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#### ABSTRACT

# THE BIOLOGY OF HERIADES CARINATA CRESSON (HYMENOPTERA: MEGACHILIDAE)

### by Robert Wendell Matthews

The life history of this bee is presented, based on observations in 1963 and 1964 on a Michigan population compared with an Oregon population observed in 1962, both nesting in trap-nests. In Michigan, a new technique, the use of Saran-covered trap-nests, facilitated observations of intra-nest adult behavior and larval development in situ. Two new terms are introduced; the cap base, constructed by the female prior to nest-capping, and the operimentum, spun by the larva prior to coccon construction.

There is one generation per year, overwintering in the prepupal stage. Adults are active between June 23 and August 15 in Michigan and from July 11 lasting into September in Oregon; nesting reached a peak on June 30 in Michigan and July 28 in Oregon. Oregon females averaged 6.4 cells per nest and 2.7 days per cell compared to 4.6 cells per nest and 1.1 days per cell for Michigan females.

Partitions between cells and nest caps are of resin. Pollen used by the Michigan population over 19 days during the nesting season peak was almost exclusively staghorn sumac (<u>Rhus typhina</u>). Nest construction activities and adult behavior are presented in detail and the phenomenon of nest raiding is discussed.

Larval development, lasting 30 days, and comparative post-diapause

development of males and females in Michigan are discussed. The mature larva is described.

Parasites included <u>Stelis vernalis</u> Mitchell and <u>Sapyga louisi</u> Krombein; their biology and behavior is discussed. <u>Melittobia chalybii</u> Ashmead was a laboratory contaminant.

## THE BIOLOGY OF HERIADES CARINATA CRESSON

(HYMENOPTERA: MEGACHILIDAE)

Ву

Robert Wendell Matthews

### A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Entomology

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#### ACKNOWLEDGEMENTS

It is with much appreciation that I acknowledge the encouragement and guidance given me by my graduate committee, the Doctors Gordon E. Guyer, Ethelbert C. Martin, and John E. Cantlon. I am especially indebted to Dr. Roland L. Fischer, my major professor, for his continued interest and helpful suggestions freely given throughout this study.

Dr. B.D. Burks of the United States National Museum kindly identified the chalcid parasite; Dr. R.M. Bohart of the University of California, Davis, determined the sapygid parasite. I am grateful also to Dr. A.T. Cross and Wm. T. Gillis for their assistance with the pollen identification.

Equipment and labor involved in preparation of the 1963 trap-nests were furnished by Consumers Power Company through the efforts of my father-in-law, Stuart Rittenhouse; his aid is gratefully acknowledged. A special thanks is also due Julian P. Donahue for the numerous excellent photographs taken for me in connection with this research.

Finally, I wish to thank my wife Janice for her suggestions and invaluable aid in the typing and preparation of the final copy. Her help and continued encouragement are greatly appreciated.

ii

### TABLE OF CONTENTS

Acknowledgements	ii
List of tables	v
List of figures	vi
Introduction	1
Procedure	3
Nesting habitat	3
Nest block description	5
Seasonal History	6
Abundance	6
Period of nesting activity	6
Adult emergence	7
Recovery and population size	7
Adult longevity and nests per female	8
Adult Activities	11
Pre-nest activity and mating	11
Availability of natural nest sites	11
Nest site selection and preparation	12
Provisioning	13
Pollen placement behavior	15
Construction of cell partition	17
Oviposition	18
Cap base construction	19
Nest closure	21
Nest defense	22

Nest raiding and supersedure	23		
Miscellaneous behavior	27		
Period of daily activity	28		
Nest structure	30		
Growth and Development	34		
Techniques of study	34		
The egg			
The larva	<b>3</b> 5		
Description of mature larva	<b>3</b> 9		
Post-diapause development	40		
Parasites	46		
Summary and Discussion			
Literature cited			

# LIST OF TABLES

Table 1.	Female longevity and nesting data for	
	H. carinata in Michigan, 1963.	9
Table 2.	Resin foraging trips before and after	
	oviposition.	20
Table 3.	Nest supersedure by H. carinata.	26
Table 4.	Comparison of volume (mm-in <sup>2</sup> ) of provisioned	
	cells and nest caps for Michigan and Oregon	
	nests, using Student's t-test.	33
Table 5.	Post-diapause development for Michigan	
	H. carinata refrigerated 115 days, then	
	maintained at $72^{\circ}$ F.	42
Table 6.	Combined records of sex and position in	
	cell series for all reared <u>H</u> . <u>carinata</u> ,	
	Michigan and Oregon.	44
Table 7.	Rearing data for <u>H</u> . <u>carinata</u> from 55 Oregon	
	and 77 Michigan nests.	45

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### LIST OF FIGURES

Figure 1.	H. carinata breaking through recently	
	completed nest cap.	56
Figure 2.	Nesting habitat at target range.	56
Figure 3.	Oregon nest of $\underline{H}$ . carinata, freshly split.	56
Figure 4.	Same from Michigan, Saran-covered bore.	56
Figure 5.	Operimentum, larva removed.	56
Figure 6.	Typical H. carinata cocoons.	56
Figure 7.	Prepupa in saran-covered cell.	56
Figure 8.	Pupa.	56
Figure 9.	Seasonal distribution of H. carinata	
	nests in Oregon, 1962.	57
Figure 10.	Seasonal distribution of <u>H.</u> carinata	
	nests in Michigan, 1963 and 1964.	57
Figure 11.	Five-day arrival and departure records for	
	female H. carinata construction of single	
	7-celled nest.	59
Figure 12.	Resin placement prior to oviposition.	61
Figure 13.	Position of freshly laid egg of <u>H</u> . <u>carinata</u>	
	on pollen.	61
Figure 14.	Slumped position of egg immediately prior	
	to hatching.	61
Figure 15.	Egg of <u>H</u> . <u>carinata</u> .	61
Figure 16.	Egg of Sapyga louisi.	61

Figure 17.	Position and method of attachment of	
	S. Louisi egg on host egg.	61
Figure 18.	<u>H. carinata</u> , mature larva.	63
Figure 19.	Dorsal view of head of same.	63
Figure 20.	Lateral view of head of same.	63
Figure 21.	Inner view of mandible of same.	63
Figure 22.	Ventral view of mandible of same.	63
Figure 23.	Spiracle of same.	63

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### INTRODUCTION

The biology of the megachiline bees has attracted considerable attention, as it may elucidate phyletic relationships within the family and add to our knowledge of comparative behavior of bees. Knowledge of the biology and behavior of <u>Heriades</u>, because it is regarded as one of the more primitive genera of the Megachilidae (Michener, 1938), may be especially valuable.

The genus <u>Heriades</u> occurs throughout the world except in the Australian region and in South America. A total of eleven species is known from North America, belonging to two subgenera, <u>Physostetha</u> and <u>Neotrypetes</u>. <u>Heriades</u> (<u>Physostetha</u>) <u>carinata</u> Cresson ranges throughout most of the United States from Quebec south to Georgia, west to British Columbia, Oregon, Utah, Arizona and Texas. Its range was mapped by Hurd and Michener (1955).

The only biological information on this species is a note by Rau (1922), recording the emergence of two individuals from a nest in a hollowed-out stem of sumac but giving no other details. A single nest of <u>Heriades (Neotrypetes) variolosa</u> (Cresson), also a wide-ranging species in North America, in a hollow twig of <u>Rhus glabra</u> was described and figured by Fischer (1955). Apparently nothing is known of the biology of any other North American <u>Heriades</u>, but the biology of a South African species, <u>H. freygessneri</u> Schletterer, is reported by Taylor (1962). It largely agrees with the biology of <u>H. carinata</u> reported here. Some biological data also exist for the European species, <u>H. truncorum Linnaeus and H. crenulatus Nylander. Grandi (1934)</u>,

reporting on the biology of these species, noted them nesting in canes of <u>Phragmites</u>; he also described and figured the mature larva of <u>H. crenulatus</u>, the only larval description of any species of <u>Heriades</u>.

The material presented here was obtained during the summers of 1963 and 1964 at the Michigan State University W.K. Kellogg Biological Station in Kalamazoo County, Michigan. These data are compared, where possible, with data obtained on a population of the same species from Corvallis, Oregon, during the summer of 1962, a study made possible by a National Science Foundation undergraduate research award (NSF G21612).

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#### PROCEDURE

<u>Nesting Habitat</u>. In the summer of 1963, five nesting sites were chosen along a 700 yard strip of land bordered by cultivated fields on the west and by marsh on the east. Thickets of staghorn sumac  $(\underline{\text{Rbus typhina}})^1$  formed a nearly continuous border along the fields, and occurred with sassafras (<u>Sassafras variifolium</u>) through the central areas to the marsh edge, where elderberry (<u>Sambucus</u> <u>canadensis</u>) thickets predominated. Mixed young hardwoods occurred intermittently along the strip, continuing at each end around the marsh.

Common herbacious plants of the area which flowered throughout the nesting season were <u>Melilotus alba</u>, <u>M. officinale</u>, <u>Trifolium</u> <u>pratense</u>, <u>T. repens</u>, <u>Potentilla recta</u>, and, less commonly, <u>Hypericum</u> <u>perforatum</u>, <u>Apocynum androsaemifolium</u>, and <u>Verbascum thapsus</u>. The field adjoining the area to the southwest was in alfalfa.

No nesting site was completely shaded: all received shade for at least part of the day, except site 4 (Figure 2) which was situated under full sun at the open end of a target range excavated from the side of a small hill. Site 1 was bordered on the north and east by staghorn sumac and sassafras thickets, and by an open abandoned field to the south and west. A young catalpa tree shaded it in late afternoon. Sites 2 and 5 were in small clearings surrounded by thickets of staghorn sumac and sassafras. Site 3, opposite site 4 in the target range, was at the end of a short path through mixed hardwoods. Site

<sup>&</sup>lt;sup>1</sup>Authority for all plant names is <u>Gray's Manual of</u> Botany, 8th ed., 1950.

