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BIOLOGY OF *PYEMOTES PARVISCOLYTI* [*ACARINA* : *PYEMOTIDAE*]

BY

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Pyemotes parviscolyti CROSS & MOSER is phoretic only on *Pityophthorus bisulcatus* EICHHOFF; it attacks all stages of this insect except the adult. Females, which contain little or no venom, prey on other scolytids if galleries overlap. Males copulate with females of *Pyemotes ventricosus* NEWPORT and vice versa, but only males of the mother species result. Copulation with *Pyemotes scolyti* OUDEMANS was not successful.

During studies of mite predators on *Dendroctonus frontalis* ZIMMERMAN and *Ips* spp. on southern pines (MOSER & ROTON, 1971), we discovered and closely observed a *Pyemotes* associated with one of the minor bark beetles, *Pityophthorus bisulcatus*. The species was named *Pyemotes parviscolyti* by CROSS & MOSER in 1971. *Pityophthorus bisulcatus* is one of several minor bark beetles that occur in dead or dying southern pines following successful attacks by *D. frontalis* and 3 *Ips* species. In large trees it is found on the periphery, infesting twigs and branches from 4 to 75 mm in diameter. It is often abundant in weakened young plantations where it may infest sapling trunks as large as 270 mm in diameter.

Host specificity

Although the mite readily attacked any bark beetle in the laboratory, it rarely did so in nature. Apparently, the mite's phoretic behavior keeps it from contacting the larger bark beetles in the field.

Pyemotes parviscolyti females ride both sexes of *Pityophthorus bisulcatus*, but no other pine insects, including *Pityophthorus annectans* LE CONTE, which often infest the same tree. Several females (1-11, usually 2-3) attach to setae at bases of beetle coxae with claws of tarsi I (fig. 1). When crowded, however, a few may overflow to the abdomen. Single females are often overlooked because of the many

Pygmephorus bennetti CROSS & MOSER females, which have a similar appearance and ride in the same manner. Presumably, a few phoretic females of *Pyemotes parviscolyti* are virgin, as evidenced by the all-male progeny in occasional *Pityophthorus* egg niches.

Since successive generations were reared in the laboratory, phoresy is not a prerequisite for attack behavior. In the field the first generation of mites leaving beetles attacked eggs, the second attacked larvae, and so on until immatures became unavailable. Adult beetles were never attacked. Parent adults of *Pityophthorus bisulcatus* rarely carried mites, which were common on brood adults. WALTERS & CAMPBELL (1955), studying mites in general, found that parent adults of *Dendroctonus pseudotsugae* HOPKINS become free of mites soon after establishing first brood.

