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Review article

Xyleborus Ambrosia Beetles: A Symbiotic Ideal Extreme Biofacies with Evolved Polyphagous Privileges at Monophagous Prices

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Abstract

Symbiotic *Xyleborus* ambrosis beetles (Family: Scolytidae) have evolved into nearly the ideal extreme biofacies. Such an animal puts much of its energy into the evolutionarily desirable reproduction of its genes. *Xyleborus* feeds "monophagously" on its perpetuated ectosymbiotic microorganisms that it grows on many diverse botanical substrates; thus, it need not expend much energy on seeking specific substrates. It achieves a desirable very high degree of relatedness of potential mates, without incurring genetic loading of deleterious genes from inbreeding, though endosymbiote-dependent arrhenotokous parthenogenesis in which males are haploid; thus, harmful genes are exposed to selection in the male. Because mating is brother:sister or son:mother, dispersal for mating is not necessary; thus, an ultimate level of energy-saving philopatry is practiced. Brood rearing is in a common chamber tended by the mother; thus, a single male can readily mate with many sisters or with a mother if she was not previously inseminated. A sex ratio of 20–30:1 (F:M) is thus allowed, and this further assures that a species expends most of its energy on replicating "self" genes in the female sex. The overall life history allows non-mated females to reproduce asexually, and then mate with a son. This establishes "clones" which may be perpetuated as a species through resultant diploid daughters. The competitiveness of this process for speciation is illustrated by more than one-third of all scolytid beetles being in the genus *Xyleborus*.

Keywords: *Xyleborus*, symbiosis, microorganisms, substrate, sex, sex ratio, shelter

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1. Introduction

The paramount evolutionary goal of an organism is perpetuation of its genes, but such can only occur if requisite substrate and shelter are available. The most reliable reproductive means for achieving this goal is through inbreeding, combined with haploid asexual reproduction (cloning). However, it has commonly been considered that inbreeding for the sake of perpetuating one's genes is undesirable because such reproduction supposedly results in loading the genome with deleterious genes (Darwin, 1868; 1876). This "detrimental" hypothesis regarding inbreeding has approached the status of law (Learner, 1954; Maynard Smith, 1978; Mayr, 1963; Crow and Kimura, 1970; Wilson, 1963, 1975; Wright, 1969). Shields (1982), however, concluded that these many efforts at explaining selective effects of inbreeding using a nonselective model are logically inconsistent, and that reliance on evidence from such 'artificial' situations apparently has resulted in a potential misinterpretation of the consequences and importance of inbreeding in natural populations. More reasonable attitudes toward inbreeding seem to include that it is not inherently bad, and that its real worth is dependent upon the specific circumstances of its use. In this paper, the highly successful use of inbreeding by *Xyleborus* beetles in evolving an overall life style which optimally conserves resources for perpetuating its genes is described. The symbiote-dependent evolution of a requisite highly dependable nutrient substrate and effective physical shelter from environmental stresses (threats) is also detailed.

2. Optimal Perpetuation of *Xyleborus* Genes

Arrhenotokous parthenogenesis

An optimal reproductive process for perpetuation of one's genes is arrhenotokous parthenogenesis (Shields, 1982). With this inbreeding method, virgin females (diploids) can reproduce asexually to produce males that are haploid. Such haploid males can prevent the genetic loading which classical genetic thought has considered as a deleterious parameter of inbreeding. If inseminated, the female can then fertilize eggs to yield female (diploid) progeny. *Xyleborus* spp. practice this style of reproduction (Fig. 1). This asexual reproduction capability of *Xyleborus* is allowed by endosymbiotic microorganisms that activate haploid embryonic development in the virgin female (Peleg and Norris, 1972). Specific antibiotic treatment of the adult female will kill endosymbiotes and will thus render the female non-reproductive (Norris, 1975; Norris and Chu, 1990). The involved endosymbiote is a rod-shaped bacteroid (Norris and Chu, 1980). It also has been shown that when inseminated with

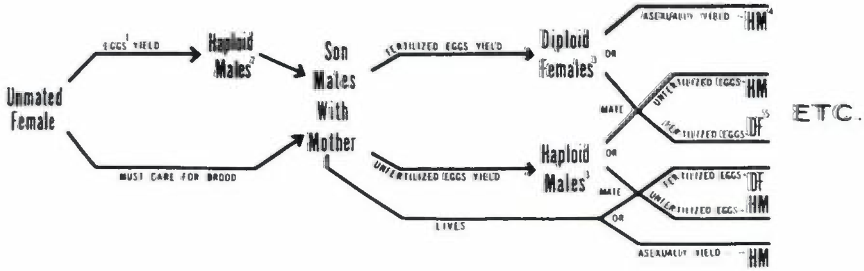

Figure 1. Arrhenotokous parthenogenesis as practiced by ecto-endosymbiotic *Xyleborus* ambrosia beetles.

sperm, the maternal female can anatomically control fertilization of oocytes to yield a mixed brood skewed toward females (e.g., 20–30:1, females:males) (Norris, 1972; Norris and Chu, 1985).

