LIFE HISTORY & NEST BIOLOGY OF THE MASON BEE OSMIA (ACANTHOSMIOIDES) INTEGRA CRESSON IN COASTAL DUNES (HYMENOPTERA: MEGACHILIDAE).

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Abstract. — Nest and cell architecture, pupation season, adult behavior, and floral visitation are reported for a population of the mason bee Osmia integra Cresson nesting in coastal dunes near Arcata, Humboldt County, California. Shallow nests were constructed in sand with one to five cells per nest formed from masticated leaf pulp mixed with sand. Most nests were scattered individually but a loose aggregation was found in one area. Photographs, descriptions and measurements of nests, cell architecture and cocoons are provided. Adults exhibited protandry, flew from late April to July, with peak activity in May. Cells observed in vitro overwintered as adults, completing pupation by November. Males displayed territorial behavior at foraging resources but not at nest sites. Males and females visited several flower species but females appear to prefer legumes, especially Lathyrus littoralis (Nuttall) Endlicher, based on observations and SEM study of four provisions and three foragers. This population lacked the dark red thoracic hairs characteristic of the species. Nest architecture differed markedly from previously reported mud nests plastered to a rock. Results suggest that synonymy of O. novomexicana with O. integra may need to be re-evaluated. More biological information is needed to clarify relationships within and among subgenera.

Key Words. — Hymenoptera, Megachilidae, Osmiini, solitary bee conservation, pollen

The only previous nest description for Osmia integra Cresson reported a cluster of mud cells plastered beneath a rock in Colorado (Hicks 1926, reported as O. novomexicana). Sugden (1985) referred to an O. integra population nesting beneath plants in Mono County, California, but provided no information regarding nest structure. No behavioral information has been reported for this species. This paper describes the nest architecture and reports aspects of the life history and behavior of a population from coastal dunes of northern California.

MATERIALS AND METHODS

The study was conducted near Arcata, Humboldt County, California within the original 76 hectares of the Lanphere-Christensen Dunes Preserve on the North Spit of Humboldt Bay. The site included the least disturbed coastal dune system in the Northern Pacific Border Region (Sweet 1981). The 1 km wide peninsula is composed of drifted beach sand that ranges in elevation from slightly below sea level to about 28 m. Cover ranges from barren sand or sparsely vegetated dunes to lodgepole pine/ Sitka spruce forests with dense underbrush. Descriptions and photographs of the study site are provided by Gordon (2000, 1992, 1984), Barbour & Johnson (1988), Barbour et al. (1985), Wiedemann (1984), and Sweet (1981).

Bees were observed and collected during daily or weekly site visits throughout the flight seasons 1979-1983. In June, 1982 fifteen fresh brood cells were placed in a screened jar of sand and kept in an unheated room until the following spring to study developmental progression. In June, 1983 additional nests were excavated and fifteen cells from these nests were refrigerated (2 degrees Celsius) for 19 days before they were dissected and the cells, provisions and eggs were measured with a Vernier caliper. Additional measurements were made from dried cells and by projecting photographs of fresh cells that included metric rulers. A total of 40 cells were measured from 21 nests. In 1988-89, a survey conducted to determine the distribution of nests of another bee species (Gordon 2000) provided additional cells and information regarding the distribution of and predation on O. integra nests.

Pollen samples from four provisioned brood cells taken from different nests and from three foragers with full or nearly full scopae were examined in a scanning electron microscope (ETEC Autoscan, Hayward, CA.). Three cells were collected on June 1 and one cell on June 22, 1983. One forager was collected on June 2 and two on June 6, 1983. Samples were compared to reference samples collected from fresh flowers of eight species in bloom that foragers might have utilized. Pollen grains were examined at 1,000 to 1,500 diameters for characteristic sculpturing and pore shapes to determine the floral source. Counts of pollen grains were taken at five random locations in each sample and the total number of pollen grains for each species was counted at 200 diameters magnification to determine the percent composition. Samples were prepared according to Lynch and Webster (1974), with the exception that specimens were air dried overnight from 100% ethanol rather than critical point dried (Peng et al. 1987).

