Associates of the native bee, *Halictus (Seladonia) confusus* Smith *(Hymenoptera: Halicitidae)*

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Introduction

The ecological life history of a local population of *Halictus (Seladonia) confusus* Smith, a common halictine bee of the eastern United States, was studied near West Lafayette, Indiana, from 1963 to 1965 (4). This species is a ground-nesting bee that nests in aggregations, primarily in open fields, and prefers bare or sparsely vegetated sites. In central Indiana, the species is primitively social: Nests are begun by solitary females and have the potential to develop into matriarchal associations with a mother queen and daughter workers. The workers enlarge the nest and construct and provision cells in which the immature stages develop. Two to three broods are produced each summer.

The female castes are morphologically inseparable, and range from 6 to 8 mm long. Whitish fasciae on the apical margins of the tergites of this dark metallic green bee give the abdomen a banded appearance. Adult females, including inseminated insects that overwinter in parent nests, are present throughout the year. Males are present in all broods but do not overwinter. The species is polylectic, and adults may be found frequenting many field and woodland flowers from mid-March to late September.

Several predators and parasites were noted attacking larvae and adults of *H. confusus* during 3 summers of observations of a nesting site. Because mortality of the bee species seemed more the result of predators and parasites than other causes, special attention was given to these biological agents and their interrelationship with *H. confusus*.

One advantage to the bee species of a social nest rather than a solitary nest is the presence of a guard at the entrance to repel predators and parasites (6). Another advantage of the social nest is that the queen, which stays in the nest, is less subject to the attacks of above-ground predators and parasites. In the nest, a defending bee is able to cope with an intruder effectively since the bee body nearly fills the nest entrance and the adjoining horizontal tunnel, and the bee mandibles serve as formidable defensive weapons. The females can also brace themselves tightly against the tunnel walls with the basitibial plates and, in this position, cannot be easily dislodged nor bypassed by intruders. In contrast, during the spring solitary phase, predators, parasites, and alien bees often entered an open nest during the absence of the foraging bee. Such invasions subsequently became uncommon due to the presence of a nest guard once a worker caste was produced.

Predators.—A mummified male *H. confusus* found in a flower suggested that some bees fall victim to crab spiders and ambush bugs common on field

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flowers. However, ants were the major predators of the nesting area, and 4 species were observed attacking bees resting in the nesting area or the nest-guard bee. Ants also entered open, unguarded nests, but most ant attacks could be avoided by flight of the bee that was outside the nest or by aggressive action of an adult bee that was within the nest. One attack was witnessed in which a cluster of about 10 *Aphaenogaster rudis rudis* Emery engaged the guard bee at a nest entrance in direct attack. Several of the ants enlarged the entrance by removing particles of soil which were transferred from one ant to another and passed to the outside. Time passed, and more ants arrived and continued to remove soil. Eventually, the ants overwhelmed the guard and thereafter entered and left the nest at will. Several ants left the nest dragging the mutilated guard now stripped of her wings and with 1/3 of her abdomen removed. Another ant carried a white pupa of *H. confusus* in its mandibles. Until dusk, the ants entered and left the nest periodically. The next day, the ants were gone, and, suprisingly, a female *H. confusus* without a pollen load entered the nest. The nest then remained closed for 11 days and then reopened attended by a guard. Two days later, provisioning workers were present, and the nest remained active for the remainder of the summer. Lone individuals of this ant species have been observed attacking a nest guard in other nets, but these attacks were always successfully repulsed.

Lasius alineus (Foerster) was another common invader of the *H. confusus* nests. This ant frequently entered nest entrances but retreated quickly when contact was made with the guard. Also, in one instance, an ant of this species started to enter an unguarded nest but then retreated rapidly as if a repellant secretion was deposited around the inside of the entrance by the bee that constructed the nest. This ant species was in newly-abandoned *H. confusus* nests. It quickly located the closed cells and removed both the pollen provisions and the immature stages by cutting off and removing pieces of these stages until no trace remained. Open abandoned nests were quite vulnerable to this species, and ants were observed entering and departing from such nests as long as salvageable nutrients remained. However, nests with no signs of bee occupancy other than deserted burrows and empty cells often had these ants present in the tunnels. In these cases, ant tunnels intersected with the nest burrows and the ants had free access to the bee nest from their own nest.