Endosymbiote-dependent philopatry

The ideal extreme biofacies (Hamilton, 1967) minimizes dispersal. Philopatry means that propagules (e.g., progeny) remain at, or very near, their origin; such conserves energy. Regardless of an organism's mobility, ecology or trophic status, many remain at, or near, their birthplaces. Philopatry thus apparently is adaptive. Shields (1982) has concluded that the primary, but not sole, function of philopatry is to favor inbreeding. If philopatry is adaptive because it promotes inbreeding, then inbreeding must also be adaptive. For this discussion, inbreeding is defined as a system in which mates are regularly more similar genetically than a pair chosen at random from a reference population or species (Crow and Kimura, 1970). The classically argued disadvantage of inbreeding is its tendency to reduce heterozygosity thereby speeding the chance (nonadaptive) fixation of alleles. If an organism could overcome this disadvantage of inbreeding, then it might be expected to evolve toward extreme philopatry. As discussed in the previous section, *Xyleborus* beetles have overcome the genetic loading of deleterious genes associated with inbreeding by practicing it within an arrhenotokous parthenogenetic reproductive system in which males are haploid. This process guarantees that deleterious genes are regularly selected against in the haploid male and are thus not accumulated in the genome.

Ectosymbiotes: a homogenous substrate

Another prerequisite for the practice of extreme philopatry is the organism's ability to utilize a broad range of substrates. Among the scolytid beetles, their breadth of acceptable botanical substrates correlates strongly with the level of their evolved nutritional dependence on ectosymbiotes (i.e., mycetophagy) versus phloemphagy (Wood, 1982). Thus, the highly mycetophagous *Xyleborus* spp. have the broadest range of botanical substrates among the scolytids (Browne, 1962). Some species of *Xyleborus* (e.g., *X. ferrugineus*) show little, if any, selection of substrate (Samuelson, 1981). This use of a wide range of botanical substrates is allowed especially through the obligatory ectosymbiotes of the beetles being able to grow on such diverse botanical materials and still provide an adequately homogeneous nutrient source of microbial growth to the beetles. This evolved situation where *Xyleborus* are "monophagous" on the same ectosymbiotic microorganismal diet regardless of which of dozens or hundreds of distinct botanical substrates it grows on, is here termed "polyphagous privileges at monophagous metabolic prices." This extraordinarily dependable substrate situation seemingly has contributed very significantly to the extreme philopatry practiced by *Xyleborus*. With these ecto-endosymbiotic beetles there normally is no dispersal of progeny (i.e., ultimate philopatry) until after brother:sister mating. If a virgin female does disperse, she initially can only reproduce haploids asexually because males (mates) cannot fly. If this occurs, she tends her haploid (male) brood to maturity and can then mate with a son to enable continuation of the genes via diploid daughters (Norris 1972; Norris and Chu, 1985). Each female that mates only with a son yields an isolated genome which may lead to a new species. Thus, more than one-third (i.e. > 2000) of all scolytid species (i.e., $\sim 6,000$) are found in the genus *Xyleborus*.

Ectosymbiote-dependent shelter from environmental threats

To perpetuate one's genes, satisfactory shelter also must be provided. Ectosymbiosis has allowed *Xyleborus* to evolve nearly ultimate shelter. Whereas, scolytid bark beetles only shelter their progeny individually in tunnels at the phloem-sapwood interface or in the inner bark, *Xyleborus* ambrosia beetles make their brood galleries, or chambers, significantly deeper in highly lignified (i.e., woody) tissues (Saunders et al., 1967). This is possible because such ambrosia beetles eat the nutritious ectosymbiotic microorganisms growing on the walls of their gallery system in wood, and thus are not restricted to the nutritious phloem (inner bark) tissues of trees (Norris, 1975). Being housed in wood usually protects *Xyleborus* from all but the few highly specialized parasitoids or predators. The ectosymbiosis also has allowed the evolution of a common (single) brood chamber (Fig. 2) for a mother's progeny, as seen with many *Xyleborus*. Because the mother and the progeny exclusively eat the

