Nesting Behavior, Ecology, Seasonal and Geographic Distribution of the Sand Wasp, *Stictiella emarginata* (Hymenoptera: Sphecidae)*

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The nesting behavior and ecology of *Stictiella emarginata* are documented for the first time based on field studies made mainly at Canadian Forces Base Borden, Simcoe County, Ontario. Type of soil, natural community, temporary closure, mound leveling, orientation flight, prey transport, nest structure and dimensions, and kind and number of prey per cell are defined. Museum and field collection records support a geographic bridge from northern Michigan to the Atlantic Coast and dispel the previously held notion of a disjunct distribution for this species. A late June-July-early August flight season is inferred from observations and collections made in Ontario, New York and Michigan. The nesting behavior and ecology of *S. emarginata* and several other *Stictiella* species from the western United States, Mexico and Florida are compared.

Key Words: Sand Wasp, *Stictiella emarginata*, Noctuidae, Hesperiidae, Ontario.

The tribe Bembicini includes moderate to large-sized, stout-bodied sand wasps that are often conspicuously marked with yellow or white (Parker 1917). All species of Bembicini nest in the ground, usually in sand or gravel. The subtribe Stictiellina of the tribe Bembicini includes five genera in the Nearctic Region: *Stictiella*, *Glenostictia*, *Microstictia*, *Xerostictia* and *Steniolia* (Bohart and Gillaspy 1985). *Stictiella* contains 13 species that range collectively from Mexico into southern Canada.

Species of *Stictiella* attempt to level the mound of soil that accumulates in front of an entrance from burrow excavation. The species temporarily close the entrance with soil following burrow excavation and then make an orientation flight before going in search of prey. Species of *Stictiella* hunt and stock underground cells with adult Lepidoptera (moths, skippers, butterflies). *Stictiella* nests are one-, two- or many-celled depending on the species. The number of prey per cell is often inversely related to prey size. Most *Stictiella* species practice delayed mass provisioning; i.e., they lay an egg on the first prey placed in the cell before other prey are put inside (Evans 1966).

Stictiella emarginata (Cresson) is the most widely occurring species in the genus. It ranges from Baja California through the United States into southern Canada (Bohart and Gillaspy 1985). This species was illustrated as having a disjunct geographic distribution with separate populations extending from the Great Plains to the Pacific Ocean and from the Appalachian Mountains to the Atlantic Ocean. *Stictiella emarginata* is the only congener found in the northeastern United States and southeastern Canada.

Stictiella emarginata is virtually unknown ecologically and behaviorally. The species is seldom seen in the field or collected east of the Rocky Mountains. Nothing is known of its nesting behavior except for a single prey record, an adult *Euxoa* [Noctuidae] from the western United States (Gillaspy et al. 1962). Bradley (1908) described a sleeping aggregation of *S. emarginata* from California. Our paper documents the nesting behavior and ecology of *S. emarginata* for the first time based on observations made mainly at a single locality in southern Ontario. Our paper redefines the geographic and seasonal distribution of *S. emarginata* in the northeastern United States and southeastern Canada.

Methods

Nearly all field research on *S. emarginata* was done at Canadian Forces Base Borden, Simcoe County, Ontario. We spent 15 days in the field, sometimes from 0530 to 2000 hrs (EDT), at this site. We made field observations of wasps on 26-28 July 1996, 13-14 July 1997, 5-7, 17-19 July 1998, and 29 June-2 July 1999. We found no adult *S. emarginata* nesting at Base Borden on 11-12 August 1995, 28-30 June 1996, and 27-30 June 1997.

Field observations covering four hours were made on two females of *S. emarginata* at South Glens Falls, Saratoga County, New York, on 31 July 1993. We did not find any *S. emarginata* at this locality during three visits on 18 July 1997, 14 July 1998, and 23 July 1999. We observed one female of this species for less than an hour at the Fort Drum Military Reservation, Jefferson County, New York on 22 July 1997. We did not find any *S. emarginata* at Fort Drum during 56 hrs of observation on 2-3 August and 18 October 1996 and 3 April, 5-6, 12 July and 4 Oct 1997 (Kurczewski 1998, 1999). The trips in October were made to ascer-

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tain that there was no fall flight of 2nd generation adults. The trip in April was made to ensure that the species did not winter and reappear in the spring in the adult stage.

Two other sites with potentially favorable habitat for *S. emarginata* were investigated but the species was not found at either locality. Seven trips were made to the Rome Sand Plains, Oneida County, New York on 27 June 1992, 28 July 1993, 13 July 1995, and 2 June, 26 July and 10, 27 September 1997 (Kurczewski 1998). Time spent observing and collecting sphecid wasps at this site on Windsor loamy fine sand totaled 35 hrs. Four trips were made to the Albany Pine Bush, Albany County, New York on 29 June 1991, 18 July 1997, 14 July 1998, and 23 July 1999. We spent 17 hours collecting and observing sphecid wasps at that locality on Colonie loamy fine sand.

