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ETHOLOGY OF THE BEE *EXOMALOPSIS NITENS* AND ITS CLEPTOPARASITE (HYMENOPTERA: ANTHOPHORIDAE)

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Abstract.—The nesting biology and other aspects of the natural history of *Exomalopsis nitens* (Exomalopsini) are described and compared with the ethology of other members of the genus. This bee nests in walls of cracks in claylike soil in southern California; cells range in depth from 20 to 54 cm. Numerous females use a single surface entrance to the fissures, but each apparently constructs an individual nest in the crack face. Cells are arranged either singly or in series of two and agree in shape and other details with cells of other species in the genus. Provisions are formed into smooth elongate loaves, each supported by a 'foot' at the front. Elongate, curved eggs are deposited on top of the food masses toward the front and feeding larvae crawl around the masses. Fully fed larvae either defecate and pupate immediately, or spin cocoons incorporating fecal material and then enter diapause, depending upon factors not fully understood. The structure of the cocoon differs in certain respects from that of other *Exomalopsis*. An undescribed species of cuckoo bee belonging to the genus *Melanomada* (Nomadini) attacks the host nest by entering just after the *Exomalopsis* females depart to forage, and then depositing eggs in the cell wall. *Melanomada* larvae crawl as they feed and enter diapause without cocoon spinning.

This is the first account of the nesting biology of *Exomalopsis* (*Anthophorisca*) *nitens* Cockerell (Exomalopsini). This species ranges from Santo Tomas, Baja California, Mexico, north to Monterey County, California, and, in southern California, inland to Oak Grove, San Diego County, and the Gavilan Hills, Riverside County. *E. nitens* has also been taken at Bagby, Mariposa County, in the western foothills of the Sierra Nevada (Timberlake, 1980). We also present data on an undescribed species of cuckoo bee belonging to *Melanomada* (Nomadini). This association, considered highly probable before (Rozen, 1984), is now confirmed, but the cleptoparasite was thought to be *Hesperonomada melanantha* Linsley. We will name and describe our species, which is closely related to *H. melanantha,* in a taxonomic revision of *Melanomada.* The monotypic *Hesperonomada* is a junior synonym of *Melanomada* as proposed earlier by Rodeck (1945).

Samples of burrows, cells, cocoons and immature stages are in the collections of the American Museum of Natural History.

NESTING ETHOLOGY OF *EXOMALOPSIS NITENS*

This species nested about 0.5 mile west of Interstate 15 along Indian Truck Trail Road, 12 miles south of Corona, Riverside County, California. R. R. Snelling first discovered the site in 1983, and we made our study on May 22, 24–26, 1985.

Description of nesting area. All nests were in cracks (Figs. 2, 3) in sloping ground

on a hillside that was partly covered with clumps of herbaceous plants about one meter high, consisting predominantly of grasses, *Eriogonum fasciculatum,* and *Hemizonia fasciculata* (Fig. 1). The vegetation cast little shadow on the surface entrances to the nests, which were not in areas that would be subject to flooding or man-made disturbances. We found six surface entrances altogether, four within a meter of one another and the other two, 20 cm apart, approximately 30 m away. More than one female used each surface entrance, as is characteristic of other *Exomalopsis,* and we captured a maximum of 12 females coming to or leaving one surface entrance. All surface entrances allowed access to deep crevices that were often closed at the surface. These long, essentially vertical fissures (Fig. 3) penetrated the ground well below where cells were recovered (20–54 cm), ran in various directions, and occasionally interconnected. They presumably resulted from shrinking of the claylike substrate as it lost water with the advancing dry season. The surface entrances (Fig. 2) represented places where surface debris did not obscure the crack, so that the bees, by entering at that spot, were then able to descend into the crevice and construct nests. All the entrances lacked tumuli and turrets. The vertical, uneven opposing faces of a fissure were separated in some places by several centimeters so that females, once in the crack, had available to them much of the two faces in which to start nests. As a consequence, females did not construct composite main burrows as is the case with most *Exomalopsis.*

The fine, claylike soil contained irregularly shaped, small stones that were abundant toward the surface but gradually became less abundant below. At the cell level the soil was moist and difficult to excavate because its sticky nature caused it to adhere to trowels and knives, and we could not easily fracture small soil clumps when we attempted to twist them apart. The soil in many ways was reminiscent of the clayey soil in which *Exomalopsis chionura* Cockerell was also found nesting in vertical fissures (Rozen and MacNeill, 1957).

