FEEDING AND REPRODUCTIVE BEHAVIOR
OF IPS AVULSUS¹

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ABSTRACT

* Ips avulsus * (Eichhoff) parent adults were introduced into pine inner bark-glass plate observation units where they periodically fed as follows: chips of excised inner bark were taken into the buccal cavity, compressed, and the resulting pellet of exhausted tissue was expelled from the mouth. Microscopic examination of sectioned and whole guts showed contents consisting principally of symbionts, starch grains, and small amounts of very fine material. Ventral dilator muscles of the pharynx were well-developed and the alimentary tract was of the elongate type reported in liquid-feeding insects.

Gelatinous feces were produced and deposited on the roof of the male's nuptial chamber, where they were consumed by consorting beetles or adhered to their bodies.

Reproductive behavior was similar to that reported for *Ips pini* (Say) and *Ips paraconfusus* Lanier. *I. avulsus* copulation lasted an average of 35 sec (range, 22.45 sec) at 30°C. Pairs mated 3 times at about 10 min intervals, after which each female isolated herself from the associated male in his nuptial chamber by packing the egg gallery behind her with boring material.

Generalized accounts of behavior in North American bark beetles (*Scolytidae*) have been given by Beal and Massey (1945), Blackman (1922), Chamberlin (1939), and Swaine (1918), but detailed accounts of reproductive behavior in North American *Ips* spp. have been reported for only a few species such as *Ips confusus* (LeConte) (= *Ips paraconfusus* Lanier) from California (Hall 1969), *Ips pini* (Say) from Idaho (Schmitz 1972), and *Ips calligraphus* (Germar) from Florida (Wilkinson et al. 1967).

* Ips avulsus * (Eichhoff) is a small species which commonly infests the thinner-barked portions of *Pinus* spp. in the southeastern USA. Its reproductive habits (Beal and Massey 1945, Blackman 1922, Thatcher 1960) have been reported as follows. *I. avulsus* is polygamous, but the male alone usually initiates attacks on host material by boring an "entrance tunnel" through the outer bark and excavating a small, irregular, flattened "nuptial chamber" in the soft inner bark (phloem) next to the sapwood. He may then tunnel-out the basal portion of one or more "egg galleries", which are subsequently extended through the inner bark by the 1 to several females which join him in the nuptial chamber. The basal portions of the egg gal-

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⁶Body length of alcohol-preserved teneral adults from north-central peninsular Florida (n = 50 spms/sex): X ± s = 2.9 ± 0.1 (2.7-3.2) mm for female; X ± s = 2.9 ± 0.1 (2.5-3.1) mm for male (unpublished data).
⁷Egg dimensions (n = 69 eggs from 18 females): X ± s = 0.80 ± 0.04(0.7-0.92) mm long; X ± s = 0.46 ± 0.03 (0.37-0.54) mm wide (unpublished data).
leries radiate out from the nuptial chamber and commonly do not follow the grain of the underlying sapwood, but the more distal, egg-bearing portions of the egg galleries tend to parallel the wood grain. As females extend their egg galleries through the inner bark, they deposit relatively large eggs singly in cup-shaped "egg niches", cut at intervals into either or both sides of the galleries. The eggs are covered and sealed in the egg niches by bits of inner bark tamped together in the form of a plug (called "phloem plugs" in our study).

Data on egg gallery construction and oviposition are given by Yearian (1966) and Yearian et al. (1972). Egg gallery construction in individual log bolts (2 females and 1 male in consort) was completed within 10 days after introduction of females, and most reproductive activity took place during the first 5 days. The average space between egg niches in the egg galleries was 5.9 mm and the mean length of 46 egg galleries was 13.5 ± 1.4 cm. In more extended tests, each of 10 females oviposited successively in 3 log bolts and consorted with a different male in each bolt. The total length of galleries constructed per female averaged 51.2 ± 5.75 cm, and females laid a mean of 77.0 ± 13.8 eggs. Females oviposited in both sides of their egg galleries when only 1 egg gallery was extended into an area of non-infested inner bark. When 2 egg galleries were concurrently extended side by side and close together, oviposition was concentrated on the opposite (farthest removed) sides of the respective galleries and not any or relatively few eggs were laid in the narrow phloem strip separating the 2 galleries. Males abandoned their nuptial chambers about 10 days after females were introduced with them, and most females left their galleries 15-20 days after introduction into the nuptial chambers.

*I. avulsus* larvae feed in relatively short and broad "larval galleries" which extend laterally from the egg gallery through the inner bark and are greatly enlarged at their distal ends where pupation occurs. Callow adults have been reported to feed on inner bark before leaving brood logs, but detailed accounts of parent or immature (F1) adult feeding behavior are lacking. Adult feeding and reproductive behavior of *I. avulsus* are described here.