We spent over 1000 hours searching unsuccessfully for *S. emarginata* in sandy and gravelly habitats in the following states and counties in the northeastern United States and southeastern Canada: INDIANA, Lake, LaPorte, Porter (21-22 June 1999); MASSACHUSETTS, Franklin (30 June 1991, 1 August 1993); MICHIGAN, Allegan, Alpena, Antrim, Arenac, Barry, Berrien, Cass, Cheboygan, Chippewa, Clare, Crawford, Emmett, Gladwin, Grand Traverse, Gratiot, Iosco, Kalamazoo, Kalkaska, Lake, Luce, Manistee, Mason, Mecosta, Menominee, Midland, Missaukee, Montcalm, Montmorency, Muskegon, Newaygo, Oakland, Oceana, Ogemaw, Osceola, Oscoda, Otsego, Ottawa, Presque Isle, Roscommon, Van Buren, Washtenaw, Wexford (15-20 June 1991; 9-12 June, 28 June-6 July, 7-10 August 1992; 10-16 June, 8-12 July, 10-12 August 1993; 12-23, 26-27 June 1994; 25-30 June 1995); NEW JERSEY, Atlantic, Burlington, Cape May, Ocean (19-21 August 1993, 14-21 June 1995, 14-16 June 1996, 21-22 June 1997, 24-25 June 1998); NEW YORK, Herkimer, Lewis, Oneida, Onondaga, Oswego, St. Lawrence, Suffolk (3-5 July 1994; 2-5 August 1996; 10 July 1997; 22, 25-27 June 1998); OHIO, Fulton, Lucas (28 June 1994; 14-20, 23-25 June 1999); ONTARIO, Elgin, Essex, Grenville, Grey, Haldimand-Norfolk Regional Municipality, Lambton, Northumberland, Prince Edward, Renfrew, Simcoe (20-27 June, 1-4, 12-25, 28 July 1996; 24-27 June, 1-2 July 1997; 15-16, 19 July 1998); PENNSYLVANIA, Erie (30 June 1994, 26 June 1999); QUEBEC, Kazabazua (31 July-1 August 1996), WISCONSIN, Adams, Bayfield, Douglas, Jackson, Juneau, Monroe (24-26 June 1994).

Females of *S. emarginata* nested mainly on warm, sunny days. Wasps excavated burrows, searched for prey, provisioned cells, and closed nests at air temperatures of 20.6-28.9°C and sand surface temperatures of 28-51°C. At Base Borden, females worked at nests from 1005 to 2005 hrs. The last female to leave her nest in the evening to join a sleeping aggregation on vegetation departed at 2006 hrs on 5 July 1998. No nesting or any other wasp activity occurred after that time. We unearthed two nests at Base Borden that evening but did not find any adult wasps in them. Collection of this species at Fort Drum was made at 1515 hrs at an air temperature of 26.7°C. At South Glens Falls, wasps provisioned nests and excavated burrows from 1321 to 1531 hrs at sand surface temperatures of 44-49°C.

All wasps from 1998 and 1999 field studies at Base Borden were color-coded by applying different colored paint to the thorax, except for two females collected as voucher specimens. All nests were flagged with numbered wooden stakes. Type of wasp activity was noted, described and quantified. Emphasis was placed on burrow excavation, temporary closure, mound leveling, orientation flight, prey transport, final closure, and evening activity. Wasps entering nests with prey were timed between consecutive provisioning trips, from entry to exit, and during temporary closure, leveling and orientation flights.

The burrow and cell(s) of each nest were excavated, examined, measured and drawn. Burrow length and design, number of cells per nest, cell depth, number of prey per cell, and position of prey in a cell and egg on a prey was recorded in the field. Prey, wasp cocoons, fly maggots and puparia were removed from the cells, placed in individual vials according to nest and cell number, put in an ice cooler, transported to a laboratory, and weighed [wet] on a Mettler balance. The aggregate prey weight of each cell was summed. The prey Lepidoptera were then pinned, code labeled, and, later, hand carried to Tim McCabe, New York State Insect Museum, for generic and specific determination. One of the two voucher specimens of *S. emarginata* was sent to Howard Evans, Colorado State University, for species confirmation. Miltogrammini cleptoparasites were compared with specimens in the State University of New York College of Environmental Science & Forestry collection determined by Margery Spofford. Wasp and prey specimens were deposited in the New York State Insect Museum, Albany.

Ecological communities and habitats were defined using Varga and Schmelefske (1992) for Canadian Forces Base Borden, Ontario, Reschke (1990) for Karner and South Glens Falls, New York, and Kurczewski (1998) for the Fort Drum Military Reservation, New York. Soil type for Base Borden was identified using the Soil Map of Simcoe County [Base Borden Area] (Soil Research Institute of Canada 1959). Soil types for Fort Drum, Karner and South Glens Falls, New York were identified from soil samples sent to Ed Stein, United States Department of Agriculture, National Resources Conservation Service.

