ADULT-JUVENILE ALIMENTARY RELATIONSHIPS IN PASSALIDAE (COLEOPTERA)

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ABSTRACT

The results reported in this paper show that larvae of passalids are unable to feed directly from wood. Their main source of food is a mixture of adult faeces and powdered wood fragments produced by adults during galleries excavation. Newly emerged adults are also unable to use wood as their source of food unless they have previously ingest faeces from older adults. This fact suggests the existence of a symbiotic relationship with microorganisms for degradation and/or assimilation of wood in adults. On the other hand, I also found that, usually, adult faeces has a higher nitrogen concentration than ingested wood. In larvae faeces, this phenomenon may also take place but less frequently; besides, increases tend to be considerably less than with adults. Differences found between larvae and adults regarding their ability to use wood for feeding are probably due to some important variations existing in their digestive tracts. The main difference concerns the existence, in aduts, of a structure that could be a fermentation chamber; this structure is absent in larvae. The importance of these alimentary relationships, in regard to the evolution of social behavior in passalids, is discussed.

KEY WORDS: Passalidae, Coleoptera, Parental Behaviors, Subsocial Behavior, Nutrition, Xylophagy.

RESUMEN

Los resultados reportados en este trabajo muestran que las larvas de los pasálidos son incapaces de alimentarse directamente de la madera. Su fuente principal de alimentación es una mezcla de excrementos de adultos y fragmentos de madera producidos durante la excavación de las galerías. Los adultos recién emergidos tampoco pueden sobrevivir con una dieta a base de madera si no tienen la oportunidad de ingerir, previamente, excrementos de otros adultos. Estos resultados sugieren la existencia de relaciones simbióticas con microorganismos para la degradación de la madera en los adultos. Se encontró también que los excrementos de los adultos poseen, generalmente, un mayor contenido de nitrógeno que la madera de que se alimentan. Este mismo fenómeno ocurre en los excrementos de las larvas, pero con menor frecuencia que en los adultos; por otra parte, dichos incrementos son considerablemente mayores en el caso de los adultos que en el de las larvas. Estas diferencias entre larvas y adultos, concernientes a su capacidad de poder aprovechar la madera como fuente de alimentación, probablemente sean originadas por las variaciones existentes en sus tubos digestivos. La diferencia principal radica en la presencia de una estructura, que probablemente funciona como una cámara de fermentación, en el intestino de los adultos; dicha estructura no existe en las larvas. Por último, se discuten algunos aspectos de la importancia que la xilofagia puede haber tenido en la evolución del comportamiento social en estos insectos.

PALABRAS CLAVE: Passalidae, Coleoptera, Comportamientos Parentales, Comportamiento Subsocial, Alimentación, Xilofagia.

INTRODUCTION

Parental behaviors in Passalids include: 1) care and protection of the eggs, 2) excavation of galleries, 3) pupal cell building and 4) feeding. (For several aspects of the biology and behavior of the group, see: Miller, 1931, 1932; Gray, 1946; Reyes-Castillo, 1970; Schuster, 1975; Schuster & Schuster, 1985; Reyes-Castillo & Halffter, 1984; Jarman & Reyes-Castillo,1985; Valenzuela-Gonzalez & Castillo, 1984; Valenzuela-González, 1986a, b).

The nature of the interactions between adults and young, concerning nutrition, has not been well elucidated yet. Apparently, the main source of food for Passalids is a mixture of powdered wood fragments produced during gallery excavation and faeces (Pearse *et al*, 1936; Gray, 1946; Reyes-Castillo & Halffter, 1984; Valenzuela-González 1986a); these detritus are constantly compressed by adults against the gallery walls, which are usually lined with this mixture.

Ohaus (1900, 1909) was the first to propose that larvae depend on adults for their feeding, due an insufficient adaptation of their mandibules to xylophagous nutrition. More recently, some studies have shown that adults have a mandibular force that is far superior to that of the larvae (Reyes-Castillo & Jarman, 1981; Jarman & Reyes-Castillo, 1985), a fact which could give some support to Ohaus's ideas. However, Heymons (1929) reported that the larvae's mandibules were well-adapted for this regime, and he claimed that, concerning their feeding, larvae were independent from adults. Pearse *et al* (1936) and Gray (1946) made some additional observations, but their results are inconclusive concerning the participation of adults in larvae nutrition. Finally, Burnett *et al*, (1969) and Mason & Odum (1969) showed the importance of coprophagy in adults nutrition.