Description of nests. Nest entrances were scattered along the vertical surfaces of the cracks. One series of five entrances, 20–22 cm below the ground surface, was grouped so that some holes were as close as 2 cm and the greatest distance between any two was 7 cm. Elsewhere entrances were probably more widely scattered, both horizontally and vertically. Although some were found as deep as 54 cm, we suspect that even deeper ones would have been found had we had time to dig deeper.

The entrances in the crack faces were circular, not filled with soil and approximately 3.5–4.0 mm in diameter. The relatively few cells associated with some entrances suggested that a single female was responsible for the tunnel and associated cells. The main tunnel, unfilled, penetrated in a meandering fashion usually more or less horizontally (Fig. 3), but some burrows at greater depths descended almost vertically. Both main tunnels and laterals were 3.3–3.5 mm in diameter (four measurements) and had a non-waterproof wall that generally showed no indication of having been masoned and that was so rough that we could not detect signs of pygidial plate prints. Laterals were filled with soil after completion. Several clusters of cells, presumably nests, were close to the crack wall. One such cluster (Fig. 3) ranged horizontally from 3 to 6 cm from the crack. The largest single nest, still incomplete, contained six cells, and another five cells.

Cells were arranged both singly (Fig. 4) and in linear series of two (Fig. 5) and had the front end always higher than the rear, although the slope of the long axis varied.

Figs. 1, 2. 1. Nesting site of *Exomalopsis nitens,* 12 miles south of Corona, California, showing general vegetation type and R. R. Snelling examining nesting surface. 2. Pencil pointing at surface entrance to nest of *Exomalopsis nitens,* in partly obscured crack extending from lower left hand corner to upper right hand corner of picture.

The cell ceiling was vaulted whereas the floor was flatter, so the cells were not symmetrical around their long axes. Cell length (from rear of cell to middle of closure) ranged from 7.0 to 8.0 mm (five measurements); maximum cell diameter, 4.8–5.0 mm (seven measurements); and diameter of entrance, 2.9–3.5 mm (five measurements), so that the entrance was generally smaller than the burrow diameter. The cell wall did not show definite signs of having been masoned, and was neither harder nor softer than the substrate. The lining was smooth but uneven because of small stones protruding into the lumen. We could not easily peel the somewhat shiny coating from the surface, and it seemed waxlike when scraped with fine forceps. When heated on a hotplate to 700°F, however, the coating did not melt and remained otherwise unchanged.

