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DANIEL WOJCIK

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A Natural History of *Pleotomodes needhami* Green (Coleoptera: Lampyridae): A Firefly Symbiont of Ants

John M. Sivinski
USDA-ARS
Center for Medical, Agricultural and Veterinary Entomology
Gainesville, FL 32608 U.S.A.

James E. Lloyd
Entomology and Nematology Department
University of Florida
Gainesville, FL 32611 U.S.A.

Samuel N. Beshers
Boston University Biological Science Center
Boston, MA 02215 U.S.A.

Lloyd R. Davis
USDA-ARS
Center for Medical, Agricultural and Veterinary Entomology
Gainesville, FL 32608 U.S.A.

Robert G. Sivinski
Steven R. Wing
Entomology and Nematology Department
University of Florida
Gainesville, FL 32611 U.S.A.

Robert T. Sullivan
Paula E. Cushing
Zoology Department
University of Florida
Gainesville, FL 32611 U.S.A.

Erik Petersson
USDA-ARS
Center for Medical, Agricultural and Veterinary Entomology
Gainesville, FL 32608 U.S.A.

Abstract

A firefly, *Pleotomodes needhami* Green, lives in the nests of two, possibly three, species of ants. These ants are the fungus-growing *Trachymrmex septentrionalis* (McCook), the carnivorous *Odontomachus clarus* (Roger), and perhaps a *Dorymyrmex* sp. All known specimens of *P. needhami* have been collected on the grounds of the Archbold Biological Station, Highlands County, Florida. Larvae, pupae, and adults of both sexes were excavated from the brood-queen-fungal chambers of *T. septentrionalis*. Ants appeared to ignore the fireflies, and the fireflies were not seen to feed on ants or their brood. Larvae in captivity consumed snails on the soil surface at night and a single larva was captured on the surface in the field. Pupation begins in late March and the earliest collections of adults took place in the first half of April. Neotenous females emerge from ant colonies soon after dark and emit light while waiting near the nest

entrance. Males luminesce in the presence of females. Larvae also produce light, both on the surface and underground in ant colonies.

Lampyrid larvae often live underground or under debris (Sivinski 1981). There they feed upon molluscs, earthworms and other invertebrates (Wing 1989). A number of brachypterous, apterous, and larviform adult females also spend most of their lives sheltered in burrows (*e.g.* Wing 1984). Presumably, the regular occurrence of "glowworms" (*i.e.*, larvae and wingless females) with organisms other than their prey is due to an overlap in habitats, such as decayed logs, swampy mud or leaf-litter. An exception is *Pelania mauritanica* L., a North African species which lives in the nests of the granivorous ant *Messor barbarus* (L.) (Cros 1924). The larvae and neotenous females of *Pleotomodes knulli* Green may also live in association with ants. Adult females have been collected on vegetation above colonies of the ponerine ant *Odontomachus brunneus* (Patton) in Alachua County, Florida, and a larva was discovered in the nest material of the same species (J. E. Lloyd and S. R. Wing pers. obs.).

A related species, *Pleotomodes needhami* Green, occurs in the scrub forests of the Archbold Biological Station near Lake Placid, Florida (Fig. 1). Over several years we have collected immature and adult *P. needhami* in association with 3 species of ants. In addition, captive ants and firefly larvae were observed together over periods of weeks. The following includes host-ant records for *P. needhami,* information on periods of activity and development, interactions with ants, foraging behavior of larvae, bioluminescence, and mating behavior.

Methods

All specimens were obtained from the grounds of the Archbold Biological Station. The station is located in Highlands County, Florida about seven miles from the southern terminus of the Lake Wales ridge, a region of relict dunes that reach up to 90 m above present sea level (Deyrup 1990). Sandy soils support xeric woodlands of pines and oaks, notably the scrub-oak, *Quercus inopina* Ashe. The biota is exceptionally diverse. For example, the area is believed to hold more species of ants than any comparable location in the eastern United States (M. Deyrup, pers. comm.). The ridge contains an unusual number of Florida endemic plants and animals, including *P. needhami,* which has not been collected outside of the Archbold Biological Station.