Thief ants, *Solenopsis molesta* (Say), were too small to pose a threat to a defending female *H. confusus* and were never observed attacking en masse. However, they were common and joined with *L. alienus* in attacking the immature stages in the cells during a nest dissection if a nest undergoing dissection was left untended for several hours. In natural situations, the thief ants normally were not found in the main tunnels of the nest or contacting adult bees. However, on occasion, they entered cells from tunnels that penetrated the cell walls and cleaned out the contents of the cells.

Formica pallidefulva nitidiventris Emery workers were conspicuous in the nest area due to their large size. The ants were never observed in the nests and did not probe the nest entrance, as did other species. The only time they were attracted to the entrance was when a grass straw was inserted in the entrance by the author and left there for a period of several minutes or more. Even under artificial conditions, the ants did not attempt entry or engage the guard. The

only observed physical contact was with inactive adult bees in the nest area. Several times an ant was seen approaching and touching a resting female bee, which responded by flying a short distance. Ants carrying moribund female bees in their mandibles have been observed, but it is not known if the bees were functional adults captured by the ant or bees that were spent or parasitized and nearing death before capture.

Paratrechina parvula (Mayr) ants were casual probers of nest entrances but always left when repulsed by the guard. They were never found in the nests.

All ant species were determined by D. R. Smith (AR, SEA, USDA).

Adult parasites.—Dipteran parasites of the family Conopidae were the major parasites of adult female *H. confusus.* It was not uncommon to find female bees that had died and were in various stages of decomposition within the nests. If the responsible parasite had emerged, the abdomen of these bees was likely to contain a puparium or its remains, which completely filled the abdominal space. If decomposition was advanced, the abdominal sclerites separated, and the puparium was evident without dissection of the bee. Dead bees containing live conopid puparia have been found at the base of the nest in digging position, embedded in the sides of the nest, and in old cells. If the nests were active, the dead bees were walled off or their bodies were apparently bypassed in further excavation of the nest, depending on the position of the body in the nest. One cell containing a dead bee was filled in with soil by active workers.

Larvae of 2 species of Conopidae have been recovered from the haemocoele of the abdomens of active female bees; in addition, an adult fly reared from a puparium has been identified as *Thecophora occidensis* (Walker) by G. Steyskal (AR, SEA, USDA). Both of the larvae differed from *Occemyia* reported by Kirkton (5) as a parasite of the bee *Halictus ligatus* (Say), which was found in the same locality. The first dead parasitized bee was found on May 10, 1964, at the base of a new nest under construction at the time of death. In nest dissections during midsummer 1965, several marked bees of the spring solitary phase that would later become queens and also some first-brood workers were parasitized by conopids. Only 1 parasite per bee was found. The conopid larvae did not mature and pupate until after the death of the host.

Adult conopid flies were usually present in the nest area during favorable weather. They rested on the vegetation and struck at passing female bees in flight. Quite often the fly and bee tumbled to the ground during these brief encounters. Bees returning to the nest were often attacked, but bees leaving the nest were not approached. During the nesting seasons of 1964 and 1965, 9 of 58 nests dissected were found to contain live or dead females that had been parasitized by conopids.

Phalacrotophora halictorum (Melander and Brues) (Diptera: Phoridae) (det. By W. W. Wirth, AR, SEA, USDA) were frequently observed near the entrances of *H. confusus* nests. On a number of occasions, a small phorid adult was observed attempting to enter a nest, only to be repulsed by the guard. Eventually, the fly assumed an immobile stance near the nest entrance; then when a returning worker entered the nest the parasite followed close behind. It

would remain in the nest for several minutes. Similar behavior by this dipteran species has been reported by Melander and Brues (8) for nests of the bee, *Lasioglossum pruinosum* (Robertson) and by Batra (2) for *L. zephyrum* (Smith).

On two occasions, small nondescript maggots were recovered from the abdomen of healthy females. These were determined to be parasitic Phoridae by G. Steyskal (AR, SEA, USDA). In one instance, 2 maggots were recovered from the abdomen of 1 female.

One nondescript nematode was found in the abdomen of a healthy larva on July 18, 1964. It was determined by J. M. Ferris (Entomology Department, Purdue University). Gregarine sporozoans (Eugregaria, cephalina) were often present in the intestine of the bee anterior to the rectum. These unicellular bodies were translucent, oval, and partitioned unequally into 2 regions. They measured about 0.1 mm long and were visible at 15X magnification.