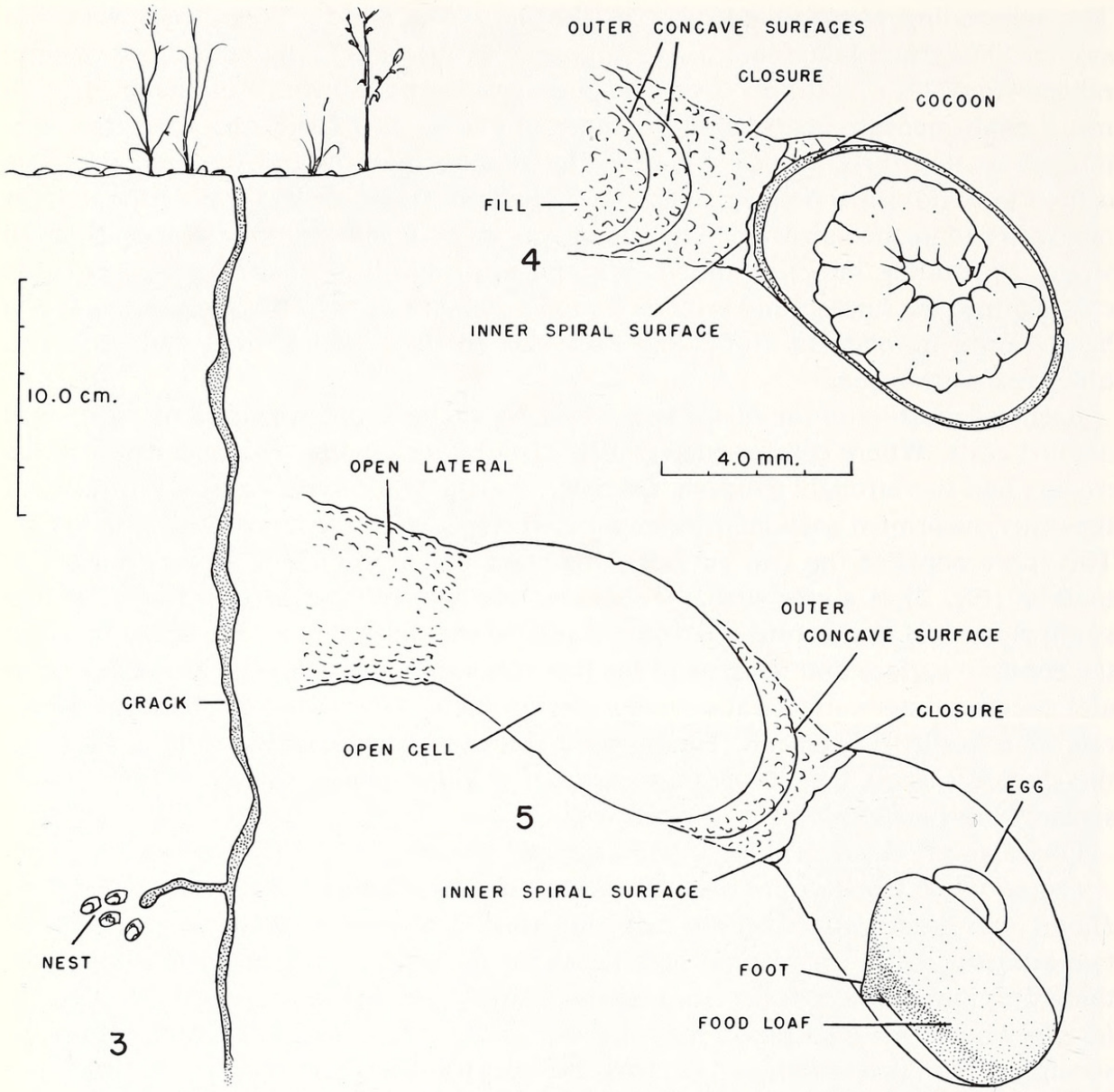
Each cell closure on the inside consisted of a slightly concave spiral of 4 to 5 well defined coils. Where cells connected directly to laterals (Fig. 4), the outside of the closure had two strongly concave, specially worked, smooth surfaces, one in front of the other, imprinted particularly around the periphery by the female's pygidial plate. The space between the two surfaces was filled with soil. Where two cells were in tandem (Fig. 5), a single strongly concave, smooth surface appeared between the spiral closure of the second cell and the rear of the first cell, and the space between the concave surface and the rear of the first cell was filled with soil. The spiral inner and concave outer surfaces absorbed water droplets, although at a somewhat slower rate than freshly broken soil. The pygidial plate embossings on the outer surfaces of the closure suggest that the female uses her pygidial plate to work not only these surfaces but presumably also the cell wall.

Laterals were filled with loose soil after cell closure.