Our field observations took place during March and April of 1988 through 1993. Nests of *T. septentrionalis* were excavated by digging a trench to one side of a mound and then carefully removing intervening soil with a trowel. The contents of the brood, queen and fungal mass chamber were removed entire and then sifted to separate ants, lampyrids and fungi. Specimens are held in the collection of J.M. Sivinski.

Larvae maintained in captivity were placed in an artificial nest ("ant-farm"), constructed of two-450 and one-250 ml plastic cups. The smaller cup was placed inside a larger. Soil was poured in the space formed between the two and this was shielded from light by a second large cup painted black. Each of three farms were populated with several dozens of *T. septentrionalis,* each cohort being from one of three colonies. The fungal-detritus mass and the firefly larvae captured from the same colony were included. Subsequently, larvae were occasionally moved from "colony" to "colony." Ants were fed

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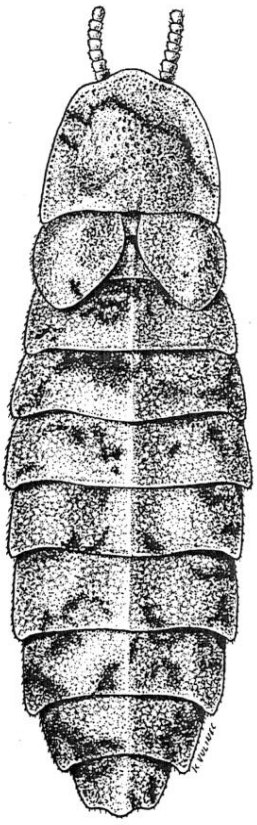

Fig. 1. *Pleotomodes needhami,* adult female, collected April 14, 1991, Highlands County, Florida, in nest of *Trachymyrmex septentrionalis,* dorsal view.

on a sucrose solution. *Pleotomodes needhami* larvae were provided with unidentified snails taken from a fresh water aquarium. Shells were cracked before introduction. Larval behavior and locations within the nest were noted on a total of 21 nights over a period of six weeks.

Results

Location of fireflies relative to ants. Twenty late-instar larvae, two pupae, three adult females, and four male *P. needhami* were found in the queen, brood and fungal chambers of 11 *T. septentrionalis* colonies. *Trachymrmex septentrionalis* often constructs multiple chambers at different depths. In 8 colonies only one, presumably the shallowest chamber, was excavated. Two others had only one chamber, both at depths of 25 cm. A third completely excavated nest contained 2 larvae in the deeper of two chambers at a depth of 40 cm. The only immature *P. needhami* captured outside of a *T. septentrionalis* nest was a large luminescing larva discovered at night on the forest floor.

Four female *P. needhami* were collected in 3 excavated nests of *Odontomachus clarus* Roger. Nest structure in this species is more loosely-knit and

we could not determine whether fireflies occupied any special location in the colony.

Adult *P. needhami* use light signals in sexual interactions. Females were seen steadily glowing near the entrances of five *T. septentrionalis,* six *O. clarus* and one *Dorymyrmex* sp. nests. There was only one instance where an ant nest could not be located at the signaling site; however, *T. septentrionalis* ants and disturbed soil, typical of ant excavations, were found nearby. It is possible that the beetle emerged from an abandoned nest. In another case without an obvious burrow entrance, the signaling site was found to be above an *O. clarus* nest (in which a second female was discovered). Entrances to such nests are sometimes obscure. The presence of signaling females only or primairily at ant colonies is strong evidence of an obligatory relationship between *P. needhami* and ants. That is, the firefly might occupy burrows of any sort and larvae were discovered with ants simply because those were the burrows being excavated. If however, fireflies were in other types of burrows the luminous signal of the female would betray their presence.

