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Fricke: Factors Influencing Length and Volume of Cells Provisioned by Two

FACTORS INFLUENCING LENGTH AND VOLUME OF CELLS PROVISIONED BY TWO *PASSALOECUS* SPECIES (HYMEMOPTERA: SPHECIDAE)

John M. Fricke[1]

ABSTRACT

Length of cells provisioned by *Passaloecus areolatus* and *Passaloecus cuspidatus* decreased as bore diameter increased, but volume of provisioned cells increased with increasing bore diameter. Activity of the parasitoid *Omalus aneus* increased length of provisioned cells. Wasp senescence did not result in increased cell length.

Danks (1971) suggested that the availability of nesting sites was one of the factors limiting populations of wood inhabiting aculeate Hymenoptera. If this is true, it should be possible to identify strategies used to optimize available nesting material. One of these strategies could be the decrease of cell length as bore diameter increases. Such a strategy would increase the number of cells possible in a given nest. Fye (1965), Krombein (1967) and Vincent (1978) gave bore diameter and cell length data for cells provisioned by *Passaloecus cuspidatus* Smith. Krombein (1967) reported 58 provisioned cells from 3.2 mm bore diameter trap-nests (mean length, 16.3 mm; range, 8 – 52 mm.); four cells from 4.8 mm bore diameter were 7, 8, 13, and 126 mm long; and one 6.4 mm bore diameter trap-nest had four cells 6, 7, 7, and 9 mm long, respectively. Fye (1965) reported a 6.4 mm bore diameter trap-nest of four cells, with a mean cell length of 15 mm. Vincent (1978) reported data from 83 soda straw nests with 4.0 mm bore diameters. One hundred-eleven female cells had a mean length of 10.09 ± 2.19 mm and 110 male cells had a mean length of 8.82 ± 2.16 mm. These data suggest that *Passaloecus* spp. would optimize nesting material by decreasing cell length as bore diameter increases.

METHODS AND MATERIALS

To test whether *Passaloecus* spp. optimize their use of bore volume, trap-nests of several bore diameters were made available as nesting sites on the campus of Concordia College from 1984 through 1987. Trap-nest design has been previously described (Fricke 1991). Cell length and volume data were collected from trap-nests provisioned by *Passaloecus annulatus* (Say), *P. areolatus* Vincent, *P. cuspidatus* Smith, and *P. monilicornis* Dahlbom. Cell length was determined by measuring the distance from the innermost surface of a cell to the exterior surface of the cell closure. Cell volume was determined

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Table 1. Cell length data from trap-nests provisioned by *Passaloecus areolatus* and *P. cuspidatus*, 1984–1987.

Passaloecus spp.	Bore (mm)	Number of Cells	Cell Length	Median Cell Length	Mean Cell Length
	1.6	49	9–70	16.25	19.79±12.79
areolatus	2.0	73	7.5–41	13.19	14.33±5.31
	2.4	30	7–36	13.19	15.57±7.27
	2.4	40	8–39	12.96	14.34±5.29
cuspidatus	3.2	210	6–82	12.73	14.17±8.30
	4.0	180	5–101	10.03	15.09±17.00
	4.8	95	5–116	10.23	20.58±26.33

by using the formula for a cylinder and the length and bore diameter of each respective cell.

RESULTS AND DISCUSSION

Lengths of provisioned cells produced by *P. areolatus* and *P. cuspidatus* were varied and skewed. This should be expected since one tail of the distribution of provisioned cell length is closed (no cell can have a length shorter than 0 mm) and the open end of the distribution is limited by the actual length of the trap-nest bore (120 mm). Data for *P. areolatus* and *P. cuspidatus* are summarized in Table 1. Ranges and medians for these respective species and trap-nest bore diameter classes show median cell lengths much shorter than mid-point cell lengths of respective ranges. In normal distributions equal proportions of measurements above and below the mean would be expected. However, the percentage of cell lengths shorter than respective mean cell lengths for *P. areolatus* were 71.4, 68.5, and 73.3%. For *P. cuspidatus* these values were respectively 72.5, 61, 80, and 81.5%.