Sample bee specimens were deposited in the USDA ARS Bee Biology and Systematics Lab at Logan Utah, the California Academy of Sciences, and the Bohart Museum of Entomology at the University of California, Davis.
RESULTS AND DISCUSSION

Nests. — In 1979 a number of nests were concentrated in a situation approaching an aggregation at the edge of a forest in “Inland Dunes” habitat (Figs. 1, 2, 3). A systematic survey of the study site in 1988 revealed single nests were distributed throughout sparsely vegetated areas within the “Foredunes,” “Transitional Dunes” and “Inland Dunes” habitats (Fig. 4, see Gordon 2000 for habitat descriptions). Most of the 44 nests recovered were widely dispersed. 93% were from the “Foredunes”, 2% from “Transitional Dunes” and 4% from “Inland Dunes” habitats (Gordon 2000). During that study a number of O. integra nests were discovered that had been excavated by rodents which had chewed open the cells and consumed the bee larvae.

In all nesting sites examined nest tunnels consisted of unlined burrows constructed in loosely consolidated sand within the root zone of sparse annual herbs and grasses (Fig. 5). Many nest entrances were obscured under the base of a plant, but tumuli often were visible (Fig. 6). The loose sand collapsed so readily that it was difficult to determine the tunnel diameter except for three nests (11 mm each). Tunnels generally descended at an angle of about 40 degrees, were about eight cm in length, less than five cm deep (Figs. 7, 8). Some tunnels curved to the side around obstructions such as plant roots and one had a short side branch. Thirty-seven nests contained one to five cells constructed in a linear series, although the axis of each cell varied with respect to adjacent cells and the alignment of the central axis of the tunnel. In one nest a fresh cell was attached to two cells from the previous season from which the adults had already emerged.

Cells, Provisions and Eggs. — Cells ranged from 8.7 to 20.1 mm in diameter at the widest point (mean = 13.5 ± 1.9 SD, median = 13.2, n = 40). Cell length ranged from 10.1 to 26.1 mm (mean = 16.3 ± 3.2 SD, median = 16.1, n = 40). Cell walls were constructed of masticated leaf material with sand grains incorporated throughout the pulp matrix (Figs. 9-14). Two females that were captured returning to nests carried pulp wads which contained no sand, so it appears the sand is incorporated as it is plastered into the nest tunnel. Completed cells are urn-shaped with a coarse, fibrous external surface and an inner surface that is smooth but not polished (Figs 9, 10). Longitudinal section revealed that the roof of the cell was thinner than the floor, which was thickened at the entrance (Figs. 10-12). The cap is smooth and concave externally; coarse and protruding internally (Figs. 10, 11). The entrance of unfinished cells was flattened dorsoventrally into an oval with a rounded threshold (Fig. 13).

One cell in the early stages of provisioning contained a thin layer of buff-colored pollen plastered evenly over the floor and partly up the sides of the entire cell. Another, containing more pollen, had the provisions restricted to the posterior end, forming a thicker (3 mm) mass with a sloped surface. In both cases the provisions had apparently been mixed with liquid, were dry and hard, not sticky, and contained no loose pollen grains. Completed provisions from nine cells all were formed into basically rounded balls (Fig. 14), but six had flattened, sloped faces, and three were somewhat cuboidal. Sizes ranged from 7.6 to 14 mm in diameter (mean = 10.1 ± 2.8 SD, median = 9.5, n = 6). All the pollen balls were light orange, firm with dry, sticky surfaces, had no free pollen grains, and adhered loosely to the cell floor. In six cells the provisions contacted and stuck to the walls. In three cells the provisions were only attached to the floor and did not contact the walls or ceiling. Eggs were quite small (two 3 x 1 mm and one 4 x 1 mm) considering the size of the adult. The posterior ends of the eggs were slightly imbedded into the top of the provision, with the anterior end more free. SEM examination of four cells revealed that they contained pure Lathyrus littoralis (Nuttall) Endlicher pollen (Figs. 15, 16).

Cocoons and Development. — The cocoon is oval and is closely appressed to the posterior half of the cell. The space at the anterior end of the cell is filled with intact fecal pellets, which are round in cross-section, long, and abruptly taper to a point at each end (Figs. 17, 18). The cocoons are composed of three layers: an outer network of loose hyaline fibers, some of which attach to the cell wall, a middle layer that is dense and non-fibrous with an uneven surface, and a thin, dense, non-fibrous inner layer that is highly polished on the inner surface (Figs. 17-22). The middle and outer layers are delaminated, forming a flattened nipple on the anterior end of the cocoon (Figs. 19, 20) with a few fine fibers stretching between the layers. This nipple is obscured by the outer layer of fibers in unweathered cocoons (Figs. 20, 21). In the center of the nipple a round pore penetrates only the inner layer; there is no evidence of it on middle or the outside layers. This pore is filled with a dense network of fine tan fibers (Fig. 22).

It appears that O. integra pupates in the fall and overwinters as adults. Two cells that were stored in a jar of sand opened on August 5 contained pupae that were partially melanized. Two more cells opened on November 18 contained fully developed adults.