To fill in gaps in the geographic distribution of *S. emarginata* we examined specimens and collection records from the University of Guelph, Royal Ontario Museum and Canadian National Collection for Ontario, Cornell University, American Museum of Natural History and New York State Museum for New York State, and National Museum of Natural History, Smithsonian Institution, Pennsylvania Department of Agriculture, Carnegie Museum of Natural History, and The Penn-

sylvania State University for the northeastern United States.

Weather information for Canadian Forces Base Borden, Ontario was unavailable from the base and nearby Angus weather stations as they were not operational. In order to simulate weather conditions at our research site (latitude 44°16'N, longitude 79°55'W, elevation 221 m) for May-June 1996-1999, we obtained temperatures from weather stations within 15 km of the base: Alliston Nelson (latitude 44°9'N, longitude 79°52'W, elevation 221 m), Egbert Care (latitude 44°13'N, longitude 79°46'W, elevation 252 m), and Essa Hydro (latitude 44°21'N, longitude 79°49'W, elevation 216 m), Ontario. We averaged May-June 1996-1999 temperatures from these weather stations and used these averages in a discussion of *S. emarginata* seasonal distribution.

Results

Geographic distribution

We searched 10 insect museums in Ontario and the northeastern United States and found the following unreported specimens of *S. emarginata*: ONTARIO—Regional Municipality of York, Toronto, August 1918, 1; Dufferin County, Primrose, June 1955, D. H. Pengelly, 3; Hastings County, Sydney Field Station near Foxboro, 8 July 1970, J. L. McAlpine, 1 female; NEW YORK: Albany County, Center [Karner], 28 July 1870, J. A. Lintner, 1 female. These collection records coupled with those from Pennsylvania (Parker 1929), northern Michigan (O'Brien 1989), Simcoe [Canadian Forces Base Borden] County, Ontario (Kurczewski 2000), and Jefferson [Fort Drum Military Reservation] and Saratoga [South Glens Falls] Counties, New York, when plotted on a map, reveal a contiguous, transcontinental population of *S. emarginata* in the United States and southern Canada (Figure 1).

Habitat and soils

Canadian Forces Base Borden

Two females were observed nesting at Base Borden in 1996 and 1997 in a sandy two-track running through a Red Pine [*Pinus resinosa* Aiton]—Scotch Pine [*Pinus sylvestris* L.]—graminoid savanna at the end of an airport runway (Figure 2). This two-track trail was the focal point of our 1998 and 1999 field studies. It was kept open by intermittent military vehicle use. In the early to mid-19th century droughty Tioga loamy sand (Soil Research Institute of Canada 1959),

FIGURE 1. Geographic distribution of *Stictiella emarginata* in the northeastern United States and southeastern Canada. Black circles represent collection localities as follows: MICHIGAN: Ontonagon County, Bruce Crossing; Marquette County, Huron Mountain Club (O'Brien 1989); ONTARIO: Dufferin County, Primrose; Simcoe County, Canadian Forces Base Borden; Regional Municipality of York, Toronto; Hastings County, Sydney Field Station near Foxboro; NEW YORK: Jefferson County, Fort Drum Military Reservation; Saratoga County, South Glens Falls; Albany County, Center [Karner]; PENNSYLVANIA: Cumberland County, Carlisle Junction (Parker 1929). Inset depicts geographic distribution of *S. emarginata* as illustrated by Bohart and Gillaspy (1985).

FIGURE 2. Nesting site of *Stictiella emarginata* at Canadian Forces Base Borden, Simcoe County, Ontario.

continuous pine plains, and periodic fires characterized the area. The coarse loamy sand coupled with ground and crown fires supported large Red Pine and White Pine [*Pinus strobus* L.] forests, savanna and barrens (Varga and Schmelefske 1992). Military activity on the Camp Borden Sand Plain in the 20th century maintained the savanna, barrens and sandy openings (Kurczewski 2000).

Karner

Stictiella emarginata records from 1870 exist in the form of a female specimen in the New York State Insect Museum, Albany [see above] and a male recorded in *A List of the Insects of New York with a List of the Spiders and certain other Allied Groups* (Bradley 1928). The locality of these collections is Center, an old name for Karner, a 19th century railroad stop in the heart of the Pine Bush between Albany, Albany County and Schenectady, Schenectady County, New York. Pine barrens, pine plains, and shrub savanna or pitch pine [*Pinus rigida* Miller]-scrub oak [*Quercus* spp.] barrens (Reschke 1990) still persist in preserved areas on Colonie loamy fine sand. Fires occur regularly every eight to 11 years (Benton 1976). Pitch Pine-shrub oak was a dominant plant community of the 19th century Pine Bush (Milne 1985). We found no *S. emarginata* at Karner probably because of extensive habitat destruction and expansion of alien vegetation due to fire suppression.