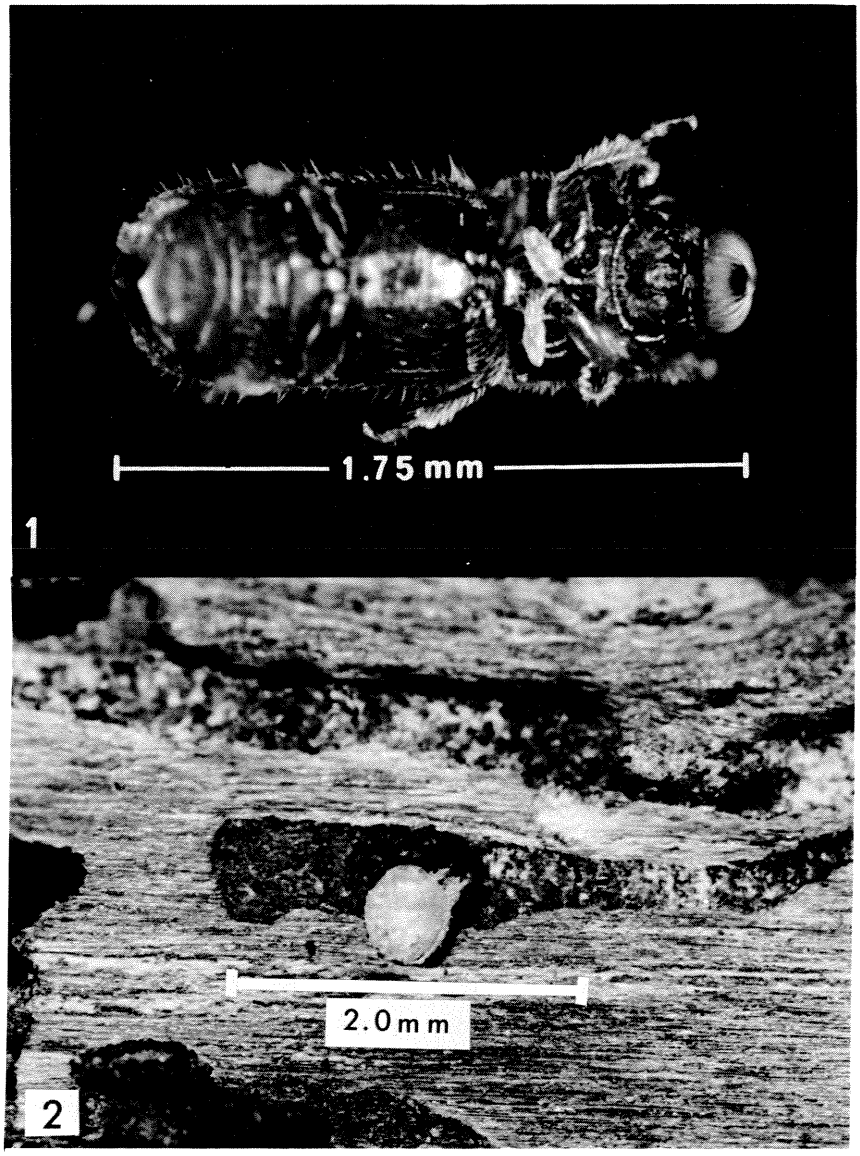
Galleries of *Pityophthorus bisulcatus* sometimes overlapped with those of *Ips avulsus* (EICHHOFF) and *I. grandicollis* (EICHHOFF) in twigs, and rarely with those of *I. calligraphus* (GERMAR), and *Dendroctonus frontalis* ZIMMERMAN in larger branches and sapling trunks. When overlap did occur, *Pyemotes parviscolyti* attacked brood of the other scolytids. In general, however, *Pyemotes parviscolyti* occurs only on the periphery of trees and is ecologically isolated from most potential host material.

Laboratory observations

ATTACK BEHAVIOR AND SURVIVAL.

In laboratory cultures females readily fed on brood of any scolytid. In addition, pupae of a pine weevil, *Pissodes nemorensis* GERMAR, were attacked, but not its large and active larvae which tended to crush the fragile mites. Females would not feed on brood of other subcortical insects such as *Corticeus glaber* LE CONTE, *Thanasimus dubius* (F.), *Temnochila virescens* (F.), *Cerambycidae* spp., *Roptrocerus xylophagorum* (RATZEBURG), and *Reticulitermes flavipes* KOLLAR, but females did feed on pupae of the town ant, *Atta texana* (BUCKLEY). Swollen females were cannibalized if host material was scarce. Numbers and sex ratios of progeny from these cannibals were normal when only one fed on a mother, but if 3 were present, only 20-30 females and 1-2 males were born. One attacked mother continued to give birth while 3 other females were feeding on her.

Laboratory cultures exposed to the air in open stender dishes were easily maintained under the normal laboratory temperatures and humidity of about 21 °C and 40 % R. H. When dishes were covered, higher humidities resulted, and fungi often overwhelmed cultures. In the field, humidities under twig bark were usually less than under trunk bark, which was usually damp to wet. For this reason, swollen female mites probably could not survive well under



FIGS. 1-2. — *Pyemotes parviscolyti.*

1. Females attached to setae at coxal bases of *Pityophthorus bisulcatus* with claws of tarsi I.

2. Single physogastric female and shrunken larva of *P. bisulcatus* in larval gallery. Parent gallery is at top.

the more humid thick bark even if they were phoretic on the bark beetles that infest large stems of pines.

However, virgin and mated unswollen females, as well as males, lived much longer under high than moderate laboratory humidities (table 1). Maximum survival time for males at room humidity and temperature was 0.39 days; it was 9 days at 100 % humidity. The increase in survival time for females was from 2 to 22 days. Surprisingly, survival times of virgin and mated females at 100 % humidity did not differ significantly at the 0.05 level.

