PP-F								
D	A	PB-U	Larva-U	Larva-U	Larva-U						
	B	Empty	Larva-U	Larva-U							
DD	A	PP-M	Dead-U	PP-M	Parasitized	UP-F	Empty	Parasitized			
	B	PP-F	UP-M	UP-U	UP-M	UP-M					
	C	Parasitized	UP-F	Empty							
E	A	Larva-U	Larva-U	Larva-U							
	B	Dead	Dead	Larva	Larva-M	Larva-U					
EE	A	PP-M	PP-M	PP-M	PP-M	PP-U	PP-M	PP-U			
	B	UP-M	UP-M	UP-M	UP-U	UP-U	UP-F	UP-U			
F	A	Larva-U	Empty								
	B	Parasitized	Parasitized	Parasitized	Empty	Larva-U					

FF	A	PB-F	PB-F	PP-M	PP-U	PP-U	PP-M	PP-M	PP-M	UP-M	UP-F
GG	A	UP-F	UP-F	UP-F	UP-U	UP-F					
	B	Empty	UP-U	Empty	PP-f	Empty	PP-U				
H	A	UP-F	UP-F	UP-F	UP-M	Larva-U	Larva-M				
	B	Dead									
I	A	UP-F	UP-M	PP-M	Dead						
	B	UP-F	UP-M	UP-M	UP-F	Dead					
	C	Larva-U	Parasitized								
J	A	Parasitized	Larva-F								
K	A	Parasitized	Larva-F								
	B	PB	UP-F	UP-M							
	C	Parasitized	PP-U	Parasitized	UP-M						
L	A	UP-M	UP-F	PB	PB	Parasitized					
	B	UP-M	UP-F	UP-F	UP-F						
M	A	Parasitized	UP-F	UP-F	UP-F	UP-M	UP-F				
	B	UP-M	UP-F	UP-M	UP-M	Parasitized	Parasitized				
N	A	UP-M	UP-F	UP-F	UP-M						
	B	Larva-M	Dead	Larva-F	Larva-M						
O	A	Larva-U	Larva-F	Larva-U							
P	A	Empty	Empty	Empty	Empty						
Q	A	UP-M	Parasitized	UP-M	UP-U	UP-F	UP-M	UP-M	UP-U	UP-U	
R[a]	A	UP-M	UP-F	UP-M	UP-F						
	B	UP-U	UP-M	UP-F	UP-M						
S	A	UP-M									
	B	UP-F	UP-M	UP-M	UP-M	UP-F					
	C	UP-M									

Table 1 (continued)

Nest	Branch	Cell 0	Cell 1	Cell 2	Cell 3	Cell 4	Cell 5	Cell 6	Cell 7	Cell 8	Cell 9
T	A	UP-F	UP-F	UP-U	UP-U	UP-U	UP-U	UP-M	UP-U	UP-U	
	B	UP-U	Parasitized								
	C	PP-M	PP-M	PP-M	dead						
U	A	PP-F	UP-F	Parasitized	UP-F	Dead					
	B	Dead									
V	A	UP-M	UP-F	UP-M							
	B	Dead	PP-U	PP-U	PP-F	PP-F	UP-M	UP-F	UP-F		
W	A	UP-M	Parasitized	UP-M	UP-M	UP-M	UP-U	UP-F			
	B	PP-U	PP-M								
	C	Parasitized									
X	A	Parasitized	UP-F	UP-U	UP-M	UP-F					
Y	A	Parasitized	Parasitized	UP-M	Parasitized	Parasitized	Larva	UP-M			
	B	UP-F	Larva-U	UP-F							
Z	A	PB	PB	Parasitized	Parasitized						
	B	PP-F	PP-M	Parasitized	Larva	PB					
	C	PP-U	PP-U	UP-U	dead	UP-F	Parasitized				

[a] Nest R contained a third branch but brood could not be assigned positions

each individual. Earlier developmental stages were assigned lower values. We also assigned a number value to each cell that reflected its position within a terminus. These numbers were assigned sequentially from the terminus to the entrance gallery along each branch so that lower numbers indicate a greater distance from the gallery.

We examined the relationship between developmental stage of offspring and their position within a terminus, and a nest, to test the hypothesis that brood are laid starting from the end of a terminus and ending near the entrance gallery. Since developmental stage reflects laying order, younger brood stages were expected near the entrance gallery (i.e., in cells of higher number).

