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NOMADA ANNULATA SMITH (HYMENOPTERA: ANTHOPHORIDAE), A CONFIRMED CLEPTOPARASITE OF *ANDRENA MACRA* MITCHELL (HYMENOPTERA: ANDRENIDAE) AND OTHER *NOMADA-ANDRENA* ASSOCIATIONS

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Abstract.—*Nomada annulata* Smith is a cleptoparasite in the nests of *Andrena macra* Mitchell. This relationship was confirmed when *N. annulata* adults were found inside *A. macra* brood cells in winter, *N. annulata* prepupae were found inside brood cells in summer, and prepupae were reared to the adult stage by the fall season. Other *Nomada-Andrena* associations, reported in North America north of Mexico, are discussed.

Key Words: *Nomada,* cleptoparasites, *Andrena,* bees

Nomada is the largest genus of Nomadinae in North America north of Mexico and contains approximately 300 species (Hurd 1979). Less than 15% of the North American species have any aspect of their biology reported. *Nomada* are cleptoparasites in the nests of other bees, mainly *Andrena.* Other Andrenidae (*Nomadopsis, Panurgus*), Anthophoridae, Halictidae, and Melittidae also contain members utilized as hosts (Bohart 1970, Eickwort and Abrams 1980).

An earlier study of *Nomada annulata* Smith reported the identification of a sex-specific compound in the cephalic secretions of males (Duffield et al. 1990). It was in this study that *Andrena macra* Mitchell was implicated as the host of *N. annulata.* This current paper outlines the research that confirmed the *N. annulata-A. macra* association.

The definitive and putative *Nomada-Andrena* associations, reported in America north of Mexico, are tabulated and discussed. The methodology presented herein can be used to accurately associate *Nomada* species with *Andrena* hosts, in future investigations.

MATERIALS AND METHODS

Nesting sites were found on the United States Marine Corps Reservation at Quantico, Virginia, by walking alongside roadways and noting bee and cleptoparasite flight activity, in May 1983. All sites were on sun-exposed roadsides, had soil of a clay-like consistency, and had sparse amounts of grasses in them. The approximate distance between nesting sites ranged from 1 mile, between sites I and III, to 5 miles, between sites I and IV.

Andrena macra are solitary, univoltine bees that conduct nesting activities from early May until the middle of June, in Virginia. Their nests display an aggregated or clumped distribution within each site. A typical *A. macra* nest contains an entrance, tumulus, main vertical shaft, lateral shafts, and 4–12 brood cells (Riddick 1992).

Winter dormant bees were excavated from nests at nesting site I from March to May

1984. A trench was dug in front of a m^2 area of the site, where *A. macra* nest entrances were aggregated on the surface in the previous nesting season. Soil particles were then removed from the wall of the trench with a microspatula. Brood cell depth was approximately 30–70 cm beneath the surface of site I. A cell is an oval to urn-shaped chamber in which an immature bee is reared. Each is composed of two walls: an outer wall of compacted soil and a thin, shiny inner lining of a wax-like composition. Cells were located and checked for prepupae and adult bees, which became visible when the cell wall was broken with a microspatula. No attempt was made to distinguish cells of a nest from those of another.

Adult *N. annulata* and *A. macra* were collected while they flew over the surface of nesting sites in May 1984, in order to estimate their relative abundance. Standardized trapping of bees occurred with a sweep net, while traversing the sites. The time and temperature were recorded for each session.

Prepupae involved in the rearing trials were excavated from nesting sites II and III from July to August 1984; and site II in June 1985. Brood cell depth beneath the surface of these sites ranged from 30–70 cm. Each prepupa, with most of its brood cell, was carved out of the ground with the microspatula and placed in a 4-dram glass shell vial. Vials were transported to the laboratory inside an ice chest on the same day.