TABLE 1

Life spans of Pyemotes parviscolyti *under various conditions* (1) (*in days*)

SEX AND ENVIRONMENT	MEAN ± S.E.	OBSERVED RANGE
Males		
On mothers	3.45 ± 0.225	0.05[3] – 9.0
Dry vial (2)	0.28 ± 0.017	0.15 – 0.39
Wet vial	4.50 ± 0.655	1.0 – 9.0
Virgin females		
Dry vial	1.3 ± 0.076	1.0 – 2.0
Wet vial	6.8 ± 1.386	1.0 – 22.0
Mated females		
Dry vial	1.4 ± 0.112	1.0 – 2.0
Wet vial	7.5 ± 1.170	1.0 – 20.0

(1) Averages presented in table are based on 97 observations of males on mothers and 20 observations of all other classes.

(2) From individuals removed from mothers immediately after birth, and placed in 25 × 8 mm specimen vials with corks. Dry vials were at room temperature and humidity (21°C, 40 %); wet accumulated on glass, thus maintaining 100 % humidity.

(3) None were born dead.

In the field no more than 7 (usually 1 or 2) females were seen attacking individuals of *Pityophthorus bisulcatus* (fig. 2). In the laboratory, as many as possible covered a host; 35 were counted on a single pupa of *Dendroctonus frontalis*. Under crowded conditions, first females to attack swelled larger and gave birth to more progeny than those feeding later. In bark beetle galleries, swollen *Pyemotes* could easily be distinguished from the more common *Pygmephorus bennetti*. Only the conjunctival folds separating the smooth from the ridged plates of the opisthosoma of *Pyemotes* (fig. 6) swelled, in contrast