Provisioning. During our excavations, we only observed bees collecting pollen from *Hemizonia fasciculata* (Compositae), but most food loaves and feces consisted of two kinds of pollen, one being three times the diameter of the other. We conclude, therefore, that another pollen source was visited, very possibly *Eriogonum fasciculatum,* which was also blooming adjacent to the nests. Recorded floral visits on specimens we have examined include the plant genera *Calochortus, Malvastrum, Opuntia, Bloomeria, Chlorogalum, Grindelia, Hemizonia, Heteromeles,* and *Clarkia.* at our site it had been taken on *Eriogonum fasciculatum, Hemizonia fasciculata, Raphanus* sp., *Opuntia prolifera, Malvastrum fasciculatum,* and *Calochortus catalinae.* Early in the season (May to early June), females foraged primarily on *Hemizonia* and *Malvastrum.* In late June, foraging switched primarily to *Eriogonum fasciculatum.*

Females transported pollen in a dry state on the large scopae on the hind legs and stored it at the rear (bottom) of the cell as a partly moist, partly dry unshaped mass. Finished provisions (Fig. 5) were shaped into an elongate, homogeneous, semimoist, smooth-surfaced, yellow loaf attached by its rear to the rear of the cell and supported on the floor by a well-formed foot, as typical of most but not all *Exomalopsis.*

Development. White and strongly curved eggs (2.20 mm long and 0.55 mm in maximum diameter, one measurement) (Fig. 5) with a smooth chorion were attached to the top front end of the food loaves, by the anterior and posterior ends. The middle of each egg arched upward so that its venter did not touch the loaf. The anterior of the egg was closest to the cell closure as in all known *Exomalopsis.* Feeding larvae crawled over the food mass, channeling the provisions beneath them. Intermediate



Figs. 3–5. Nest components of *Exomalopsis nitens*. 3. Sketch diagraming relationship of nest to crack, side view. 4. Single cell containing postdefecating larva within cocoon, side view. 5. Two cells in tandem, first one open, second one containing food mass and egg, side view. Scales refer to Figure 3, and Figures 4 and 5, respectively.

stage larvae cradled the now elongate and reduced provisions so that the food no longer touched the cell wall, as seems characteristic of other species in the genus. Fully grown larvae sometimes retained a very small mass of food attached to their venters.

Some mature larvae spun cocoons and others did not. Those that did not pressed their feces as elongate pellets to the rear (bottom) of the cell, so that the fecal material extended part way toward the closure, as illustrated for *Exomalopsis sidae* (Rozen, 1984, fig. 31). They remained active and pupated a few days after completing defecation.

All larvae that spun cocoons diapaused for the season after completing the cocoon.

They usually, if not invariably, started defecating before they had consumed all of their food. In early stages of construction the cocoon fabric consisted of a webbing of gauzelike, fine, white silk with elongate, flattened yellow fecal streaks applied here and there, around the entire inner surface of the cell. However, in early stages of construction, the webbing was so thin as to be nearly invisible, but still several fecal smears were present on top of it rather than on the cell wall. This indicates that silk production commenced synchronously with, or just before, defecation, in contrast to the silk production/defecation timing of other known *Exomalopsis* (see Rozen, 1984). Although in *Exomalopsis nitens* a near synchrony exists, still a conspicuous outer layer of silk was laid down before most of the meconial mass was deposited, as revealed in completed cocoons. Hence the early fecal smears were only a minor part of the entire meconium.

In completed cocoons, the thin outer and inner layers of matted, semitransparent, fine silk sandwiched a thicker, opaque layer primarily of yellow feces consisting of vaculated pollen grains. The combined three layers were roughly 0.1–0.2 mm thick in most places. The outer layer had fine silk strands on the surface, giving it a slightly fuzzy appearance and reducing the surface reflection somewhat; the inner silk layer lacked such fine loose strands and was shiny but crinkly.

With most cocoons, light transmitted through the fabric showed that the front and rear of the cocoon were more opaque because of somewhat thicker fecal layers there. One cocoon had more fecal material at the front end, so that the casing there was approximately 0.5 mm thick, and few fecal deposits elsewhere. Hence considerable variation exists with respect to fecal placements and a larger sample needs investigation.