5 was above site 4 on the remains of the hill from which the target range had been excavated. Sites 3, 4 and 5 were all relatively close, linearly situated with site 3 about 50 feet northwest of site 4 and with site 5 about 25 feet southeast of site 4.

In 1964, sites 1 and 5 were abandoned because of poor nesting results the previous year, and nesting site 6 was established midway between sites 2 and 3. It was bordered immediately to the west by young hardwoods and by marsh about 50 feet to the east. Between the nest site and the marsh was a stretch of grass and clover (<u>Trifolium</u> <u>repens</u>) periodically mowed to admit traffic to a dumping area previously established along the marsh edge. Adjacent to site 6, a large patch of dogbane (<u>Apocynum androsaemifolium</u>) attracted a variety of hymenopterans throughout the nesting season.

In 1963, <u>Heriades carinata</u> made 58 nesting attempts, 7 of which were at site 1, 16 at site 2, 31 at site 3, 3 at site 4, and 1 at site 5. Of 19 nesting attempts in 1964, 3 were made at site 2, 9 at site 3, none at site 4, and 6 at the newly established site 6. In addition, one nest was constructed on the window ledge of my office.

In Corvallis, Oregon, in the summer of 1962 trap-nests were placed in three widely separated locations. Sites 1 and 2 were typical suburban backyards, in which the nest-blocks were placed in tree crotches, along fences and stairways, etc. The yard at site 2 was ill kept with numerous overgrown shrubs and hedges and few flowers. Adjoining yards contained a variety of flowering plants, however. The yard at site 1, in contrast to site 2, in a newer urban development contained very little woody vegetation and was well kept; as with site 2, pollen sources were available in neighboring yards. Site 3 was a

small, triangular old field with a few large trees, bordered by a small creek on one side and a well-grazed pasture on the other. Most nests were placed on the window ledges and beams of an abandoned livestock shed shaded about half the day.

Of the 55 nesting attempts by <u>H</u>. <u>carinata</u> in Oregon, 47 were at site 2, 6 at site 3, and 2 at site 1. The majority of those at site 2 were constructed in nests placed along a stairway on the east side of the house and all observations were made here.

<u>Nest Block Description</u>. Trap-nests such as described by Cooper (1953), with bores of 1/8, 5/32, 7/32, and 1/4 inch diameter and variable length were used in Michigan, combined into blocks of nine wired together for ease of handling. Every block, containing at least two nests of each bore diameter, was given a number and the nine nests in each block lettered from A through I, thus identifying each nest (e.g., 150-C). Approximately equal numbers of these blocks were placed at each nesting site, with bores horizontal from eight inches to four feet above the ground.

<u>H. carinata</u> readily accepted these nests, 86% preferring those with 1/8 inch bores 101 mm long in Michigan, where 77 nesting attempts were made in 1963 and 1964, of which 24 were in Saran-covered bores of the type described by Matthews and Fischer (1964). In Oregon in 1962, where no 1/8 inch bores or Saran-covered nests were used, <u>H. carinata</u> constructed 55 nests, primarily (62%) in 9/64 inch diameter bores 71 mm long. Glass tubes of appropriate inner diameter inserted into larger bores resulted in only one nesting attempt in three years with <u>H. carinata</u> although Taylor (1962) obtained very good nesting success with <u>H.</u> freygessneri in glass vials.

### SEASONAL HISTORY

<u>Abundance</u>. Never abundant in either Michigan or Oregon, <u>H</u>. <u>carinata</u> was only occasionally picked up in general collecting. However, at the nesting sites where the bees' activities were concentrated, it was not uncommon to have several nests under construction concurrently within three or four square feet.

<u>Period of Nesting Activity</u>. In Michigan there is one generation per year. In 1963, nesting began on June 23 and reached its peak on June 30 when 23 nests were under construction (Figure 10). Except for two apparent nesting attempts toward the end of July (July 24 and 28-31) all nests were constructed between June 23 and July 18. In 1964, the records show a similar pattern although it was a much wetter season with fewer nests made.

In Oregon, there is apparently also one generation per year; however, the period of adult nesting activity occurred later in the summer and was of longer duration. The first <u>Heriades</u> observed to nest in Oregon were three on July 11. Nesting reached a peak near the end of July (Figure 9) with 26 nests active concurrently and remained at this level, with minor fluctuations, throughout the entire month of August. When the nests were removed from the field on August 30, 20 were still in various stages of construction.

Examination of 38 males and 73 females of <u>H</u>. <u>carinata</u> in the Entomology Museum at Michigan State University revealed a flight period in Michigan's lower penninsula of about two months. The earliest records are those of a male on June 13 and of four females

on June 23 (the same date upon which I first saw female <u>Heriades</u> active at Gull Lake). The latest male record is for August 3, while the latest female was collected on August 15.

<u>Adult Emergence</u>. The first adults reared from 1963 nests kept outside over the winter emerged on June 23, 1964: the period of emergence was one week, June 23-29, during which 32 males and 12 females emerged. Males were first, emerging three days before the females; they were also more variable, appearing over a six day interval while female emergence was confined to a four day period. Under natural field conditions, emergences probably extend over a longer period, since the reared <u>Heriades</u> had been maintained under fairly uniform conditions.

<u>Recovery and Population Size</u>. The reared adults from 1963 were marked and released, as soon as possible after emergence, at site 3. Marking was done with quick-drying paints, applied in two-color combinations to the thorax. During the emergence week, sweep samples in the nesting vicinity were made periodically in an attempt to estimate population size and dispersal rates.

Of the 29 bees marked and released, only a single female was recovered; she was collected in vegetation around the release area three hours after release on June 27. In addition to this recovery, two unmarked <u>H</u>. <u>carinata</u>, one female and one male, were collected in other sweep samples in the nesting vicinity.

Of the ten females marked and released, one returned to construct a nest in a trap-nest in 1964. This female, reared in a Saran-covered nest, emerged and was marked and released at 10:00 a.m. on June 26;

she began to work in a Saran-covered nest about 30 hours after release.

This would seem to indicate that while the native <u>Heriades</u> population was not excessively large, trap-nesting activities probably had little overall effect on the population structure. Also, there is some evidence that the paint spots could wear off in time and so it is possible that more than one 1964 nest was made by a reared female.

Adult Longevity and Nests Per Female. Known longevity and number of nests constructed for seven marked female bees from Michigan in 1963 are summarized in Table 1. The oldest marked bee lived for 23 days and constructed four nests (15 provisioned cells). However, females may often live a month or longer, for caged females were also kept alive for 23 days, and the flight period in southern Michigan, based on collection records, is about two months.

Males are apparently fairly long-lived, judging from the large number of male collection records through late July, although reared caged males only survived for 12 days.

Based on marking records, it appears that in Michigan <u>Heriades</u> constructs at least two nests per female and often more. The most known cells constructed by a single bee was 16 for bee 1. Time to complete a single nest in Michigan averaged 5.2 days (range 2-15 days). In general, the first nest of a female's series tends to contain more cells than subsequent nests (Table 1). There were too few successful rearings from any one nest series to suggest whether the offspring sex ratio changed as the bee aged.

Table	1.	Female	longevity	and	nesting	data	for
					-		

• H	carinata	in	Michigan,	1963.

		Days	Cells	Cell Contents			
Bee	Nests	per nest	made	Male	Female	Aborted	
1	150 <b>G</b>	2	6	5	1	0	
	159B	3	6	<b>3</b>	0	3	
	300	6	4	0	0	4	
2	150B	2	5	4	1	0	
	300	1	1	0	0	1	
3	159 <b>G</b> 159E 150I 302	4 2 1 11	7 3 1 4	3 1 0 0	0 0 2	2 2 1 4	
4	<b>2</b> 32в	5	6	0	0	6	
	232н	4	1	0	0	1	
5	231A	3	3	0	0	3	
	301	3	2	0	0	2	
6	150E 150IR 231C 302 *	6 4 1 1	5 2 0 0	0 0 2	1 0 0 0	2 0 0	
7	163 <b>G</b>	3	5	0	0	5	
	164C	3	<b>3</b>	0	0	3	

\* Nest break-in, no cells constructed.

After one nest is completed, the bee wastes little time finding and beginning another one; in most cases the changeover occurred in less than a day. The following are representative records of nest changeover:

- Bee 1 Nest 150G completed 1:50 p.m. on 6-27; first pollen for 159B brought two hours later at 3:50 p.m. Nest 159B completed at 4 p.m. on 6-30; at 7 p.m. the same day the female was resting in nest 300.
- Bee 3 Nest 159G completed at 3:15 p.m. on 6-3; by 7 p.m. the same day the bee had completed the bottommost resin partition in nest 159E.

Where gaps longer than one day between nests occur it seems possible that the bee completed another undiscovered nest in that period.

The bees apparently exhibit high fidelity to their first nest site as long as suitable nests are available, for no marked bee was found nesting at more than one site, although nest sites were relatively close. Furthermore, the series of nests made by a single female were usually in a localized part of the nest site (e.g., at one end of the table at site 3) and often in adjacent nest blocks or even adjacent holes of the same nest block.

No Oregon bees were marked, but the time to complete a single nest in Oregon averaged 17.2 days (range 3-35 days), with several nests requiring over 30 days. One nest was under construction for 38 days and still unfinished. No data on the number of nests by a single female <u>Heriades</u> from Oregon are available, but since the average number of days required to complete a nest was higher, it seems likely that a female would seldom construct more than two nests during her life.

