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Specialization, Foraging Efficiency and Nutritional Relationships in a Solitary Bee, <u>Heriades carinata</u> Cresson (Hymenoptera: Megachilidae)

presented by

Jonathon Michael DeNike

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# SPECIALIZATION, FORAGING EFFICIENCY, AND NUTRITIONAL RELATIONSHIPS IN A SOLITARY BEE, <u>HERIADES</u> <u>CARINATA</u> CRESSON (HYMENOPTERA: MEGACHILIDAE)

By

Jonathon Michael DeNike

## A THESIS

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

## MASTER OF SCIENCE

Department of Entomology

### ABSTRACT

# SPECIALIZATION, FORAGING EFFICIENCY AND NUTRITIONAL RELATIONSHIPS IN A SOLITARY BEE, HERIADES CARINATA CRESSON (HYMENOPTERA: MEGACHILIDAE)

By

Jonathon Michael DeNike

Pollen foraging preferences of <u>Heriades carinata</u> Cresson were investigated by trap nesting in field sites near Pellston, Michigan during the summers of 1988-1990. During the peak of the nesting season, females of <u>H. carinata</u> provisioned exclusively with pollen from <u>Rhus typhina</u> L. (Anacardiaceae). The flight season of <u>H. carinata</u> was synchronized with the flowering of <u>Rhus</u>, and nesting activity by <u>H. carinata</u> was only found in study sites containing <u>Rhus</u>. <u>H. carinata</u> is at least regionally specialized on <u>Rhus</u> and may be oligolectic on this plant genus.

Timed flights of <u>H. carinata</u> females foraging for <u>Rhus</u> pollen were not different from those foraging from other plants. Survival by offspring of <u>H. carinata</u> to adulthood was higher on provisions consisting of <u>Rhus</u> pollen than on other pollens.

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#### INTRODUCTION

# Biology of <u>Heriades carinata</u> and <u>Rhus typhina</u>.

Heriades carinata Cresson is a small megachilid occurring throughout much of North America (Mitchell 1962, Matthews 1965). Two other species of the genus occur in eastern North America (Mitchell 1962). The biology of H. carinata was studied by Matthews (1965). Females of this bee nest in pre-existing holes of approximately 3-5 mm inside diameter, usually in hollow twigs, and will readily accept trap nests of the appropriate size as nesting sites, making it a convenient animal for study. After a female has chosen a nest hole, she constructs a linear series of cells, divided by partitions constructed of plant resins. Within each cell, the female places a ball of pollen mixed with nectar, obtained from multiple foraging flights. Once the appropriate amount of pollen is in place, an egg is laid on the food mass, the cell is sealed, and construction and provisioning of the next cell proceeds. Larvae feed for an average of 30 days before molting to a prepupa. As this species is univoltine, this stage will overwinter; pupation occurs in spring. Adult bees emerge in early summer; mating occurs, and females begin to construct nests throughout the rest of the summer, while males do not participate in nesting activities. Females may live up to a month

or longer, while males live to a maximum age of around 12 days.

Matthews (1965) found that the pollen in his trap nests in the vicinity of Kellogg Biological Station near Battle Creek, Michigan during the peak of the nesting season was almost exclusively from staghorn sumac (Rhus typhina L.: Anacardiaceae). Adult emergence of this bee also corresponded well with the beginning of the blooming period for staghorn sumac. R. typhina grows as a tall shrub or small tree, often in thickets; other members of the genus exhibit similar growth forms, although some may be more prostrate or vine-like (Barkley 1937). R. typhina is dioecious; the inflorescences are terminal, usually several per plant, and densely crowded with hundreds of small (about 5 mm in diameter) flowers, presenting an obvious target for pollen- and nectar-seeking insects. As this plant is usually abundant in those open field habitats where it occurs, it provides an extremely important source of nectar and pollen when in bloom, which is usually 2-3 weeks in a given habitat. This plant can be considered a "cornucopian species" in the sense of Mosquin (1971) in that it provides an extremely abundant source of pollen and nectar and is attractive to several orders of insects. including a diverse assemblage of Hymenoptera, Diptera, Lepidoptera and Coleoptera.

**Specialization and Oligolecty.** Many insects exhibit specialization in their foraging, in contrast to generalists which exhibit a broad range of acceptable food choices. Trophic relationships between specialists and their preferred food

sources can be very intricate and dynamic, and can vary considerably in degree of specificity. Many of these relationships can impact the overall ecology of the local ecosystems by regulating populations of their food organisms, either through predatory/parasitic interactions or by assisting in propagation by dispersal of seeds or pollination (Prescott and Allen 1986).

Trophic relationships of specialists may be a driving force in speciation of both insects and host plants (Ehrlich and Raven 1964, Cruden 1972, Cane and Eickwort in press). Many pest insects are specialists, having both cued in on the characteristics and overcome the defenses of their host organisms (Fraenkel 1959, Price 1984). Understanding foraging specialization in insects is thus an important area of study for both basic and applied research. Solitary bees (Apoidea) are a group of insects that contains examples of all degrees of foraging specialization, including opposite extremes within genera. Studying foraging relationships of solitary bees is not only important in an evolutionary sense (Cane and Eickwort in press), but also in agriculture, where these bees are being increasingly used for crop pollination (Bohart 1972, Torchio 1976, 1981, 1990a, b).

Overall, most solitary bee species (64.1%) exhibit oligolecty, or pollen specialization (Hurd 1979, Schemske 1983). Oligoleges are generally distinguished from polyleges (bees that do not specialize in pollen foraging) in that the former confine the bulk (if not all) of their pollen foraging to a single plant family across their entire range (and in the presence of other

pollen sources), whereas polyleges will collect pollen from plants in more than one family, without demonstrating consistent preferences across their range (Linsley 1958, Thorp 1979, Eickwort and Ginsberg 1980). These categories have no sharp distinction, as the pollen foraging habits of solitary bees form a continuum from monolecty (exclusive use of a single plant species for pollen) to broad polylecty (use of many plants in different families for pollen) (Eickwort and Ginsberg 1980).

This issue is further confused by local specialization of polyleges on highly abundant sources of pollen (Torchio 1976, 1981, Johnson 1984, Cripps and Rust 1989, Rust 1990). Even in broadly polylectic species such as the social Apidae, individual bees often exhibit floral constancy, foraging consistently from a particular plant species and bypassing others (Grant 1950, Waser 1986). Cane and Payne (1988) base their decision that <u>Habropoda</u> <u>laboriosa</u> (F.) (Anthophoridae) is oligolectic on blueberries (<u>Vaccinium</u> spp.) on criteria including visitation rates, floral handling behaviors and efficiencies, pollen provisioning, and phenology in relation to the host plants.

Some families contain more specialists than others. In the Andrenidae, 83% of the species studied are oligolectic, while the Megachilidae appears to contain the lowest proportion of oligolectic species at 43% (Hurd 1979, Schemske 1983). The degree of specialization is also variable: 15.3% of all solitary bees studied specialize on pollen at the species level; 36.6% show preferences for plants at the generic level; and 12.2% confine

their pollen foraging to a single family of plants (Hurd 1979, Schemske 1983).

