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SOCIAL BEHAVIOR IN PASSALID BEETLES  
(COLEOPTERA: PASSALIDAE): COOPERATIVE  
BROOD CARE

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## ABSTRACT

A brief summary is given concerning passalid social behavior in relation to their life cycle. Passalid pairs defend log tunnels and remain with offspring from egg to adulthood. Parent-offspring cooperation involving care of other offspring is a step in the evolution of eusociality. Young adult passalids cooperated with their parents in repair of sibling pupal cases. Cooperative brood care between parents and juveniles has not been reported previously for non-Hymenopterous or non-Isopterous arthropods. The presence of overlap of generations and cooperative brood care by at least temporarily non-reproductive adult individuals in certain passalid species suggest that we might consider these passalids to possess one of the highest levels of subsocial behavior known for arthropods. Habitat, trophic rela-

tions between individuals, and sex determination mechanisms suggest parallels with the evolution of termite sociality.

#### RESUMEN

Se resumen brevemente lo que se conoce acerca del comportamiento social de passalidor en relación a su ciclo de vida. Parejas de pasálidos defienden túneles en palos y se quedan con su prole desde huevo hasta adulto. Cooperación entre padres y prole involucrando cuidado de otra prole, es una etapa en la evolución de la eusocialidad. Jóvenes adultos cooperaron con sus padres en la reparación de capullos pupales de sus hermanos. Cuidado de la cría en cooperación entre padres y juveniles no ha sido reportado anteriormente para los artrópodos no-Hymenopteros o no-Isopteros. La presencia de traslape de generaciones y cooperación entre adultos y prole que son temporalmente no-reproductivas en algunas especies de pasálidos, sugiere que estos pasálidos poseen uno de los niveles conocidos más altos de comportamiento subsocial entre los artrópodos. Habitat, relaciones tróficas entre individuos y mecanismos de determinación de sexo, sugieren paralelas con la evolución de la eusocialidad en termitas.

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Cooperative brood care, overlap of parental and offspring generations, and the presence of reproductive castes are the basic characteristics which define truly social (eusocial and hypersocial) behavior in arthropods (Batra 1966, 1977). These high levels of social behavior are recognized among the arthropods primarily in the Hymenoptera and Isoptera. Some arthropods have forms of subsocial or quasisocial behavior with 1 or rarely 2 of these characteristics developed to varying degrees (Wilson 1971, Eickwort 1981). Passalid beetles are among the most highly subsocial insects because they possess, in at least some species, both overlap of generations and, as we report here, cooperation in brood care between parent and offspring. Young adult passalids cooperate with their parents in repair of sibling pupal cases. Cooperative brood care is rare (unknown?) for arthropods other than Hymenoptera or Isoptera. Habitat, trophic relations between individuals, and sex determination mechanisms suggest parallels with the evolution of termite sociality.

The family Passalidae contains approximately 500 species of primarily tropical, wood-eating beetles that tunnel in rotting logs (Reyes-Castillo 1970, Schuster 1978). One beetle (either sex) arrives at a log and begins a tunnel. The other beetle which will form the pair arrives later. The beetles are monogamous and the pair remains together at least through the development of the first brood. They will defend the tunnel against other passalid intruders (Schuster 1975). Acoustical communication is highly developed in the colony, especially associated with courtship and aggression. One species has at least 17 signals, more than is known from any other arthropod (Schuster 1983).

Eggs are placed in a nest of finally triturated wood in the tunnel. Though Krause and Ryan (1953) mention 100 eggs and juveniles of the first larval instar in a nest of *Odontotaenius disjunctus* (Illiger) (formerly *Passalus cornutus* Fabricius and *Popilius disjunctus* Ill.), Gray (1946) noted nests of this species usually contain 20-35 eggs. In various countries we examined a total of 28 natural passalid nests by carefully dissecting the tunnel systems; the maximum number of progeny (eggs and young larvae)

in a nest was 42 for *Chondrocephalus purulensis* (Bates) in Guatemala. In some tropical species a pair can produce 3, and perhaps 4, egg clutches in a year (Schuster 1975). We observed courtship of *O. zodiacus* (Truqui) in the presence of third instar larvae; occasionally, we found pupae and eggs in a tunnel system without any intermediate larval stages. Apparently, therefore, when a brood is in or near the pupal state, another egg clutch may be produced. It is not necessary, however, for the male to be present (though apparently he usually is) for subsequent egg clutch production. A female *Publius agassizi* (Kaup) collected in May and maintained completely isolated from other passalids produced a clutch of fertile eggs at 4 months and another a year after capture. Nevertheless, it is rare to find single beetles in a tunnel system except at the initial stage of excavation.