Larval parasites.—The parasitic beetle, *Rhipiphorus walshi* LeConte (det. T. J. Spilman, AR, SEA, USDA) was the primary parasite of the larvae of *H. confusus*. The adults were common in the nesting area, and their immature stages were present in many cells of active nests. This species of parasite has a complex life history: Adult female beetles lay eggs on the blossoms of field flowers. The eggs produce active, 2 mm, first-instar larvae (or triungulins). When a female bee visits the flowers, the triungulins use their mandibles to attach themselves tightly to parts of the bee. From 1 to 4 triungulins have been found attached to 1 bee, most of them in the wings near their base. A few have been found clinging to the hair of the legs and abdominal sternites.

Triungulins were most common on bees during the spring solitary phase (immobile and inactive state) prior to the construction of cells. They were then in a phoretic association with the hibernating females for 8 to 9 months, from August or September until the following April or May. In spring, as the solitary females constructed the first pollen balls of the year, the triungulins left the bee and remained in the sealed cell with the pollen ball and egg. Several active triungulins were observed on a fresh pollen ball before the egg had hatched. As the egg hatched and the bee larva began to grow, the triungulins burrowed into its abdomen. There it remained relatively inactive and did not attain much growth as the bee larva developed into a prepupa. However, after a molt, it burrowed to the outside and attached itself at a point just behind the head with its body curled around the thoracic segment of the host. One parasite per host was the usual number though 2 were observed in one instance. Parasitized bee larvae never matured beyond the prepupal stage and all died, whether the parasite larvae survived or died. As an ectoparasite, the larva fed continuously, with a conspicuous bellow-like action of its head and thoracic region; so in 3 to 5 days, the host was reduced to a small bladder-like body of liquid. By 6 to 7 days, the parasite was fully grown, and the host was reduced to a dried mass of exoskeleton. The fully-grown parasite was comparable in size to a bee prepupa. During the feeding process, the parasite was not observed molting, nor were any cast skins found.

The fully-grown parasite was quiescent for 1 to 2 days and then molted to a white pupa. Sex of the pupae could be determined since antennae of the female

are shorter and narrower than those of the male. One day after pupation, the eyes darkened to a tan color; by the 2nd or 3rd day they darkened further. On the 4th or 5th day, the pupa began to darken. Until it emerged at 6 to 8 days, the abdominal segments had alternating dark and light bands. Within a short time after emergence, the newly-emerged adult discharged a large amount of a white liquid from its mouth onto the cell floor or rearing chamber. The adult beetle remained in the cell for 1 to 2 days while it dried and became better able to walk about; its abdomen darkened further and contracted somewhat until most unsclerotized regions of the abdomen were telescoped internally. The adult beetles then pushed out the soil plugs of the cell and emerged as free-living adults. A newly-emerged female was strongly attractive to males of the same species, possibly because of a sex pheromone: when a female beetle was captured and held in a net for several minutes, as many as 17 males were attracted to the female, and collected. These males had a remarkable range of size, from 2.6 to 5.7 mm.

After mating and egg maturation, the female beetle oviposited upon field flowers to complete the cycle. Then triungulins were again transported from the flowers to cells. However, the association with a worker at this time could be as short as a few minutes, unlike the long fall to spring association. For this reason, in the summer triungulins were not found as often attached to bees as in spring before the cells were constructed.

There appeared to be 2 to 3 generations of beetles each year. In a density-dependent mechanism, the presence of this parasite became more common as the season progressed. The highest percentage of parasitism recorded in a nest was 50% in late summer. The extent of parasitism could not be accurately determined since many immature larvae died during laboratory rearing or were preserved without checking for endoparasites. Freedom from parasitization could not be assumed until the bee entered the pupal stage.

Rhipiphorid parasitism was apparently the major population-limiting factor for the *H. confusus* in the study area. A similar host-parasite relationship for an undetermined *Phipiphorus* was reported by Barber (1) upon *Augochlora pura* (Say) and by Linsley, MacSwain, and Smith (7) for *R. smithii*, upon a parasite of *Diadasia consociata* Timberlake. Batra (2) reports the occurrence of *Rhipiphorus fasciatus* (Say) in the nests of *L. zephyrum*.