### ADULT ACTIVITIES

<u>Pre-Nest Activity and Mating</u>. In the laboratory, a male and female were kept alive together for twelve days, but no mating activity was observed during that time. However, mating in the field presumably occurs soon after emergence, probably before nest building is begun. Exceptions may occur, for in some nests no eggs hatched and in others eggs in the first one or two cells constructed did not hatch (or in one instance were apparently not laid) while they did in all subsequent cells. Whether mating occurs more than once is unknown; however, once mated, the female alone does the nest building and males were never observed in the nesting vicinity.

<u>Availability of Natural Nest Sites</u>. An examination of the staghorn sumac thickets predominant in the nesting vicinity revealed an abundance of hollow twigs which presumably would be acceptable nest sites to <u>Heriades</u>. When split open, these hollow twigs contained nests of solitary Aculeata and most showed evidences of having been used several times. However, of over 100 such twigs examined, only one showed any evidence of having been used by <u>Heriades</u> --- the remains of a <u>Heriades</u> cocoon and resin plug in the bottom, and additional resin along the bore.

Other potential nest sites might be found in hollow elderberry twigs in the thickets along the marsh edge, although a number of these twigs split open failed to show any evidence of <u>Heriades</u>. Also, it is possible that the dead stalks of some of the herbaceous annuals and perennials of the vicinity may have provided natural nest sites.

<u>Nest Site Selection and Preparation</u>. Initial discovery of the trap-nest is probably by chance. The bees probably encountered the weathered tables, planks, etc., on which the trap-nests rested before discovering the nest blocks. A female bee's search for a prospective nest site may be generalized as follows:

Upon discovering a nest site, such as a table, the bee spent about 45 minutes entering numerous bores and quite thoroughly investigating the table's surface cracks and crevices, ends, underside, and legs. She tended to work in spurts, entering several adjacent bores in fairly rapid succession. While at first she entered all size bores, she rarely crawled all the way down the larger diameter bores. She apparently could not distinguish whether a particular bore was already in use; this is discussed again later. During this time the bee frequently circled the nest area as though orienting. Occasionally she disappeared from sight but always returned almost immediately.

Eventually, nearly all her attention was directed to two or three 1/8 inch bores, in which she tended to remain for longer periods. Increasingly more time was also spent hovering near the nest blocks containing the favored bores. Finally she settled in a particular bore.

The first step in nest preparation was usually cleaning the bore of drill filings and splinters, and the telltale pile of sawdust beneath the nest entrance was often the first outward indication that a new nest was underway. The bee dragged or kicked the chips to the nest entrance, then intermittently backed up and kicked the pile out. The time spent at this activity varied depending on the condition of the individual bores; one bee worked for forty minutes, while some did

practically no bore cleaning. During this activity, the bees occasionally left on short flights, rarely longer than three or four minutes duration and usually for only a few seconds, in the nest area.

Finally the bee began to make regular trips for pollen or resin. Some bees found the bottom of the bore acceptable and began to store pollen directly on it, while others chose to begin by placing a plug of resin in the bottom, storing the first pollen above this.

One bee observed continuously throughout this activity seems representative of the time sequence involved. Between first searching for a prospective nest site and returning with the first pollen load, just over two hours elapsed. Half an hour was spent cleaning the bore. After one of her frequent short flights of this period, she returned with a chunk of resin in her mandibles and began plugging the bottom of the bore; six additional resin trips were made in the next hour. Between these trips she usually spent five to ten minutes working the resin inside the nest; after the last resin trip, she remained in the nest for 17 minutes. On the next trip she returned with a load of pollen and provisioning began.

<u>Provisioning</u>. The pattern of provisioning the cell, laying the egg and closing the cell follows a fairly predictable sequence. Several successive pollen loads are stored in the cell bottom; then the bee switches to collecting resin which is placed around the bore 3-4 mm beyond the edge of the pollen mass, forming a rim which ultimately becomes the cell partition. When an opening about the size of the bee's body remains, the bee prepares the pollen, reverses, and deposits the egg. She then completes the partition, thus sealing the cell, and begins

construction of the next cell.

The amount of time required to collect a single pollen load is undoubtedly influenced by such factors as distance of pollen source from nest site, availability of pollen, time of day, and weather. Also, it is probable that the bees often stopped to suck nectar while on foraging trips. In general, the time required to collect pollen loads was shortest during the middle hours of the day. Foraging for pollen in Michigan averaged 9' 57" per trip (range 2' 08" to 31' 53", 97 observations).

Random samples of pollen taken from cells constructed between June 23 and July 12 in 1963 were found to be almost entirely staghorn sumac (<u>Rhus typhina</u>) although other kinds of flowers were abundant in the area; this would suggest an oligolectic population, as defined by Linsley and MacSwain (1957). Although the pollen from Oregon nests was not analyzed, the source was probably garden flowers in neighboring yards. <u>H. carinata</u> has, however, been collected on a wide variety of flowers. In addition to flower visitation records of Hurd and Michener (1955) and Mitchell (1962), the following have been obtained from Gull Lake: <u>Asclepias syriaca, Monarda fistulosa, Melilotus alba, Rhus</u> <u>glabra, Cichorium intybus</u>, and <u>Apocynum</u> sp. Thus, the species as a whole should probably be regarded as polylectic, although many of the records may have been only nectar sources.

Since the principal source of pollen in Michigan was staghorn sumac which flowered abundantly in the nesting area, it seems unlikely that the bees travelled more than a quarter mile for pollen. Furthermore, <u>Rhus</u> flowers occur in large masses and therefore probably enabled the bees to collect large amounts of pollen with relative ease.

Much of the information on the timing of various nest construction activities in Michigan is summarized in Figure 11, which presents the comings and goings of a single bee watched continuously over a five day period in which she constructed a nest containing seven provisioned cells. This example probably represents optimum conditions, for the five days were near the peak of the nesting season, pollen sources were abundant, and weather conditions were ideal with sunny skies and temperatures of 85-90 degrees daily. Under these conditions, the bee was active nearly twelve hours daily and completed an average of two cells per day. (The seasonal mean number of cells constructed per day per bee was about 0.9 in 1963 and 1.1 in 1964.) The average number of trips for pollen to provision a single cell was 17 (range 13-19, 7 observations). The total of 115 pollen foraging trips accounted for 55% of this bee's nestbuilding time.

Little provisioning data were obtained, and the records represent only a few hours' observation, for the Oregon bees: however, some inferences may be drawn. In general, the number of pollen foraging trips per cell was greater for the Oregon nests, there being no less than 41 consecutive trips by one bee, all apparently for the same cell. The most pollen trips for a single day by a Michigan <u>Heriades</u> was only 36. Also, both the pollen and resin foraging trips were of noticeably shorter duration for the Oregon bees. It is unfortunate that a more complete picture of the adult nesting activities of Oregon Heriades is not available.

Pollen Placement Behavior. Upon returning with pollen, the bee enters the bore head first and incorporates the pollen deposited the previous trip into the mass, probably adding nectar at this time.

Chewing back and forth, typewriter-fashion, the bee works rapidly and rhythmically from the base to the top of the mass. During this process, the bee's face and mandibles become covered with pollen dust, so she often grooms momentarily before backing out to unload the pollen. The time spent incorporating pollen into the mass was relatively constant, ranging from 23" to 1' 30" (average of 108 observations, 52").

When crawling along the bore either frontwards or backwards, the female rarely travels in a straight line, but rather from side to side and occasionally completely around the bore. Crawling backwards was two to three times slower than crawling frontwards, or even slower when the bee was heavily laden with pollen. Since the 1/8 inch diameter bores were too small to permit the bees to turn around inside, they were forced to come outside, turn around, and back down the bore in order to unload pollen. However, those <u>Heriades</u> in Oregon which nested in bores of larger diameter were able to turn around inside and thus did not exhibit this behavior.

To remove the pollen from her scopa the female crawls backwards until the tip of her abdomen touches the pollen mass, then, balancing on the front two pair of legs, frog-kicks both legs together and simultaneously bends her abdomen downward stiffly into the thrust. She continues kicking about 23" (range 16"- 1' 41", 101 observations). When the pollen is largely removed from the scopa she moves forward about 1/8 inch, brushes the hind tarsi together, removing any pollen that may have clung to them, then crawls out, occasionally stopping to groom.

The completed pollen mass, situated against the lower cell partition,

fills about two-thirds of the average cell and is thoroughly mixed with nectar, forming a compact mass. The freshly completed provisions are firm and pliable and hold their shape well. The mass of staghorn sumac pollen was yellow-orange, but in other localities the pollen color would depend on the kind used. Usually the pollen at the bottom and sides of the cell is not wholly incorporated into the mass, retaining its powdery looseness and appearing as a lining into which the mass fits; apparently the females find it difficult to work the loose pollen from the cracks and crevices of the bore into the mass. This lining is usually quite obvious in fresh provisions since it tends to be distinctly lighter than the pollen to which nectar has been added.

<u>Construction of Cell Partition</u>. After storing pollen, the bee begins to bring resin. In Michigan, resin must have been relatively close and readily available, for the bee required only about five minutes (4, 47, average, 72 trips) to obtain it. The source of the resin remains unknown but it may, in part, have come from the sumac. Taylor (1962) reports that <u>H. freygessneri</u> used pine resin and the nests had a distinct pine odor, but no pine was present in the nesting vicinity here.

The number of resin-gathering trips per cell varied greatly (range 7 - 25, 7 observations). The duration of the trips also varied, but the 57 resin trips for the nest in Figure 11 (not including trips for resin used in the nest cap) accounted for 21% of the nest construction time.

The resin brought before egg-laying was placed around the bore 3-4 mm beyond the edge of the pollen mass, forming a circular rim. Successive resin placement and rim construction are illustrated in Figure 12. Often the bee used her front feet to remove the resin from

her mandibles, and generally she spent several minutes molding the resin and working it around the rim, finally leaving only a hole large enough to pass through.