The incorporated feces gave the cocoon fabric rigidity so that it did not collapse as in *Exomalopsis sidae.* The cocoon shape conformed to the entire cell wall except for the front where the cocoon was rounded and loosely connected to the truncation of the cell closure, as seen in side view (Fig. 4), by fuzzy strands of loose, white silk. Larvae removed from their cells prior to cocoon construction spun malformed cocoons in artificial containers, an indication that the shape of a normal cocoon is determined by the shape of the cell. As in the other Exomalopsini, cocoons of *E. nitens* lacked both opercula and nipples.

Diapausing postdefecating larvae (Fig. 4) were curled, each with its posterior end toward the rear of the cocoon and its curved anterior end toward the front of the cocoon (i.e., cell closure), as in other cocoon-spinning *Exomalopsis.*

Adult activity. Adults flew during the late morning and early afternoon. Both sexes were seen occasionally on the flowers and several males were captured emerging from surface entrances of nesting cracks, although whether these were freshly emerging individuals leaving for the first time or males departing from their overnight sleeping quarters is uncertain. No matings were observed.

Seasonal activity. The presence of larvae starting to spin cocoons before hibernating and of other larvae pupating soon after consuming all their food suggests that this species is both univoltine and bivoltine, at least at this nesting site. In one nest all larvae pupated immediately without spinning cocoons, raising questions as to what factor or factors, external or endogenous, control voltinism.

On the basis of adult specimens, Timberlake (1947) noted that the flight period extends from mid-May to mid-August in southern California.

ETHOLOGY OF *MELANOMADA*

We oberved a number of males and females of the unnamed cleptoparasitic *Melanomada* flying at the nesting site of *Exomalopsis nitens,* first in 1983 and again at the time of nest excavation in 1985. We saw them primarily in the immediate vicinity of the surface entrances rather than widely distributed over the hillside. It was the apparent interest of several females in a crevice that attracted our attention and led to the discovery of the first nest in 1985. Female parasites flew back and forth around and close to entrances and often landed on a stem or rock, more or less facing the entrances. On a number of occasions perched females immediately and swiftly flew into entrances just after a female *Exomalopsis* departed. The occurrence of numerous cuckoo bees examining one nest area for a while and then departing to another suggested that females had already identified various entrances and were patrolling (i.e., trap-lining) from one to another, so as to find one that was 'appropriate' in which to descend. *Melanomada* females may have waited outside the entrances for *Exomalopsis* females to depart so that the cleptoparasites could follow scent trails created by the *Exomalopsis* females as they ascended from their nests along the faces of the crevice. This matter is further explored in the Discussion. During three days of nest digging we saw only one live female *Melanomada* leaving our excavations, a fact suggesting that cleptoparasites do not wait underground for nests to become available for attack.

Like all Nomadinae, *Melanomada* females probably entered still-open cells of their host and inserted their eggs into the cell wall. Egg punctures in the walls of three cells occupied by *Melanomada* larvae were situated almost next to the closures; one was a deep oblong puncture with a raised cell lining on one side, as if the soil had been very moist when the hole was made; another was a raised flap of cell wall still attached to the wall on one side, beneath which was a hole, as has been described for *Melanomada sidaefloris* and *Nomada* (Rozen, 1977).

A number of cell walls had deep irregular holes that suggested that *Exomalopsis* females may have detected and attempted to destroy *Melanomada* eggs by excising them. The shape and roughness of the holes indicated that the *Exomalopsis* females had used their mandibles to dig out the eggs. Among other taxa of host bees attacked by Nomadinae, imperfections in the cell walls indicate that this means of defense against Nomadinae parasites may be broad ranging. In the current study we saw one cell from an active nest that had been filled completely with soil, presumably by the host female, after it had been partly provisioned. This phenomenon has also been noted in nests of other ground-nesting bees (see for example Rozen, 1977, with respect to *Brachynomada*), and may be another mechanism by which host bees eliminate eggs of cleptoparasites.