Mean cell lengths are longer than median cell lengths and variances are exceptionally high. This reflects the statistical effect of a small number of provisioned cells of extraordinary length. These cells were usually found to be, but not limited to, the last provisioned cell in a trap nest. Frequently such a trap-nest did not have a vestibular cell, although in a few cases an extraordinarily long cell was followed by a vestibular cell. To eliminate the statistical effects of cells of extraordinary length, a 10% exclusion rule was applied to the analysis of cell length data. For each species, 10% of the cell length values from the open end of the distributions were excluded in subsequent analysis. The results of this analysis are given in Table 2.

With the application of the 10% exclusion rule mean values are clearly more representative of cell length measurements and demonstrate an inverse relationship between bore diameter and cell lengths. One-way ANOVA for differences in cell lengths associated with differences in bore diameter were significant for *P. areolatus* ($F = 3.30337$, df $= 134$, $p < .01$) and for *P. cuspidatus* ($F = 19.51697$, df $= 472$, $p < .001$). However, these mean values do not reflect the extreme variation observed in provisioned cell length and we can only speculate on possible causes for such variation. One possible cause could be a declining prey population. As prey numbers decrease, additional time and energy are expended during provisioning. In this case an optimal closure or partition strategy would be reduction of time required to move from the trap-nest bore opening to the partition or closure. A partition or closure placed

Table 2. Cell length data from trap-nests provisioned by *Passaloecus areolatus* and *P. cuspidatus*, 1984–1987 using a 10% exclusion rule.*

Passaloecus spp.	Bore (mm)	Number of Cells	Cell Length	Median Cell Length	Mean Cell Length
areolatus	1.6	41	9–25.5	14.17	15.13±3.81
	2.0	71	7.5–25	13.06	13.51±3.79
	2.4	25	7–21	12.81	12.68±3.26
cuspidatus	2.4	38	8–22	12.89	13.43±3.19
	3.2	195	6–23	11.93	12.39±3.45
	4.0	164	5–23	9.90	10.33±2.38
	4.8	79	5–23	9.825	9.47±2.72

*Ten percent of the cell length values from the open end of cell length distributions were excluded in these analyses.

closer to the bore opening will produce a cell of disproportionate length and volume.

Previous research on *Passaloecus* has made no reference to cell volume, and no anaylses have been done on relationships between number of prey per cell, cell length, cell volume and bore diameter. If *Passaloecus* spp. made maximum use of available bore space, constant volume for cells from trap-nests of different bore diameters should be observed. This hypothesis was evaluated by determining cell volume for provisioned cells of mean cell length from each bore diameter used by *P. areolatus* and *P. cuspidatus* (Table 3). These data show that cell volume increased as bore diameter increased for both species.

A related question is whether or not increased cell volume is associated with a larger number of provisions. Data were available from 3.2 and 4.0 mm bore trap-nests provisioned by *P. cuspidatus* with *Myzus monardae* (Davis) (Aphididae). Cells with extraordinary length and cells in which larval feeding had occurred prior were excluded from this analysis. Such feeding would reduce the number of aphids by an uncertain amount. Ranges and means for number of aphids per cell, cell length, and cell volume were determined for 58 cells of 3.2 mm bore trap-nests and 59 cells from 4.0 mm bore trap-nests (Table 4). There was no significant difference in the number of aphids provisioned in 3.2 and 4.0 mm bore trap-nests. However, differences in cell length and volume were signficant. As bore diameter increased, cell length decreased and cell volume increased. While no data were collected on actual volume of aphid provisions, a relative index to utilization of available space is cell volume (mm3)/aphid. The index for 3.2 mm bore trap-nests was 2.895 and for 4.0 mm bore trap-nests, 3.336. If an equal volume per provisioned aphid is assumed,

Table 3. Trap-nest bore diameters and provisioned cell volume for two *Passaloecus* spp.