**METHODS AND MATERIALS**

Behavior was studied by the use of phloem-glass plate units, a modification of the "sandwich" technique described by Hopping (1961) for rearing *Ips* spp. Each unit consisted of 3 layers; (1) a 25 X 36 X 0.95 cm glass plate which was placed on the bottom, (2) a 15 X 24 X 0.5 cm sheet of phloem from the inner bark of typical slash pine, *Pinus elliottii* Engelm. var. *elliottii* which was placed in the middle, and (3) a 25 X 36 X 0.95 cm glass plate with a 6 mm hole in the center, which was placed on top. The 3 layers were held together at their edges with no. 10 binder clips. A 6 mm plug of outer bark was inserted in the hole in the top plate and nonabsorbent cotton was packed around the edges of the phloem sheet in the middle to prevent desiccation. All observation units were held at 30°C throughout the study.

All test beetles were collected as callow adults from or near their pupal chambers and reared in isolation on inner bark until mature. It was assumed that they had not mated prior to the tests. To initiate each test, 1 male was placed on the outer bark plug and a 10mm cover slip was placed over the hole in the top plate. Males that did not become "established" by boring an entrance tunnel and constructing a nuptial chamber in the
inner bark sheet were replaced by other males, as required. Twelve hr after a male was introduced and established in a unit, a female was placed on the bark plug where the male had bored his entrance tunnel.

Feeding, mating, and oviposition behavior were observed for each of the 10 pairs of I. avulsus, until each female had isolated herself from the associated male in his nuptial chamber by packing the egg gallery behind her with boring material.

Ten beetles of each sex, newly-emerged from pine logs, were fixed, sectioned, and stained by a modified Gram-Weigert procedure (Gouger 1971), then sections were examined microscopically to determine whether mycangia were present and to determine contents of the alimentary canal.

Results

Feeding.—I. avulsus males rotated about their longitudinal axis while boring a round entrance tunnel through the plug of outer bark in the upper plate. Boring material was passed back under the beetle by means of the mandibles, maxillae, and prothoracic legs, then pushed to the rear with the meso and meta-thoracic legs. Feeding began when the inner bark was reached. Chips of bark tissue were excised from the inner bark, taken into the buccal cavity, and appeared to be compressed by squeezing action of the mandibles. After compression, the residual pellet of host tissue was expelled from the head and passed to the rear of the body as described above. Periodically, chips of inner bark were excised but passed to the rear without being taken in and compressed. Similar feeding behavior was observed in females and males.

Microscopic examination of fresh whole guts and stained sections of newly-emerged adults showed that contents of the gut consisted principally of microorganisms, starch grains, and very fine host material (Fig. 1); only small amounts of the coarser inner bark tissues were present. Asco-

![Fig. 1. Contents of foregut of newly-emerged I. avulsus adult, showing light-colored starch grains in a matrix of very fine material. Starch grains are ca. 10μ across.](image-url)
spores of the bluestain fungus, *Ceratocystis iphys* (Rumbold) C. Moreau, were universally present in the gut and especially within the hind gut, but no mycangial bodies or unusual concentrations of microorganisms were detected anywhere in the adult body. The alimentary canal was of the elongate scolytid type and ventral dilator muscles of the pharynx were present and very well-developed (Fig. 2).

*I. avulsus* adults of both sexes produced gelatinous feces which were commonly deposited on the roof of the nuptial chamber where they were frequently eaten by consorting beetles entering the chamber or adhered to their bodies.

![Image](image)

**Fig. 2.** Median sagittal section through *I. avulsus* adult head. Intake of inner bark (solid arrow); ventral dilator muscles of pharynx (hollow arrow VDM). Head is ca. 1 mm across dorso-ventrally.

**Mating.**—An *I. avulsus* female placed on the bark plug of an observation unit became visibly excited upon contacting boring material (chips, pellets, and some gelatinous feces) expelled from the entrance tunnel by a male established in his nuptial chamber, and burrowed into this extruded material until she was at the entrance to the tunnel. The male blocked entry into the tunnel by backing into it and bringing his elytral declivity nearly even with the entrance. The female pushed vigorously against the male’s declivity while forcing her way into the tunnel and stridulated with her head and pronotal organs as in other *Ips* spp. (Barr 1969, Wilkinson et al. 1967). The pushing-stridulating behavior of the female was repeated several times and the female occasionally “bit” the margins of the male elytra until the pair had reached the nuptial chamber (Fig. 3, A). The female immediately began construction of an egg gallery extending off the nuptial chamber and the male assisted by removing material produced during this
tunneling operation (Fig. 3, B, C). The female was not observed to stridulate with her head and pronotal organs after she had once begun an egg gallery.

Copulation in *I. avulsus* first occurred after the female had constructed 2.5-3.0 mm (or about 1 body length) of egg gallery. The male periodically butted the female's elytra, which apparently stimulated her to receive him, and copulation occurred at the junction of an egg gallery and nuptial chamber with the male above at an angle of ca. 100° (Fig. 3, D). Copulation lasted an average of 35 sec (range: 22-45 sec) at 30°C. Pairs mated 3 times at about 10-min intervals, ending when the female abruptly packed the tunnel behind her with boring material.