All the adult males found on the surface were also in the vicinity of ant nests. In one instance, five males were seen tightly clustered at an entrance to an *O. clarus* nest. Ants could be seen in the burrow. One walked over the clump of beetles and did not appear to be disturbed by the aggregation in the entrance. We did not see these or other males pursue females into nests; however, we did find four adult males in brood-fungal chambers of three excavated *T. septentrionalis* colonies. Females were not present. Whether these were newly eclosed individuals that had never left the nest or if they had returned for shelter was not determined.

The behavior of fireflies inside ant colonies. Two attempts were made to keep the larvae in the laboratory. In the first, four larvae collected by S. N. Beshers crawled about the nest periphery, and after two weeks were found dead and desiccated. Larvae pressed themselves to the substrate when encountered by ants but were not molested. In the second attempt, 15 larvae in three artificial nests lived six weeks, but did not pupate when expected. These insects were found throughout the colonies during nocturnal observations. In two nests with fungal chambers there were 19 instances of larvae in the fungal chamber, 41 in tunnels, and 14 on the surface. The latter were often feeding on snails. In a third nest, without a fungal chamber, there were 18 observations of larvae in tunnels and 7 of larvae on the surface. Although larvae failed to develop during the survival of the colony, they fed, moved and even crawled into crevices in the fungal masses.

Interactions between fireflies and ants. There were no obvious interactions between the ants and firefly larvae. Larvae were generally motionless in the presence of ants and ants often squeezed past beetles in partially blocked tunnels. We saw no evidence of trophallaxis. The only morphological peculiarity detected was the ability of larvae to retract their head deeply into the prothorax, which gave them the appearance of open bottles. This might be a defensive adaptation for living among ants.

Phenology. The stage of development of *P. needhami* varied with the time of year at which collections were made (Fig. 2). During the first half of March only larvae were found, in the first week of April, both larvae and pupae. On April 15 a pupa was unearthed. The earliest adults seen were a copulating pair and an associated single male collected on April 11.

Larval luminescence. Larvae of *P. needhami,* like all lampyrid larvae, emit light from paired organs on the penultimate (8th or more rarely 7th and 8th)

DATE	Location	*T. septentrionalis*	*O. clarus*	*Dorymyrmex* sp.
March 6	Excavated	15 larvae	-	-
	Surface	1 larva	0	0
April 2	Excavated	1 larva, 1 pupa	-	-
	Surface	0	0	0
April 6	Excavated	6 larvae	-	-
	Surface	-	-	-
April 11	Excavated	-	-	-
	Surface	0	4 ♂♂, 1 ♀	0
April 12	Excavated	-	-	-
	Surface	1♀	7 ♂♂	0
April 13	Excavated	1♀	-	-
	Surface	0	1 ♀	0
April 14	Excavated	0	1 ♀	-
	Surface	2♀♀, 1 ♂	3 ♀♀, 3 ♂♂	1 ♀
April 15	Excavated	2 ♂♂, 1 pupa	-	-
	Surface	0	0	0
April 17	Excavated	2 ♂♂	-	-
	Surface	0	0	0