Examples of bees that forage only from a single plant species and refuse all other sources of pollen include species such as <u>Hoplitis anthocopoides</u> (Schneck) (Megachilidae) which refused to forage on all plants other than its preferred host, Echium vulgare (Boraginaceae), in an experimental study (Strickler 1979), and Evvlaeus galpinsiae Cockerell (Halictidae) which did not forage during a year when its host plant, Oenothera pallida (Onagraceae), did not flower (Bohart and Youssef 1976). Other bees considered oligolectic will gather pollen from other plant species only when their preferred host is not in bloom, as does Andrena ervthronii Robertson (Andrenidae); this bee gathers pollen from <u>Quercus</u> (Fagaceae) as well as other plants after its preferred host, Ervthronium (Liliaceae), wilts (Michener and Rettenmeyer 1956). Cruden (1972) discusses three species of Andrena oligolectic on Nemophila (Hydrophyllaceae) that will, in times of low host plant abundance, forage on other genera of the Hydrophyllaceae or members of other plant families . Thorp (1969) cites other examples and advances the idea that collecting pollen from non-host plants is adaptive for survival of oligoleges during periods of low host plant availability.

**Nectar Foraging.** Many, if not most, oligolectic bees will also forage on plants other than their host for nectar (Linsley 1958, Eickwort and Ginsberg 1980). Although nectar is more complex in composition than merely an aqueous solution of sugars

(Baker and Baker 1975), this composition is not as variable between plant species as pollen (Cane and Eickwort in press) and thus probably does not have as important an effect on the nutrition of the bee. Nectar is primarily used as adult flight fuel (and also in larval provisions to a varying extent), whereas pollen is the primary protein source for growing larvae.

In many bees, assumptions of polylecty are based upon flower records (Krombein et al 1979) which may in fact be nectar foraging (Cane and Eickwort in press). Pollen preferences can only be determined with certainty by examining pollen carried by females, provisioned in nests, or in larval feces (Johnson 1984). Foraging for nectar on non-host plants by oligoleges may lead to "contamination" of otherwise pure host pollen loads with small percentages of non-host pollen (Cripps and Rust 1989, Rust 1990, Cane and Eickwort in press).

**Evolution of Oligolecty.** The evolution of oligolecty in solitary bees has been a subject of debate for a long time. Robertson (1914, 1929a) proposed that oligolecty evolved as an adaptation to reduce competition by partitioning the pollen resources, believed to be limiting, amongst many non-overlapping specialists. This view was questioned by Lovell (1914, 1918), who speculated that pollen was not limiting and that oligolecty allowed for greater efficiency in foraging by focusing behaviors on particular plant morphologies. This in turn would enable the production of a greater number of offspring. Thorp (1979) discussed the possibility that each hypothesis could apply to

certain situations and are not necessarily mutually exclusive. In some habitats, such as arid regions with seasonally limited rainfall, pollen resources may indeed be limited and oligolectic species that are more efficient harvesters may have an advantage (Linsley and Cazier 1963, Thorp 1979, Parker 1981). Michener (1954) believes that oligolecty may have been derived through a combination of competitive pressure and preadaptive morphology or behavior that made particular polylectic bee species better harvesters on some plants than on others, thus driving these polyleges to specialize on plants to which they were most suited. This in fact combines the theories of Robertson and Lovell in explaining the evolution of oligolecty.

One could speculate that solitary bees had their evolutionary beginnings when pollen resources were limiting, and thus competition was a driving force in the evolution of oligolecty. Oligolecty is much more common amongst bees that live in arid regions, where pollen resources are likely to be limited (Linsley and MacSwain 1958, Linsley and Cazier 1963). However, in other situations pollen does not appear to be a limited resource (Cane and Eickwort in press). Some flowers are visited by a large number of bee species, both oligolectic and polylectic, in several families. <u>Helianthus</u> is visited by a total of 284 bee species, of which 39 species (in 12 genera) are oligolectic on the genus and 92 more are oligoleges of the family Asteraceae (Hurd et al 1980). Even in a single locality, such as a commercial plantation (which does provide more than ample

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resources), 7 species (all in different genera) of oligoleges visit <u>Helianthus annuus</u> (Parker 1981). <u>Larrea tridentata</u> (Fabaceae) is visited by 22 oligoleges (in 9 genera) and 68 polyleges (Hurd and Linsley 1975). <u>Phacelia</u> is visited by 20 different lineages of bees, and 11 lineages each visit <u>Oenothera</u>, <u>Salix</u> and <u>Sphaeralcea</u> (Cane and Eickwort in press). Cripps and Rust (1989a, b) concluded that a community of <u>Osmia</u> (Megachilidae) species partitioned their floral resources and overlapped on the most abundant flowers, but found no evidence of competition for pollen. Raw (1974) found that each of three <u>Osmia</u> species nesting in the same locality did collect pollen from different plant species. Thus, pollen may be a limited resource in some situations but not in others.

Location and Assessment of Host Plants and Relationship to Offspring Investment. Host-plant finding by oligolectic bees may rely on either visual or olfactory cues, or a combination of stimuli, although literature on sensory cues in solitary bees is limited. Learning may be involved (Linsely et al 1963, Thorp 1979) but evidence is scarce. Some authors have speculated that bees may imprint on the chemical composition of the pollen in their nest cells and thus use the same chemical cues to locate their appropriate host plants (Linsely 1958, 1978, Thorp 1979). Some oligoleges investigate the unopened flower buds of their host plants (Linsely 1958, Linsely et al 1963, Eickwort 1973), indicating that olfactory cues are important. Dobson

(1984) demonstrated that pollen coat lipids from <u>Grindelia</u> alone were as attractive as pollen and bagged flowers to a local specialist of this plant, <u>Colletes fulgidus longiplumosus</u> (Colletidae).

Visual cues also appear to be important in some cases. <u>Megachile brevis</u> Say, a broadly polylectic species, prefers blueviolet flowers and takes little pollen from flowers of other colors, even when abundant (Michener 1953). <u>Megachile rotundata</u> Fabricius (Megachilidae), which is polylectic, prefers alfalfa (<u>Medicago</u>) with normal purple flowers over yellow-flowered variants (Golpen and Brandt 1975). Ultraviolet patterns also play an important role, as speculated by Linsley (1958) about the pollination of the green, odorless orchid <u>Helleborus viridis</u>. This apparently unattractive flower was nonetheless visited by four species of solitary bees and one bumble bee species, while being ignored by honey bees, in a garden filled with brightly colored and aromatic violets (Leclercq 1945). Alteration of normal ultraviolet patterns deters foraging behavior on normally preferred plants (Jones and Buchmann 1974).

Oligolectic bees assess their pollen resources and respond to the changing availability of host plant pollen. <u>Evylaeus</u> <u>galpinsiae</u> emerged but did not forage during a year in which its host plant (<u>Oenothera pallida</u>) did not bloom, but instead the adults returned to their natal burrows after filling up on nectar (from other flowers) and overwintered a second year (Bohart and Youseff 1976). <u>Calliopsis persimilis</u> (Cockerell) (Andrenidae), an

oligolege of <u>Physalis Wrightii</u> (Solanaceae), provisions its nest at the astonishing rate of up to six cells per day (one to three is typical for most solitary bees). Early in the day, when pollen is abundant, <u>C. persimilis</u> constructs cells for female offspring; towards the end of the day, when the pollen of its host plant becomes depleted, <u>C. persimilis</u> begins to produce cells for male offspring, which require 33% less pollen than female cells (Danforth 1990). Male solitary bees are usually smaller than females and require less food (Mitchell 1962, Krombein et al 1979). Production of more males late in the season as either resources dwindle or female pollen harvesting efficiency declines is considered to be a strategy for maximization of reproductive success (Torchio and Tepedino 1980, Sugiura and Maeta 1989).