The Relationship between Nest Architecture and Sex Allocation

We examined whether there were patterns of sex allocation with respect to the sex of an individual offspring and its position within the nest. We counted the number of instances in which cells were provisioned in a particular sequence (male followed by female, female followed by female, female followed by male, male followed by male). These frequencies were compared to an expectation that all sequences were equally likely using a chi-square-goodness of fit test performed in Microsoft Excel.

Relationships between Nest Architecture and Parasitism

Prager (2008) found no influence of parasitism on the social behavior of *X. virginica.* However, because relationships between parasitism and nest architecture are commonly studied, and because it is possible that the architecture of a nest protects against parasitism, we examined these relationships further. Similarly, it is possible that nest architecture influences the degree of parasitism in a nest indirectly by its influence on brood size. We tested four hypotheses relating nest architecture to parasitism. We tested the hypotheses that (1) branched nests would contain more *Xenox tigrinus* (the most common parasite of *X. virginica*) compared to linear nests using Wilcoxon 2-sample tests; (2) longer nests would contain fewer parasites, because it is more difficult to reach brood cells; (3) nests containing larger broods (more individuals) would also contain more parasites, and (4) any cell within a nest is equally likely to be parasitized.

Sample Availability Considerations

Not all variables were available for all analyses. In particular, some nests were collected without foundresses ($n=3$) or brood ($n=3$); one nest contained neither. For three other nests, it was not possible to assign foundresses to a particular nest. Sex could not be determined for parasitized individuals, nor for larvae that failed to pupate.

Statistical Analyses

All analyses were performed in SAS 9.1.3 (SAS Institute Inc, Cary, NC) unless otherwise stated. Logistic regression was performed using SAS PROC Logistic. All models used Fisher's scoring technique (Stokes et al. 2000) and either binary (male, female) or cumulative (male, female, unknown) logits as was appropriate. Regression, ANOVA and ANCOVA were performed using PROC GLM. Effects are reported as type III sums of squares.

Results

Relationships between Nest Architecture and Brood

Branched nests ($n=13$) contained significantly more brood cells (11.1±4.9) than linear nests ($n=14$) (7.2±4.1) (Wilcoxon 2-sample test: $W=236.5$, $n=26$, $p<0.01$); 73% (16/22) of nests showed an ordered pattern of laying in which a single terminus was provisioned before moving to the next (Table 1). In 86% (19/22) of nests age was sequential within a branch (Table 1). We examined whether laying was sequential within termini and among termini using ANOVA with a model where the dependent variable was brood stage (converted to a rank), and the predictor was termini nested within nest. The overall model was significant (ANCOVA: $F_{56, 187}=5.68$, $p<0.01$), as was the effect of nest (ANCOVA: $F_{29, 187}=9.41$, $p<0.01$), which suggests that the age of broods varies among nests. The terminus (nest) factor was also significant (ANCOVA: $F_{27, 187}=1.68$, $p<0.05$), indicating that the variability between termini was greater than the variability within a terminus and that termini are provisioned sequentially.

Relationship between Nest Architecture and Sex Allocation

We found no significant pattern of sex allocation (Fig. 2). The number of instances in which cells were provisioned consecutively with females ($n=16$), consecutively with males ($n=22$), with a female followed by a male ($n=18$), or males followed by females ($n=16$) were not different from the expectations of an equal probability (Table 1) (Chi-square goodness of fit: $\chi_3^2=1.33$, $p>0.7$). We also found that the pattern of sex allocation is not statistically associated with an offspring's position in the nest, and therefore with the order in which it was laid. These patterns are consistent when the model treated sex as a binary category (male or female) using binary logits (Logistic regression: $Q_{w1}=0.81$, $p=0.37$) and when the model treated individuals of unknown sex as an additional category using cumulative logits (Logistic regression: $Q_{w1}=0.59$, $p=0.44$). Finally, when individual cell positions were tested using either chi-square or Fisher's exact test, no position exhibited a significant bias.