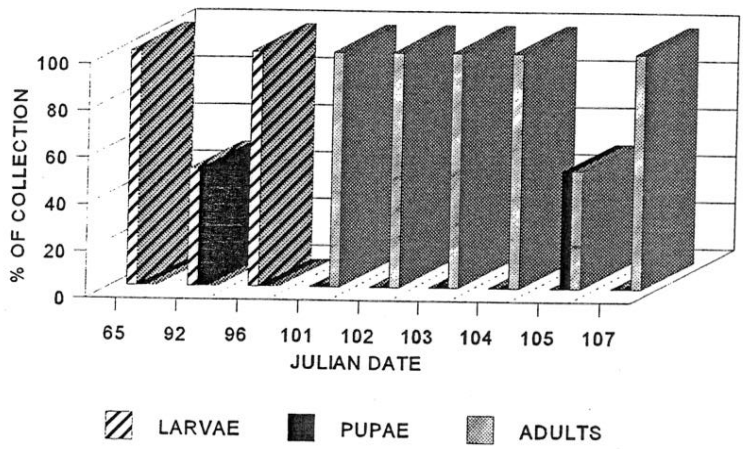

Fig. 2. Above, tabulation of numbers of *Pleotomodes needhami* collected from surfaces of ant colonies and excavated from nests. Below, graphic representation of percent of larvae, pupae, and adults in collections of *P. needhami* made on different dates.

abdominal segment (Sivinski 1981). A luminescing larva was captured on the floor of the Archbold scrub forest, and 3 larvae underground in ant-farms were seen to emit a steady glow over observation periods of several minutes.

Adult luminescence. Females emerged from ant nests and maintained positions near the entrances. Light organs near the abdominal tip were held aloft as the insect assumed a C-shaped position. Thus, the ventrally located organs faced the sky. If no males arrived, her light would dim and she would retreat into the nest. One female escaped down a nest entrance when disturbed by an observer. Lights continued to glow during mating, but went out when the insects separated. The signaling period was about one hour long. On our most productive night, April 14, 1990, the first of 6 female glows was discovered at 20:19 (EST) and the last at 20:52 (*i.e.* 1.4–2.8 crep units: One crep unit equals the duration of civil twilight at a particular time and place. Civil twilight is the time required for the upper limb of the sun to descend 6 degrees below the horizon).

Males also luminesce. They produced a steady glow in the presence of females and were seen to emit light near ant nest entrances in the absence of females. In these latter cases females may have been present earlier or males were responding to some nonluminescent cue such as a pheromone or kairomone. On two occasions luminescing males were found near mating pairs.

Discussion

It seems remarkable that *P. needhami* coexists with ants of such different temperaments and habits as the gentle, fungus-farming *T. septentrionalis* and the predaceous *O. clarus*. The accomplishment is made more noteworthy because of their frequent occupation of brood, queen, and fungal-mass chambers. These centers of reproduction are generally well guarded and breached by only the most sophisticated adaptations (Holldobler and Wilson 1990).

Why the fireflies are ignored remains to be determined. By comparison, milichiid flies found in *T. septentrionalis* nests are instantly attacked and dismembered (S. N. Beshers, pers. obs.). Anonymity is sometimes obtained by ant symbionts through adsorption of colony odors onto the surface of the cuticle (Vander Meer and Wojcik 1982); however, when *P. needhami* larvae were moved from one *T. septentrionalis* colony to another no obvious period of "suspicion" occurred while the correct scent was acquired. The seeming lack of cues suggests a sort of chemical "invisibility" or a special resemblance to some innocuous material.

Despite the implied danger to ants of a large predator in their nest, there is no evidence that *P. needhami* eats ants. While larvae were commonly observed near ant brood, they were not seen to consume any. All feeding witnessed in captive specimens was on snails and on the soil surface. This is probably indicative of a broad prey range rather than a specialization for capturing snails. Although molluscs are commonly eaten by lampyrid larvae, there are only pin-head sized, arboreal snails in the scrub oak habitat and slugs are rare (M. Deyrup pers. comm.).

Feeding bouts often included multiple larvae; four in one instance. No indications of aggression occurred among larvae nor were there attempts to cache prey, phenomena that are found in other lampyrids such as *Photuris* spp. (Sivinski 1981). Given what must be a patchy distribution of this relatively sedentary insect, the larvae in a nest might be siblings and prone to evolve

prey-sharing. Group feeding also occurs in *Photinus* spp. larvae (S. S. R. Wing, pers. obs.).