Bore (mm)	*Passaloecus* spp. provisioned cell volume (mm^3)	
	areolatus	*cuspidatus*
1.6	30.42± 7.66	–
2.0	42.44±11.90	–
2.4	57.36±14.77	60.76±14.43
3.2	–	100.53±28.87
4.0	–	131.57±39.08
4.8	–	182.22±60.98

Table 4. Number of aphids [*Myzus monardae* (Aphididae)] provisioned per cell, cell length and cell volume in 3.2mm bore and 4.0 mm bore trap-nests provisioned by *Passaloecus cuspidatus*, 1987.

				t(II) statistic		
	Bore	Range	Mean	t value	df	prob
# of aphids per cell	3.2	22 to 66	35.81 ± 10.25	1.3098	115	p > .05
	4.0	14 to 74	38.67 ± 13.03			
Cell length (mm)	3.2	7 to 23	12.89 ± 3.29	4.2796	115	p < .0005
	4.0	6 to 23	10.27 ± 3.28			
Cell volume (mm^3)	3.2	56.30 to 184.98	103.67 ± 26.49	3.9331	115	p < .0005
	4.0	75.40 to 289.03	129.02 ± 41.19			

these indices show a more efficient use of the 3.2 mm bore trap-nests. These results agree with the subjective observation that the free space above the aphid provisions was larger in 4.0 mm bores.

Scatter plots of number of aphids provisioned per cell and cell volume for 3.2 and 4.0 mm bore trap-nest are given in Figures 1 and 2. Simple linear regression of cell volume on number of aphids provisoned per cell gave the respective regression equations: ($Y = 54.88 + 1.36X$, $r = 0.53$) for 3.2 mm bores and ($Y = 86.75 + 1.09X$, $r = 0.35$) for 4.0 mm bores. Cell volume is weakly related to the number of aphids provisioned. In the case of 3.2 mm bores, 25% of the variance of cell volume is accounted for by the variance of the number of aphids provisioned; in 4.0 mm bores only 12.25% of the variance of cell volume is accounted for by the variance of the number of aphids provisioned. Cell volume is not greatly affected by the number of aphids provisioned.

In addition to bore diameter, several other factors could contribute to variations in length of provisioned cells. Wasp behavior, influencing the placement of cell partitions and closures, could be altered by age, prey availability, proximity of prey, weather conditions, competition for nesting sites, and the activity of parasites. To determine whether extraordinary cell lengths were a result of wasp senescence, cell length data for trap-nests with known closure dates were examined from *P. cuspidatus* trap-nests of 1984 and 1987. If extraordinary cell length is a result of senescence, increased length would be noted in late-season nests. Provisioned cells of extraordinary length (24 – 116 mm) were found in trap-nests provisioned throughout *P. cuspidatus* nesting season, and in all but three cases the extraordinary cell was the last cell provisioned (Table 5). Senescence can thus be excluded as a principal factor contributing to increased cell length.

Another possible cause for increased cell length is the activity of parasites. Data from *P. cuspidatus* nests of 1984 were examined for evidence that activity of *Omalus aeneus* (Fabricius) (Chrysididae) contributed to increased cell length. Ranges of provisioned cell length from trap-nests of respective bore diameter classes were as follows: 3.2 mm (6 to 31 mm, n = 79); 4.0 mm (6 to 101 mm, n = 29); 4.8 mm (5 to 116 mm, n = 52); and 6.4 mm (5 to 20 mm, n = 10). Cell length data for eight of 170 cells (approximately 5% of all values) were excluded in the analyses of these data because they were characterized as cells with extraordinary length. No cell lengths were excluded from 3.2 mm bore data, 3 cell lengths (56, 94, and 101 mm) were excluded from 4.0 mm bore data, and 5 cell lengths (56, 72, 78, 108, and 116 mm) were excluded from 4.8