Trips for resin following egg-laying were characteristically fewer, of shorter duration, and more regular than those made prior to egg-laying. One representative example, Table 2, compares resin gathering before and after oviposition.

Oviposition. The behavior connected with egg-laying was observed several times in Saran-covered nests. Instead of leaving the nest after disposing of the pollen or resin in the usual manner, the bee moves forward and begins to chew vigorously at the outermost portion of the pollen. This chewing continues for several minutes (6' 30" average, 4 observations), taking one or more short pauses to clean and groom. Chewing apparently adds nectar, for when the female has finished, the pollen has a soupy consistency in the area where the egg is to be laid.

Next, the bee backs out of the nest, turns around, and backs in until her abdomen touches the pollen mass. For 13 to 25 seconds, her abdomen makes several noticeable rhythmic contractions. Then the egg begins to appear and the abdomen remains practically motionless for the 20 to 35 seconds during which the single egg is deposited, attached by one end to the pollen mass. The female then quickly crawls out, turns around, and re-enters head first. Usually she pokes her head through the aperature and touches the pollen mass and egg with her antennae. This behavior is brief and the female turns almost immediately to chewing at the resin partition base, moving resin chunks and remolding the resin to close off the cell partition. Usually there is not enough

resin available to completely close the cell and additional trips to gather resin are necessary. However, on at least two recorded occasions, <u>Heriades</u> completed the cell partition using only the resin brought prior to oviposition.

Egg-laying occurred whenever the pollen mass was complete and the resin ring formed, and was observed as early as 9 a.m. and as late as 6:45 p.m. Generally resin was brought to the nest on the last trip before egg-laying. Occasionally, however, the bee switched back to pollen after several resin trips (see cells 2, 3, 4, 5 in Figure 11) and oviposited following a pollen trip.

<u>Cap Base Construction</u>. As Figure 11 illustrates, the last few foraging trips of the afternoon invariably were for resin, regardless of the cell's stage of construction. All bees observed began bringing it almost simultaneously, but the resin was disposed of in different ways. Often it was used to lay a cell partition foundation. Sometimes it was placed in chunks apparently randomly along the bore. In Sarancovered nests it frequently was used to caulk along the junction of the Saran and bore, particularly when the Saran did not tightly cover the nest.

Sometime during nest construction and almost invariably in late afternoon a circular base of resin was laid just inside the nest entrance. This often incomplete rim of resin, which forms the foundation for the nest closing plug, I have termed the "cap base". The early formation of such a cap base, often several days before the nest is actually completed, seems to be a unique feature to <u>H. carinata</u> and its characteristic appearance just inside the nest entrance was sometimes the first sign that Heriades was nesting. (In only three instances, the closure was not

Cell	Before	Oviposition	After	Oviposition	То	tals
number	Number	Average time	Number	Average time	Trips	Average time
l	7	7 <b>'</b> 33"	4	2' 29"	11	5' 32"
2	3	31 29"	4	2' 31"	7	2' 56"
3	8	5' 07"	1	21 4 <sup>1</sup> t"	9	4' 35"
4	6	4' 10"	4	3' 48"	10	<b>3'</b> 59"
5	20	5' 09"	5	2' 37"	25	4' 55"
6	6	5 <b>'</b> 09"	5	5' 09"	11	5' 09"
7	7	7 <b>'</b> 46"	2	2' 25"	9	6' 26"
Average	8.1	5' 29"	3.6	3' 06"	11.7	4  47"

Table 2. Resin foraging trips before and after oviposition.

preceded by cap base construction.) Taylor (1962) does not mention any similar phenomenon for <u>H</u>. <u>freygessneri</u>; for that species, the nest closure apparently is not begun until the nest is finally capped.

Cap base construction occurred any time from the first to the last day of nest construction. In one instance the cap base was even constructed before any pollen had been stored. In the example noted (Figure 11) the cap base was formed during the fourth day of construction. Bees occasionally were observed to add resin on successive days, increasing the size and extent of the cap base, but generally it was constructed in a single afternoon and remained unchanged until the nest was finally capped. Only once was a bee observed to remove resin from the cap base for use in a cell partition.

<u>Nest Closure</u>. Heriades began adding more resin to the cap base, first to one side of the bore, then to the other, until the resin plug became nearly flush with the entrance. In about half of the nests from both Michigan and Oregon, the bees stuffed sand grains, paint chips, dirt, slivers of wood, dried plant fragments, and other miscellaneous detritus into the nest entrance, sticking them to the outer surface of the resin cap plug. Often the fragment was larger than the bee and, after unsuccessful attempts at maneuvering, she abandoned it.

The materials were usually from the immediate vicinity, often debris which had accumulated in the crevices of the surface on which the nests rested. One bee made 26 consecutive detritus-collecting trips to the same crack 1.5 feet from the nest. On other occasions, bees were observed to enter an unused bore, grasp a projecting splinter with their mandibles, tear it loose, and transport it back to their nest. Sometimes after stuffing the end, the bee brought more resin and packed it around

the debris. The time occupied in nest closure ranged from about two hours to two or three days.

Stuffing the nest entrances with detritus has been noted for a variety of solitary Aculeata, and generally is considered a nest camouflage adaptation. This may well be the case for H. carinata also.

<u>Nest Defense</u>. The close proximity of the nest blocks, with the consequent nesting of several females in a small area, probably increased the number of intraspecific encounters. In some instances when two female <u>Heriades</u> returned to (or occasionally left from) their nests simultaneously, they scuffled briefly; usually these struggles were short and both bees immediately returned to their nests. Occasionally after such scuffles one or both bees showed reluctance to leave the nest, remaining inside for periods up to 45 minutes, the greater part of the time being spent poised just inside the entrance. Taylor (1962) notes similar behavior by H. freygessneri.

Sometimes a female searching for a nest site entered the nest of another <u>Heriades</u> and crawled down the bore, feeling with her antennae as she went. Upon touching the owner bee or cell provisions, the intruder rapidly backed out and flew to another nest. The owner bee usually seemed undisturbed and continued as though nothin had happened. In the only observed instance of <u>Heriades</u> entering the nest of another species, the behavior exhibited was essentially the same.

If the owner bee was away when the intruder entered and returned while the intruder was still in the nest, a struggle nearly always ensued. Only once was the owner observed to permit the intruder to leave its nest without a fight. In one instance involving marked bees, neither gave any ground at first, but soon the owner succeeded in
forcing the intruder down into the bore, badly disrupting and scattering the pollen. Then the owner backed nearly to the entrance and stopped; when the intruder, following close behind, backed into her, the owner's mandibles opened as though to bite the intruder's abdomen and in apparent response the intruder moved back down the bore. the owner then left the nest, permitting the intruder to exit, and immediately re-entered without giving further chase. Without hesitation she began to repair the damage and later that day completed the cell and capped the nest. The entire episode occurred within four minutes.

On another occasion a marked intruder bee blocked the entrance for 7 minutes, preventing the returning bee from entering until she finally rushed in, locked mandibles with the intruder, and dragged her out. This owner did not continue provisioning activities but rested at the entrance for over 16 minutes before reversing to unload her pollen; another 29 minutes elapsed before she finally left the nest.

Sometimes a distinctly audible buzzing sound was heard during these encounters, apparently emitted by both bees as they stood deadlocked midway along the bore. A very similar buzz can be induced when a bee is grasped tightly between the thumb and first finger.

<u>Nest Raiding and Supersedure</u>. A puzzling phenomenon noted in both Michigan and Oregon was the break-in and take-over of nests previously completed by <u>Heriades</u>. This usually occurred within one or two days after the nest was completed. Why the bees would raid nests of their own species when numerous nest sites are available is very perplexing. Malyshev (1936) noted this phenomenon when the bees were nesting in close proximity but suggested it might be due to senility in the participating bees. Fabre (1914), noting it in Osmia tricornis Latreille

suggested that the bees' ovaries were exhausted.

Twenty-four hours after the original female was collected from a finished nest in Oregon, a second female Heriades was discovered removing the nest cap piece by piece and sticking the pieces around the entrance (Figure 1). Usually she would bite off a small resin chunk, back up slightly, scrape her mandibles with her front legs, then pass the resin back to her hind legs and kick it off. Sometimes she carried the resin outside and deposited it on the nest face without the aid of her feet. After an aperature large enough to allow her body through was chewed out of the cap, she broke into the last cell and cleared out the egg and provisions. Following a night spent in the nest, she brought fresh pollen and remade the last cell; the next morning she capped the nest using both freshly obtained resin and old particles from the nest face. About twenty-four hours later, a third female was found breaking into the nest in the same manner. Five days later she finished restocking and recapping the nest. This raiding occurred during the peak of the nesting season, and the last cell contained a prepupa when opened so at least the third female was still producing viable eggs.

Another example of raiding was observed in Michigan shortly after the peak of the nesting season. One marked female, known to have constructed eleven cells, was found breaking into the outermost cell in a Saran-covered nest capped only an hour earlier. She destroyed the egg, laid another, and resealed the cell; then, before recapping, she constructed two more cells and began a third. The female was much slower in this than in previous nest building, requiring eleven days to complete this nest whereas in earlier nests she had averaged nearly two cells per day. The three eggs she laid were viable but the last cell, which

appeared nearly complete, contained no egg, suggesting that her ovaries may have become exhausted.

Nest raiding may also take the form of appropriation of incomplete nests from other <u>Heriades</u>. In one example involving marked bees in a Saran-covered nest, the original <u>Heriades</u> was provisioning the first cell at 2:30 p.m.; by 7:00 p.m., the first cell was complete and an egg laid, but a different bee (which had capped another nest earlier in the afternoon) was resting in the nest. This second bee completed six additional cells and capped the nest.