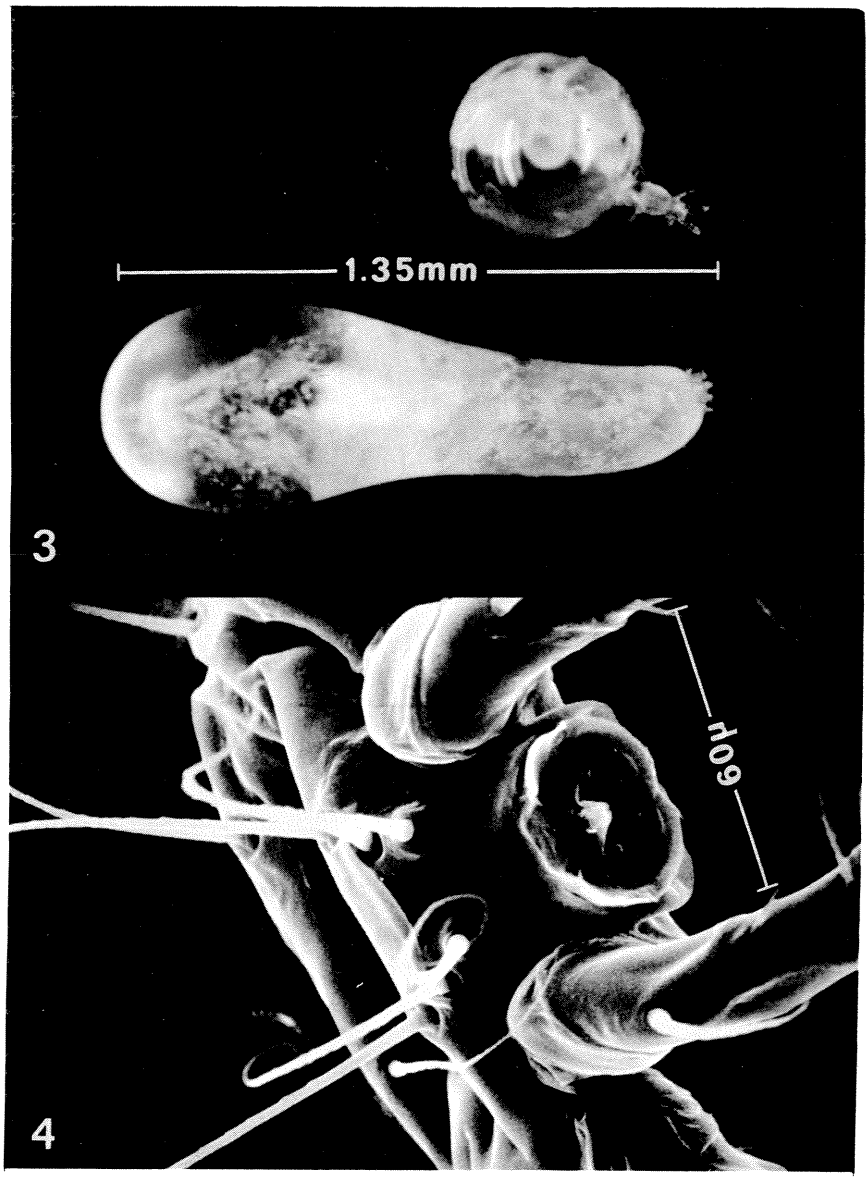


FIG. 3. *Pyemotes parviscolyti* (top), *Pygmephorus bennetti* (bottom). Only the opisthosomal area of *P. parviscolyti* swells, whereas the whole hysterosoma of *P. bennetti* balloons.

FIG. 4. *R. parviscolyti.* Male genital capsule showing a) dorsal plate which pushes newly born female out of birth canal, b) penis.

to *Pygmephorus bennetti* in which practically the entire hysterosoma ballooned (fig. 3).

In laboratory cultures, females at first moved actively on the body of the host, feeding intermittently. As HERFS (1926) observed, first swelling of abdomen was noticed at about 24 hours. Swelling progressed rapidly, and after 2 days movement was greatly hampered by size. By the third day, the female had settled in one place and permanently inserted mouthparts; swelling continued until birth during the 9th day. Abdomens of fully swollen females reared on a single larva averaged 760 μ with extremes of 480 μ to 1.040 μ. These measurements agree better with those of the smaller *Pyemotes herfsi* (OUDEMANS), (HERFS, 1926), than with those of *Pyemotes scolyti* (KRCZAL, 1959). The large variation of maternal size is probably, as HERFS (1926) suggested, dependent upon the site and efficiency of attachment, rate and type of decomposition of the host, as well as the degree of competition from other females attacking the same larva. Nine of 10 undernourished mothers removed from hosts after 3 days gave birth to females only, whereas mothers fed for 6 days gave birth to normal ratios (table 2). REUTER (1909), in contrast, found that malnourishment increased number of offspring in *Siteroptes cerealium* AMERLING.

TABLE 2

Effect of mother's nourishment (1) *on number and sex of progeny.*

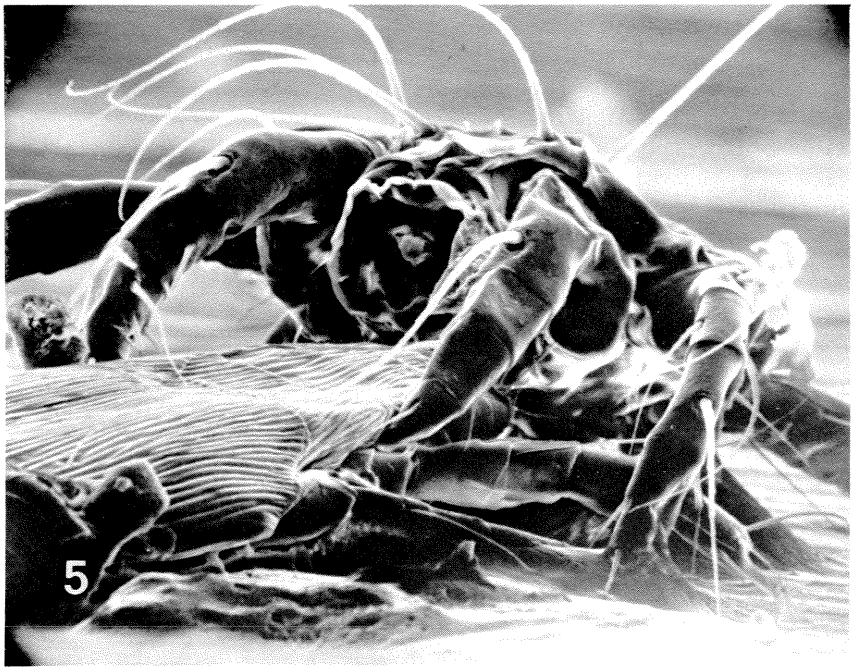
DAYS FED AND SEX OF PROGENY	MEAN ± S.E.	OBSERVED RANGE
3 days		
Males	< 1 — — —	0 — 1 (2)
Females	14.7 ± 2.810	3 — 32
6 days		
Males	2.14 ± 0.50	1 — 4
Females	13.3 ± 12.26	103 — 166

(1) From fully swollen mothers fed 9 days on larvae of *Dendroctonus frontalis* in laboratory. Only one mite was placed on each beetle larva. The 3-day feeding period represented by 10 mothers, the 6-day by 5.