In Passalidae, black (mature) adults are found in tunnels with all ontogenetic stages, including red (teneral) adults. In 76 passalid tunnel systems containing juveniles of 37 species in Peru, Costa Rica, Mexico and Guatemala, mature adults were present in all except 2 systems. Of 17 systems with at least 1 teneral adult, 16 also contained at least 1 mature adult. Since teneral adults require a few weeks to many months to blacken entirely, this suggests a minimal duration of parent-adult progeny contact. Usually, only completely black adults migrate (Schuster 1975). Of 51 migrating passalids captured in Guatemala, 40 were black, 11 were intermediate in color and none were red. The presence of more than 2 black adults in 1 tunnel system indicates that migration may not necessarily occur immediately upon blackening. This inference is strengthened by the aggressive behavior of colonists toward intruders, reducing the probability of foreign beetles joining the colony; thus all black beetles in a colony should be either parents or progeny. The maximal duration of generation overlap may depend on resource availability and consumption rate, or on adult longevity. Adults live more than 2 years in the field, and in the laboratory a pair of *Passalus affinis* (Percheron) survived 4 years. Individuals of *P. punctiger* Lapeletier & Serville and *O. zodiacus* continued reproducing after 2 years.

Very little is known concerning the life and behavior of the larvae until pupation. A third larval instar pupates in a case of fine-textured, compacted excrement and wood shreds constructed with adult aid (Fig. 1). This case may be important in protecting the pupa from predation or parasitism. Reduviids and tachinids are known to attack passalids (Schuster 1975). About 5 days prior to pupation, the larva ceases feeding, becomes whiter, and enters a pre-pupal stage. In the absence of adults, the prepupa will roll over and over, forming a depression in the feces and wood shreds. It will pupate in this depression. When adults are present, they will aid the larva in pupal case construction, as described by Miller (1932) from laboratory observations of *O. disjunctus*, by piling case material on the prepupa and shaping it from the outside. Two or more adults may work on the same case concurrently, or a single adult may work alone. Males and females may participate in construction.

The presence of parental brood care and generation overlap allows the possibility of cooperative brood care between parents and adult offspring, apparently quite rare outside the Hymenoptera and Isoptera. In Passalidae, parents, teneral adults, pupae and older larvae are commonly found together in the same tunnel system, a situation obviously conducive to cooperative brood care. In some cases, even greater overlap occurs, e.g. a chamber ap-

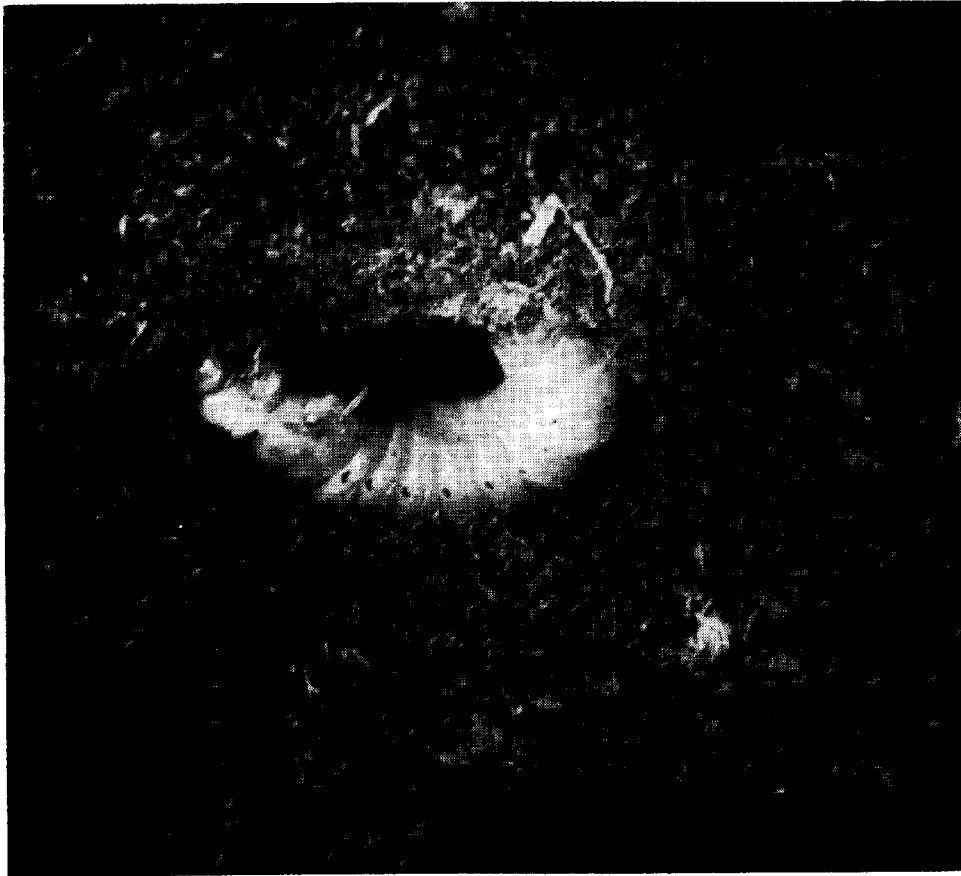


Fig. 1. *Passalus punctiger*—pupal case containing prepupa.

proximately 18 cm long in a Mexican log contained 22 *Heliscus tropicus* (Perch.) eggs, 4 first instar and 1 third instar larvae, 3 pupae, 10 teneral adults, and 3 black adults. Passalid iteroparity augments the potential for cooperation.