Concerning the participation of symbiotic microorganisms in the nutrition of these insects, Lewis (1926) and Pearse *et al* (1936) looked, unsuccesfully, for cellulotic protozoires in the gut of *Odontotaenius disjunctus* (Illiger). However, it is well known that bacterians and fungi are very common in the intestines of Passalids, but it is unknown if they could have a significant participation in the nutrition of these insects (Lewis, 1926; Heymons & Heymons, 1934; Patterson, 1937; Lichtward 1957 & 1968; Baker, 1968).

In this paper I present results which show that larvae and young adults cannot survive on a diet made exclusively of wood; furthermore, I illustrate the importance of the ingestion of adult faeces for both larvae and adults.

METHODOLOGY AND RESULTS

In order to evaluate the preferences of larvae when allowed to choose between different kinds of food, the following selection tests were made: in glass Petri dishes 10 cm in diameter, equal amounts of the materials being tested were placed, symmetrically, in both sides of said dishes; then, one first instar larvae of *Passalus interstitialis* Eschscholtz was put in the center of each dish. 24 hours later, the material which larvae were eating was registered.

Three types of selection tests were made: a) between adult homospecific detritus (a mixture of wood and adult faeces) and fragmentated wood without faeces (n=27), b) between adult heterospecific detritus and wood without faeces (n=20) and, c) between homospecific adult and larvae detritus (a mixture of wood and larvae faeces; n=20).

Table 1
Results of three different types of selection tests made with larvae of *P. punctiger* for different kinds of food. The number of larvae feeding in each substratum after 24 hrs is represented.

Type of Food	Num. of larvae		X^2
Adult homospecific detritus	23		13.4; $p<0.01$
Wood detritus		4	
Adult heterospecific detritus	18		12.8; $p<0.01$
Wood detritus		2	
Adult homospecific detritus	16		7.2; $p<0.01$
Larvae homoespecific detritus		4	

Results are shown in table 1. Significant differences were found in all cases. Larvae always prefered to feed on adult detritus (homo or hetrospecific) than on wood or larvae detritus.

In order to determine if larvae can survive on a diet made exclusively of wood, the following experiment was carried out with first instar larvae of *Passalus punctiger* Lepeletier et Serville. Three groups of larvae were used. In the first (n=18), the larvae were fed with bits of wood. In the second (n=19), larvae were also fed on wood, but in this case it was in the form of fine sawdust in order that the larvae could better ingest it. The purpose of using this group was to determine if,in event that the larvae might exhibit a feeding dependance on the adults, it could have a mechanical origen as suggested by Ohaus (1900, 1909). The third group (n=35) was fed from adult detritus. In order to avoid the effect of cannibalism, the larvae were placed individually in small plastic containers covered with a fine mesh.

The results concerning longevity during the first twenty days are shown on figure 1. As no differences were observed between larvae fed on wood, in bits or in sawdust, the results of both groups were assembled under one heading (larvae fed on wood). As can be seen in figure 1, none of the larvae fed with wood survived over 8 days, while over 40% of those nourished on adult detritus were still alive twenty days after the beginning of the test. None of the larvae of the first group attained the second instar; in the second 13 larvae reached second instar, 7 the third and 5 pupated.

In the case of certain xylophagous insects, digestion of wood is possible due to the presence of symbiotic microorganisms (Hungate 1975, Wigglesworth 1976 and Chararas 1979). In some of them, like termites and xylophagous cockroaches of genus *Cryptocercus*, young individuals acquire these microorganisms by means of the ingestion of feces from the individuals which already have them. In order to investigate the possibility of a similar phenomenon in Passalids, the following test was carried out with *P. punctiger* larvae.

A lot of 29 newly born larvae was fed adult detritus (containing abundant feces) during 24 hours and later they were supplied only with wood. The adult detritus used was mostly excrement. Most of the wood contained in it was removed but, because of the small size of some of the wood particles, it was difficult to obtain a complete separation. Larvae were kept individually in small plastic containers covered with fine mesh.