Oviposition.—The mated *I. avulsus* female extended her tunnel until it ran parallel with the phloem grain in most cases, then excised phloem tissue from the left or right side of the egg gallery with her mandibles to form an egg niche. The egg niche was cut to approximately the same size as her head capsule by rotary motion of the extended head. Tissue removed from the niche was packed into a phloem plug located at the end of the egg gallery (Fig. 3, E). She then backed out of the gallery (F), turned around in the nuptial chamber (G) and backed up to the egg niche (H) where a single egg was quickly deposited (I). She then reversed her position (J,K,L) and removed pieces of the phloem plug which were then tamped tightly over and around the egg with her mouthparts (M).

**Discussion**

Butts (1951) studied morphological differences between “liquid-feeding” and “solid-feeding” coccinellid beetles and other insects, and reported ventral dilator muscles were well-developed in liquid-feeding species such as the Mexican bean beetle, *Epilachnus varivestis* Mulsant, but absent in solid-feeding species. He also observed that “... those insects that take liquids only have a greatly elongated alimentary canal”, as illustrated by *E. varivestis*. Butts did not report that *E. varivestis* also produces liquid feces, which behavior would appear to be concomitant to liquid-feeding in many insects (e.g., aphids and scales).

*Ips avulsus* is evidently a “liquid-feeding” species at least in the adult stage, based on its feeding behavior of intake-compression- and regurgitation of inner bark from the buccal cavity, the presence of very well-developed ventral dilator muscles of the pharynx, and especially the presence of only very fine, semi-liquid material, and almost no solids in the gut. *Ips avulsus* has the elongate alimentary canal typical of liquid-feeding insects such as the Mexican bean beetle (illus. by Butts 1951), and also typical of scolytid beetles as illustrated by Hopkins (1911) in the red turpentine beetle, *Dendroctonus valens* LeConte.

Liquid-feeding, the deposition of gelatinous feces on the walls of the nuptial chamber, and consumption of feces by consortig adults was also observed by us in *Ips calligraphus* (Germ.) (unpublished), which suggests that this behavior is common in *Ips* spp. Leach et al. (1934) reported that the sticky fecal pellets of *Ips grandicollis* (Eichh.) and *I. pini* were deposited and adhered to the nuptial chamber wall. Barr (pers. comm.) reported that *I. paraconfusus* defecated principally in the nuptial chamber.

Two important consequences of this behavior would be (1) transmission of bluestain (*C. ips*) spores and other symbionts between consortig adults
and (2) concentration of the male-produced aggregating pheromone in feces deposited in the nuptial chamber, which virgin females must find and enter in order to mate and reproduce.

The universal presence of viable bluestain fungus ascospores in the gut and feces of *Ips* adults emerging from brood logs or colonizing new host material is explained by their extensive feeding on *C. ips* perithecia in the inner bark of brood logs prior to attacking new host material (Leach et al. 1934, Yearian et al. 1972). Such spores germinate in new host tissues surrounding the nuptial chamber soon after deposition of feces (Leach et al. 1934), thus ensuring establishment in new host material. Feeding on perithecia and interchange of symbionts through feeding on gelatinous feces deposited in the nuptial chamber thus ensures transmission and dispersal of

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Fig. 3. Reproductive behavior of *Ips avulsus*:—A. Male *I. avulsus* preceding female into nuptial chamber; B. Female *I. avulsus* assisting male in constructing nuptial chamber; C. Male removing frass from nuptial chamber; D. Copulation in nuptial chamber; E. Female constructing egg niche in egg gallery.
Fig. 3 (Cont'd.) F. Female backing out of egg gallery; G. Female turning around in nuptial chamber; H. Female backing into egg gallery; I. Female ovipositing in egg niche; J, K, L. Female reversing her position and re-entering the egg gallery; M. Female packing phloem around the egg.
such symbionts throughout a population of consorting adults; this would serve an important function in species such as *Ips avulsus* which lack mycangia for the transport of symbionts.

Reproductive behavior of *I. avulsus* was identical to that illustrated by Schmitz (1972) for *I. pini*, a not surprising result since both species belong to Hoppings taxonomic Group IV (Hopping 1963, Lanier 1972). Reproductive behavior is apparently quite generalized in pine-feeding *Ips* spp. from North America, since it has now been observed to be similar in species from Group IV (*pini* from Idaho and *avulsus* from Florida), Group IX (*paraconfusus* from California) (Barr 1969, pers. comm.), and Group X (*calligraphus* from Florida) (unpublished study by authors).

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**Literature Cited**


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NOTICE


(For a review of the book by E. O. Wilson, see Science 158:622, 1967.)