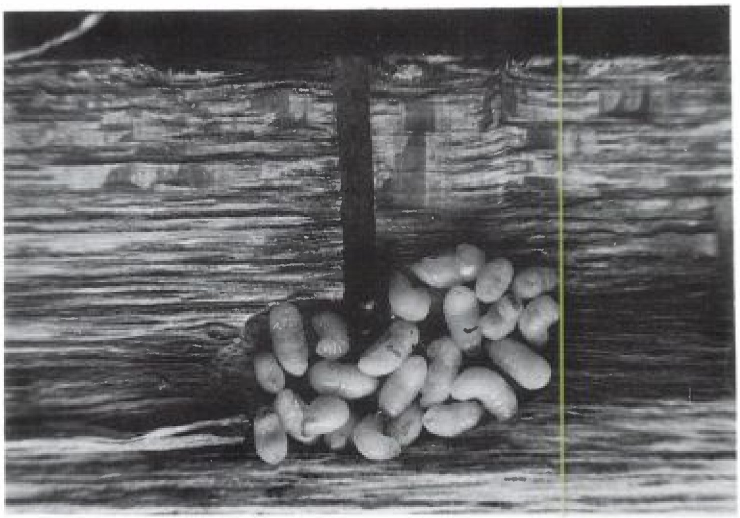

Figure 2. *Xyleborus* larvae in a common brood chamber in woody substrate.

growth of ectosymbiotes on the gallery (chamber) walls, individual progeny tunneling is not required for nutrient intake, as it is with bark beetle scolytids. Thus, a mother's progeny can effectively be housed and protected in a common chamber (Norris and Chu, 1985). Among *Xyleborus* ambrosia beetles, but not among all bark beetles, the maternal beetle must live to tend her brood to maturity in such a common chamber buried in wood. In such a relatively well protected common chamber, the highest skews in the sex of progeny are seen (i.e., 30:1, females to males) (Norris and Chu, 1985). In such brood situations, the single, or very few, males (haploids) are especially degenerate in such parameters as vision and flight, and cannot disperse (Norris and Chu, 1985). The mother beetle oviposits the haploid (male) egg(s) first when producing a mixed haploid-diploid brood. This is evolutionarily significant because this assures that the non-dispersive male(s) will become a sexually mature adult before their sisters who must be inseminated by a brother (or a son, as a last resort).

3. Conclusions

Xyleborus ambrosia beetles have become a nearly ideal extreme biofacies (Hamilton, 1967) through evolution of endo-ectosymbioses with microorganisms (Norris, 1972; Norris and Chu, 1985; Norris et al., 1986). Their association with endosymbiotes has especially enabled arrhenotokous parthenogenesis. This reproductive process allows the mother beetle to control (e.g., skew) the sex of her progeny; and her asexual production of haploid male progeny exposes, and thus selects against, deleterious genes. This facultative haploid reproduction thus may overcome the genetic loading otherwise associated with inbreeding. Without the threat of deleterious genetic loading *Xyleborus* symbiote-dependent arrhenotokous parthenogenesis has enabled the cloning (i.e., the ultimate replication) of the insect's genes.

To optimize the use of resources for such efficient perpetuation of one's genes, an organism (i.e., *Xyleborus* spp.) must also make special provisions for both substrate and shelter. *Xyleborus* has evolved metabolically a "monophagous" substrate relationship with a predictable, perpetuated complex of ectosymbiotic microorganisms that grows adequately on many available botanical (especially woody) substrates. Thus, *Xyleborus* only expends the energy inherent in nutritionally utilizing a highly predictable, quite homogenous substrate of ectosymbiotes, but the beetle obtains the "polyphagous" substrate privileges of the ectosymbiotes that can grow adequately on many diverse substrates. The overall resultant substrate situation is that *Xyleborus* beetles can reproduce indirectly on dozens and hundreds of botanical substrates. This means that the beetles do not need to disperse significantly to obtain requisite nutrition, and thus they can practice near ultimate philopatry which greatly conserves energy for reproducing one's genes.

Regarding optimizing shelter for perpetuating one's genes, *Xyleborus* beetles evolved to feed in a monophagous manner on their evolved ectosymbiotic microorganisms that grow adequately on a variety of botanical, especially wood, substrates. As a result, the beetles can shelter their progeny in a common chamber (Fig. 2) deep in wood where only a few very specialized parasitoids or predators can succeed. This situation has also allowed the evolution of compulsory brood tending by the maternal beetle which increases the safety (shelter) of her progeny and enables the maternal female to mate with a son if she is still a virgin (Norris, 1972, 1979; Norris and Chu, 1985). This brother:sister, mother:son compulsory mating facilitates the isolation of a genotype which may become perpetuated, and may ultimately be recognized as a new species (Norris, 1979; Norris and Chu, 1985). The significance of such evolved cloning to speciation is clearly revealed by the facts that

Xyleborus beetles are both the ultimate practitioners of such mating, and more than one-third ($> 2,000$) of the ($\sim 6,000$) described scolytid species (Browne, 1961; Bright, 1968; Samuelson, 1981; Wood, 1982).

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