South Glens Falls

Two *S. emarginata* females nested in 1993 in recently bulldozed Windsor loamy sand of a construction equipment parking lot. The wasps nested near the road in a 5B slope that was too loose for heavy vehicles. This loamy sand contained many pebbles. Vegetation was similar to that at Karner, i.e., pitch pine-scrub oak barrens (Reschke 1990) with a preponderance of Pitch Pine, White Pine, shrub oaks, and Sweet Fern [*Comptonia peregrina* (L.) J. M. Coulter].

Fort Drum Military Reservation

One female was netted while flying with a noctuid moth held beneath her body in an area of Plainfield sand. The Fort Drum site contained open grassland and woodland of Pitch Pine, White Pine, Red Pine, and shrub oaks bordered by Sweet Fern (Kurczewski 1998). Original land surveys from the 1790s indicate that the area was once covered with White Pine, Pitch Pine, and oak forests with some sandy openings (Kurczewski 1997, personal observation). The site is now kept open by constant military activity. Three species of psammophilous sphecid wasps that prefer vast expanses of barren sand, *Ammophila harti* (Fernald), *Bembix pallidipicta* Smith, and *Philanthus albopilosus* Cresson, were collected at this site in addition to *S. emarginata* (Kurczewski 1998).

TABLE 1. Average temperature (ºC) at Alliston Nelson, Egbert Care and Essa Hydro, Ontario weather stations, May-June 1996-1999 and first observed nesting date during those years at Canadian Forces Base Borden, Ontario.

	1996	1997	1998	1999
Alliston	15.30	17.10	17.90	17.75
Egbert	14.35	13.65	16.90	16.80
Essa	14.60	13.80	17.40	16.95
Average	**14.75**	**14.85**	**17.40**	**17.17**
1st Nesting	**26 July***	**13 July**	**5 July**	**29 June**

*First observations by us, not first nesting by wasps at site.

Flight season

Stictiella emarginata has one emergence of adults per year in the Great Lakes Region according to collection dates on museum specimens and field observations. The flight season of this species encompasses the last few days of June, July, and, rarely, early August. At Base Borden adult development, emergence and flight season was influenced by May-June temperature. Wasps nested earlier (5-7 July 1998, 29 June-2 July 1999) following warmer springs (May-June 1998, 1999 average temperature, 17.40º, 17.17º C, respectively) and later (26-28 July 1996, 13-14 July 1997) after cooler springs (May-June 1996, 1997 average temperature, 14.75º, 14.85° C, respectively) (Table 1). Similar phenology in 1998 and 1999 *S. emarginata* broods at Base Borden was probably related to similar May-June average temperatures for those years. Unsuccessful attempts to find adults of this species at Base Borden following cooler springs (28-30 June 1996, 27-30 June 1997) supports the contention that emergence is tied to May-June temperature.

Nest spacing and false starts

Four females of *S. emarginata* nested at Base Borden in 1998 in a sandy two-track, 2.5 m wide, with a grassy median, 0.9 m wide. Each track was about 0.8 m wide (Figure 2). *Stictiella emarginata* was uncommon at this site compared to other sphecid species. More than 24 *Tachysphex similis* Rohwer, eight *T. tarsatus* (Say), four *T. pechumani* Krombein, 10 *Plenoculus davisi* Fox, 12-14 *Bembix americana* (Lepeletier), and 18-20 *Philanthus politus* Say nests were scattered through the area of the two-track where *S. emarginata* nested.

Seven active nests of *S. emarginata* occupied the two tracks over three days. One section of the N track had one active nest and 10 false starts in an area 4.5 m long and 0.4 m wide. The distance between adjacent false starts ranged from 13 to 102 cm (Mean = 41.4 ± 26.37, N = 14). A section of the S track had three active nests and 26 false starts in an area 3.9 m long and 0.8 m wide. The three active nests were 25, 33 and 30 cm apart, respectively. The distance between adjacent false starts ranged from 2 to 90 cm (Mean = 27.5 ± 17.58, N = 52). Three other nests were located 4 m farther west on the S track. These nests, of different ages and possibly belonging to a single female, were only 15-18 cm apart. Four active nests at Base Borden in 1999 were spaced 1.2-7.1 m [Mean = 3.5 ± 2.52] apart. Two females nested about 1 m apart in 1993 at South Glens Falls.

Nesting behavior

Burrow excavation

Four females at Base Borden excavated burrows between 1035 and 2005 hrs in 1998. The wasps made two to eight false starts before remaining in one place and completing a burrow. One female made seven false starts in an area 0.5 m^2 before finishing a burrow. Three other wasps moved as far as 0.5-3.0 m between consecutive false starts. One female at South Glens Falls started digging a new burrow at 1531 hrs at a sand surface temperature of 44ºC after nesting elsewhere from 1321 to 1530 hrs at sand surface temperatures of 45-49ºC.