Torchio and Tepedino (1980) and Frohlich and Tepedino (1986) speculated that increasingly male-biased sex ratios late in the nesting season of <u>Osmia lignaria propinqua</u> Cresson (Megachilidae) were the result of declining resource availability, and Torchio (1985) confirmed this. By experimentally increasing provision masses, Plateaux-Quenu (1983) caused females of <u>Evylaeus calceatus</u> (Halictidae) to produce more female offspring. Conversely, Torchio and Tepedino (1980) also speculated that aging of females, and subsequent wear and tear, reduce the abilities of females to gather pollen as effectively as earlier in the season. Tepedino and Torchio (1982) proved this, and Sugiura and Maeta (1989) demonstrated this with photographs comparing young and old females of <u>Osmia cornifrons</u> (Radoszkowski)

(Megachilidae), showing that age does indeed reduce the density of scopal hairs and therefore pollen carrying capacity.

However, Strickler (1982) found that, even though Hoplitis anthocopoides handled flowers of its host Echium vulgare more slowly as females aged (and possibly due to declining quantities of pollen), investment per individual offspring did not decrease correspondingly. This bee is unusual in that there is little sexual dimorphism in size (Strickler 1979). Males of <u>H. anthocopoides</u> are territorial (Eickwort 1973), and Strickler (1982) speculates that smaller males would be at a disadvantage in territorial competition. Small females would also be less efficient at gathering pollen from the host plant (Strickler 1979, 1982). Cowan (1981) found that larger females of two eumenid wasps, Ancistrocerus adiabatus (Saussure) and Euodynerus foraminatus (Saussure), had higher reproductive success than smaller females by collecting more food and provisioning more offspring. This may also be true for some solitary bees, but Johnson (1990) found that larger females of the small carpenter bee Ceratina calcarata Robertson (Anthophoridae) did not produce either more total offspring or more female offspring, and speculates that in this species larger female offspring have a greater chance of surviving through the winter. Tepedino and Torchio (1982) also found no correlation between female size and fecundity in the solitary bee Osmia lignaria propingua Cresson (Megachilidae).

**Pollen Harvesting Efficiency.** Oligolectic bees have variously adapted to the characteristics of their host plants

(reviewed by Thorp, 1979). Bees that specialize may have become behaviorally adapted to the particular flower morphology of their host plants so that they can harvest pollen more efficiently than non-specialist, or polylectic, bees visiting the same plants. Hoplitis anthocopoides was shown to be more efficient at collecting pollen from its host plant, Echium vulgare, than four polylectic species (Strickler 1979). Habropoda laboriosa (Anthophoridae), an oligolege of blueberries (Vaccinium), forages more rapidly on its host plants than competing polylectic Bombus species (Cane and Payne 1988). This would appear to convey an advantage to a specialist in localities where abundance of the preferred host plant is high. Most solitary bees are believed to limit their foraging ranges to within a few hundred meters of their nests (Eickwort and Ginsberg 1980, Rust 1980, Neff et al 1982, Cane and Eickwort in press). One would therefore expect to find oligolectic bees only in habitats containing sufficient quantities of their host plants to sustain a population. Superior efficiency of oligoleges on their host plants when compared to polyleges supports Lovell's (1914, 1918) hypothesis about the advantages of oligolecty, but evidence is still scanty.

**Diurnal Synchrony.** Many oligolectic bees show a high degree of diurnal synchrony of activity with the anthesis (shedding of pollen) of their host plants. This is especially true in desert habitats, where the incidence of oligolecty is high and floral resources are limited both temporally and in abundance (Linsley 1958, 1978; Linsley and Cazier 1963). Several different

temporal foraging periods can be distinguished in desert habitats, especially amongst bee species that forage from plants presenting their pollen at specific times and for limited periods such as members of the Solanaceae and Onagraceae (Thorp 1979). Oligoleges often arrive at their host plants and extract pollen and nectar before competing polyleges arrive (Linsley and Cazier 1963, Thorp 1979, Parker 1981). Learning may be involved with diurnal synchrony (Thorp 1979) but many oligoleges exhibit morphological adaptations to their temporal foraging periods, such as crepuscular or nocturnal bees with large ocelli (Kerfoot 1967).

Seasonal Synchrony. Other oligoleges show seasonal synchrony of emergence with the blooming phenology of their host plants. Robertson (1929b) cites numerous examples of oligolectic species with flight periods that are shorter than, and overlap perfectly, the blooming period of their host plants. Many oligoleges, however, are not perfectly synchronous with host plant flowering. Andrena ervthronii females emerge before Ervthronium begins blooming and continue to forage after the plants are no longer in flower (Michener and Rettenmeyer 1956). Proteriades (Megachilidae) species in California are not synchronous in flight period with peak blooming of their host plants in the genus Crvptantha (Hurd and Michener 1955). Diadasia olivacea begins flight two weeks earlier than first bloom of its host plant Sphaeralcea (Eickwort et al 1977) while Perdita maculigera maculipennis Graenicher (Andrenidae) begins

foraging too late to catch peak bloom of its host <u>Salix nigra</u> (Michener and Ordway 1963). In many of these cases, it is possible that mate finding and nest construction delay the onset of actual foraging for nest provisions (Cane and Eickwort in press).

The environmental cues used by oligolectic bees to achieve synchrony of flight with the flowering of their host plants are not well known. As solitary bee larvae are somewhat insulated from the outside environment by their nest enclosures, the stimuli used by host plants to flower and bees to pupate or emerge may not be perceived in the same manner. Moisture may be an important stimulus for emergence. A normally vernal, univoltine desert oligolege. Hesperapsis fulvipes Crawford, emerged as a second generation in October to forage on an unique autumnal flowering of its host Geraea (Asteraceae) after unseasonally heavy rainfall (Hurd 1957). Other oligoleges did not emerge during drought years when their host plants did not flower (Thorp 1979). Temperature may also play an important role; it is known to be the primary factor in the emergence of Megachile rotundata (Thorp 1979). Cane and Eickwort (in press) suggest that loose synchrony with host-plant flowering is adaptive in bracketing blooming which may be highly variable between years.

**Morphological Adaptations to Host Plant Pollens.** Some oligolectic bees have specialized structures for collecting and transporting the distinctive pollen grains of their host

plants. Bees that specialize on members of the Malvaceae and Cactaceae, which produce relatively large pollen grains, have loosley plumose scopal setae to accommodate the large grains (Linsley 1958). Some oligoleges of <u>Solanum</u>, species of which produce relatively small pollen grains, have much more densely plumose scopal hairs to securely hold the small pollen, while others mix the pollen with regurgitated nectar to hold it in place (Linsely and Cazier 1963, Roberts and Vallespir 1978). Species of Xenoglossa, a genus oligolectic on species of Cucurbita, have stout, unbranched, and grooved scopal hairs to hold the large, oily pollen grains of their host plants (Roberts and Vallespir 1978). Perhaps the best examples of morphological adaptation to host plant pollen morphology involve oligoleges of the general Oenothera, Camissonia, and Clarkia in the Onagraceae. Several genera of bees, from different families, that specialize on these plants all have unbranched scopal setae with hooked tips that function well in holding the pollen grains of their hosts, which are large and connected together by sticky threads (Roberts and Vallespir 1978, Thorp 1979). Finally, there are examples of oligolectic bees that have morphological adaptations of their proboscis for extracting nectar from their host plants (Linsely 1958, Cruden 1972), although others are apparently not well adapted to collect their host plant's nectar (Bohart and Youssef 1976).