Adults. — Notal hairs on the adults collected or observed (more than 100 individuals) ranged from slightly reddish to golden on the dorsum of the thorax, indicating that this population lacks the dark red hairs characteristic of the species. All of the pinned specimens examined in 2001 had blonde notal hairs, indicating that the ones collected with reddish color had faded during storage. The adult population began to appear in early April, built rapidly in May, dropped off quickly by the end of June and was gone in early July. Protandry was evident, and males were usually not seen after the second week of June. Males were collected between April 2 and June 20,
peaking in abundance between the fourth week of April and the second week of June (n = 14). Females were collected between March 27 and July 5, peaking in abundance between the third week of May and the first week of June (n = 24). Although a variety of flowers were visited (Table 1; Fig 23, 24), observations and pollen analysis suggest a preference for legumes, especially beach pea (L. littoralis), which is very abundant on the Preserve during the flight season (Fig. 4) and whose bloom phenology closely coincides with the flight season of O. integra (Gordon 1984).

Although nest initiation was not witnessed, some females were observed excavating sand from established nests (Fig. 25) and it appears the females dig their nest burrows. Several females were observed collecting leaf material from three plant species (Table 1) and entire leaves had been consumed on some strawberry plants (Fragaria chiloensis Duchesne, Fig. 26). Three nests that were excavated in the early morning before flight began contained inactive females. Two were in tunnels with no cells and the third was inside a completed, unprovisioned cell, indicating that females spend the night inside their nest.

Table 1. Plant utilization records for Osmia integra Cresson in coastal dunes of northern California. Floral visitation, territorial mating behavior exhibited by males around floral resources, and sources of masticated leaf material used by females. Nectar or pollen collection was not distinguished.

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Flower Visitation</th>
<th>Leaf Material</th>
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<tbody>
<tr>
<td>Abronia latifolia Eschscholtz</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Cakile maritima Scopoli</td>
<td>F, P</td>
<td></td>
</tr>
<tr>
<td>Convolvulus soldanella L.</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Fragaria chiloensis Duchesne</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Lathyrus littoralis (Nuttall) Endlicher</td>
<td>F, P</td>
<td></td>
</tr>
<tr>
<td>Lotus sp. a</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Mesembryanthemum chilense L.</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>Oenothera cheiranthifolia (Sprengel) Raimann</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Trifolium wormskioldii Lehmann</td>
<td>F</td>
<td></td>
</tr>
</tbody>
</table>

a F = foraging, P = patrolling behavior.
b L. micranthus Bentham or L. purshianus (Bentham) FE Clements & EG Clements.

Males exhibited territorial behavior at floral resources: patrolling, taking nectar, and perching on the sand. One interaction was observed in which an intruding conspecific male was chased away and the patrolling male returned to his perch. Males were regularly observed patrolling foraging resources for females, and once a male was observed pouncing on a female visiting L. littoralis, but no mating occurred. Although males were usually not seen around nests or patrolling nesting sites, on one occasion three males were observed in a nest site. No matings were observed, but circumstantial evidence suggests that mating occurs at floral resources.

Distribution. — During the study period, O. integra was not observed when a few collecting trips were made to nearby coastal dunes at Big Lagoon, Elk River Spit or the South Spit of Humboldt Bay.Specimens were collected approximately five miles south of the preserve near the U.S. Coast Guard station in Samoa. A faunistic survey at the University of California Bodega Marine Reserve showed that O. integra was not present in those dunes (Thorp and Gordon 1992).

Taxonomic Confusion. — Hicks (1926, reported as O. novomexicana) collected a female in Colorado on a single mud nest plastered to the underside of a rock. There were six cells with no mud wall between the provision masses and the rock. Nest architecture in this California population differs markedly from that only previous report. The nest descriptions and habitat for the Mono County population were similar to those reported here from the Humboldt County population (E. Sugden, personal communication). Hicks did observe the female going under the rock before he collected her, but does not provide much more information. The biology of two California populations suggest that synonymy of O. novomexicana with O. integra may need to be re-evaluated, or that the bee Hicks collected with the mud nest may not have constructed that nest. Comparing nest behaviors within Acanthosmioides, Rust et al. (1974) reported that some members of the subgenus use mud and others use masticated leaf material and that constructing burrows is unusual. Frolich (1983) suggested that comparing nesting behaviors should help sort out the taxonomic confusion among subgenera. Clearly, more biological information is needed to clarify relationships.
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LITERATURE CITED