Females searching for a place to dig walked on the sand, tapped the surface with their antennae, and dug with the mandibles. One wasp turned completely on her side while using the mandibles. She produced an audible buzzing sound for >1 min. After the mandibles loosened the sand crust, she used the forelegs in unison to fling the loosened sand backward. Her body, especially the abdomen, moved synchronously up and down to allow the sand to pass underneath.

At Base Borden and South Glens Falls, where the soil contained loamy sand mixed with gravel, females constantly removed pebbles from their excavations. One wasp at Base Borden pulled pebbles backward with the mandibles nine times. She pulled them to the top of the sand mound in front of her entrance. The pebbles rolled down the sides of the mound and, later, became incorporated in the leveling process. The wasp then moved from the top of the mound straight into the burrow flinging sand backward with the forelegs. Females that dug nests in loamy sand without gravelly inclusions did not remove pebbles or make intermittent buzzing sounds while loosening the pebbles underground.

After removing a pebble, most wasps made a hovering flight while facing the open entrance. The female that removed nine pebbles from her excavation made a hovering flight following eight of the nine sand removals. Most hovering flights were 2-4 sec in dura-

tion but some lasted 5-10 sec. After removing sand or a pebble, some females paused and cleaned their antennae, eyes and mandibles with the forelegs.

One wasp at Base Borden removed sand from her burrow 20 times in 50 min, or an average of once every 2.5 min. A second female removed 62 sand loads in 63.5 min, or about one load per minute. A third wasp dragged backward 49 loads of sand in 50.5 min. Other females spent 69 and 60 min to excavate a burrow. At the beginning of an excavation, females were inside their burrows loosening sand with the mandibles for as long as 5-6 min before moving sand onto the surface. Toward the end of a dig, wasps often spent less than a minute for this behavior. After clearing loose sand and pebbles from the burrow, females made a temporary closure of the entrance. They appeared in the opening headfirst flinging sand backward with the forelegs in unison while tamping the fill with the end of the abdomen. Three wasps took 15, 18 and 45 sec to temporarily close their entrances, resulting in one-third to one-half of the sand mound being put back in the opening.

After closing, females leveled the mound of soil in front of the opening. They walked across the mound in various directions flinging sand backward beneath the body with the forelegs until the mound was, more or less, flattened. Wasps nesting in mixed sand and gravel then placed pebbles on the fill with the mandibles interspersed with making hovering [orientation?] flights. This sometimes involved moving debris out of the way. The hovering flights, 10-50 cm high, were 15-50 sec in duration and made 10 sec to 2.5 min apart. During mound leveling as many as 10 hovering flights were interspersed after which a wasp rested for several seconds and then flew away. Mound leveling in five females took 5.5-11.0 min (Mean = 8.2 ± 2.22).

Provisioning

Sixteen hours over three days were spent at Base Borden in 1998 and 1999 observing females bringing prey to nests. Four wasps provisioned nests from 1044 to 1820 hrs at sand surface and air temperatures of 28-36° and 22-25°C, respectively. They spent 9-77 min [Mean = 28.6 ± 22.70, N = 18] between consecutive returns to a nest with prey. Females flew into the nesting area from a distance of >10 m. Such a wasp circled slowly in flight holding the prey ventral side upward with the middle legs while producing an audible buzzing sound. She then landed on the sand mound directly in front of an entrance or as far away as 50 cm before making a second flight to the mound. Two females at South Glens Falls brought prey to their nests at 1321 and 1442 hrs at sand surface temperatures of 44ºC and 49°C.

Retaining their grasp of the prey's body with the middle legs, wasps raked open the temporary closure using the forelegs in unison. Removal of a closure usually took 5-10 sec unless the area had been disturbed. Then, some females walked straight into the burrow holding the prey as described. However, most wasps released the prey ventral side upward just inside the burrow with its abdomen projecting from the entrance. Such females then turned around in the burrow, grasped the prey by its front end with the mandibles, and dragged it backward down the tunnel. Females spent about 2 min to remove the temporary closure, deposit the prey inside, *oviposit*, and remake the closure for the first prey for the cell. Not having to oviposit, a female taking subsequent prey into a nest spent only 15-45 sec [Mean = 31.6 ± 13.24, N = 18] inside and remade the closure in 6-9 sec. She then flew off immediately toward the hunting grounds making an audible buzzing sound. Some females rested on the sand before flying away. Other wasps made an orientation flight, rested on the sand, and flew away.

Final closure

After placing the full complement of prey in a cell, a wasp filled her burrow with sand and leveled the area of the entrance. One female at Base Borden appeared headfirst in her entrance 3 min after placing prey in the nest, walked onto the sand mound, and began raking sand backward into the opening with the forelegs. She repeated this behavior eight times at intervals of 15-97 sec [Mean = 65.0 ± 30.24]. This wasp made brief hovering flights, facing the entrance, following her third and fourth trips onto the mound to get sand. Near the end of the closure, the female raked sand backward from the sides as well as the top of the mound. Always facing away from the opening, she pulled several pebbles into the burrow with the mandibles and packed in sand with the end of the abdomen. She spent nearly 11 min to fill the burrow, flew a short distance away, and rested on the sand. The wasp returned to the area 1.5 min later and finished raking sand and pulling pebbles onto the filled entrance. She then flew away, 13 min after taking her last prey into the nest.