Relationships between Nest Architecture and Parasitism

We found no significant relationships between nest architecture and parasitism. The number of parasites did not differ significantly between branched and linear nests (Wilcoxon 2 sample test: $W=176.5$, $n=27$, $p=0.79$); on average linear nests contained 1.4±1.6 parasites while branched nests contain 1.2±1.5 parasites. In addition, the number of parasites was not related to brood, and large broods did not contain more parasites than smaller broods (Regression: $F_{1, 22}=0.76$, $p=0.39$). Nest length did not influence the rate of parasitism and no statistical relationship existed between the number of parasitic flies and the total length of the nest (Regression: $F_{1, 25}=0.62$, $p=0.44$). Finally, there was no significant relationship between the position of a brood cell within a terminus and whether it was parasitized (Logistic Regression: $Q_{w1}=2.4$, $p=0.12$) (Fig. 3, Table 1).

Relationship between Nest Architecture and Number of Females

The number of females occupying a nest was significantly greater in branched nests than in linear nests (Wilcoxon 2-sample test, $W=94$, $n=27$, $p<0.05$). On average, branched nests contained 3.3±2.1 foundresses while linear nests contained 1.9±1.0 females.

We tested the hypothesis that nest architecture influences the number of foundresses in a nest using ANCOVA. The model included the total length of the nest, the amount of space occupied by brood cells, the space not occupied by brood cells that could accommodate them and whether nests were branched or linear as predictors, and the number of foundresses as a dependent variable. Initially, interaction terms were included for all variables, but no interactions were significant and the final model excluded these terms with no noteworthy difference. The measure of space occupied by brood cells was log transformed to meet the assumptions of GLM. While the overall model was significant (ANCOVA: $F_{4, 18}=3.34$, $p=0.03$), none of the effects terms were significant (Table 2). When a similar analysis was performed replacing foundresses with the number of females that exhibited wear in either their wings or mandibles (indicators of work), the model

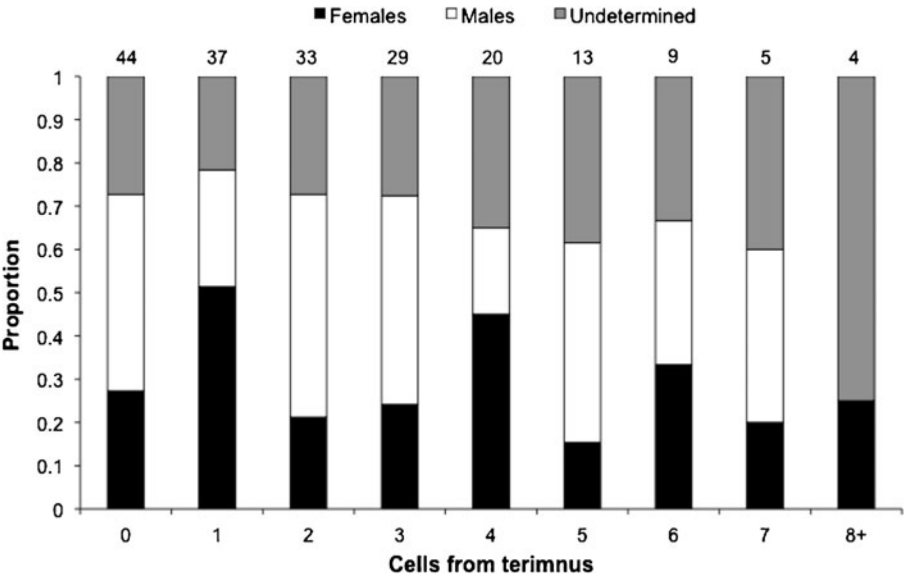

Fig. 2 The relationship between sex and position within a nest. Cells from terminus (x-axis) were measured as the number of cells from the end of a branch farthest from the entrance gallery. Numbers above bars indicate the total number of cells in that position across all nests. None of the positions exhibited a significant deviation from even sex ratio