(2) i.e. only one male was born to 1 of the 10 mothers.

MATING BEHAVIOR, NUMBER AND RATIO OF PROGENY.

In 37 rearings of fully swollen females, a male was always born first. He rested quietly on the opisthosoma of the mother, usually with gnathosoma in vulva (slit-like opening of birth canal). When males were plentiful, they often clustered near the birth canal. As



FIGS. 5-6. *P. parviscolyti* :

5. Male grasping female abdomen with hind legs just prior to copulation.

6. Male and female copulating. Only the conjunctival folds between the smooth and ridged plates swell when the mite feeds (figs. 2, 3).

The scanning electron microscope photos were made at the USDA Forest Service Forest Products Laboratory at Madison, Wisconsin, by Dr. IRVING SACHS.

many as 5 were seen with gnathosomae in a single vulva. Perhaps they were feeding on the mother as KRCZAL (1959) suggested for *Pyemotes scolyti*. Mouthparts of slide specimens of males appeared to be well developed and functional. Mean life span on mothers was 3.45 days, which was not significantly different from that for those kept at 100 % humidity (table 1). Maximum survival time was 9 days. Means for mother-reared males significantly exceeded those for mites reared in " dry " vials. Since the males on mothers were exposed to about the same air humidities as those in " dry " vials, the greater life span of mother-reared males may be due to water imbibed rather than food intake. HERFS (1926) recorded that *Pyemotes herfsi* males averaged 14.5 (maximum 32) days on a mother at 25°C. He also found that males placed on host larvae or in glass dishes lived no longer than 24 hours at 25°C. He attributed the short life span of the latter to starvation rather than desiccation.

When present, the male always assisted birth of females, which emerged head first. He removed his gnathosoma from the maternal vulva, turned around, and pushed nascent females from the birth canal with successive jabs of the dorsal plate of the genital capsule (fig. 4). Birth of a female took about 20 seconds, after which he immediately grasped the female abdomen with his hind legs (fig. 5) and copulated for about 30 seconds (fig. 6), a time similar to that HERFS (1926) recorded for *Pyemotes herfsi*. When multiple males were present, they competed briefly, but one always dominated and finished copulation. No female was observed mating more than once.

When a male was not present, birth was accomplished by peristalsis, taking as long as 6 hours for the first born and 10 minutes for those born later. *Pyemotes herfsi* birth time was 171 seconds with a male and 217 without a male; copulation time was 20-30 seconds (HERFS, 1926). *Pyemotes scolyti* birth took 40-50 seconds, including the 5-10 seconds spent in copulation (KRCZAL, 1959).

Single males mated with an average of 53.7 (s.d. 34.7) females in 54 cases where virgins were present; extremes were 1 and 131. Although no statistical test was made, it was obvious that the longer a male lived, the more matings he would accomplish (table 1). The four males that lived 8 days fertilized from 65 to 120 females each, and the two that lived 9 days fertilized 90 and 131. One that lived only 4 days succeeded in fertilizing 106, but he had a backlog of 63 virgins when he was born. Single males of *Pyemotes herfsi* averaged 25-20 matings, and one was observed to mate 78 times (HERFS, 1926); KRCZAL (1959) records a *Pyemotes scolyti* male that mated with 258 females.

When numerous swollen females clustered on a host, two or more males per mother usually accumulated. In such cases the males

often moved from mother to mother, or wandered about and mated with stray virgins — a mechanism that may reduce inbreeding.

In the absence of a male at birth, virgins clustered on or near the mother until arrival of a male, which copulated with each. Copulation released searching behavior of the females, who immediately left to attack suitable hosts. HERFS (1926) and KRCZAL (1959) recorded a similar behavior for *Pyemotes herfsi* and *Pyemotes scolyti*.

Virgins clustered near mothers usually wandered away and died after 8-12 days if a male did not appear. In several cases, virgins left and attacked a beetle brood after remaining on the mother for 7 days; progeny were all males. As stated earlier, all-male progeny were also found in a few egg niches of *Pityophthorus bisulcatus* in the field.