In the first rearing trial, 71 prepupae were collected then stored at 3.0°C for two to three months, because it was assumed that prepupae would normally overwinter as prepupae, and therefore required months of cold exposure in the laboratory before development could resume. Rearing at room temperature (24–27°C) began on 29 October and ended on 21 December 1984, when all prepupae had metamorphosed into adults or died. The rearing chamber consisted of a plastic container (26 × 36 × 14 cm) covered with a dark trash can liner. Each shell vial was examined at least once a week to notice whether prepupae had died and if brood cells were dry. Water droplets were added directly to the outer cell wall as needed, to maintain moisture within individual vials.

The second rearing trial involved 47 prepupae excavated from nesting site II between 22–29 June 1985. The second trial began on 30 June, without any prior cold exposure, and ended by 24 October. The rearing chamber was a styrofoam ice chest (14 × 30.5 × 14 cm) which had a strip of plastic between the body and lid. This chamber was designed to keep moisture inside. Maintenance procedures were the same as those used in the first trial.

Reared adults were sacrificed, preserved, and stored in the Insect Collection, Department of Zoology, at Howard University.

Results

Nomada annulata overwintered inside *A. macra* brood cells. Thirteen brood cells (3.37%) contained a *N. annulata* adult, all alive, in winter 1984. Live *A. macra* were found in 121 cells; 72 (18.65%) contained a prepupa, 49 (12.69%) contained an adult. Dead *A. macra* were found in 36 cells; 04 (1.03%) contained a prepupa, 32 (8.29%) contained an adult. Notice that 216 cells (55.96%) contained fungus, covering the contents. Empty cells (195) were also present, but not included in the calculation of percentages.

Nomada annulata were first observed at the surface of *A. macra* nesting site I on 10 May 1984, days after *A. macra* major emergence. Within a 32 min collecting session at site I, a single male *N. annulata* and 26 *A. macra* (males > females) were captured as they flew above the surface. Air temperatures ranged from 29–34°C. Male *N. annulata* were apparently searching for females to mate with.

By 15 May, *N. annulata* were more abundant at the nesting sites. Forty *N. annulata* (males and females) were captured, with 11

A. macra (males < females), in 41 min at site I. Air temperature was at least 21°C. On 19 May, 24 *N. annulata* were captured, with 8 *A. macra* females, in 38 min (temp. 29–30°C) at site I; 23 *N. annulata,* with 4 *A. macra* females, in 35 min (temp. 30–40°C) at site II; 22 *N. annulata,* with 11 *A. macra* females, in 37 min (temp. 48–49°C) at site IV; and 14 *N. annulata,* with 16 *A. macra* females, in 21 min (temp. 38–39°C) at site V.

When investigating *A. macra* nests, female *N. annulata* flew above the surface at a height of 5–8 cm, under sunny to partly sunny skies, if air temperatures were at least 20°C. Each cleptoparasite landed on the nest tumulus, vibrated the distal portion of its antennae down into the opening, entered it, but usually retreated at once. The maternal host bees sometimes appeared at their entrances soon thereafter. At other instances, *N. annulata* entered nests and remained within them for a minute or more.

Bee prepupae were present within *A. macra* brood cells, in the summer. Of a total of 71 cells containing live bees, excavated in July and August 1984, 1 cell (1.4%) contained a *N. annulata* prepupa and 70 cells (98.6%) contained an *A. macra* prepupa. Of 47 cells containing live bees, excavated from 22–29 July 1985, 7 cells (14.89%) contained a *N. annulata* prepupa and 40 cells (85.11%) contained an *A. macra* prepupa.

The first rearing trial began on 29 October 1984, proceeding a period of cold exposure. One *N. annulata* (male) prepupa metamorphosed into a pupa by 21 November, and then into an adult, with expanded wings and complete pigmentation, by 10 December. Six *A. macra* (2 males : 4 females) were reared to mature adults, by 21 December.

The second rearing trial began on 30 June 1985, without prior cold exposure. Two *N. annulata* prepupae metamorphosed into pupae by 26 September, and metamorphosed into adults, with expanded wings and complete pigmentation, by 29 October. Eighteen *A. macra* (10 males : 8 females) were reared successfully by 29 October as well.