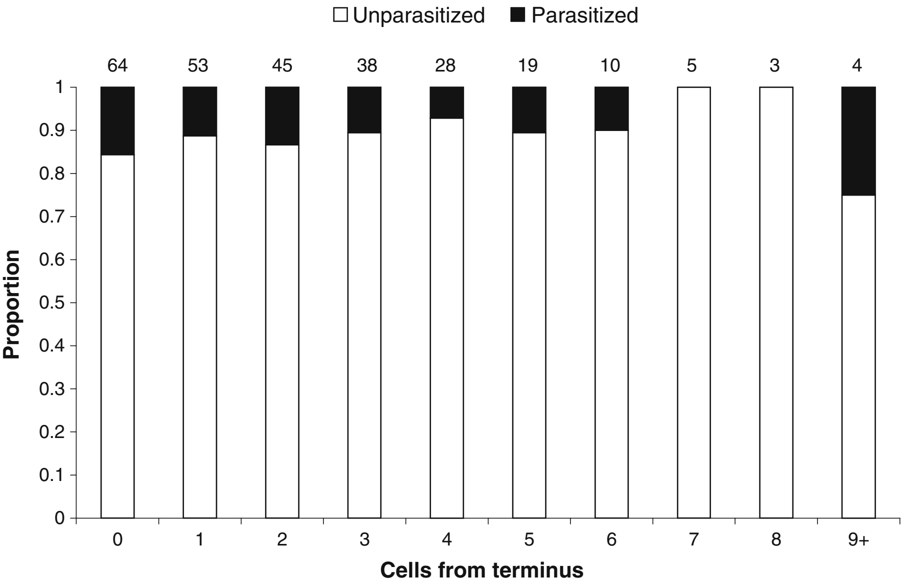

Fig. 3 The relationship between parasitism and position within a nest. Cells from terminus (x-axis) were measured as the number of cells from the end of a branch farthest from the entrance gallery. The y-axis gives the number of parasitized cells in that position across all nests. Numbers above bars indicate the total number of cells in that position across all nests

was not significant (ANCOVA: $F_{5,\ 15}=0.98$, $p=0.45$). Finally, to determine if females worked cooperatively to construct longer nests, which would have more room for brood cells, we tested the relationship between the number of foundresses with worn mandibles (those that constructed or renovated nests) and total length of a nest and again found no significant relationship (ANOVA: $F_{2,\ 17}=0.23$, $p=0.8$).

Discussion

Brood Development and Nest Architecture

Many authors have speculated on the developmental rates of *Xylocopa*, concentrating on the order and mechanisms of emergence (Gerling and Hermann 1976; Rau 1933; Skaife 1952). Specifically, Gerling and Hermann (1976) claimed that *X. virginica* nests

Table 2 The effects of nest architectural characteristics on the number of foundresses within a nest. Results are based on type III sums of squares

Characteristic	F	p-value	df
Total length	0.16	0.7	1
Unused (empty) space	0.00	0.99	1
Length occupied by brood cells (log transformed)	3.59	0.07	1
Branched or linear	2.31	0.15	1

in Georgia have a mechanism that synchronizes the development time of individuals, but offered no empirical evidence. In Ontario, individuals varied significantly in developmental stage, within and between branches; the oldest individuals were at the end of a branch. However, the order of brood stages within a branch was not perfect suggesting no synchronizing mechanism exists in Niagara populations. This finding also indicates that some variation may exist in developmental rate; although, it seems unlikely that individuals in the same nest would develop at substantially different rates. It is not clear if lack of synchronization results from rearing brood in the lab.

In *Xylocopa* that provision cells sequentially, it is not possible to access a previously provisioned cell without destroying the cell partitions built after it, although these cells could be rebuilt later as is seen in some species of *Ceratina* (Michener 1974; Michener 1990; Sakagami and Maeta 1977), and Halictini (Michener 1974). In solitary cavity nesting bees, such as some species of *Osmia* (Bosch and Vicens 2006) and *Ceratina* (Sakagami and Maeta 1977) a pattern exists where cells are ordered by age within the nest; the oldest progeny are located at the branch's terminus. We observed the same pattern in *X. virginica*, which provisions cells sequentially, a single branch at a time, and does not appear to revisit cells once completed. We detected some variation within branches, which may have been caused by differing developmental rates or variation in nutritional value of pollen masses. Variation may be expected if pollen masses differ in nutritional value, and thus individuals develop at different rates. Variation may also have resulted from egg replacement, although this implies that cells are revisited for which there is little evidence. Finally, in strictly communal species, we would expect to find multiple nest branches with broods of equivalent ages, as is reported for *Xylocopa sauteri* (Iwata 1964; Michener 1969). We did not detect such a pattern in *X. virginica*; therefore brood age patterns do not support communal social organization in this species.