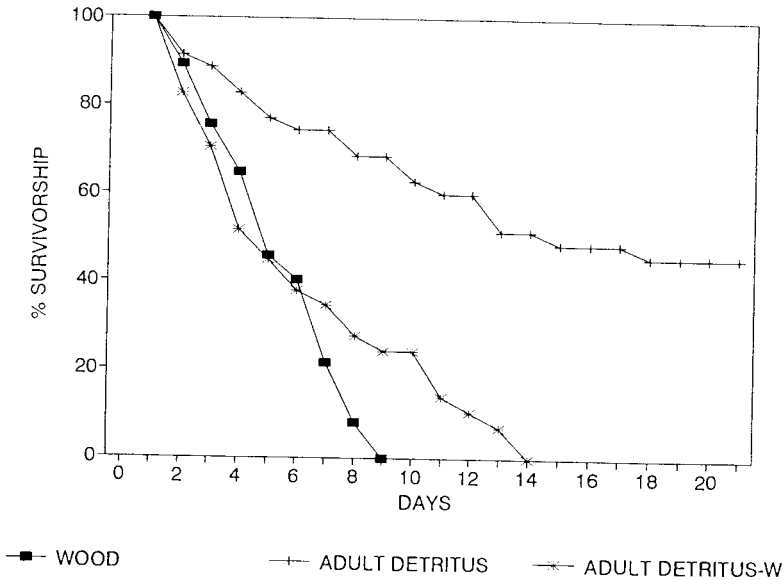


Fig. 1. Survivorship (in %), during the first twenty days, of new-born larvae fed with: a) wood (n=37), b) adult detritus (mainly fecal pellets) (n=35) and c) adult detritus for the first 24 hrs and then with wood (n=29).

Results concerning the longevity of these larvae are also shown in figure 1. As can be observed, the longevity was slightly greater than in the case of larvae fed exclusively with wood; however, all individuals died before attaining the age of 15 days. On the other hand, none of the larvae reached the second instar. These results prove that after a temporary but abundant ingestion of adult excrement, the larvae are still incapable of using wood as their only source of food.

With regard to adults, the insects collected in the field were able to survive for several months, under laboratory conditions, having wood as their only nourishment. However, it is known that actually they need to reingest their own excrement for feeding (Mason and Odum, 1969), but they also need a constant supply of wood for the production of excrement suitable for feeding. In the absence of wood, adults die after some time, even if they are able to reingest their feces (personal observations not published). In order to explore the possibility of a transmission of symbionts by excrements in the case of adults, the following experiment was carried out:

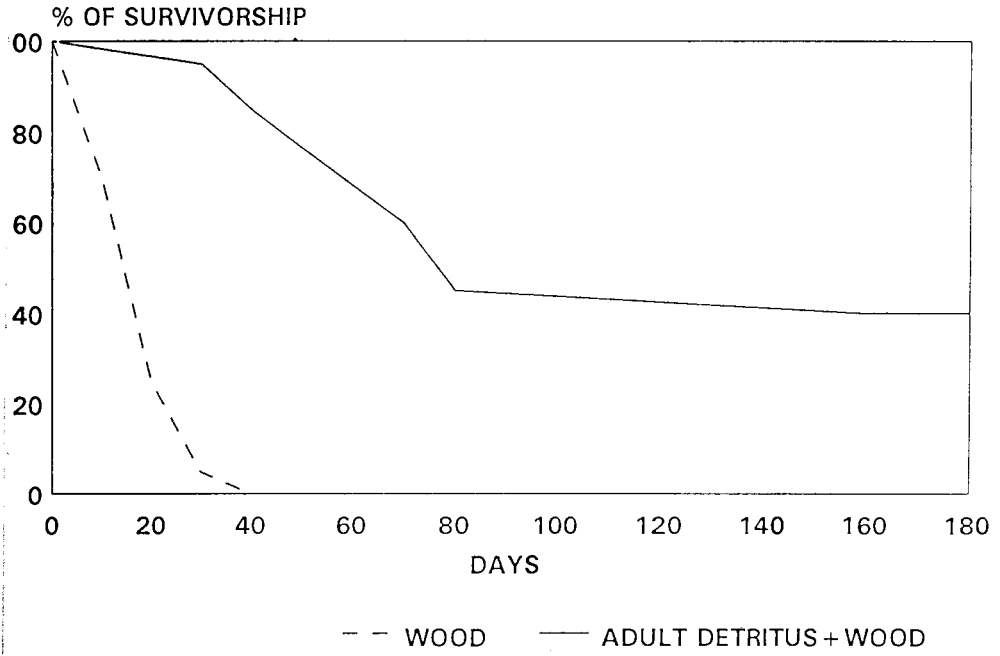
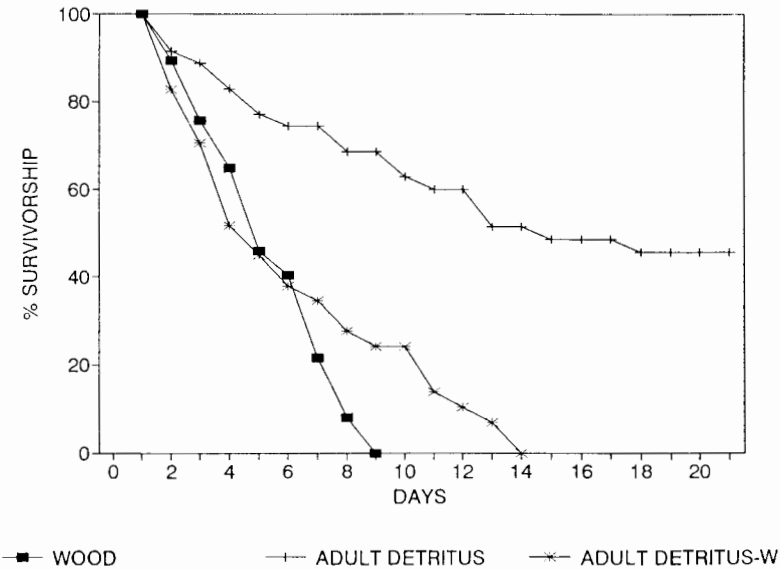