On other occasions, two bees, apparently owner and intruder, were noted deadlocked in nests. Often afterwards, the pollen in the last cell (in one case, last three cells) was in a pile below the nest entrance; subsequently, the cell was restocked and completed. Piles of pollen below nest entrances were noted on several occasions throughout the nesting season in both Oregon and Michigan, and whether each was the result of a nest takeover or struggle is uncertain.

Occasionally, nests were found which were begun by some other solitary bee or wasp and superseded by <u>Heriades</u>. Since this behavior was never observed, whether the original occupant abandoned the nest or was forced out by <u>Heriades</u> is unknown. None of the cells of the superseded nests appeared to have been first cleared out by <u>H</u>. <u>carinata</u>, although Taylor (1962) reports that this is usually the case for <u>H</u>. freygessneri when superseding Megachile gratiosa nests.

Superseded nests, the original occupants and number of cells completed by each are listed in Table 3. In four of the six Oregon usurpations, <u>Heriades</u> constructed no basal partition for her own series of cells. In the other two cases, she left a space, then constructed a

Table 3. Nest supersedure by <u>H</u>. carinata.

Nest	Original occupant	Number of cells by original occupant	Number of cells by <u>H. carinata</u>
Oregon:			
lllE	Hylaeus sp.	1 (inc.)	6
112E	Hylaeus sp.	3	5
112F	Hylaeus sp.	4	4
113C	Osmia (Chalcosmia) coerulescens (L.)	4	7
115E	Megachile (Chelostomo angelarum Cockerell	ides) 2	3
116G	<u>Osmia</u> ( <u>Nothosmia</u> ) sp.	2	6 (inc.)
Michigan:			
1501	Hylaeus sp.	2 (inc.)	l

resin plug before her cells. In the one Michigan case, <u>Heriades</u> deposited its pollen mass directly on the incomplete pollen mass which the original occupant deserted seven days earlier. This one case, at least, was clearly abandonment.

<u>Heriades'</u> chief competitor for 1/8 inch diameter bores in Michigan was a sphecid wasp, <u>Soleriella</u> sp. A quick and efficient nest builder, this wasp was able to complete two or three nests to every one of <u>Heriades</u>. Of lesser importance as competitors were bees of the genus <u>Hylaeus</u>. Only once was a nest of <u>Heriades</u> superseded, apparently by <u>Trypoxylon</u>. This nest contained five completed <u>Heriades</u> cells and some pollen in the bottom of a sixth; in this same cell were numerous spider remains (the prey used by <u>Trypoxylon</u>) and a Chrysidid parasite cocoon. A thin mud partition sealed cell six and served as the only nest cap, although it was quite far in from the entrance.

<u>Miscellaneous Behavior</u>. A notable feature of the behavior of some bees was the repeated return to nests which they had constructed previously. For nine days one marked bee returned several times daily to its first nest, although during this time she constructed two subsequent nests. These visits were short, the bee only hovering (or occasionally alighting) momentarily before returning to the nest currently under construction. These trips occurred only when returning to the nest from foraging trips, perhaps serving to orient the bee to its new nest. However, since this behavior did not occur after every foraging trip, it may have been the result of conditioning.

On several occasions, <u>Heriades</u> alighted on me to suck my perspiration, or crawled slowly about the surface of a recently handled nest block avidly licking the surface, apparently also for perspiration. This

behavior, which appeared to be initiated by chance discovery, often lasted for several minutes and provided an excellent opportunity to mark the bees. At one point, nearly half the bees nesting at site 3 had been marked in this manner.

<u>Period of Daily Activity</u>. On warm sunny days, <u>H. carinata</u> was active from early morning to late afternoon, beginning as early as 7:30 a.m. and ending about 7:00 p.m. Under less optimal conditions the period of daily activity was proportionately shortened. Apparently the bees exhibit a kind of circadien rhythm or diurnal periodicity, for bees kept in a cage in the laboratory were very active between 9 a.m. and 5 p.m. but at night showed no activity or response even though the lab lights burned late.

On overcast but mild days, the bees were still active, though not as early and sometimes only intermittently; strong wind had a very pronounced effect on flight control and undoubtedly decreased provisioning efficiency. When it rained the bees ceased activity entirely and remained in their nests.

Between June 23 and July 18, the rain fell on six days in 1963, compared with 15 days in 1964. Of the 19 nesting attempts for 1964, eight were incomplete and three of these contained dead females. Several of the other incomplete nests were abandoned during one of these rainy periods. The poor nesting in 1964 is probably attributable to the increased precipitation, for only two nests were begun after the very rainy first week in July.

Females constructing nests invariably spent the night just inside the nest entrance until nest capping when not enough space remained to permit them inside, when they often rested in a nearby empty bore.

Their "sleeping position" was head first in the bore, abdomen blocking the entrance (just inside the rim of resin when the cap base was present.) On rare occasions the bees were found reversed, with head facing out, but still just inside the entrance. <u>Heriades</u> was never observed to rest farther down inside the bore or to curl against the pollen mass. This "sleeping position" afforded an easy means of determining when a nest was occupied.

No field evidence regarding how males spent the night was obtained. Step (1932) reports finding males, and sometimes females, of a European species of <u>Heriades</u> curled in a ball asleep in a flower or clinging by their mandibles to a twig or grass stem. In cages, both males and females curled up, often in groups, in one of the corners of the cage. Although grass was present, it was not utilized.

Generally, all bees at a nest site became active within a period of about half an hour in the early morning, probably in response to temperature or a combination of temperature and light. The possible occurrence of an orientation flight was difficult to perceive, for the bee, being small and black, is difficult to follow and quickly disappears from view. Nest construction is immediately begun where it left off the previous afternoon.

At day's end, the bee simply ceases to leave the nest, often working down inside the bore for long periods after the last foraging trip. Usually her behavior gives no indication that activity is about to cease. On two occasions, however, a very striking and unusual behavior was noted. In both instances, the bee left its nest, alighted nearby, and stood motionless with antennae erect, as though sensing weather conditions. The bees remained in this position less than a minute, then returned

immediately to the nest. A short while later both were in the nocturnal resting position. Once, a very soft, rather high-pitched continuous buzz like the hum of a small motor was emitted by the bee during this behavior, although no motion was perceived. The motionless, antennae erect, position assumed by the bees was most striking, resembling no other aspect of the bees' behavior.

<u>Nest Structure</u>. The typical <u>H</u>. <u>carinata</u> nest (Figures 3 and 4) consists of a linear series of cells followed by an empty space (the vestibule cell) and the nest cap. Resin partitions 0.5 to 1.0 mm thick separate the cells. The freshly opened nest containing diapausing larvae is readily identified by the distinctive feces-covered cocoons, their associated operimenta, and the resin partitions.

Fischer (1955), noting the presence of a cellophane-like material covering the inner side of the cell partitions in a <u>H</u>. <u>variolosa</u> nest, termed it the cap support, presuming the mother bee constructed it prior to the cell partition. However, this study has revealed it to be secreted by the larva prior to cocoon spinning (see section on larval development) and in order to avoid confusion with the term "cap base" it is deemed best to reneme it the "operimentum".

The operimentum (Figure 5) appears as a thin hyaline cover extending inward from the partition around the bore about 1-3 mm and resembles the secretion used by <u>Hylaeus</u> to line their cells. Against the Saran, the operimentum is barely perceptable but is readily seen if the Saran is peeled away. Taylor (1962) notes no similar structure in nest of <u>H</u>. freygessneri.

The vestibule cell which usually characterized <u>H</u>. <u>carinata</u> nests was occasionally lacking; in these cases, the last cell partition was often

thickened like a normal nest cap. Of the 33 completed Oregon nests, 10 lacked the vestibule cell, while only 2 of the 56 completed Michigan nests did. In a few nests, two vestibule cells were found; in others varying amounts of pollen were stored in the bottom of the vestibule cell but no egg laid.

The resin used by <u>H</u>. <u>carinata</u> for partitions and nest cap was pure, and an outer ring of sand and soil such as reported for <u>H</u>. <u>variolosa</u> partitions (Fischer, 1955) was never present. Rarely, splinters of wood or other fragments were incorporated into the cell partitions. The resin source remained undiscovered, but two different types (oxblood-red and whitish-translucent) were used in the Michigan nests; 35 nests employed the reddish resin, 26 the whitish, and 9 were weak read, as though the resin were a mixture of the two. In general, the resin in a nest was consistently of one type or the other, but 6 nests contained resin of both colors. In the Oregon nests, the resin used was whitish-translucent throughout.

The nest caps, which are much thicker than the cell partitions, were consistently constructed more or less flush with the nest entrance by both populations. About half of those nests occupying the entire bore contained a plug of resin 0.5 to 6.0 mm thick at the inner end, probably a phenomenon of the irregular bottoms of the trap-nests, but perhaps a function of the time of day since the bees tended to carry resin exclusively in the late afternoon. Occasionally, nests did not utilize the entire bore; in these cases, a resin partition part way along the bore was first constructed as a base for the cell series.

The average number of provisioned cells per completed nest for the Oregon population was 6.4 (range 2-13) and for the Michigan population, both years combined, was 4.6 (range 1-10). Inversely related to this was

the average length of the vestibule cells, 47.9 mm (range 10.0-89.0 mm) in the Michigan nests (Figure 4) and 13.0 mm (range 4.5-55.0 mm) for the Oregon nests (Figure 3). Drawing meaningful conclusions on the basis of these figures alone is difficult since the bore lengths of the preferred 1/8 and 9/64 inch bores differed by 30 mm. However, more striking are comparisons of the average volumes of the provisioned cells and nest caps since they should not depend on bore length. Table 4 shows that the Oregon population constructed significantly larger cells and nest caps.