Relationships between Nests and Sex Allocation

We did not detect any pattern in the allocation of sexes within brood cells with respect to position or laying order. There was neither a pattern with respect to nest, or within consecutive brood. These findings contradict those of Stark (1992b) for *X. sulcatipe*s and those of Watmough (1983) for the average of 15 *Xylocopa* species; both studies found female biased broods. While Gerling and Hermann (1976)) did not report sex ratios directly, they noted that in Georgia overwintering nests of *X. virginica* on average contained 4.5±2.21 females and 3.4±2.15 males. Since broods overwinter in their natal nest, this would suggest a female biased sex ratio. However, this number likely includes old foundresses (those attempting to overwinter a 2nd time) in addition to newly emerged brood. Hence, the number of females may be inflated. Similarly, Steen (2000) did not give analyses but reported data for two species of *Xylocopa* in the subgenus *Lestis* in which she showed nests with both more male brood and nests with more female brood. It is possible that sex ratio varies with species of *Xylocopa*; this may be related to social organization, differences in the relative "value" of males versus females in a given environment, or it may reflect seasonal variation.

The primary source of mortality in southern Ontario populations of *X. virginica* brood is bombyliid parasitism (Prager 2008), and nest architecture may influence these parasitism rates. Packer (1988) compared mortality from parasitism between ground nesting sweat bees and trap nesting megachilid bees and concluded that mortality from parasites is higher in trap nesting bees. This contradicts Michener (1985) who suggested that ground-nesting bees should suffer greater mortality from parasites. Among nests collected in this study, 41% were parasitized, which corresponds to the range observed in other twig nesting bees (40%-44%) (Packer 1988).

In multi-foundress nests of *X. virginica*, females do not appear to guard by plugging or blocking the nest entrance (SMP, personal observation). Females, however, may guard brood within branches, which is the proposed use of extra space in *X. fenestrata* (Dhaliwal and Kapil 1968) and is similar to Daly's suggestion for some *Ceratina* (Daly 1966). While, we found extra space in some *X. virginica* nests, Prager (2008) has demonstrated that nests with multiple females do not benefit from reduced parasitism. Similarly, in a study of *Halictus ligatus* in southern Ontario, Packer (1988) found no difference in levels of parasitism for pleometrotic nests, which were guarded versus solitary nests. These similar results may suggest that, in general, guarding by a female is not an effective defense against bombyliid parasitism in *X. virginica*.

If a single female founds a nest, a branched nest may not be necessary until there are additional adult females to benefit from branches. Conversely, more space may be required to accommodate additional foundresses. We did not detect a relationship in which larger nests or those with more unused space are associated with more foundresses. Similarly, longer nests are apparently not the result of more females performing construction (more females with worn mandibles). Therefore, we conclude that additional foundresses do not benefit a colony by creating nests that can accommodate larger broods.

Numerous authors have discussed potential interactions between social behavior and nest architecture (Gerling and Hermann 1976; Michener 1974; Michener and Kerfoot 1967; Steen and Schwarz 2000). Some have suggested that branched nests may allow for variable laying strategies, as females may choose to either lay in alternating termini or sequentially in a single branch at a time. Sequential laying may explain the larger broods seen in branched nests; using a single branch at a time may allow a foundress to work with less obstruction from other females than in linear nests. In her study, Steen suggested that polymorphisms in provisioning strategies (laying sequentially vs. alternating between branches), and nest branching are associated with social behavior (Steen 2000; Steen and Schwarz 2000). In branched nests, workers can provision cells simultaneously, as in *X. sulcatipes* (Stark 1992a). This is not possible in linear nests where at maximum two cells can be accessed at a time. In multi-foundress nests of *X. virginica*, a single female (or occasionally more) perform(s) most brood related tasks including nest construction (Gerling and Hermann 1976; Rau 1933). This form of task allocation would negate the benefits of alternating between branches, as only a single cell is provisioned at a time and thus order is less pertinent. It is possible that branched nests may be useful in reducing the number of interactions between foundresses, because additional foundresses can reside in those branches of a nest not being provisioned. This would reduce the number of passing events required and in turn the time required to deposit pollen. However, in observations of foraging, Prager (2008) found no difference in the total handling time per female for solitary and multi-foundress nests. This indicates that unlike many wasp species, the efficiency with which *X. virginica* provisions cells is not influenced by nest architecture.

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