This searching and clustering behavior permitted the tabulation of numbers of females mated by individual males and male longevity on the mother. Observations were made daily and searching females were counted as mated, after which they were killed and removed. Newly born males were killed as they were born, but the older males had to be marked, because the newly born males could not be distinguished from their older brothers unless the observer happened to see one being born. Marking was done with spray paint, as described by MOSER & ROTON (1970).

It was demonstrated that copulation, not fertilization, triggered searching behavior. Virgin females of *Pyemotes parviscolyti* were mated to males of *Pyemotes ?ventricosus* (*), and vice versa. They readily copulated and females searched for hosts in a normal manner, but the all-male progeny in both cases confirmed that no fertilization had resulted. The progeny were always of the same species as the mother.

Mating behaviors of *Pyemotes parviscolyti* and *Pyemotes ?ventricosus* were essentially the same. When males of one species were placed on the vulva of a gravid female of the other species, males performed as if the mother were of the same species. When a female was born, she was dutifully shoved out by the foreign male and copulation followed immediately.

Gestation period from commencement of feeding to birth was 9-10 days in uncovered stender dishes in the laboratory. Parturition lasted an average of 6 days, with extremes of 3 to 11 days for 26 fully swollen mothers. The above figures are short compared to those for *Pyemotes herfsi* according to HERFS (1926). At room temperature 17 mothers averaged 20.5 days (extremes 5-38); at 25°C the average was 17 days (extremes 2-33).

(*) From laboratory cultures of *Lyctus planicollis* LECONTE at Gulfport, Mississippi, furnished by JOE K. MAULDIN and RICHARD V. SMYTHE. Since type specimens of *Pyemotes ventricosus* have been lost, and since no lectotypes have been designated, the identity of this as well as all other literature records of "*ventricosus*" are in doubt.

Mothers usually died before all progeny were born, but 10 of 19 mothers continued to give birth, to as many as 47 individuals, for as long as 18 hours after death. Although a male was invariably born first, subsequent males were spaced rather evenly throughout the birth period. The average number of males from 20 mothers mated immediately after birth was 10 (6 % of total offspring) with extremes of 1 to 89 (table 3), figures that approximate those of HERFS (1926). Average number of females born was 162 with extremes of 64 to 229. The greatest number of progeny from any mother was 286 (12 were males), which exceeded previous maximums of 269 for *Pyemotes scolyti* (BEAVER, 1967) and 280 for *Pyemotes herfsi* (HERFS, 1926) (table 3), but was less than the 322 recorded for *Pyemotes ventricosus* (MONTEROSSO, 1934).

TABLE 3

Effect of delayed matings on sex and number of progeny (1).

DELAY IN DAYS AND SEX OF PROGENY	MEAN ± S.E.	OBSERVED RANGE	GRAVID FEMALES OBSERVED
0 days			20
Males	10.3 ± 4.28	1 — 89	
Females	161.7 ± 11.73	64 — 229	
Total offspring	172.0		
Percent males	5.7		
3 days			24
Males	2.5 ± 0.18	1 — 4	
Females	107.0 ± 9.92	9 — 183	
Total offspring	109.5		
Percent males	3.2		
6 days			24
Males	20.0 ± 2.98	2 — 46	
Females	175.0 ± 6.87	86 — 274 (2)	
Total offspring	195.0		
Percent males	11.4		

(1) From fully swollen mothers fed 9 days on larvae of *Dendroctonus frontalis* in laboratory. Only one mite was placed on each beetle larva.

(2) These 274 females were accompanied by 12 males, a total of 286.

Since virgin females cluster around the mother for about 8 days waiting to mate, we decided to see whether age of the virgin at mating affected progeny. Virgins were mated immediately after birth and 3 and 6 days thereafter. Differences in progeny that are difficult to explain were observed (table 3). Duncan's new multiple range test

at the 0.05 level indicates that both number of males and total number of progeny were smaller for females mated 3 days after birth than for those mated immediately or after 6 days. The proportion of males was significantly higher for females mated 6 days after birth than for those mated after 0 or 3 days. Mating delays of 9 days could not easily be tested because virgins started to wander away from the mother within 8 days.

INTERSPECIFIC BEHAVIORAL COMPARISONS.