Nutritional Properties of Host Plant Pollens. Nutritional relationships between oligolectic bees and their host plants are not well studied, but a few cases involving oligoleges as well as polyleges deserve discussion. Bohart and Youseff (1976) were able to rear larvae of <u>Evylaeus galpinsiae</u>, an oligolege of <u>Oenothera</u>, to adulthood on <u>Medicago</u> (Fabaceae) pollen. However, larval growth was slower (8 days versus 6 on <u>Oenothera</u>), and both prepupal (3 days versus 2) and pupal periods (13 days versus 8) were longer on <u>Medicago</u>. <u>Andrena astragali</u> Viereck and Cockerell is oligolectic on <u>Zigadenus</u> (Liliaceae), a plant with pollen that has proven toxic to honey bees (<u>Apis</u> <u>mellifera</u> L.) and possibly to other polylectic species as well (Tepedino 1981).

<u>Osmia lignaria</u> is narrowly polylectic (foraging from a few plant families) but its larvae do not develop equally well on different pollens. Optimal development (maximum weight and shortest larval period) occurs on <u>Hydrophyllum</u> (Hydrophyllaceae), growth is slower on <u>Brassica</u> (Brassicaceae), <u>Pisum</u> (Fabaceae) and <u>Medicago</u>, and larvae die when fed on <u>Grindelia</u>, <u>Iva</u>, <u>Sarcobatus</u>, and <u>Taraxacum</u> (Levin and Haydak 1957). This bee also appears to do well on almond (<u>Prunus</u>: Rosaceae) pollen, as nests with provisions averaging 96% almond pollen yielded an average survival rate of greater than 90% (Torchio 1981). Rust (1990) reported a survival rate of only 47% for <u>O</u>, <u>lignaria</u> offspring feeding on <u>Taraxacum</u> pollen.

The alfalfa leafcutter bee <u>Megachile rotundata</u> is also considered to be narrowly polylectic, but prefers alfalfa (<u>Medicago sativa</u>) pollen when present (Stephen and Torchio 1961). This bee is able to reproduce successfully on pollen and nectar from other plants, such as carrot (Daucus carota), but when released in carrot fields in a pollination experiment the bees flew to relatively distant (500 m) alfalfa fields for pollen (Tepedino 1983). Larvae of this bee exhibited maximum growth when fed alfalfa pollen, grew slightly less when fed on pollen of the related legumes <u>Melilotus</u> and <u>Galega</u>, and died when fed pollen exclusively from the composite <u>Haplopappus</u> (Guirgus and Brindley 1974). Larval growth is faster on pollen from <u>Medicago</u> than from <u>Melilotus</u> (Tasei and Masure 1978). The larvae of <u>M.</u> rotundata are extremely efficient (in terms of energy and nitrogen utilization) at using alfalfa pollen in nutrition (Wightman and Rogers 1978).

It has long been known that the chemical composition of pollen varies between plant species and that these differences affect nutritional value to bees (Todd and Bretherick 1942, Vivino and Palmer 1944, Haydak 1970). The ability of insects to evaluate the nutritional quality of their food sources was not given much consideration (Fraenkel 1959) until House (1967, 1970) demonstrated that insects can choose the most nutritious diet when given a choice among diets of varying nutritional suitability. Essential nutrients, not merely secondary compounds (Fraenkel 1959), have been demonstrated to be important phagostimulants (Thorsteinson 1960, Beck 1965, Davis 1968). Larval bees cannot chose their own diet, their food being provided by their mothers. Adult honey bees do show preferences when

pollen foraging (Levin and Bohart 1955), and adult honey bees demonstrate differential longevity on different plant pollens (Schmidt et al 1987). Perhaps adult bees can detect nutritional differences in pollen and provision only those pollens most nutritious for their offspring, although it is unknown if there is any correlation between larval and adult nutrition.

Conversely, it has been speculated that oligolectic bees are imprinted on their host plant from the pollen in their nest provisions (Linsely 1958, 1978). Pollens do indeed contain components that have been shown to be attractive (Lepage and Boch 1968, Hopkins et al 1969, 1975) or phagostimulatory (Dobson 1984, Schmidt 1985) to bees. However, examples of oligolectic bees that forage from non-host plants during years of host plant flowering failure and then return to their host plants the following year (Thorp 1969) do not support host plant imprinting through pollen (Cane and Eickwort, in press).

**Objectives.** The objectives of my study were:

1) To determine if <u>H. carinata</u> specializes on <u>Rhus typhina</u> or similar congeneric species for pollen for larval provisions in trap nests.

2) To evaluate possible mechanisms of specialization with respect to three hypotheses: a "cornucopia" hypothesis, behavioral specialization, and nutritional specialization.

a) "Cornucopia" hypothesis: <u>H. carinata</u> females forage on <u>Rhus</u> because it is the most obvious and abundant source of pollen, and share similar foraging habits with other bees that appear to be local specialists, foraging on other plants in other habitats as well.

b) Behavioral specialization: <u>H. carinata</u> females are able to gather more pollen per unit time on <u>Rhus</u> than from other plants.

c) Nutritional specialization: <u>H. carinata</u> larvae survive to adulthood at a higher rate when feeding on <u>Rhus</u> pollen than on pollen from other plants.

These hypotheses are not mutually exclusive, as <u>Rhus</u> pollen may be a basically nutritious food for any pollen forager, and the abundance of <u>Rhus</u> at the study sites may affect the time necessary to collect sufficient amounts of pollen for provisioning. Other potential explanations for specialization by <u>H. carinata on Rhus</u>, such as morphological specialization and diurnal synchrony, were not examined in this study. <u>Rhus typhina</u> pollen is rather typical in size and shape, and it is unlikely that any special morphological adaptations would increase transportation efficiency of this pollen.

#### METHODS

**Field Sites.** Four study sites, each with distinctive vegetational and ecological characteristics, were established on the property of the University of Michigan Biological Station (UMBS) near Pellston, Michigan. These sites were chosen because of their differing plant communities related to soil moisture and surrounding habitat.

The moist site (MS) was located in a clearing in the extreme southwest corner of Section 5, Burt Twp., Cheboygan Co; it consisted of an old field with a moderately diverse flora of insect-pollinated plants, including staghorn sumac (<u>Rhus typhina</u> L.), surrounded by mixed deciduous/conifer woodland.

The Colonial Point site (CP) was established in an abandoned apple orchard located southeast of the intersection of Lathers Road and Indian Point Trail in Colonial Point Forest. This semi-virgin timber tract was located in Section 28, Burt Twp., Cheboygan Co., and consisted of old-growth mixed woodland with a very rich community of spring ephemeral wildflowers. In addition to apple trees, this site contained plant species not found on the other three study sites, including a small population of <u>Rhus glabra</u>.

The wet site (WS) was located in the extreme southeast corner of UMBS property along Greenstar Trail in Section 35, Munro Twp., Cheboygan Co.; it consisted of a seasonally wet meadow bordered by cattail marsh, willow/alder swamp, and

farmlands to the south of the trail. This site had a high diversity of insect-pollinated plant species, but no nearby <u>Rhus</u>.

The dry site (DS) was located just north of Douglas Lake Road near Van Creek in Section 26, McKinley Twp., Emmet Co. This was an open, dry field habitat occupied by scattered white pines and red maples, shrubby hawthorns, cherries, serviceberries, and willows, and a low diversity of insectpollinated herbaceous plants. No <u>Rhus</u> was present within approximately one-half mile of this site.