Other Associates.—An anoetid mite species of the genus *Histiostoma* (det. by E. W. Baker, AR, SEA, USDA) had an obligatory commensal relationship with *H. confusus* and did not noticeably interfere with the various life stages. These mites were oval and reddish-purple in color. They fed upon the pollen balls in the cells at the same time as the bee larvae were feeding and growing. As the adult bee emerged, the mites attached themselves to the body of the bee, sometimes the wings, but usually to the first abdominal tergite, and became inactive. A latticed aggregation of 85 mites was counted on one such mass of the abdomen of an overwintering female. The mites eventually left the host female bee to feed upon the pollen ball of another cell in completion of the life cycle. These mites were in phoretic association on workers for brief periods in the summer, and the association on the overwintering females lasted for periods of 8

to 9 months. The mites were common on spring females before cells were constructed but were uncommon on summer workers.

A number of irregular visitors, saprophytic organisms and scavengers were observed on *H. confusus* from time to time. Particularly, the overwintering nest served as a refuge for species other than *H. confusus*. A small spider and a 6 mm *Dialictus* sp. female were noted in nest dissections.

Moldy pollen balls supported numerous scavengers such as nematodes and spherical-bodied mites.

A tiphiid, *Myrmosula parvula* (Fox) (det. by K. V. Krombein, Department of Entomology, Smithsonian Institute) was captured in 1 nest burrow during a nest dissection, and several others entered unguarded spring nests. No parasitic association was demonstrated, however, and the parasite may have been searching for another bee species.

Dialictus imitatum (Smith) females sometimes entered *H. confusus* nests during the absence of the female in the spring solitary period. However, they never remained in the nests for more than 30 minutes and left when or before the owner returned. Occasionally, male *Calliopsis andreniformis* Smith struck at *H. confusus* females in flight but made no attempts to follow the females into the nests.

One dead and soil-covered female *H. confusus* was found packed full of spherical bodies filled with moisture. These bodies may have been some species of fungus.

During rainy periods, excessive moisture accumulated in some cells and a fungus would become established on the pollen ball and grow into a mass of white hyphae. Eventually, all of the pollen was destroyed, and as the fungus grew, the larvae died. In time, the fungus attacked the body of the larva also. Chandler (3) reported *Gibellula pulchra* in the nests of *H. ligatus* by the fungus. In the present case, many of the cells bearing fungal deposits had been filled with loose soil, which indicated that the fungus had been detected by the nest bees and blocked off in the same manner that dead parasitized adults are sealed off with soil. Since fungus grew on fecal deposits in old cells, which had served to produce the brood, the practice of the worker bees of filling these cells with loose soil was probably related. In all of these cases, the end result was the isolation of fungus growths from the rest of the nest.

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Literature Cited

1. BARBER, H. S. 1931. A new parasitic beetle from California (Rhipiphoridae). Bull. Brooklyn Entomol. Soc. 34:17-20.
2. BATRA, S. W. T. 1965. Organisms assocated with *Lasioglossum zephyrum* (Hymenoptera: Halicitidae). J. Kansas Entomol. Soc. 38:367-89.
3. CHANDLER, L. 1955. The ecological life history of *Halictus* (H.) *ligatus* Say with notes on related species. Unpublished Ph.D Thesis, Purdue University Library.
4. DOLPHIN, R. E. 1966. The ecological life history of *Halictus (Seladonia) confusus* with Smith (Hymenoptera: Halicitidae). Unpublished Ph.D. Dissertation. Purdue University, Lafayette, IN 47907.
5. KIRKTON, R. M. 1964. Conopid parasitization and its effects on *Halicitus ligatus*. Proc. North Cent. Branch, Entomol. Soc. Amer. 19:75-7.
6. LIN, H. 1964. Increased parasite pressure as a major factor in the evolution of social behavior in halictine bees. Insectes Soc. 11-187-92.
7. LINSLEY, F. G., J. W. MACSWAIN, and R. F. SMITH. 1952. The life history and development of *Rhipiphorus smithi* with notes on their phylogenetic significance. Univ. California Publ. in Entomol. 9:291-314.
8. MELANDER, A. L., and C. T. Brues. 1903. Guests and parasites of the burrowing bee *Halictus*. Biol. Bull. 5:1-27.