Morphologically, *Pyemotes parviscolyti* resembled *Pyemotes scolyti* more than *Pyemotes ?ventricosus* (CROSS & MOSER, 1971), but the behavior of *Pyemotes parviscolyti* was mixed (table 4). The mating behavior of *Pyemotes parviscolyti* was so similar to *Pyemotes ?ventricosus* that males of both species readily mated with their female counterparts. In addition, females and males of both were born gnathosoma first. *Pyemotes parviscolyti* closely resembled *Pyemotes scolyti* in host preferences and in having little or no venom. A single *Pyemotes ?ventricosus* female paralyzed a host within 5 minutes; mouthpart insertion was accompanied by violent movements of host. Hosts of *Pyemotes parviscolyti* and *Pyemotes scolyti* (*) moved as long as 24 hours if attacked by a single feeding female; 2 hours with 25-30 females. Host movements were not violent.

The phoretic behavior of *Pyemotes parviscolyti* resembles neither of the other two *Pyemotes*. It is limited to a single scolytid, whereas *Pyemotes scolyti* apparently rides any species of the genus *Scolytus*. There are no records of phoretic behavior for *Pyemotes ?ventricosus*.

TABLE 4

Behavioral differences and similarities among 3 species of Pyemotes.

BEHAVIOR	*P. parviscolyti*	*P. scolyti*	*P. ?ventricosus*
Mating position relative to birth canal	outside	inside	outside
Birth	gnathosoma first	opisthosoma first	gnathosoma first
Venom	little or none	little or none	highly toxic
Feeding preference in laboratory	scolytids	scolytids	wide variety of insects
Phoresy	*Pityophthorus bisulcatus*	*Scolytus* spp.	?
Will attack adult hosts in laboratory	no	no	yes

(*) From under bark of *Ulmus americana* L. infested with *Scolytus multistriatus* (MARSHAM) at Delaware, Ohio, furnished by BRUCE H. KENNEDY.

Considering their tendency to attack adults (in the laboratory, at least) it is difficult to see how they ride adult hosts. We observed swelled females feeding on adults of *Lyctus planicollis*, *Anobium punctatum* DE GEER (*,) and teneral adults of *Anthonomous grandis* BOHEMAN (**). Literature records of adult parasitization include *Tineola biselliella* (HUMMEL) (HERFS 1926), *Anagasta kuehniella* (ZELLER) (VUKASOVIĆ 1947), and *Harmolita tritici* (FITCH) (WEBSTER 1910).

Males of *Pyemotes parviscolyti* and *Pyemotes ?ventricosus* tried to mate with virgin females of *Pyemotes scolyti* clustered around the mother, but were unsuccessful. When placed on a *Pyemotes scolyti* mother without a *Pyemotes scolyti* male imbedded in the birth canal, foreign males assisted birth by pushing with the dorsal plate of the genital capsule even though the female was coming out opisthosoma first. They then attempted to mate, but copulation was never achieved.

Males of *Pyemotes scolyti* placed on mothers of *Pyemotes parviscolyti* or *Pyemotes ?ventricosus* briefly tried to enter the birth canal, but never were successful, perhaps because the vulva was too small. They then usually wandered off. If a male was still on a foreign mother when a virgin female happened to be born, he did not assist birth, but made clumsy, unsuccessful attempts to mate outside the birth canal.

Conclusions

Historically, the taxonomy of *Pyemotes* has been confused, and species have been difficult to identify (CROSS, 1965). We show here that at least 3 species are quite distinct, both in morphology and behavior. At this point it seems doubtful whether morphologically indistinguishable *Pyemotes* taken from new hosts should be described unless laboratory studies show them to be behaviorally or genetically incompatible with closely related forms already described.

RÉSUMÉ

Biologie de *Pyemotes parviscolyti* [*Acarina : Pyemotidae*]

Pyemotes parviscolyti CROSS & MOSER est phorétique seulement sur *Pityophthorus bisulcatus* EICHHOFF; il attaque tous les stades de cet insecte à l'exception de l'imago. Les femelles, qui possèdent peu ou pas de venin, s'alimentent aux dépens d'autres scolytides si les galeries se recoupent. Les mâles s'accouplent avec les femelles de *Pyemotes ?ventricosus* NEWPORT et réciproquement. La copulation avec *Pyemotes scolyti* OUDEMANS n'a pas de succès.

(*) From the material used by MEYER (1970). Specimens furnished by STEEN RASMUSSEN.

(**) From material collected at Sonora, Mexico, furnished by W. H. CROSS, State College, Mississippi.

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