Trap Nests. A sampling grid was established in each site. In DS, MS and WS, the grid measured 60 m by 60 m. In CP, the grid measured 30 m by 40 m because of the smaller area of this site. At each 10 m interval within the grid, a cluster of six trap nests (Krombein 1967) held together by wire was positioned in a tree or shrub branch or attached to a wooden stake, to provide artificial nesting sites for twig nesting bees. Trap nest clusters were located between 0.3 and 1.5 m above the ground; this both approximates the likely foraging height of these bees and is convenient for examination. Individual trap nests averaged 150 mm in length and 20 mm square, cut from pine or fir. To attract as many different species of twig-nesting bees as possible, six sizes of inside bore diameter were used (drill bits were in English measurements; approximate metric equivalents follow): 5/32" (4mm), 3/16" (4.75mm), 7/32" (5.5mm), 1/4" (6.25mm) 9/32" (7.25mm), and 5/16" (8mm). One of each size was used per cluster.

During preliminary work in 1988, DS, MS, and WS each received a full compliment of 49 trap nest clusters. In 1989, I decided to reduce the number of trap nest clusters at DS and WS to 20 each, because of substantially lower nesting activity at these sites compared with MS. CP also received 20 trap nest clusters, because of the smaller size of the sampling grid in this site. In 1990, only MS was used, because of the high amount of nesting activity by <u>H. carinata</u> when compared with the other sites. Only the two smallest sizes (4mm and 4.75mm) of trap nest bores were used, as <u>H. carinata</u> did not use the larger four sizes. These small bores were randomly mixed in clusters of six, and the site (MS) received a full compliment of 49 clusters.

Vegetation Sampling. Insect-pollinated flowering vegetation was sampled weekly by placing a 1 m square quadrat twice at each grid point, with one corner touching the grid point. Within each quadrat, flowering plants were identified to species and the number of flowers or inflorescences (for plants such as composites with highly compact inflorescences of minute flowers) of each species was recorded. Voucher specimens were collected for all insect-pollinated plants occurring within the study sites. A reference collection of pollen from all insectpollinated plants occurring within the study sites was made by collecting fresh anthers and preparing them using the same techniques as outlined for the nest pollen samples (see Pollen Provision Sampling below).

**Sampling Chronology.** During preliminary work in 1988, trap nests were placed in WS on 28 April, and in DS and MS on 29 April. Weekly sampling continued for 4 weeks. Nests were not removed from the field sites until 8 October. In 1989, trap nests were placed in DS, MS, and WS on 4 May and in CP on 10 May; weekly sampling was initiated immediately and continued until 29 August on all sites. Trap nests remained in all field sites until 30 September. In 1990, only MS was used based upon the abundance of nesting activity by <u>H. carinata</u> in 1988 and 1989; trap nest placement and weekly sampling began on 30 June (when individuals of this species became evident in the site) and continued until 18 August.

Pollen Provision Sampling. Each site was visited weekly to examine the trap nests for occupation (and sample flowering vegetation, previously described). Trap nests were examined with an otoscope; completed nests were removed; marked with a code indicating site, date, and grid point location; and replaced with empty nests of the same bore size. The occupied nests were brought into the laboratory and split open to examine their contents. A small sample of pollen was removed from as many cells as possible without disturbing the larvae. These pollen samples were prepared for preservation on microscope slides using the acetolysis method (Erdtman 1943) with the following modifications: following acid treatment and distilled water washing, the pollen was

1. washed with a 1% solution of NaOH;

2. stained with a 0.2% solution of safranin;

3. washed again with distilled water;

- 4. washed with tertiary butanol to remove remaining water;
- 5. placed in glass vials with silicone oil for a few days to allow remaining alcohol to evaporate.

These samples were then mounted on microscope slides and labeled for cross-reference to adult bee voucher specimens from nests. Pollen samples were examined using bright field microscopy. Pollens were identified to species (when possible; otherwise, to genus or family) using a prepared pollen reference collection (see Vegetation Sampling), and approximate proportions of different pollens in provisions were estimated. Pollen samples were categorized with respect to the approximate abundance of <u>Rhus</u> pollen: 100%, 50-99%, 1-49% and 0%.

After removal of pollen samples, the number of cells constructed in each trap nest was recorded for nests of <u>H</u>. carinata. The trap nests of all bees were then resealed and capped with glass vials to allow for continued larval development to obtain adult bee specimens for identification, and also to determine the number of individuals of <u>H</u>. carinata surviving to adulthood on different pollens. Nests were overwintered outdoors in southern Michigan to provide for normal diapause and development. Emerging adults were killed, pinned, and labeled according to the code of the trap nest from which they emerged; they were retained as voucher specimens.

Foraging Flight Timings. In 1990, foraging flight timings were taken on nesting females of <u>H. carinata</u>. Timinas were taken on warm, sunny afternoons with minimal wind to reduce variation due to climatic factors. An active nest was located, and timing was begun when the female left the nest. While she was away, a grass stem was carefully inserted to determine the depth of the cell being provisioned; this measurement was recorded. The timing was terminated when the female returned with a pollen load (recognized by the bright yellow or white mass of pollen on her abdominal scopa). Each observed female was timed for up to five consecutive foraging flights; flights for resin, nectar or other purposes were not The depth measurement was used to determine which included. cell was being provisioned during the timed flights when the completed nest was removed and brought into the laboratory for opening, and a separate pollen sample was prepared to identify the plant species being foraged upon during the timed flights.

#### RESULTS

Nesting Activity and Pollen Provisioning. Forty-five nests of <u>H. carinata</u> were constructed at the moist site (MS) between 25 June and 12 August 1989. The onset and peak of nesting activity of H. carinata was synchronous with the flowering period of <u>Rhus typhina</u> (Figures 1a, 1b). Nests constructed during the peak (first three weeks) of nesting activity and Rhus bloom were provisioned exclusively with Rhus pollen. Although nests continued to be constructed after Rhus had ceased blooming, nesting activity was highest during this plant's flowering and declined steadily after Rhus was no longer in bloom. The blooming period of <u>Rhus</u> was longer than these data indicate, since some plants outside the actual sampling quadrats were observed coming into bloom a week earlier and some may have continued to flower a week later. This would explain the ability of <u>H. carinata</u> females to find <u>Rhus</u> pollen after the floral sampling data show it to be no longer available.

Only after <u>Rhus</u> flowering had severely declined did <u>H</u>. <u>carinata</u> females begin to include other pollens in their nests. Plant species used for provisioning after <u>Rhus</u> included <u>Satureja</u> <u>vulgaris</u> (Lamiaceae), <u>Hypericum perforatum</u> (Guttiferae), <u>Trifolium</u> sp. (Fabaceae), and several species of composites (Asteraceae) that were difficult to identify from pollen. In spite of their abundance (Figure 1a), these plants were totally unexploited as pollen sources by <u>H. carinata</u> females while <u>Rhus</u>







Figure 1b. Percent <u>Rhus</u> pollen in nests of <u>Heriades carinata</u> from the moist site from 25 June - 12 August, 1989.

was in bloom. Nesting activity declined steadily after peaking in early July, except for a minor resurgence the second week in August; no nests were found after 14 August. It is doubtful that this brief revival in nesting activity is due to bivoltinism; no adults were observed to emerge from any nests brought in from the field until the following summer during the three years of this study.