Four *N. annulata* failed to develop to the mature adult stage for several reasons. A parasitoid (mutillid wasp) egg was attached to the cuticle of one; the mutillid immature died several days later in the laboratory, and the paralyzed *N. annulata* prepupa soon succumbed. Another *N. annulata* prepupa was found covered with an unidentified fungus. Another had died for no apparent reason. One *N. annulata* female developed to the premature adult stage, but failed to expand its wings.

Discussion

Nomada annulata overwintered as adults within *A. macra* nests. Other *Nomada* overwinter as prepupae or as adults inside host nests. Rozen (1977) indicated that members of Nomadinae typically pass the winter as prepupae in the nests of their hosts, and then resume development in the spring season. However, Eickwort and Abrams (1980) have determined that this pattern is variable. They found *Nomada* overwintering both as prepupae and as adults, in the nests of *Agapostemon* (Halictidae) hosts. Also, *Nomada* adults were found within *Andrena* brood cells in the fall season, and presumably overwintered within the cells (Linsley and MacSwain 1955, Osgood 1989).

Overwintering within host brood cells can be advantageous since: (1) the wax-lined brood cells may deter microbial infestations (Duffield et al. 1984), thus providing a better hibernaculum than crevices in the ground; (2) it insures that opposite sexes are in the vicinity for mating soon after spring emergence; and (3) it eliminates the need to depart the emergence site to search for host nests, if *Andrena* offspring construct their nests in the site from which they emerged.

Nomada annulata emerged in May, several days after the major emergence of *A. macra. Nomada* sp. emerges days after the emergence of males of its potential host, *A.*

Table 1. *Nomada-Andrena* associations in America north of Mexico; an asterisk (*) denotes a definitive host, lack of an asterisk denotes a putative host.

Nomada sp.	*drena* host	Reference
N. annulata Smith	*A. macra* Mitchell	Hurd 1979, Iwata 1976
N. annulata Smith	**A. macra* Mitchell	This study
N. calloxantha Cockerell	**A. nivalis* Smith	Miliczky et al. 1990
N. cressonii (Robertson)	**A. crataegi* Robertson	Osgood 1989
N. crudelis Cresson	*A. obscuripennis* Smith	Linsley & MacSwain 1955
N. edwardsii Cresson	**A. perimelas* Cockerell	Linsley & MacSwain 1955
N. imbricata Smith	**A. vicina* Smith	Packard 1868
N. morrisoni Cresson	*A. irana* Cockerell	Hicks 1934
N. obliquella Fowler	*A. suavis* Timberlake	Linsley & MacSwain 1959
N. obliterata Cresson	*A. vicina* Smith	Hurd 1979
N. obscurella Fowler syn. *N. fowleri* Cockerell	**A. caerulea* Smith, syn. *A. complexa* (Viereck)	Linsley & MacSwain 1955, Rozen 1966
N. opacella Timberlake	**A. caerulea* Smith	Linsley & MacSwain 1955
N. opacella Timberlake	**A. suavis* Timberlake	Linsley & MacSwain 1955
N. pulchella Smith	**A. vicina* Smith	Packard 1868
N. vallesina Cockerell	*A. irana* Cockerell	Hicks 1934
N. vicina Cresson	*A. vicina* Smith	Hurd 1979
Nomada sp.	*A. basilicis* Viereck	Rozen 1966
Nomada sp.	**A. chalybaea* (Cresson)	Thorp 1969
Nomada sp.	*A. chylismiae* Linsley & MacSwain	Linsley et al. 1963b
Nomada sp.	*A. deserticola* Timberlake	Linsley et al. 1964
Nomada sp.	**A. flexa* Malloch	Rozen 1966
Nomada sp.	*A. helianthi* Robertson	Parker & Bohart 1982
Nomada sp.	*A. linsleyi* Timberlake	Linsley et al. 1963a
Nomada sp.	*A. miserabilis* Cresson syn. *B. bipunctata* Cresson	Michener & Rettenmeyer 1956
Nomada sp.	*A. raveni* Linsley & MacSwain	Linsley et al. 1963b
Nomada sp.	*A. rozeni* Linsley & MacSwain	Linsley et al. 1963a

macra, at a site in North Carolina (Sivik 1954). Emergence after *A. macra* can be advantageous because it provides time for mating and building of nests by the maternal host.