A possible explanation for the greater number of cells of larger size per nest in the Oregon nests is that more time was spent on cell construction by the Oregon bees. By dividing the total days spent in construction by the number of provisioned cells, a rough average of 2.7 days per cell in Oregon and 1.1 days per cell in Michigan is obtained. However, the time required for cell construction varied from a minimum of just under four hours to several days, and in one instance of bad weather over six days were required to complete one cell. Table 4. Comparison of volume (mm-in<sup>2</sup>) of provisioned cells and nest caps for Michigan and Oregon nests, using Student's t-test.

48 Michigan nests, 1/8 inch diameter bores, 243 provisioned cells. 24 Oregon nests, 9/64 inch diameter bores, 175 provisioned cells.

	Mean Oregon	Volumes Michigan	Popul <b>a</b> tion <u>mean</u>	t-value	
Provisioned cells	.1252	.1067	.1145	<b>8.3</b> 484**	
Nest cap	•0900	•0337	.0525	12.6556**	

## GROWTH AND DEVELOPMENT

<u>Techniques of Study</u>. Records of the developmental stages of <u>Heriades carinata</u> were taken primarily from Saran-covered nests which permitted ready, easy observation under as nearly normal conditions as possible with minimum disturbance to the cells. To enhance visibility, the Saran was often pulled back or removed during observations. This technique also lent itself nicely to photography of the various stages <u>in situ</u>. Some problems with mold were encountered, particularly with nests which had been exposed to heavy rain, but it could be checked by manual removal and temporary exposure of the nests to permit drying.

All developmental data were obtained at room temperature. Most larvae were observed once daily, so that timing accuracy for certain activities was not always precise. Gently dusting the larvae with dry pollen grains, thereby "marking" them, yielded the information on number and duration of larval stages.

The Egg. Deposited on the outer surface of the provisions (Figure 13), the egg is cream-colored, opaque, smooth and shiny. It is cylindrical, slightly curved with both ends uniformly rounded, and measures 2-2.3 mm long and 0.75 mm in diameter at the middle (Figure 15).

The incubation period is about 5 1/2 days. By 48 hours after deposition, the egg's cloudy contents pull away from both ends and become concentrated in the central portion. The ends become translucent and in the free end a faint internal constriction is evident. By 96 hours, the chorion becomes constricted at the same point, forming a distinct nipple which ultimately will become the larval head. Also at this time, segmentation

begins to appear. Regular pulsating movements originating at the attached end are evident along the length of the egg, and a more rapid localized throbbing can be seen in the head. By about 120 hours, the free end slumps downward until the egg lies at full length on the pollen (Figure 14). Determining exactly when the chorion is shed is difficult, but shortly after hatching the intestinal tract becomes yellow from the ingested pollen.

The Larva. The mature larva (Figure 18) is a legless whitish grub. Dull yellowish for the first day or two after hatching, it gradually becomes dull grayish-white and three to four days after hatching, small sub-cuticular white spots become evident through the integument. These remains throughout the feeding period of the larva, increasing in size to maturity, and are still apparent after pupation though they disappear soon after.

The number of larval instars was not definitely determined but there are at least four. Throughout the first two instars the larva remains attached to the pollen mass, little changed in position from the slumped egg. Probably as a result, the early larval development proceeds quite uniformly and it is easy to determine when a molt occurs. From the onset of defecation following the second molt to maturity the larva moves about considerably and the posterior portion of its body is no longer in contact with the pollen mass. There is considerable individual variability in the rate of development, and it becomes increasingly difficult to perceive molts even if the larva is dusted with pollen. Furthermore, there was some evidence that the later larval exuviae are eaten soon after ecdysis, while the earlier ones are not.

The first and second larval stadia are each about two days in duration. The length of the third and fourth stadia is less certain, appearing to vary greatly. The body and head setae become apparent for the first time after the second molt. Defecation begins within one or two days after the second molt, or an average of about 6 days (range 4-11) after hatching. Grandi (1934) mentions that defecation in a European species of <u>Heriades</u> began five days after hatching. The brownish-yellow feces are cylindrical, slightly curved, firm and quite uniform, approximately 0.75 mm long and 0.25 mm wide. The first produced are slightly smaller and often pointed at one end. Occasionally, a longer spiraled excrement having two or three coils was found. At the onset of defecation usually less than half the pollen mass had been consumed. The feces are produced c opiously throughout the remainder of larval development, ceasing about midway through the cocoon spinning.

At an average of 14 days after hatching (range 9-22) or about 7 1/2 days after the onset of defecation, the larva halts feeding temporarily, reverses itself, and spins the operimentum. Although this unique structure was usually recognizable after one day's spinning, often the larva returned to it intermittently on subsequent days, adding noticeably to it until feeding was completed. Other times no further work was observed after the original construction. When the operimentum is spun, approximately 1-2 mm of pollen remain to be consumed; after it is spun, the larva resumes feeding.

The operimentum is probably spun during the fourth instar stage but the data are inconclusive. Apparent third molts have been noted for a few larvae following the onset of defecation, but before operimentum construction, between two and nine days after the second molt was recorded.

Cocoon construction is initiated by the mature larva an average of 25 days (range 15-33) after egg hatching; the pollen mass was usually completely consumed but not infrequently some pollen was left untouched and the cocoon constructed above it. The transition from feeding to cocoon construction was not abrupt; random threads crisscrossing the cell usually appeared a few days before feeding terminated.

The cocoons (Figure 6) are cylindrical with rounded ends, lacking any conspicuous nipple on the anterior end as found in many Megachilidae. The cocoon, thin and flexible, semi-opaque with a shiny glazed appearance, is embedded in a matrix of loose threads to which the feces adhere uniformly. The texture of the <u>H</u>. <u>carinata</u> cocoon, unlike <u>H</u>. <u>variolosa</u> (Fischer, 1955), is very similar to that of the operimentum, resembling crinkled cellophane. It does not appear to be composed of layers of different thicknesses and texture; neither is the cocoon impregnated with any liquids to give it color or rigidity as with other megachilids, including its parasite <u>Stelis vernalis</u>. When the cocoon does not fill the entire cell, its posterior end is against the innermost partition, leaving between the anterior end and the outer partition a small space sparsely criss-crossed with threads attaching the cocoon to the operimentum and cell walls.

The feces become intertwined into a mass at either end of the cell through a sort of net spun over them in the first stages of cocoon construction. The material used is exuded continuously from the salivary slit; as the larva moves about, the pellets are caught up, dragged along, and pulled up into new positions where subsequent strands secure them firmly to the matrix and cocoon. The continual twisting and turning of the larval body thus distributes the feces more or less uniformly over the outer surface of the cocoon.

To determine when defecation ceased and to see what effect lack of feces and operimentum would have on cocoon construction and larval orientation, larvae in various stages of cocoon construction were transferred to empty cells where they subsequently began new cocoons. Few larvae were available, but some inferences may be drawn. In one instance, a larva was placed in a cleared Heriades-made cell after its feeding had ceased but prior to discernable cocoon spinning; by one day later, the larva had enclosed itself in a flimsy cocoon and between 30 and 40 fecal pellets had been passed. At this point the cell was again completely cleared and the naked larva replaced; twenty-four hours later, another flimsy cocoon had been spun in about the same position as the first, but very few fecal pellets had been passed. The cocoon was then allowed to go to completion; though lacking the feces blanket, it otherwise appeared identical to the normal cocoon and the larva was correctly oriented. Most other larval transplants showed similar results. However, in one instance the larva constructed operimenta which coated the inner side of both partitions. The cocoon was constructed in the center of the cell with 1-2 mm between the ends of the cocoon and the cell partitions. However, the larva was correctly oriented.

Misoriented larvae are so rare that correct orientation cannot be explained solely on the basis of chance. However, the partitions between the cells are of amorphous resin with no concave or convex sides like the mud partitions shown by Cooper (1957) to be the cue to the larval orientation for certain Eumenine wasps. The operimentum, constructed by the <u>Heriades</u> larva while the pollen remains in the bottom of the cell, covers the inner side of the only exposed cell partition, the one capping the cell. When the operimentum covered the inner sides of both partitions,

the cocoon was not situated against either partition but about equidistant from each; furthermore, when the cocoon does not fill the cell, the space between the anterior end of the cocoon and the cell cap is invariably left. Therefore, it seems logical to postulate that the operimentum serves as a vital cue to the larva in cocoon positioning and orientation.

Cocoons were completed in an average of seven days (range 3-11) after feeding terminated. Following cocoon completion, the larvae lay motionless for up to 24 hours; during this time, no spinning was done but the mandibles would open and close in response to probing. Then, transformation to the prepupal position occurred, the larva's anterior end bending back upon itself and the larva assuming a hooked or C-position (Figure 7). No molt accompanies this transformation, and the prepupa no longer shows any response to probing.

The total period of larval development averaged 30 days (range 20-41 days); thus, by the second week of August in Michigan, the last <u>H. carinata</u> larvae were in the prepupal overwintering stage. It is of note that H. freygessneri overwinters in the pupal stage (Taylor, 1962).

Description of Mature Larva. Illustrations and techniques used follow the system of Michener (1953). The larva closely resembles <u>H</u>. <u>crenulatus</u> Nylander, described by Grandi (1934), except for the lack of atrial teeth and mandibular serrations. Most of the larval characters are in agreement with those of the Anthidiini, especially the mandibular serrations. The presence of labral papillae has also been noted in Hoplitus and Stelis (Michener, 1953).

Body (Figure 18) non-pigmented, with abundant setae; posterior end swollen, tapered anteriorly. Thoracic and anterior abdominal segments

dorsally divided into cephalic and caudal annulets; other segments less distinctly divided. Ventrolateral swellings absent or only feebly present. Spiracular atria (Figure 23) projecting slightly above integument, lacking spines or teeth but bearing a few internal ridges; primary tracheal opening large with thickened collar.