Eight nests of <u>H. carinata</u> were constructed at the Colonial Point site (CP) between 25 June and 12 August 1989. These nests were temporally scattered throughout the season. This site contained a small thicket of <u>Rhus glabra</u> which flowered in early July. Except for a single nest found, partially completed, on 28 August, in the dry site, no nests of <u>H. carinata</u> were found in the dry or wet sites. Neither of these sites contained any <u>Rhus</u>.

In 1990, nesting by <u>H. carinata</u> at MS began on 1 July, and by 18 August forty-nine nests had been completed. The same seasonal synchrony between nesting activity and <u>Rhus</u> flowering was observed (Figures 2a, 2b). Peak nesting (i.e., first three weeks) again corresponded with peak <u>Rhus</u> flowering, and nests constructed during the peak of the nesting season were provisioned exclusively with <u>Rhus</u> poller. As in 1989, other plant species were ignored in spite of their abundance (Figure 2b) during <u>Rhus</u> bloom and used only after <u>Rhus</u> pollen was declining in availability. Nesting declined steadily through the season although again there was a minor resurgence of nesting activity







Figure 2b. Percent <u>Rhus</u> pollen in nests of <u>Heriades carinata</u> from the moist site from 1 July - 18 August, 1990.

in mid-August; some nests were still being provisioned when sampling was terminated on 18 August.

The average number of cells in each nest of <u>H. carinata</u> was higher for nests containing exclusively <u>Rhus</u> pollen than in nests including any proportion of other plant pollens, even when the non-<u>Rhus</u> pollen component was less than 3%, in both 1989 and 1990 (Figures 3a, b). Chi-square tests comparing nests exclusively containing <u>Rhus</u> pollen with nests containing any non-<u>Rhus</u> pollen in any proportion (Figures 4a, b) were significant for both 1989 (Chi-square=22.8, df=2, p<.001) and 1990 (Chisquare=10.5, df=2, p<.01). The average number of cells per nest also declined steadily on a weekly basis in both 1989 and 1990, with the exception in both years of a single anomalous nest late in the season (Figures 5a, b).

Pollen Provisioning By Other Bee Species. Twentytwo nests constructed by other bee species at the moist site during 25 June - 12 August 1989 yielded adult voucher specimens. Many additional nests were constructed but did not yield adult voucher specimens for identification. Due to the difficulty of identifying bee species other then <u>H. carinata</u> on the basis of nest architecture alone only those nests yielding adults for identification were examined for pollen provisioning. Two species of megachilids, <u>Hoplitis cylindrica</u> Cresson and <u>Megachile</u> <u>relativa</u> Cresson, frequently nested in the moist site as well as in the other sites; other species, including <u>Megachile rotundata</u> (Fabricius), <u>Megachile pugnata</u> Say, and two <u>Osmia</u> sp. only



Figure 3a. Number of cells per nest in relation to the proportion of <u>Rhus</u>pollen in nests of <u>Heriadescarinata</u> from the moist site for 1989.



Figure 3b. Number of cells per nest in relation to the proportion of <u>Rhus</u> pollen in nests of <u>Heriades carinata</u> from the moist site for 1990.



Figure 4a. Number of nests in relation to the number of cells per nest of <u>Heriades carinata</u> from the moist site from 1989.







Figure 5a. Weekly average numbers of cells per nest of <u>Heriades carinata</u> from the moist site from 25 June - 12 August, 1989.



Figure 5b. Weekly average number of cells per nest of <u>Heriades</u> carinata from the moist site from 1 July -18 August, 1990.

constructed a single nest each that yielded adults for identification.

<u>Hoplitis cylindrica</u> constructed twelve known nests at the moist site; eleven of these were provisioned with >90% <u>Rhus</u> pollen (three exclusively). The earliest nest contained mostly <u>Hypericum perforatum</u> pollen with a small amount of <u>Rhus</u>. No completed nests of <u>H. cylindrica</u> were found prior to 5 July, and no completed nests were found later than 19 July at this site.

<u>Megachile relativa</u> constructed six known nests at the moist site; two of these were provisioned almost exclusively with <u>Rhus</u> pollen. The other nests were provisioned with mixtures of composite (Asteraceae) species or composites mixed with <u>Vicia</u> <u>villosa</u> (Fabaceae) or other legume pollens. The earliest of these nests was completed by 29 June; the last two, which both contained primarily <u>Rhus</u> pollen, were completed by 11 July.

Both of these bee species constructed nests at the other study sites during 1989. <u>H. cylindrica</u> made a total of nine known nests at the other sites. Two nests from Colonial Point contained <u>Rhus</u> pollen, one completed by 18 July containing about 50% and the other (completed by 26 July) with about 10%; a third nest from this site, discovered 10 August, contained no <u>Rhus</u> pollen. A small thicket of <u>Rhus glabra</u> flowered briefly on this site in early July. Four nests from the dry site, completed between 4 and 18 July, were provisioned mostly (three contained >90%) with <u>Hypericum perforatum</u>, which flowered abundantly in this site throughout July and August. Two nests of <u>H. cylindrica</u> from the wet site, both completed by 12 July, contained unknown (possibly legume) pollens. Several legumes (<u>Trifolium</u> sp., <u>Melilotus alba</u>, <u>Medicago lupulina</u>) flowered abundantly in this site during July.

<u>Megachile relativa</u> constructed eight known nests at the other three sites, the earliest completed by 30 June (wet site) and the last finished by 31 July (dry site). Six of these nests contained mostly composite pollens. One nest from Colonial Point contained about 50% pollen from <u>Lathyrus latifolius</u>, which flowered abundantly on this site in July. The last known nest contained almost exclusively <u>Hypericum perforatum</u> pollen.

Foraging Flight Timings. The foraging trips of ten <u>H</u>. <u>carinata</u> females were timed in the moist site between 21 July and 13 August 1990. Five bees provisioned their timed cells with a predominance (>50%) of <u>Rhus</u> pollen, and five provisioned their timed cells with mostly other (<50% <u>Rhus</u>) pollen. Flight timings were averaged for individual bees. Because foraging flight timing data may not be normally distributed (Strickler, personal communication), a Mann-Whitney U-test was conducted on the two categories of bees. <u>H. carinata</u> females gathering predominantly <u>Rhus</u> pollen averaged 13.37  $\pm$  3.82 (SD) minutes per foraging flight. Females gathering mostly other pollens averaged 9.42  $\pm$  3.83 (SD) minutes per foraging flight. These average flight times were not significantly different (U=19; p=0.175).

**Offspring Survival to Adulthood.** The number of adults obtained was compared to the total number of cells constructed in trap nests of <u>H. carinata</u> from the moist site in 1989.

Tra or ne CC ł p: SU pri y e tes Sü be P< pr ac in Trap nests were categorized by the predominance of <u>Rhus</u> (>50%) or other (<50% <u>Rhus</u>) pollen in the provisions of the whole nest; nest cells were not sampled individually. Thirty-seven nests, containing a total of 277 cells, were provisioned with predominantly <u>Rhus</u> pollen and yielded 58 adults for a total survival of 20.9%. Eight nests, with a total of 39 cells, were provisioned predominantly with pollens other than <u>Rhus</u> and yielded only 2 adults for a total survival of 5.1%. A Chi-Square test conducted on the ratios of cells containing offspring surviving to adulthood to cells containing offspring that died before reaching adulthood was significant (Chi-square=143.6; p<.001). Larval provisions of <u>H. carinata</u> containing a predominance of <u>Rhus</u> pollen enabled a higher survivorship to adulthood than provisions with a minority of, or entirely lacking in, <u>Rhus</u> pollen.