Fig. 2. Survivorship (in %) of adults fed from emergence with wood (n=20) and with adult detritus (mainly fecal pellets) for the first 72 hrs and then with wood (n=20).

20 individual pupae of *P. punctiger* were put on Petri dishes. The resulting adults were fed exclusively with wood from the moment of emergence. With another 20 pupae a similar procedure was followed, but in this case adults obtained were fed adult detritus plentiful in excrements during the first 3 days and after they were fed only wood.

With adults, a longer time of feeding on excrements was used than in the case of larvae, the latter being very voracious froms birth, while the former are are not very active and apparently start feeding a certain period of time after emergence. For this reason, it was considered necessary to allow a period of 72 hours in order to guarantee a good ingestion of the excrements supplied. The results concerning the longevity of these insects are shown in figure 3.



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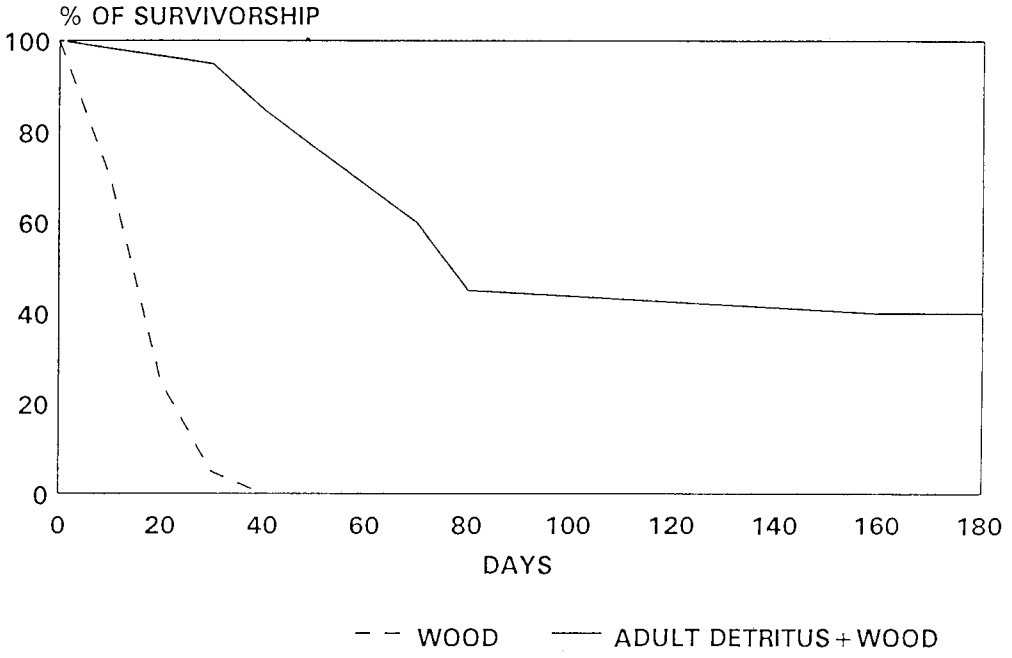

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Longevity of adults fed on wood from emergence varied from 9 to 36 days. In the case of those fed initially with excrement and subsequently with wood, when the test ended, 150 days after it had begun, 8 insects were still alive (40% of the total number). The results prove that newly emerged adults are unable to survive exclusively on a wood diet. After ingesting excrements from older adults, however they are capable of using wood for feeding. These results suggest the existence of a symbiont transmission phenomenon which allows adult Passalids to take advantage of wood as their main source of nourishment.