Head capsule (Figures 19 and 20) with scattered setae, nonpigmented except for mandible tips; marginal thickening distinct. Antennal papillae on slight prominences, more than twice as long as broad with three smaller peg-like papillae at apex. Labro-clypeal suture moderately arched, weakened medially, appearing wrinkled; epistomal suture indistinct. Labrum strongly emarginate at apex, bearing row of 6 or 7 minute peg-like papillae along apical margin, extending laterally in irregular rows of 7 or 8 on each side. Mandibles (Figures 21 and 22) bidentate, margin of inner tooth with minute blunt serrations; teeth acute, inner half as long as outer. Inner apical concavity distinct, delimited by well-defined transverse ridge. Maxillary and labial palpi similar and distinct, twice as long as broad, each with 2 smaller peg-like papillae at apex; maxillary palpi pre-apical. Salivary opening transverse, strongly protuberant with long narrow lips. Tentorium complete but tentorial bridge weak medially.

<u>Post-diapause Development</u>. In nests kept outside over the 1963-64 winter, pupation began May 20, the first adults emerging on June 23; thus the post-pupation development in 1964 required about 35 days under natural conditions. This compared with 22 days for laboratory-reared individuals. No post-diapause developmental data for the Oregon population was obtained. The pupal period of <u>H. freygessneri</u> (Taylor, 1962) varied from 22 to 138 days.

Much information on post-diapause development was obtained from prepupae removed from their cocoons and reared in small gelatin capsules, a method allowing more accurate comparative information on development rates between sexes and within cell series. Observations were made but once daily, and so do not account for slight timing differences. Table 5 summarizes the comparative post-diapause development of six males and fifteen females; the progressive stages of development listed are somewhat arbitrary but easily distinguished.

Just prior to pupation the prepupa elongates; its body contents shrink away from the anterior end and a molt occurs. The newly formed pupa (Figure 8) is white and glistening. Four to five days after pupation the eyes and ocelli turn a light cinnamon brown, becoming progressively darker to dark chocolate; at this point, the remainder of the body begins to darken. The first body pigmentation appears as faint gray areas in the head, thorax, and apical portions of the abdominal terga, giving the abdomen a ringed appearance. Darkening to black proceeds gradually throughout the body, the extremities of the legs, mouthparts, and antennae being the last. Soon, the legs and antennae become free from the body and respond to probing. Next, another molt occurs, accompanied by expansion of the wings; after a three day hardening period the adult chevs out of the cocoon.

The data in Table 5 indicate that post-diapause development proceeded slightly faster throughout for males, with the cumulative effect that males averaged five days earlier emergence than females. Because of individual variation, however, the first male to emerge preceeded the first female by only two days.

Two general observations on emergence order within single nests have

Table	<u>5</u> •	Post-diapau	ise (	develop	oment	for	Michiga	n <u>F</u>	<u>I</u> .	carinat	8
	re	efrigerated	115	d <b>a</b> ys,	then	m <b>a</b> ir	ntained	at	72'	°F.	

Nest, Cell, & Sex	Pup <b>a</b> tion occurs	Eye pigment begins	Body pigment begins	Body wholly black	Wings expand	Adult emerges	Total days	
Nest 1 1 - 3 - 4 - 5 - 6 -	18 14 13 16 13	6 4 5 + 5	- 9 8 7	- 3 3 4	14 14 14	- 4 3 3	41 39 37 37	
Nest 2 1 - 2 -	13 13	5 5	7 7	կ կ	կ կ	3 3	37 37	
Nest 3 1 - 2 - 3 -	12 12 12		- - -	) <sub>4</sub> + 3	4 5	3 3	37 36	
Nest <sup>1</sup> 4 2 -	18	6	8	4	3	3	43	
Nest 5 2 - 3 -	14 14	հ հ	8 7	5 4	2 2	3 3	37 35	
Nest 6 1 - 3 -	15 13	3 +	10	4	4	2	39	
Nest 7 1 - 2 - 3 - 4 - 6 -	12 12 12 12 12	5 5 5 5 5 5	8 8 6 5 5	+ 4 5 5 5	3 2 3 2	4 3 3 3	37 33 33 33	
Nest 8 4 <b>-</b>	12	4	6	6	2	2	33	

Days from previous stage

+ died

- inaccurate timing

been repeatedly noted in the literature --- males tend to emerge sooner than females, and the adults closest to the nest entrance tend to emerge first, although they are chronologically younger. Data in Table 5 further substantiate these findings. Many investigators have also noted a relationship between sex and position in the cell series, with males more commonly reared from the last-constructed cells. Data in Table 6 generally support this relationship, although exceptions occur. For example, in four nests, female cells were interspersed among male cells, and in one six-celled nest males occupied only the three innermost contained only males. The largest nest exhibited an alternation of sexes as follows: Cells 1-4, females; cells 5-7, males; cells 8-11, females; cells 12 and 13, males.

The rearing data are summarized in Table 7. The variation in sex ratio from year to year is worth noting. In Oregon in 1962 the sex ratio was nearly 2 °: 1 o, while in Michigan in 1963 the ratio was almost 3 o: 1 °. In 1964 the order was again reversed, over 2 °: 1 o. The low rearing success may have affected the sex ratio; however, the Oregon cells infested by the chalcid <u>Mellitobia chalybii</u> Ashmead (laboratory contamination) and the mold-ruined Michigan cells probably were affected at random. It seems unlikely that the sex ratio would be greatly changed had these events not occurred. Mortality rates in nature probably approach the same level.

<u>Table 6.</u> Combined records of sex and position in cell series

for all reared <u>H</u>. <u>carinata</u>, Michigan and Oregon.

Sex	<u>1</u>	5 Ce	ell nu <u>3</u>	umber <u>4</u>	from <u>5</u>	base <u>6</u>	to cap <u>7</u>	8	<u>9</u>	<u>10</u>	Totals
00	5	11	18	13	17	11	8	3	0	1	87
00	28	21	16	10	10	8	2	2	1	1	99

Table	7.	Rearing	data	for	<u>H</u> .	<u>carinata</u>	from	55	Oregon
	and	1 77 Mich	nig <b>an</b>	nest	s.				

	0regon 1762	Mich 1963	igan 1764	Percentage
Cells unsuitable for rearing				
Empty	• 5	8	3	3.3%
Molded	2	86	5	19.0%
Cells with unsuccessful rearing				
Egg not laid or failed to hatch	53	32	7	18.8%
Immature died, natural mortality	65	17	10	18.8%
Immature accidentally killed	17	19	15	+
Cells with successful rearing				
<u>H. carinata</u> males	41	42	6	18.2%
<u>H. carinata</u> females	70	15	15	20.4%
<u>Melittobia</u> <u>chalybii</u> Ashmead (Eulophidae)	46	0	0	+
<u>Stelis</u> vernalis Mitchell (Megachilidae)	0	5	1	1.2%
Sapyga louisi Krombein (Sapygidae)	0	2	0	0.4%

+cells not included in percentage analysis

## PARASITES

Table 7 lists the parasites reared in both Michigan and Oregon. The absence of natural parasitism of <u>Heriades</u> in Oregon is puzzling; numerous chrysidids, <u>Coelioxys</u>, <u>Anthrax</u>, and a few meloid beetles were reared from trap-nests containing other solitary Aculeata at the same locations. Forty-six Oregon cells contained <u>Melittobia chalybii</u> Ashmead; however, these records represent laboratory contamination, the small wasps entering the glass tubes through the gauze covers and ovipositing in the developing pupae. As many as 249 (239 <sup>00</sup>, 10 oo) adults were reared from a single parasitized nest. A common parasite of twig-nesting Aculeata, this small chalcid has been reported by several investigators to infest rearing chambers. Its biology is treated in detail by Buckell (1928).

Because of rearing mortality, more parasitism in Michigan was observed than indicated in Table 7. In 1963, at least nine cells were parasitized by <u>Sapyga</u> and 7 by <u>Stelis</u>: one cell contained an egg of both of these parasites, but the <u>Sapyga</u> egg failed to hatch. In 1964, 3 cells were known to be parasitized by Stelis but none by Sapyga.

Attempted parasitism by the large chalcoid wasp <u>Leucospis affinis</u> Say was observed in three completed nests in 1963; however, mold destroyed the nest contents. Medler (1958), reporting successful parasitism by <u>L. affinis</u> only from trap-nests in sumac twigs, suggests that a maximum thickness of wood exists through which the species can oviposit. It seems possible that the <u>Heriades</u> trap-nests were too thick for successful oviposition.

H. carinata represents the first host record for Stelis vernalis

Mitchell; furthermore, this apparently is also the first <u>Heriades</u> host record for any New World species of <u>Stelis</u>. <u>Stelis minima</u> Schenck and <u>S. pygmaea</u> Schenck have been recorded for the European species <u>H. campanularum</u> (Kirby) and <u>H. truncorum</u> (L.) respectively (Friese, 1923). Of reared <u>S. vernalis</u>, 5 were female and 1 male; only one nest contained more than one cell parasitized by this species.

The behavior observed for S. vernalis adults and larvae parallels that reported by Michener (1955) for Stelis lateralis; some additional behavioral observations facilitated by the Saran-covered nests seem worth noting. In one instance, Stelis repeatedly was observed in the vicinity. Then, after a Heriades female had accumulated a nearly complete pollen mass, a Stelis entered the nest while Heriades was out and burrowed along one wall of the cell almost to the bottom of the pollen mass. When the Heriades returned and encountered the Stelis, she backed out and flew off without unloading her pollen. The parasite, apparently undisturbed, continued excavation, then backed out of the nest, re-entered abdomen first, and oviposited quickly (5 seconds duration) at the bottom of the cavity in the pollen mass. She then crawled out, re-entered head first, and within less than one minute replaced the pollen she had removed, completely covering the egg. Heriades returned shortly, still laden with pollen, and entered. Apparently something seemed amiss, for an extremely long time (13'50") was spent chewing at the pollen before she finally unloaded her scopa. After this, she remained resting inside 7 minutes, then commenced constructing the resin partition rim and completed the cell in the normal manner.