Evidence of sibling cooperation has been observed in pupal case construction. Miller (1932) observed 2 or more adults of the same sex constructing pupal cases together, but he did not give any indication of their genetic relationships. We collected 1 black and 2 teneral *Popilius haagi* (Kaup) adults and 3 larvae from the same tunnel system. Two of the larvae pupated and became adults within a week before the construction of the pupal case for the third larva. The new adults were not seen to aid the construction of the third case though construction was not observed continuously. Therefore, on 1 occasion 7 days, and another 9 days, after case construction, we made a hole 3 x 5 mm in the side of the new pupal case. Both times it was repaired by older beetles working together with a newly emerged beetle pushing frass with their mandibles and head to and against the pupal case. In the second case, the teneral beetle completed the reconstruction alone after the others had stopped working. A teneral adult emerged from the case 15 days later.

In a similar experiment with *Verres hageni* Kaup, we completely destroyed a case containing a prepupa. A black adult and 2 teneral adults

worked together in completely reconstructing the case. The slightly darker teneral adult reconstructed much more than did the very red adult. All were from the same log.

In a situation with *Passalus punctiger* a pupal case was damaged several times in the presence of the black adult that had constructed it and a teneral adult 3 days out of its case. Only the black adult repaired the case. However, when the black adult was removed a rough case was constructed by the teneral adult within 21 hours; the case was well constructed within 33 hours.

In these species, as well as 2 others (*Chondrocephalus purulensis* and *P. punctatostratus* (Percheron)) with which pupal case destruction experiments were done only with black or dark intermediate adults, the mature adults often became quite active immediately on contacting the destroyed sections of a case. The teneral red adults were usually slower to begin construction.

These observations indicate that a beetle may cooperate with other siblings and/or its parents in the construction and repair of a sibling's pupal case. The only trait, therefore, that can separate passalids from eusocial insects is their lack of castes. In adult passalids, external morphological differences are minimal or non-existent, even between sexes, except for teneral redness. Exactly when adults become sexually mature is unknown. Young adult males are not sexually mature (Virkki and Reyes-Castillo 1972); they have spermatogonia but lack spermatozoa (Virkki 1965). These factors would make it difficult to distinguish if possible castes (differing only in degree of ovarian development) do occur in some insects (Plateaux-Quénu 1960, 1962).

The rate of ovarian development is unknown. Courtship occurred 3 months after male and female pupal ecdysis in *P. punctiger* and 4 months after ecdysis of both sexes in *O. disjunctus*, which may indicate maturation by this time. Reproduction by either sex can occur 10 to 11 months after pupal ecdysis in *O. disjunctus* (Schuster 1975).

What factors may have influenced the evolution of such a high level of sociality in passalids? The haplodiploidy (males haploid) sex determination mechanism of Hymenoptera is thought to predispose this group toward the evolution of sociality (Hamilton 1964). Trophic relationship regarding transmission of mutualistic intestinal protozoa and/or bacteria in some termites may be a key factor in the evolution of termite eusociality (Howse 1970). Termites pass their protozoa throughout the colony by anal trophallaxis, the ingestion of anal liquids by other colony members. Repeated anal trophallaxis is necessary because each time a worker molts it loses its intestinal symbionts.

In many respects, Passalidae resemble termites and their probable ancestors the cryptocerid roaches (Nalepa 1984) more than Hymenoptera. Termites have a conventional genic sex determination mechanism (Hamilton 1972), as do passalids, which have either XY variants or XO, depending on the species (Virkki and Reyes-Castillo 1973). Monogamy in passalids, as in termites, should result in a high degree of relatedness among individuals of a given colony. Though passalid intestines have no cellulose-degrading protozoa, they do have a well developed flora and fauna, especially various fungi and nematodes (Lewis 1926). Passalids fed only rotting wood lose weight and die much sooner than those that eat passalid feces or previously tritu-

rated wood which has been partially decomposed by microorganisms (Mason and Odum 1967). For this reason alone, it would be advantageous for the larvae to remain near the adults. This may also explain why the eggs are placed in a nest of finely chewed wood. Ohaus (1900) suggests that the larval jaws are too weak to eat wood directly, but Heymons (1929) refutes this on the basis of morphological and behavioral studies in the laboratory. Instead, the finely shredded wood exposes a greater surface area to attack by wood-digesting microorganisms. More nutrients then become available to the newly hatched larvae, either as by-products of this digestion or in the bodies of the microorganisms ingested.

Both termites and passalids live in rotting wood. Dead trunks harbor a large number of subsocial species of arthropods and are apparently the site of origin of at least 2 truly social groups: ants and termites (Hamilton 1978). Organisms in such stable, structured "bonanza" microhabitats are usually subjected to K-selection, which tends to favor longer life, large mature size, iteroparity, and small broods (Wilson 1975)—all characteristic of Passalidae. These, in turn, tend to favor the evolution of increased parental care (Wilson 1975).

The presence of overlap of generations and cooperative brood care by at least temporarily non-reproductive adult individuals in certain passalid species suggest that we might consider these passalids to possess 1 of the highest levels of subsocial behavior known for arthropods.

#### END NOTE

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