#### DISCUSSION

Seasonal Synchrony and Nest Provisioning. Adult activity of oligolectic bees is frequently synchronized with the blooming of their preferred host plants (Roberston 1929b, Thorp 1979, Cane and Payne 1988, Cane and Eickwort in press). The observed synchrony between <u>H. carinata</u> and <u>Rhus</u>, as well as the exclusive use of <u>Rhus</u> pollen by <u>H. carinata</u> during the peak of the nesting season, provides evidence for specialization by H. carinata on Rhus. Matthews' (1965) observations indicated that his study populations of <u>H. carinata</u> in the vicinity of Kellogg Biological Station, over 200 miles further south, also used Rhus pollen almost exclusively for the provisioning of nests during the peak of the nesting season. Matthews also studied a population of H. carinata in Oregon; he did not examine the pollen provisions in their nests, but speculated that "the source was probably garden flowers in neighboring yards" (Matthews, 1965). As species of Rhus do occur in Oregon (Peck 1961, Hitchcock and Cronquist 1973), it is possible that Matthews' Oregon population of H. carinata was instead foraging on a source of Rhus pollen outside his study area. <u>H. carinata</u> is minimally a regional specialist on Rhus and may be oligolectic as defined by Linsley (1958).

An alternate explanation is that <u>H. carinata</u> is a polylectic species that is only a local facultative specialist on <u>Rhus</u>, due to local abundance of this plant genus and the large quantities of

accessible pollen that these plants appear to produce. Some known polylectic bees have been shown to specialize locally on highly concentrated pollen sources while ignoring other plants no matter what their abundance (Stephen and Torchio 1961, Torchio 1976, 1981, Cripps and Rust 1989a, b). Some of these examples involve agricultural crops such as alfalfa or almonds that present extreme instances of local abundance, while others represent situations involving "cornucopia species" (Mosquin 1971).

In my field sites, several other plants were in high floral abundance during <u>Rhus</u> bloom (Figures 1a, 2a). <u>H. carinata</u> females did forage upon these other plant species when <u>Rhus</u> was no longer flowering. While some strictly monolectic bees may totally refuse to forage on other plant species when the preferred host is unavailable (Eickwort 1973, Strickler 1979, Rust 1980, Neff et al 1982), many oligolectic bees will collect pollen from non-host plant species when the preferred host species or genus is of low abundance or unavailable (Michener and Rettenmeyer 1956, Thorp 1969, Cruden 1972, Bohart and Youseff 1976).

Matthews (1965) estimated that females of <u>H. carinata</u> may live longer than a month. This is certainly supported by my field studies in 1990, when some nests were still being provisioned on 18 August, more than a month and a half after the beginning of nesting activity. Long-lived females that still have eggs to lay may have higher fitness if they lay their eggs on something, even if it is not the preferred host's pollen, than if they abstain from further nesting; this is especially true if the potential life

expectancy of some females exceeds the host's blooming period. Thorp (1969) considers the ability of oligoleges to collect other plant pollens during periods of "stress" (i. e., lack of host plant bloom) to be an adaptive trait.

**Nectar Foraging.** The exclusive use of <u>Rhus</u> pollen in nests of <u>H. carinata</u> during the peak of the nesting season indicates that these bees may be foraging exclusively on <u>Rhus</u> for nectar as well. Nectar foraging on other plants would probably lead to "contamination" of host- plant pollen provisions with 1-3% of other pollens, as speculated by Rust (1990). As the blooming period of <u>Rhus</u> was finishing, several nests of <u>H.</u> <u>carinata</u> began to show "contamination" by pollen from <u>Satureja</u> <u>vulgaris</u> and <u>Hypericum perforatum</u>, in amounts varying from traces to a few percent. It is probable that <u>H. carinata</u> females were still collecting residual pollen from senescing male <u>Rhus</u> flowers that were no longer producing nectar, forcing the bees to collect nectar from other plants. However, pollen foraging on <u>Rhus</u> appeared to continue until even residual supplies from senescing flowers had dried up.

Nesting Locality and Host Plant Abundance. <u>H.</u> <u>carinata</u> was only found in the proximity of <u>Rhus</u> and was not present at study sites DS and WS which did not contain species in this genus (with the exception of a single, very late nest in DS). It is believed that most solitary bees forage only within a few hundred meters of their nests (Eickwort and Ginsberg 1980). Thus, <u>H. carinata</u> females only nest in areas with populations of

<u>Rhus</u> within their foraging ranges, indicating specialization on this plant genus. It is known that <u>H. carinata</u> females will use hollowed-out twigs of <u>Rhus</u> as nesting sites (Matthews 1965).

Pollen Foraging by Other Bee Species. Other bees occurring in the same habitats as H. carinata do not exhibit the same restriction in host plant usage. Hoplitis cylindrica appears to be a local specialist on <u>Rhus</u> in MS and not truly oligolectic. Although the flight season of this bee also correlates well with Rhus flowering and almost all of the nests constructed in MS contained primarily <u>Rhus</u> pollen, <u>H. cylindrica</u> also nested in sites containing little or no Rhus and provisioned these nests with other locally abundant sources of pollen. This bee probably does not forage on Rhus exclusively for nectar even when it is specializing on <u>Rhus</u> pollen, as only three of the twelve nests constructed by this bee in MS contained <u>Rhus</u> provisions that were completely free of contamination by other pollens. Megachile relativa begins nesting before Rhus begins flowering, constructs nests in habitats containing little or no <u>Rhus</u>, and uses a variety of pollens in nest provisioning, including Rhus when locally abundant. <u>Rhus inflorescences are highly attractive to several</u> orders of insects and no doubt provide a highly visible and copious source of both pollen and nectar. Since the flight seasons of several solitary bees begin right around the onset of Rhus flowering, it is logical to assume that some, if not most, of these bees will exploit this abundant food source when available.

The foraging habits of these other bee species do not support the hypothesis that <u>H. carinata</u> is foraging on <u>Rhus</u> simply because it provides the most abundant source of pollen. If <u>H. carinata</u> were merely a local specialist on <u>Rhus</u> because of the abundance of this plant, it would be expected that this bee would probably switch to other sources of pollen fairly quickly when <u>Rhus</u> bloom was waning, that it would forage on other plants for nectar while <u>Rhus</u> was in peak bloom (as other bee species appear to), and that it would also occur in other habitats which did not contain <u>Rhus</u> and use other pollens in nest provisions. Even though other bee species will locally specialize on <u>Rhus</u> when it represents a highly abundant pollen source, suggesting that <u>H. carinata</u> is merely doing the same, these other species do not show the same absolute constancy in foraging and nesting location that is demonstrated by <u>H. carinata</u>.

**Parental Investment.** The decline in the average number of cells per nest of <u>H. carinata</u> as other pollens begin to be included in the nest provisions (Figures 3a, b) represents a decrease in investment per individual nest. Other bees have been shown to reduce the number of cells per nest and/or increase the number of male progeny (which require less food) as the season (or even day) progresses, either in response to dwindling floral resources (Torchio and Tepedino 1980, Torchio 1985, Danforth 1990) or because of decreasing efficiency of aging bees from wear (Sugiura and Maeta 1989). Thus, it is likely that fewer cells in late season nests is indicative of a behavioral response by <u>H.</u> <u>carinata</u> to the decreasing availability of <u>Rhus</u> pollen.