Nest structure and dimensions

Twenty-six nest entrances at Base Borden in 1998 and 1999 were mainly ovoid in shape and measured 10 × 15 mm. Below ground, the burrows were circular and 8 mm in diameter. Twenty-two burrows entered the soil obliquely at angles of 45-60B with the surface and terminated in one cell (Figure 3). One nest each at Base Borden in 1998 and 1999 was two-celled with cells 3 and 4 cm apart (Figure 3).

Base Borden burrows were significantly longer in 1998 than in 1999 [t = 3.75, df = 24, P = <0.001], ranging from 72 to 138 mm [Mean = 100.9 ± 24.35, N = 11] in 1998 and 62 to 91 mm [Mean = 71.4 ± 12.36, N = 15] in 1999. The three oldest 1998 nests had the longest burrows of 133, 138 and 135 mm. Cell depth in 1998 and 1999 at Base Borden was not significantly different, including the three oldest nests with the longest burrows [t = 0.51, df = 24, P = 0.62]. Cell depth in 1998 ranged from 43 to 73 mm [Mean = 53.3 ± 11.90, N = 11] and in 1999 from 48 to 69 mm

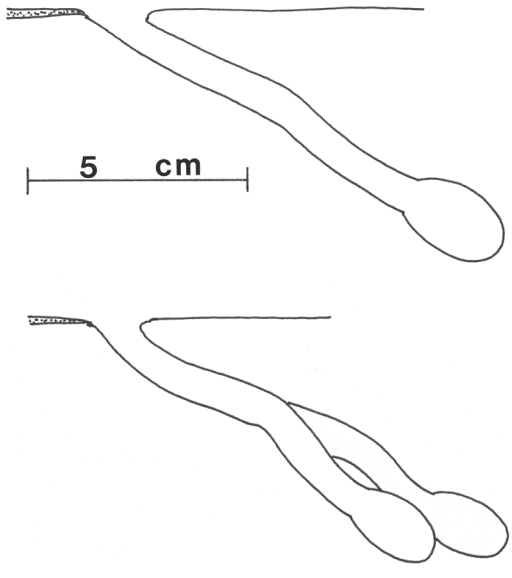

FIGURE 3. One- and two-celled nests of *Stictiella emarginata* as seen in side view. Sand mound is stippled. Scale refers to both nests.

[Mean = 51.4 ± 8.56, N = 15]. Cell size [N = 26] at Base Borden varied regardless of year: length [Range = 14-22 mm, Mean = 19.0 ± 1.71], width [Range = 13-15 mm, Mean = 14.4 ± 0.75], height [Range = 12-15 mm, Mean = 13.1 ± 0.94].

Cell contents

From five to nine prey [Mean = 6.9 ± 1.07, N = 18] were stored in fully provisioned cells at Base Borden. Individual prey weight ranged from 60.9 to 126.0 mg [Mean = 86.9 ± 17.08, N = 132]. Two wasps from Base Borden [voucher specimens] weighed 147 and 151 mg. One noctuid prey from Fort Drum weighed 93 mg. Aggregate prey weight per cell from Base Borden ranged from 456.8 to 757.9 mg [Mean = 581.6 ± 126.43, N = 18].

One cocoon from Base Borden, 69 mm deep, was 7 mm wide and 17 mm long, weighed 358.3 mg, and reared a male wasp. Two cocoons from Base Borden, 72 and 73 mm deep, were each 8 mm wide and 19 mm long, weighed 567.5 and 604.6 mg, respectively, and reared female wasps.

Of 132 prey in the cells, 78 (59.1%) were positioned head inward and ventral side upward. Fifty-four (43.5%) of the prey were placed head inward and on the side.

Females preyed on adults of seven species of Noctuidae and one species of Hesperiidae. Of 132 prey specimens, 124 (93.9%) belonged to the family Noctuidae and eight (6.1%) belonged to the family Hesperiidae (Table 2). Some prey species were associated with barren sandy and/or fire- adapted habitats. Prey individuals were probably captured on flowers or low growing herbaceous vegetation.

Egg

Stictiella emarginata eggs from four females at Base Borden in 1998 were approximately 4 mm long and 1 mm wide [N = 11]. Two recently laid eggs weighed 2.0 mg while a one day-old wasp larva weighed 2.15 mg. Eggs or 1st instar larvae were attached to the base of the prey's abdomen near its connection to the thorax or to the side of the thorax. The egg extended longitudinally along the side of the thorax toward the head. Eggs or 1st instar larvae were affixed about equally to either the left [N = 14] or right [N = 12] side of the prey.