Although from a nutritional point of view, the most remarkable adaptations of xylophagous insects are mainly related to the digestion of structural polysacharides, consumption of nitrogen products also causes problems, due to their low content in wood (see for example: Chapman 1975, Hungate 1975, Schmidt-Nielsen 1976, Chararas 1979). It was therefore interesting to effect a comparative analysis of nitrogen content in the wood consumed by Passalids as well as in their feces, considering the importance of coprophagy in these insects.

For this purpose, third instar larvae of *P. punctiger* and adults were placed individually in Petri dishes. The insects were fed on wood for a week, and afterwards the nests were cleaned in order to eliminate excrement produced from the digestion of food consumed after the experiment. Later, insects continued to be fed with the same wood.

Excrement produced in each nest was collected daily and kept in refrigeration (at -5°C), as was a sample of the wood employed as food. The Kjieldhal method was used to determine nitrogen content. To measure moisture content, 1 g of each sample was placed in an oven at 100°C for 24 hours and weighted immediatly after.

In figure 3, the percentage of increase or decrease of nitrogen in larvae and adults faeces with respect to the originally ingested wood is represented. For adults, in seven of ten repetitions, the nitrogen concentration increased from 5.8 to 72.6%; in only three cases a decrease occurred (-1 to -27.7%). In larvae, in four cases an increase was noted (3.4 to 17.6%), and in six other instances a decrease was registered (-8.3 to -52.5%) and in one case no variation was observed.

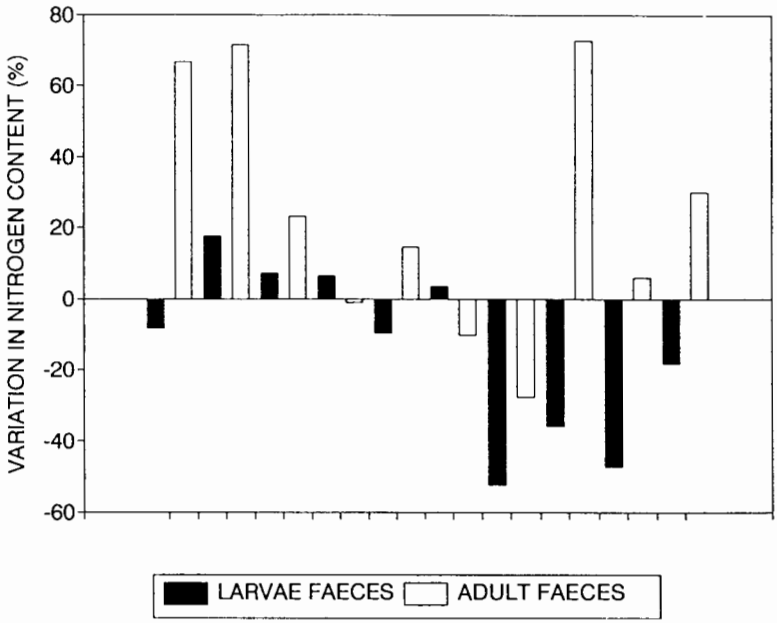

Fig. 3. Variation in nitrogen content (%) of fecal pellets produced by adults and larvae in relation to rotten wood on which beetles were fed. The nitrogen content of wood, represented as 0 in the figure, was of 0.09 %.

These results indicate that adult excrement usually has a higher nitrogen concentration than ingested wood. This phenomenon may also take place in larvae, but less frequently. Besides, increases registered in larvae tend to be considerably less than those registered in adults.

DISCUSSION

In regard to feeding, xylophagous insects present two different ways of feeding on wood (see revisions by Chapman 1975, Wigglesworth 1976 and Chararas 1979). On one hand, there are those able to use only easily assimilable glucosides like saccharose, glucose and fructose. These glucosides disappear a relatively short time after the felling of the trees; consequently, these insects tend to feed on wood that is not in an advanced stage of decay.