We found no eggs or first instars of *Melanomada* during our excavations. Feeding intermediate stage larvae were in various positions on the host food loaves, an indication that these larvae crawled as they fed. While feeding, larvae opened widely and then closed their mandibles in a strong biting action in sharp contrast to the feeding action of such Nomadinae as *Protepeolus* that scrape the food with nearly closed mandibles (Rozen, Eickwort, and Eickwort, 1978).

We excavated all larval *Melanomada* while they were still feeding. Those (four) that remained alive in laboratory containers defecated without cocoon spinning and became totally quiescent, all within several weeks of being excavated. The fact that

none pupated after defecating and that no pupae were discovered in cells suggests that *Melanomada* is solely univoltine, whereas the host is both univoltine and bivoltine. If this is true, then nests constructed by those *Exomalopsis* emerging as the second generation in a year are unlikely to be attacked (assuming that the *Melanomada* and *Exomalopsis* adults have approximately the same life span). This arrangement may be a mechanism by which the host population recovers during the second generation from the attack of a successful cleptoparasite. Such a mechanism would assure abundant hosts for the next generation of the cleptoparasite.

On the other hand, collection records for adults of this cleptoparasite extend into mid-August and early September. Hence the species may not be univoltine or it may parasitize another species of *Exomalopsis* with a later flight period.

The low adult and high immature population of *Melanomada sidaefloris* (Cockerell) attacking *Exomalopsis sidae,* as reported by Rozen (1984), may reflect that *M. sidaefloris* also has only a single annual generation and was sampled just as the progeny of the first generation were developing, by which time most of the *Melanomada* adults had died.

DISCUSSION AND CONCLUSION

The nesting biology of this species closely parallels that of other *Exomalopsis,* and especially that of *E. chionura* (Rozen and MacNeill, 1957), partly because both species nest in cracks in claylike soil. At first the double outer concave surfaces of the cell closure of *E. nitens* seemed to be a feature unique within the genus, but a further dissection of cells of *E. chionura* preserved 30 years ago in the collections of the California Insect Survey shows that it also had such an arrangement of the closure. Double-faced closures are not, however, found in cell samples of other *Exomalopsis* in the American Museum of Natural History.

As in *Exomalopsis sidae,* some progeny of *E. nitens* spin cocoons in which they diapause, whereas other larvae pupate immediately after defecation and then presumably emerge in the same season. Further study of this matter needs to be undertaken: (1) to determine how widespread it is among other anthophorid bees; and (2) to ascertain whether (as seems most likely at this time) this is a seasonal phenomenon in which progeny developing early in the year pupate, and later progeny spin cocoons; or whether both pupation and cocoon spinning occur synchronously in the nesting population throughout the year.

The structure of the cocoon of *Exomalopsis nitens* differs in some respects from that of other members of the genus. Further and more complete observations on cocoon construction of all species need to be made to test the nature and significance of the apparent differences.

How are the females of *Exomalopsis nitens* able to find their individual nest entrances along the face of the fissure where there is no light, and why do female *Melanomada* wait outside the surface entrances for *Exomalopsis* to depart before they enter? The answers may be interrelated. We suspect that female *Exomalopsis* follow individually distinctive odor trails on their way downward to their nest entrances and that these trails are identified and used by *Melanomada* females in searching out a nest that has just been vacated. (The presence of individually recognizable odor markers may well be the mechanism by which other species of *Exomalopsis* identify their sections of composite nests.) Thus *Melanomada* relies on

long range sensory perception (sight) to make certain that a host female has departed and then uses short range sensory perception (olfaction) to track down the recently vacated nest entrance in the dark along the face of the crack. The fact that only one female *Melanomada* was observed escaping from our excavations during three days of digging supports this hypothesis, in that it indicates that *Melanomada* females, once in fissures, do not wait there and search randomly for individual nest entrances.

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