A wasp's egg was affixed to the initial prey in the cell in eight nests at Base Borden. The position of the prey on which the wasp's egg or larva was affixed changed as additional prey items were added to the cell. In one incomplete cell with three moths, an egg was attached to the prey that was farthest in. In one cell with seven moths, a small larva was feeding in place on the fourth prey from the back end. In other cells, older larvae had moved around and were feeding on prey near the front end as these were the only prey left with nutrient value.

TABLE 2. Species of prey Lepidoptera of *Stictiella emarginata*.

Family and species of prey	Number of specimens	Source
NOCTUIDAE		
Apamea amputatrix Fitch	8	C.F.B. Borden
Apamea ophiogramma (Esper)	7	C.F.B. Borden
Calophasia lunula (Hufnagel)	25	C.F.B. Borden
Chytonix sensilis Grote	43	C.F.B. Borden
	1	Ft. Drum
	2	South Glens Falls
Euxoa scandens (Riley)	3	C.F.B. Borden
Euxoa incallida (J.B. Smith)	1	Gillaspy et al. 1962
Lacinipolia vicina (Grote)	14	C.F.B. Borden
Nedra ramosula (Guenee)	21	C.F.B. Borden
HESPERIIDAE		
Polites themistocles (Latreille)	8	C.F.B. Borden

Mortality

Five of 26 (19.2%) cells at Base Borden were afflicted with cleptoparasitic miltogrammine maggots or puparia. This included a one-celled nest in 1998 and two two-celled nests in 1998 and 1999. The single-celled nest held five paralyzed noctuids, no wasp's egg, two large maggots and two small maggots. The different sizes of the maggots indicate that the flies attacked at two different stages in the provisioning of the cell, perhaps a day apart. Both cells in the 1998 two-celled nest each held two miltogrammine puparia and six pairs of noctuid wings. The puparia in one cell were 5.5 mm long and 2 mm wide and weighed 21.9 and 21.3 mg, respectively. One cell of a two-celled 1999 nest contained seven pairs of noctuid wings and four miltogrammine puparia. The other cell held seven paralyzed noctuids, a small wasp larva weighing 2.15 mg, and four miltogrammine fly maggots. No maggots were reared to adult flies. Two puparia reared a male and female *Sphixapata vigilans* Allen [Sarcophagidae: Miltogramminae]. This fly species was observed on sand near *S. emarginata* nests and pursued provisioning wasps as they landed and entered nests.

Discussion

The geographic distribution of *S. emarginata*, as illustrated by Bohart and Gillaspy (1985), is disjunct (Figure 1). Specimens collected in the 1980s from the Upper Peninsula of Michigan brought these populations closer together (O'Brien 1989) and led us to believe that the disjunct distribution of *S. emarginata* was an artifact resulting from lack of collection records. Collection records from southern Ontario and Upstate New York field studies and museum specimens indeed bridge the gap between northern Michigan and the Middle Atlantic Region and provide evidence for a continuous, transcontinental geographic distribution for *S. emarginata*.

Stictiella emarginata has a flight period from early to mid-summer in southeastern Canada and northeastern United States. Collection dates for adults of this species from eight localities in northern Michigan, southern Ontario and Upstate New York range from 29 June [1999] to 31 July [1993]. There is one record from Toronto, Ontario labelled simply "August." Adult development, emergence and nesting at Canadian Forces Base Borden, Ontario seem to be tied to May-June temperature. Wasps nested earlier (5-7 July 1998, 29 June-2 July 1999) with warmer May-June 1998, 1999 average temperatures (17.40º, 17.17ºC) and later (26-28 July 1996, 13-14 July 1997) with cooler May-June 1996, 1997 average temperatures (14.75º, 14.85ºC).

Nesting information is available for six *Stictiella* taxa: *callista* Parker, *emarginata*, *evansi* Gillaspy, *formosa* (Cresson), *p. pulchella* (Cresson), and *pulchella serrata* (Handlirsch) (Table 3). Females of all species make a temporary closure of the nest. All *Stictiella* attempt to level the mound of soil in front of their entrance before flying off in search of prey. There is contradictory information about the leveling behavior of *S. formosa*. Lin *in* Gillaspy et al. (1962) observed a female "throwing…soil" behind her as she walked across the soil mound and entered the burrow. This wasp also walked across the mound in a different direction throwing soil before turning and reentering her entrance, yet Lin stated that the mound was "never leveled."