In one rearing observed daily, <u>Stelis</u> completed its development without feeding on the nost, because the Heriades egg was preserved

before the <u>Stelis</u> was discovered in the pollen mass. Thus, when the <u>Stelis</u> egg hatched in relation to its host is unknown: however, the larva was first discovered six days after the cell was completed, and was probably second instar at that time. Although smaller, less robust, and with fewer sub-cuticular white spots, the <u>Stelis</u> larva appeared otherwise quite similar to <u>Heriades</u>. The <u>Stelis</u> larva began to defecate six days later. It fed for 19 days, at which time nearly all of the pollen was consumed. Cocoon construction required four days; cocoon structure and method of construction match that described for <u>S</u>. <u>lateralis</u> (Michener, 1955). The <u>Heriades</u> larvae in the same nest lagged 4-7 days behind in their development. Post-diapause development could not be observed due to the opacity of the cocoon, but emergence was two days later than Heriades of the same nest.

<u>Heriades carinata</u> is the first host record for <u>Sapyga louisi</u> Krombein although various species of Sapygidae are known to parasitize other <u>Heriades</u> from Europe and Africa as well as other megachilid genera (Pate, 1947). Individuals of <u>S. louisi</u> were seen repeatedly about one nest site in 1963, all their parasitism occurring there after the first of July and continuing through the remainder of the nesting season. Nest parasitism was observed twice, neither instance in a Saran-covered nest; in both, the female was first observed searching along a row of nest blocks, hovering momentarily at nearly every hole and occasionally entering one. Finally, she entered an occupied nest head first, quickly reappeared, turned around, and backed in abdomen first, probably ovipositing. After oviposition, the female did not re-enter head first as did <u>Stelis</u>, but simply flew off. The total time inside the nest was about 15 seconds in both instances.

Apparently there is only a limited period during which <u>Sapyga</u> can or will parasitize a cell. In four parasitized cells, the <u>Sapyga</u> egg was attached to the <u>Heriades</u> egg (Figure 17). In another instance, a <u>Sapyga</u> egg was deposited on the Saran Wrap. In no case were <u>Sapyga</u> eggs ever found in or on the pollen mass. Furthermore, in some instances the parasite was observed to enter occupied nests but leave without turning around for oviposition. Thus, it would seem that those <u>Heriades</u> which complete the cell partition by remolding the resin brought prior to oviposition would have a distinct advantage in avoiding this parasite.

Three of the five nests parasitized by <u>S</u>. <u>louisi</u> contained more than one parasitized cell, suggesting that this parasite may learn to recognize certain nests and return to them repeatedly. This type of behavior, resulting in a high percentage of parasitism in some nests and complete absence in others, has been noted by several investigators for parasites of non-gregarious bees.

The egg of <u>Sapyga louisi</u> (Figure 16) is slightly smaller than the <u>Heriades</u> egg, measuring 1.5 mm long and 0.25 mm wide at the center. Cloudy white, it is smooth, very slightly curved, tapering posteriorly to a blunt point and rounded at the anterior end. The egg has a translucent area at the posterior end, and a cement-like material attaches the posterior half to the substrate, with the anterior end left free (Figure 17). Hatching occurs two days after oviposition.

In the first stage larva, segmentation is very apparent; the head is distinct with prominent sickle-shaped mandibles. Shortly after hatching, the larva positions itself full length along the <u>Heriades</u> egg, punctures it, and sucks out the contents. A molt then occurs and the larva subsequently devours the pollen provisions; after an undetermined number of

larval stadia, <u>Sapyga</u> spins a cocoon, requiring 3-4 days to complete this task. With the first molt the sickle-shaped mandibles are lost, and throughout the remainder of its development the larva closely resembles the Heriades larva except for the absence of body setae. The <u>Sapyga</u> larva begins defecating fecal pellets from 7-9 days after hatching continuing until cocoon spinning. Larval development and cocoon spinning for Sapyga were completed 7-10 days sooner than Heriades of the same nest.

The thin and flimsy cocoon is an opaque sating white; it consists of two layers, quite similar in texture and appearance and difficult to separate. The cocoon does not appear to be impregnated with any fluid; a few feces are distributed intermittently over its outer surface and incorporated into it. The cocoon is snug to the base of the cell, with a space usually left between its anterior end and the cell partition.

The post-diapause development of the two reared S. <u>louisi</u>, both kept outside over the winter, was considerably slower than that of <u>Heriades</u>. A male and a female S. <u>louisi</u> were reared; the male pupated 18 days after the <u>Heriades</u> in the same nest had emerged, and remained in the pupal stage for 16 days, thus following the <u>Heriades</u> emergence by 34 days. The female pupated 7 days later than the male, but remained in the pupal stage for 40 days, thus emerging 62 days after the <u>Heriades</u> in the same nest. On the basis of this information it would seem that <u>S. louisi</u> is not a very successful parasite of <u>Heriades</u> in nature, except perhaps in the lowermost cells, for otherwise the diapausing prepupae would be destroyed during emergence of the nost.

Other parasites of <u>Heriades</u> recorded in the literature are <u>Chrysis</u> (Tetrachrysis) laetabilis Buysson (Chrysididae) and Anthrax triatomus Hesse

(Bombyliidae), both parasitic on <u>H</u>. <u>freygessneri</u> (Taylor, 1962), and <u>Anthrax aethiops</u> Fabricus on <u>H</u>. <u>truncorum</u> (Laboulbene, 1873). Höppner (1904) lists <u>H</u>. <u>truncorum</u> and <u>H</u>. <u>florisomnis</u> (L.) as hosts of <u>Gasteruption jaculator</u> L. (Gasteruptionidae). Grandi (1934) records <u>Melittobia acasta</u> (Walker) (Eulophidae) from a nest of <u>Heriades</u> in Europe.

## SUMMARY AND DISCUSSION

<u>Heriades carinata</u> is considered of little importance as a crop pollinator; however, knowledge of the details of its life history is particularly significant, not only because it helps to fill existing lacunae but because it may point the direction to further fruitful study.

The significance of the early cap base construction is interesting to speculate upon, for, neither blocking nor concealing the nest entrance, it is probably of little importance as a parasite preventative. Perhaps it is a phenomenon of the late afternoon resin-carrying tendency, depposited at the entrance for lack of another suitable place, but it may help to prevent nest flooding under natural conditions.

Another interesting phenomenon is the operimentum construction; especially significant are the facts that the larva stops to construct the operimentum before completing its development, and that the cocoon, when filling less than the entire cell, always is against the opposite partition. These suggest that the operimentum is a significant clue to correct larval orientation. It is strange, in view of its obvious selective importance, that the whole problem of larval orientation in solitary twig-nesting bees has been largely ignored.

Differences in nest structure, adult behavior, and period of seasonal activity are striking between the Michigan and Oregon populations. Since <u>H</u>. <u>carinata</u> occurs throughout much of North America, additional study and biological data from other localities, along with a thorough study of morphological variability, might suggest sufficient criteria for distinguishing one or more subspecies. Because the species so readily accepts trap-nests, biological data would not be difficult to obtain. Rearing under carefully controlled environmental conditions and breeding experiments between populations might provide enlightening clues as to the extent of genetic divergence present.

The phenomenon of nest-raiding is also worthy of further investigation; perhaps this type of behavior is somehow related to the development of the parasitic habit, which has apparently arisen independently in the various phyletic lines of the Megachilidae.

Further investigation on flower relationships in different localities is sorely needed. It seems unlikely that <u>H</u>. <u>carinata</u> is ever solely oligolectic; rather it probably exhibits a decided preference for a particular type of pollen as long as it remains abundant. Knowledge of the kinds of resin utilized and the manner in which resin is obtained would also be valuabe.

The complete absence in the trap-nests of <u>Heriades variolosa</u>, the other wide-ranging species of <u>Heriades</u> in North America, is of note; this fact suggests that it occupies a different ecological habitat. Additional biological information for this species would be valuable, especially since it is in a different subgenus than H. carinata.

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Figures 1-8. 1, <u>H</u>. <u>carinata</u> breaking through recently completed nest cap (Note resin particles on nest face); 2, nesting habitat at target range, site 4 at right, site 3 at left background; 3, Oregon nest of <u>H</u>. <u>carinata</u>, freshly split; 4, same from Michigan in Saran-covered bore; 5, Operimentum (arrow), larva removed; 6, typical <u>H</u>. <u>carinata</u> cocoons; 7, prepupa of <u>H</u>. <u>carinata</u> in Saran-covered cell, head at right; 8, pupa of <u>H</u>. <u>carinata</u>.





NUMBER OF ACTIVE NESTS

Figure 11. Five-day arrival and departure records for female

H. carinata constructing single 7-celled nest.

Spaces between rectangles indicate time inside nest. Rectangles indicate time away from nest; stippled represent pollen foraging trips, solid represent trips for resin. Open rectangles indicate female returned with nothing; unshaded ends of rectangles indicate inaccurate timing. "E" indicates oviposition time.


59

Figures 12-17. 12, Placement of successive loads of resin brought prior to oviposition; 13, position of freshly laid egg of <u>H</u>. <u>carinata</u> on pollen; 14, slumped position of egg immediately prior to hatching: 15, egg of <u>H</u>. <u>carinata</u>; 16, egg of <u>Sapyga louisi</u>; 17, position and method of attachment of <u>S</u>. <u>louisi</u> egg on host egg.

60















Figures 18-23. 18, <u>Heriades carinata</u>, mature larva; 19,20, dorsal and lateral views of head of same; 21, 22, inner and ventral views of mandibles of same; 23, spiracle of same.