On the other hand, there are those insects that can use structural polysacharids from wall cells (like cellulose and hemicellulose) abundantly found in wood but which are more difficult to digest. Passalids dwell in rotting wood which is in an intermediate stage of decay (Pearse *et. al.* 1936, Gray 1946, Reyes-Castillo 1970, Schuster 1975, Valenzuela-González 1986a); this suggests that they could belong to the second group. Most insects able to feed on these polysaccharides (especially cellulose) depend on symbiotic microorganisms for feeding (Hungate 1975, Wigglesworth 1976, Martin 1983, Terra 1990).

The results obtained show that larvae of Passalids are unable to feed directly from wood. Newly emerged adults are also unable to use wood as their source of food unless they can ingest excrement from other adults first. Consequently, young adults are dependent on older adults for feeding, although this dependence is only temporary.

Pearse *et al* 1936, working with *O. disjunctus* found that adults can live on an a diet composed exclusively of wood, even if it had been sterilized. However, they did not experiment with newly emerged adults.

The fact that recently emerged adults can only use wood for feeding after the ingestion of excrement from older adults, suggests the existence of a symbiotic relationship between passalids and microorganisms for the degradation and/or assimilation of wood. Larvae, however, are not able to feed directly on wood, even after the ingestion of excrement from older adults.

This difference between larvae and adults as to their ability to use wood for feeding, is probably due to the variations in the structure of their digestive tracts (for some descriptions see: Lewis, 1926; Patterson, 1937; Pereira & Kloss, 1966; Baker, 1968). In adults the digestive tract is longer in proportion to the body length than in larvae. In addition, in the case of adults the digestive tract is rolled at several levels, a condition that does not occur in larvae, which exhibit a more or less straight digestive tract. This feature could be an important factor in the digestion of wood. One of the charasteristics of xylophagous insects, especially those able to feed on cellulose, is the great length of the digestive tract in comparison to that of other insects. This fact allows for the prolonged action of enzymes (or

symbionts) on food particles during transit (Chararas 1979).

However the most remarkable difference is observed at the proctodeum. In adults, in its upper section, there is an expansion formed by 6 rows of *caeca*. This condition does not occur in larvae. Such a structure, where a temporary retention of food particles occurs and which harbors an important intestinal flora, could be a fermentation chamber. Said chambers play a fundamental role in the digestion of cellulose in some other xylophagous insects (Chapman 1975, Wigglesworth 1976). If this structure is a fermentation chamber, its absence in larvae could explain their feeding dependance on adults.

However adults also depend on coprophagy for their feeding, although they also require the constant availability of wood, as has already been mentioned. This phenomenon could be due to the fact that the degrading of food takes place at the proctodeum, where absorption is minimal. One way to solve this problem would be with coprophagy, which allows reingestion of food that has already been submitted to microbial action. Besides, chewing and intestinal transit of the wood could favor acquisition and multiplication of microorganisms in feces, which could improve nourshing value.

Mason's results (1966, quoted by Mason and Odum 1969) and our own suggest that this is the case. In fact, faeces have a greater caloric value and higher nitrogen content than the wood from which they are made. According to Larroche and Grimaud (1988), this is also true for phosphorous. Mason and Odum (1969) have suggested that galleries where these insects live could function like an "external rumen" where transformation of food, begun during intestinal transit continues, improving the nutritional quality of the fecal pellets.

In the digestive tract of termites, phenomena of nitrogen fixation through symbiotic bacteria takes place (Benemann, 1973; Breznak *et al*, 1973; French *et al*, 1976; Bentley, 1984). In Passalid it is not known if this type of process occurs. However, the increase of nitrogen content in feces could also be due to phenomena of this type, a possibility that would be worthwile to explore in the future.

Wood is a plentiful resource in some habitats. In addition to supplying food for the insects dwelling in it, it can provide refuge against predators and a relatively protected place against environmental fluctuations.

Nevertheless, its use as food has some restrictions due to its hardness, low nitrogen content and difficulty in degrading and assimilating some of its more abundant components like cellulose. For this reason, its use requires especial adaptations that frequently imply a symbiotic relationship.

As has been pointed out by Tallamy and Wood (1986), subsociality can reduce the physical and nutritional limitations of woody resources in several ways. In Passalids, the adoption of wood as a nesting place and source of food has probably been one of the main factors in the development of the parental behaviors and, consequently, in the evolution of sociality in these insects.

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