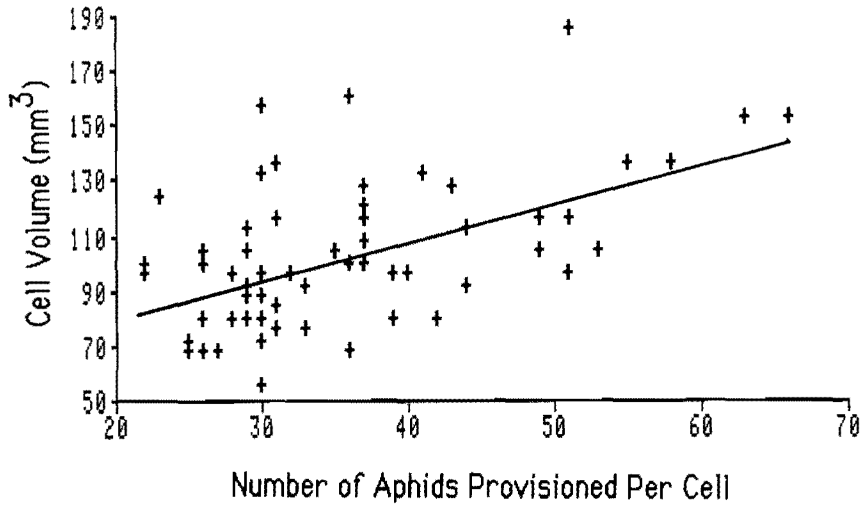

Figure 1. Scatter plot of number of aphids provisioned per cell and cell volumes (mm^3) for *Passaloecus cuspidatus* 3.2 mm bore trap-nests, 1987.

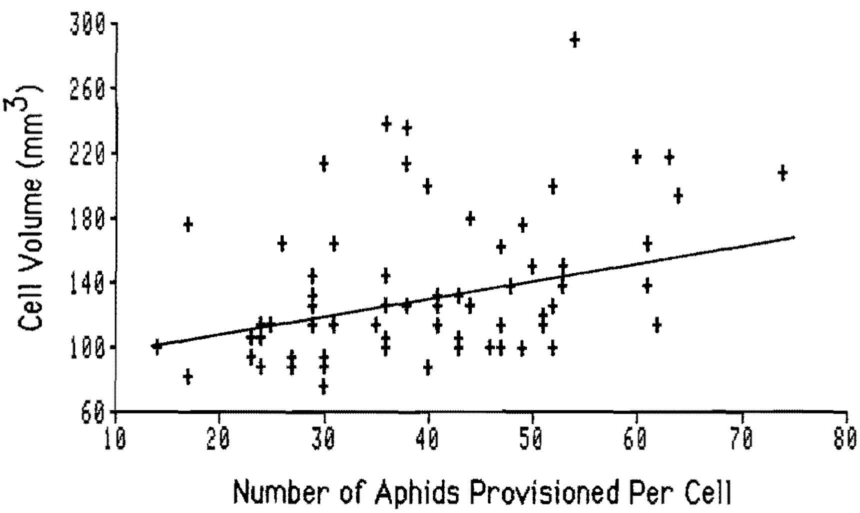

Figure 2. Scatter plot of number of aphids provisioned per cell and cell volumes (mm^3) for *Passaloecus cuspidatus* 4.0 mm bore trap-nests, 1987.

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Table 5. Seasonal distribution of *Passaloecus cuspidatus* cells of extraordinary length.

Date of closure	Bore (mm)	Cell length (mm)								
		1	2	3	4	5	6	7	8	9
6-18-84	4..0	11	11	94*						
6-18-84	4.0	15	101*							
6-20-84	4.8	116*								
6-21-84	4.8	8	108*							
7-09-84	4.0	7	56*							
7-16-84	4.8	17	24*	17	56*					
7-16-84	4.8	14	14	72*						
8-07-84	4.8	14	12	78*						
6-15-87	4.0	10	10	72*						
6-19-87	4.0	13	97*							
6-19-87	5.6	7	7	101*						
7-03-87	3.2	19	19	12	67*					
7-06-87	4.0	7	7	8.5	14	7	7	7.5	13	46*
7-08-87	4.0	13	10.5	15.5	10	10	67*			
7-08-87	3.2	47*								
7-08-87	3.2	16	47*							
7-08-87	4.8	10	13	77*						
7-08-87	3.2	23	25*	51*						
7-10-87	4.0	12	15	14	59*					
7-10-87	4.0	10	8	8	94*					
7-20-87	4.8	9	105*							
7-20-87	4.0	10	9	46*						
7-20-87	4.8	35*	88*							
7-20-87	4.8	12	12	91*						
7-20-87	4.8	13	13	44*						
7-24-87	4.0	23	75*							
7-27-87	3.2	12	16	17.5	82*					

*extraordinary cell length

Table 6. Cell length data from 1984 *Passaloecus cuspidatus* nests parasitized by *Omalus aeneus*.