Female *N. annulata* often landed at *A. macra* nest tumuli and then vibrated the distal end of their antennae into the entrance. Olfactory cues present at the entrance or within the nest are received in this manner; indicating if a partially provisioned cell is available, if the maternal host is inside, and if another cleptoparasite visited the nest (Cane 1983). *Nomada opacella* Timberlake wait near *Andrena caerulea* Smith and *Andrena suavis* Timberlake nests, and enter them after the maternal females depart (Linsley and MacSwain 1955). Successful invasions may occur when the nest becomes temporarily vacant, as females depart to collect pollen and nectar for the provision mass of each cell.

Nomada annulata were seen entering *A. macra* nests and sometimes remaining inside them for at least one minute. Similarly, *N. opacella* remained inside *A. caerulea* and *A. suavis* nests for 5–7 min maximum (Linsley and MacSwain 1955); and *Nomada* sp. remained inside an *Andrena chalybaea* (Cresson) nest for 1–4 min (Thorp 1969). *Nomada* invade nests, locate partly provisioned brood cells and oviposit in the inner cell walls (Bohart 1970).

Upon hatching, the *Nomada* larva de-

stroys the *Andrena* egg then progressively feeds on the provision mass intended for the victim (Linsley and MacSwain 1955, Rozen 1977). Each *Nomada* larva may achieve the prepupal stage of development during the summer season (Rozen 1977).

Nomada annulata prepupae were excavated from *A. macra* brood cells in the summer; three were reared to the mature adult stage in the fall. This evidence verifies that *N. annulata* is a cleptoparasite of *A. macra* nesting in Virginia. Other nesting populations of *A. macra* have been implicated as hosts for *N. annulata* (Hurd 1979, Iwata 1976), however, the methods used to confirm their associations are not given.

The 26 *Nomada-Andrena* associations reported in North America north of Mexico are listed in Table 1. Six were confirmed by rearing *Nomada* immatures, excavated from *Andrena* brood cells, to the adult stage in the laboratory. These previous associations include: *Nomada obscurella* Fowler-*A. caerulea, N. opacella-A. caerulea, Nomada edwardsii* Cresson-*Andrena perimelas* Cockerell, *N. opacella-A. suavis* (Linsley and MacSwain 1955); *Nomada calloxantha* Cockerell-*Andrena nivalis* Smith (Miliczky et al. 1990); and *Nomada* sp.-*A. chalybaea* (Thorp 1969).

Other associations were confirmed by locating *Nomada* prepupae or adults inside nests of *Andrena,* without rearing. For example, *Nomada imbricata* Smith and *Nomada pulchella* Smith larvae were found inside *Andrena vicina* Smith brood cells (Packard 1868), a *Nomada* sp. prepupa was found in an *Andrena flexa* Malloch brood cell (Rozen 1966), and *Nomada cressonii* (Robertson) adults were found in *Andrena crataegi* Robertson brood cells in the fall season (Osgood 1989).

Remaining associations were apparently determined by observing *Nomada* females as they entered *Andrena* nests. This method, by itself, is inadequate for confirming associations. It does not indicate whether parasitization had occurred. Also, this method does not reveal whether the *Nomada* immature can complete the larval stage on the pollen type in the host cell.

Effective methods for confirming *Nomada-Andrena* associations involve: (1) rearing *Nomada* immatures to the adult stage in the laboratory, or (2) locating *Nomada* prepupae in *Andrena* brood cells, when rearing is not feasible.

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