I was not able to assess intended sex ratios for H. carinata from weighed provision masses, a typical measure of offspring investment and a possible indicator of sex in dimorphic bees (Torchio and Tepedino 1980, Sugiura and Maeta 1989, Danforth 1990), because I did not weigh the provisions. Sex of a cell can also sometimes be determined by size and position, with females generally found in the innermost, larger cells and males in the outermost, smaller cells (Krombein 1967, Cowan 1981). attempted to estimate sex ratio by cell size and position after the larvae had constructed their cocoons and discovered that there was considerable variation in cell size (6-10 mm in length) without respect to cell position. Although Matthews (1965) found that the inner nest cells of <u>H. carinata</u> had a higher probability of being female and the outer cells were more likely to yield male offspring, I encountered many nests with cells containing dead larvae in central positions and other nests with very few entirely dead cells, and determining the sex of these cells was not possible with certainty.

**Foraging Efficiency.** <u>Rhus</u> inflorescences are quite densely packed with flowers, are presented in an obvious manner at the apices of well elevated branches, and are usually quite abundant given the thicket-forming growth habit of this genus. All of these features would seem to potentially enhance efficiency at finding and collecting pollen for a specialist

forager. It is possible that foraging on other plant species for pollen is more costly in terms of foraging time, and that this increases nest construction time which in turn provides more opportunities for invasion by parasites such as sapygid wasps or cleptoparasitic megachilids such as <u>Stelis</u> sp. (Matthews 1965) before a nest is finally closed. If this were the case, construction of nests containing fewer cells that took less total time to complete and seal more effectively against parasites would be advantageous. However, females of <u>H. carinata</u> do not take significantly longer to gather pollen from plants other than <u>Rhus</u>. The number of bees and the total number of flights timed were low, and timings were not obtained during peak <u>Rhus</u> bloom; thus, these observations may not be conclusive.

Offspring Survival to Adulthood. <u>H. carinata</u> offspring appear to have a significantly better chance at surviving to adulthood when feeding primarily on <u>Rhus</u> than on other pollens, supporting the hypothesis that there is a nutritional basis for specialization on <u>Rhus</u> by this bee. Other bees have demonstrated differential survival and/or development on different pollens (Levin and Haydak 1957, Guirgus and Brindley 1974, Bohart and Youseff 1976, Tasei and Masure 1978), and it appears that <u>Rhus</u> pollen confers such a survival or developmental advantage to <u>H. carinata</u> larvae. This would suggest that adult behavior evolved in response to larval nutritional requirements, those adults that feed their larvae <u>Rhus</u> pollen having a higher fitness than those feeding other pollens to their larvae. Thus, foraging for pollen on

<u>Rhus</u> is selected for in individuals of <u>H. carinata</u>. However, the converse argument could be made that the larvae have adapted to adult <u>Rhus</u> provisioning behavior. The possibility that <u>H. carinata</u> females are imprinted on <u>Rhus</u> pollen as larvae is not supported by my observations, as larvae from late-season nests would be imprinted on other plants. <u>H. carinata</u> has a fairly short emergence period of approximately one to two weeks: the first emergence in the laboratory in 1990 was a male that emerged on 26 June, and by 4 July all individuals had emerged. Matthews (1965) also observed that his populations emerged within a period of approximately one week. Thus, all females provision exclusively <u>Rhus</u> pollen during the first week or so of their lives and cannot have been imprinted on any other plants.

#### SUMMARY

<u>H. carinata</u> may be oligolectic on <u>Rhus</u>. This bee forages exclusively for both pollen and nectar on this plant genus when in bloom, taking pollen from other plants only when <u>Rhus</u> pollen is no longer available. The onset and peak flight period of this bee is synchronized with the flowering of its host plants. <u>H. carinata</u> nests only in localities containing <u>Rhus</u> species, and is completely absent in areas where its host plants are not present. Larvae of <u>H. carinata</u> more likely to survive to adulthood when fed on <u>Rhus</u> pollen.

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#### APPENDIX 1

Record of Deposition of Voucher Specimens\*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1991-02

Title of thesis or dissertation (or other research projects):

Specialization, Foraging Efficiency, and Nutritional Relationships in a Solitary Bee, <u>Heriades</u> carinata Cresson (Hymenoptera: Megachilidae)

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums: None

Investigator's Name (s) (typed) Jonathon Michael DeNike

Date <u>15 May 1991</u>

\*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original:	Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies:	<pre>Included as Appendix 1 in copies of thesis or dissertation. Museum(s) files. Research project files.</pre>

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

		NU	mber	of:		
Species or other taxon	Label data for specimens collected or used and deposited	Larvae Eggs	Pupae Nymphs	Adults 🍳	Adults d	Museum where depos- ited
<u>Heriades</u> carinata Cresson	Reared from trap nest from Sec. 5, Burt Twp., Cheboygan Co., Mich. July-August 1989		· · · · · · · · · · · · · · · · · · ·	33	24	NSW
<u>Hoplitis cylindrica</u> Cresson	Reared from trap nest from Sec. 5, Burt Twp., Cheboygan Co., Mich. July-August 1989			19	2	NSM
Hoplitis cylindrica Cresson	Reared from trap nest from Sec. 28, Burt Twp., Cheboygan Co., Mich	•		7	Ŋ	MSU
Hoplitis cylindrica Cresson	Reared from trap nest from Sec. 35, Munro Twp., Cheboygan Co., Mich. July-August 1989			4		MSW
Hoplitis cylindrica Cresson	Reared from trap nest from Sec. 26, McKinley Twp., Emmet Co., Mich. July-August 1989			4		NSM
<u>Megachile</u> relativa Cresson	Reared from trap nest from Sec. 5, Burt Twp., Cheboygan Co., Mich. July-August 1989			ø	Ś	MSU
(Use additional sheets if neces	sary)					
Investigator's Name(s) (typ	ed) Voucher No. 1991-02	.		•		
Jonathon Michael DeNike	Received the above lis deposit in the Michiga	ted spec n State	Univ	is to rersi	or Ity	
	Entomology Museum.	(ک) ر	her	194	6	
Date [5 Ma. 199]	Curator	Date				

## APPENDIX 1.1

## Voucher Specimen Data

Page <u>1</u> of <u>2</u> Pages

Number of:	where depos- ited Other Adults of Adults Q Pupae Nymphs Larvae Eggs	Sec. 4 1 MSU	Sec. 3 MSU	Sec. 2 MSU		991–02	bove listed specimens for Michigan State University	niche 15 man 1991	Date ]
	Label data for specimens collected or used and dep	Reared from trap nest from 28, Burt Twp., Cheboygan Cc Mich. July-August 1989	Reared from trap nest from 35, Munro Twp., Cheboygan C Mich. July-August 1989	Reared from trap nest from 26, McKinley Twp., Emmet Co Mich. July-August 1989		ary) ed) Voucher No. <sup>19</sup>	Received the a deposit in the	Entomology Mus	Curator
	Species or other taxon	<u>Megachile relativa</u> Cresson	<u>Megachile relativa</u> Cresson	<u>Megachile relativa</u> Cresson	311 [11]	(Use additional sneets if neces: Investigator's Name(s) (type	Jonathon Michael DeNike		Date  5 May 1991

#### APPENDIX 1.1

## Voucher Specimen Data

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