If *P. needhami* does not consume ants, then what advantage does it gain by living in their colonies? It may be that the benign environment in the center of an ant colony is superior to either the harsh, sandy surface or to anything the larvae themselves might be able dig. Predation on the lampyrid larvae might also be reduced by living among ants who defend both their nests and, as a side effect, their symbionts.

While larvae, pupae, and adults of *P. needhami* were excavated from ant colonies, oviposition was never observed. The females are soft bodied, move slowly, and are wingless. How do these fireflies disperse among nests? Observations of captive larvae feeding on the surface and the collection of a larva moving on the forest floor suggest that it is the larvae that move from nest to nest. Such "adoptions" would be facilitated by the apparent lack of response by ants to *P. needhami* larvae from other colonies. How ant nests are located is again unknown, but given the distances between colonies (from the perspective of a glowworm) perhaps immature females locate sites to pupate and eventually lay eggs by exploiting ant trail pheromones. *Lampyris noctiluca* Geoff., the European glowworm, locates snail prey by tracking slime trails (Schwalb 1960).

Relatively constant luminous larval glows, such as those of *P. needhami,* are not produced by all firefly larvae. For instance, 90% of a sample of 308 *Photuris* sp. glows were three seconds or less in duration (Sivinski 1981). Long glows have been observed in other subterranean larvae (Sivinski 1981). It may be that a continuous signal is less likely to be missed in close quarters where encounters can be brief and occur rapidly. Why larval lights are emitted and to what receiver(s) is unknown in any firefly species, although aposematism or "startle-coloration" is a frequently suggested function (see also Buschman 1988). A larva of *Pelania mauritanica,* the north African species of myrmecophilous lampyrid, was seen glowing while feeding on a snail in the company of ants (Lheritier 1955).

In addition to bioluminescent signaling to potential mates prior to copulation, *P. needhami* also luminesces while mating. This form of luminous behavior is found in some other flightless cantharoid beetles, e.g., the phengodids *Phrixothrix tiemannii* and *Dioptoma adamsi* Pascoe (Tiemann 1970 and Green 1912). Why light is emitted after the attraction of a mate is unknown, although aposematism and a courtship that continues through insemination are possibilities (see Eberhard 1994).

Another North American firefly, *Pleotomodes knulli,* may be a symbiont of ants. *Pleotomodes knulli* is more widespread than its relative *P. needhami,* and has been found sporadically in dry and well-drained habitats over the whole of peninsular Florida (J. E. Lloyd, pers. obs.). The period of female luminescence is similar to that of *P. needhami,* ca. 0.6–3.0 creps. Again, females hold their bodies in a C-shape while signaling. The pale abdomen of the female is translucent and light shines through its' dorsal surface. Unlike *P. needhami,* male *P. knulli* have not been seen to glow prior to or during mating. Ants from the host colony paid little attention to the single larva that has been held in captivity (J. Sivinski, pers. obs.).

There are a number of parallels between the natural histories of *P. needhami* and the North African myrmecophile, *P. mauritanica* (see Cros 1924; Lheritier 1955). Both occur in environments with harsh surface conditions, fossil sand dunes and rocky arid-lands respectively. They are found in the nests of multiple

ant species, *Messor barbara* and *Pheidole sinaitica* in the case of *P. mauritanica,* but not in the burrows of other local arthropods, such as crickets and tenebrionid beetles. Neither seems to be noticed by its hosts. *Pelania mauritanica* was even successfully introduced into the nest of a nonhost species, *M. instabilis.* Both will feed on molluscs and neither were seen to consume ants. Observations of *P. mauritanica* suggested that larvae do not seek out ants within their nests or require them for their survival. Both have flightless females; in *P. mauritanica* a sizable proportion of the males are brachypterous. Are these similarities due to convergent selection alone or did continental drift, separating a mymecophile ancestor into Old and New World demes, have some role? At present, phylogenetic relationships within the Lampyridae are poorly understood; it is not clear if the two genera could have an immediate common ancestor.

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