Date of closure	Bore (mm)	Cell length (mm)									
		1	2	3	4	5	6	7	8	9	10
6-14-84	3.2	31*	10	24							
6-17-84	3.2	12*	11	14	12	12	10*	10	11		
6-18-84	3.2	18*	20*	27*	24*						
6-30-84	3.2	18	19	13	9*						
7-16-84	3.2	22*	15								
7-24-84	3.2	27	8	12*							
6-18-84	4.0	32*	6	9*							
6-19-84	4.0	25*	9								
6-21-84	4.0	11	15*								
6-26-84	4.0	12	11	9	9	8*	8				
7-03-84	4.0	8*	10								
6-12-84	4.8	7*									
?	4.8	10*	10*								
6-21-84	4.8	8*	108								
6-30-84	4.8	10*	10								
7-16-84	4.8	14*	14	72							
7-16-84	4.8	17*	24	17*	56						
6-18-84	6.4	6*	6	6*	6	5*	6	6	6	5	21

*parasitized cell

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Table 7. Cell length data for cells from non-parasitized trap-nests and parasitized trap-nests provisioned by *Passaloecus cuspidatus*, 1984.

		Mean Provisioned Cell Length (mm), Standard Deviation, and Number of Cells in Each Class			
Bore (mm)		All trap-nests in bore class	Trap-nests free of parasites	Trap-nests w/ parasites	Paratized cells only
	$\bar{x}$	13.49	12.42	16.00	18.72
3.2	s	5.20	3.91	6.74	6.91
	n	79	57	22	10
	$\bar{x}$	12.19	12.8	11.80	16.17
4.0	s	6.10	4.83	6.75	9.26
	n	26	10	16	6
	$\bar{x}$	9.79	8.86	12.82	11.63
4.8	s	4.11	3.37	4.78	3.64
	n	47	36	11	8
	$\bar{x}$	7.3	–	7.30	5.67
6.4	s	4.58	–	4.58	0.47
	n	10	–	10	3

$\bar{x}$ = mean; s = standard deviaiton; n = number in class.

mm bore data. No parasitized cells were noted among excluded cells. Eighteen of 53 provisioned trapnests were parasitized and contained 27 parasitized cells. Parasitized trap-nests contained 32 cells free of parasites. Cell length data for these parasitized trap-nests is given in Table 6. Mean cell length of all bore classes were determined for: all cells, cells from trap-nests free of parasites, cells from parasitized trap nests, and parasitized cells (Table 7).

Although sample sizes were relatively small these data show that parasitism of *P. cupidatus* cells by *O. aeneus* results in increased cell length in trap-nests with bore diameters equal to or less than 4.8 mm. The *t*(II) test for differences in mean cell lengths between trap-nests without parasites and trap-nests with parasites was significant for 3.2 mm trap-nests (t = 2.343, df = 77, p <.025) and for 4.8 mm trap-nests (t = 2.5563, df= 45, p <.005). Parasitized cells from 3.2, 4.0, and 4.8 mm bores had cell lengths which were respectively 51%, 26%, and 31% longer than cells from nonparasitized trap-nests. In a single 6.4 mm bore trap-nest, parasitism did not result in increased cell lengths.

Passaloecus cuspidatus does not maximally use trap-nest bore volume. Larger bore diameter trap-nests contained cells with decreased length, while cells parasitized by *Omalus aenus* were longer than non-parasitized cells. Volume of provisioned cells increased with increased bore diameter, but number of aphids provisioned did not increase proportionately with increased cell volume. Additionally, wasp senescence did not result in increased length of provisioned cells.

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