A clearly audible, high-pitched buzz accompanies an orientation flight in *Stictiella* species (Alcock and Gamboa 1975; Evans 1966; Gillaspy et al. 1962; Krombein 1964; this study). In *S. pulchella serrata* and *S. formosa* females followed potential prey as they visited low herbs, grasses, and flowers and then captured an individual with one quick strike before carrying it away in flight (Gillaspy et al. 1962). *Stictiella pulchella serrata*, *S. p. pulchella* and *S. evansi* capture moths, *S. callista* moths, skippers and butterflies, *S. formosa* skippers and butterflies, and *S. emarginata* moths and skippers (Alcock and Gamboa 1975; Evans 1966; Gillaspy et al. 1962; Krombein 1964; Parker 1917; this study)(Table 3). One female of *S. corniculata* Mickel is pinned with a noctuid moth (Bohart and Gillaspy 1985). Some cells contained only one prey species or genus [*formosa, p. pulchella*]. In other cells

TABLE 3. Nesting characteristics of species of *Stictiella*.

Characteristics	Species of *Stictiella**					
	callista	*emarginata*	*evansi*	*formosa*	*pulchella*	*serrata*
Temporary closure	+	+	+	+		+
Leveling behavior	+	+		+?	+	+
Burrow length (cm)	68	6-14	15-24	20	25-32	15-28
Cell depth (cm)	40	4-7	11-16	8-14	12-20	10-14
Number of cells/nest	1	1-2	1	5-17	1-2	1
Number of prey/cell	>1	5-9	15	7-11	19	12->21
Prey type	LHN**	HN	SG	HML	SN	CEOPSTY

**pulchella* and *serrata* are subspecies of *Stictiella pulchella*.

**Prey families of Lepidoptera are abbreviated as follows: C, Crambidae; E, Epipaschiidae; G, Gelechiidae; H, Hesperiidae; L, Lycaenidae; M, Nymphalidae; N, Noctuidae; O, Olethreutidae; P, Pyralidae; S, Pyraustidae; T, Tortricidae; Y, Phycitidae.

the species, genera and families were mixed within the known range of prey types [*formosa*, *p. pulchella*, *pulchella serrata*, *emarginata*, *evansi*].

Prey of *S. emarginata* vary in their feeding habits and are probably captured in different places. *Calophasia lunula* (Hufnagel) feeds on Butter-and-eggs [*Linaria vulgaris* Miller]. *Apamea ophiogramma* (Esper) feeds primarily on wetland grasses. *Apamea amputatrix* Fitch and *Polites themistocles* (Latreille) are also grass-feeding but may lay their eggs on non-grasses. Adults of *P. themistocles* are commonly seen on flowers along country roads. *Nedra ramosula* (Guenee) is host-specific on St. John's-wort [*Hypericum perforatum* L.]. *Lacinipolia vicina* (Grote) is a general feeder on low-growing herbaceous plants. *Chytonix sensilis* (Grote) feeds on a variety of fungi 15-20 years after a fire. *Euxoa scandens* (Riley) occurs in areas of dry, sandy soil and feeds on dicotyledons (Layberry et al. 1998; Rings and Downer 2001; T. L. McCabe 1999 personal communication).

Prey transport in *Stictiella* species is by flying, the wasp holding the prey head forward and ventral side upward with the middle or middle and hind legs. Size of prey may influence whether the hind legs assist the middle legs in prey carriage (Krombein 1964). Prey Hesperiidae of *S. formosa* were carried with the wings partly spread while prey Pyralidae of *S. pulchella serrata* were transported with the wings folded tightly against the body (Gillaspy et al. 1962; Krombein 1964). Prey Noctuidae and Hesperiidae of *S. emarginata* were carried both ways (this study). The prey is held only with the middle legs when removing the temporary closure and entering the burrow.

Final nest closure has been described only in *S. emarginata* (this study). Such behavior involves the wasp walking onto the sand mound and flinging soil backward into the open burrow. She rakes backward the loose soil using the forelegs in unison as she backs into the burrow and occasionally tamps this soil with the end of the abdomen. She levels the area of the entrance after filling the burrow flush. The entire process takes only one-fourth as long as burrow excavation.

There is much variation among *Stictiella* species in nest dimensions (Alcock and Gamboa 1975; Evans 1966; Gillaspy et al. 1962; Krombein 1964; this study) (Table 3). Although excavated in sandy soil, burrows and cells of *S. emarginata* were much shorter and shallower than in other species. The number of prey per fully provisioned cell in *Stictiella* species is highly variable (Table 3). *Stictiella emarginata* is unique in that only five to nine prey are stored per fully provisioned cell. Wasp cocoons recovered from old *S. emarginata* cells were enswathed with only six or seven pairs of noctuid wings (this study).

Although *Stictiella* species practice mass or delayed mass provisioning, there is one record for *S. pulchella serrata* that is suggestive of progressive provisioning. In that observation, a one-third grown larva was found in an incompletely provisioned cell with 21 moths. The nest had not received a final closure (Krombein 1964). There are records of delayed mass provisioning in *S. callista* and *S. evansi* in which larval wasps occupied incompletely provisioned cells (Alcock and Gamboa 1975; Evans 1966). These cells and that of *S. pulchella serrata* were provisioned for parts of at least two days.

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