9. interactions among males, females and offspring in bark and
ambrosia beetles: the significance of living in tunnels for
the evolution of social behavior

LAWRENCE R. KIRKENDALL, DEBORAH S. KENT AND KENNETH F. RAPPA

ABSTRACT

Parental care and colonial breeding are both widespread in
two related groups of weevils known traditionally as Scolyt-
idae and Platypodidae. Within-family cooperative breed-
ing and eusociality also occur; in at least one platypodid
ambrosia beetle, non-reproductive females help presumed
relatives to raise offspring.

Although they breed in a wide variety of woody tissues, the
majority of species fall into two ecological categories, those
reproducing under the bark and feeding directly on
inner bark (‘bark beetles’), most scolytids and diverse taxa
feeding upon microbial ecomsemblates they have introduced
to the walls of their tunnel systems (ambrosia beetles, many
scolytids and all true platypodids). In both scolytids
and platypodids, females lay eggs over an extended period
of time in long tunnels. Males usually remain with females
in these tunnel systems, controlling and expelling refuse.

We examine hypotheses for prolonged male residence,
and find that the most likely explanations for long stays in
burrows are either blocking out tunnel enemies or increas-
ing the reproductive rate of the resident females.

Species reproducing in bark or wood usually breed in
large aggregations. In most species, these colonies are an
incidental effect of mutual attraction to wounds emanating
either from the tissue itself or from the beetles (pher-
omones). We suggest that the key feature predisposing these
beetles to the evolution of breeding in aggregations is the
presence of mate-attracting pheromones coupled with the
utilization of resource patches that cannot be monopolized
by simple families. In most species, sibling survivalship is
reduced by breeding in dense aggregations; however, in
species that kill trees, rapid recruitment of conspecifics is
essential to the success of the first beetles to attack a tree.
We discuss the trade-offs tree-killing species must make
when recruiting additional colonists, which are at the
same time helpers and competitors.

Although colonial behavior has been studied inten-
sively (particularly in regards to tree killing), there has
been little direct study of other forms of social behavior in
weevils and platypodids. Behaviors that increase off-
spring or sibling survivalship have evolved repeatedly in
these taxa. Living inside a well-protected food source
such as an ambrosia beetle tunnel system, we argue, is espe-
cially conducive to the evolution of parental care. We sum-
marize observations on direct and indirect forms of
parental care as well as possible instances of siblings help-
ing siblings. We suggest that key factors in the evolution of
the social behaviors we discuss are: (1) dead woody tissue is
ephemeral, divisible, patchily distributed, and relatively
infrequent; (2) bark beetles breed in tunnel systems,
which are relatively safe from predation, provide both
food and relatively favorable temperature and humidity
conditions, and are easily barricaded; (3) finding and estab-
lishing a new tunnel system is difficult and dangerous.

INTRODUCTION AND NATURAL
HISTORY

It is not generally known that complex social behaviors are
well developed in bark beetles and ambrosia beetles. Unfor-
unately, social behavior has seldom been a research focus
in these insects, and consequently we have only a superfi-
cial knowledge of the details of interactions within and
between families.

Social behavior can be so broadly defined that it covers
virtually all interactions between two organisms (see, for
eexample, Trivers 1985). Here, we will concentrate on
within-species, regular interactions between individuals
of bark and ambrosia beetles. We begin this chapter by
trying to place these beetles in a phylogenetic perspective,
in an attempt to elucidate the ecology and behavior of anim-
ial taxa. Next, we discuss (1) prolonged contact between
females and offspring; (2) prolonged male residence in gallery systems; (3) interaction among offspring; (4) colonial breeding facilitating aggregation; and (5) evolution. We conclude with a general discussion and suggestions for future research.

Phylogenetic background

Forest entomologists have traditionally treated teclorids (‘bark beetles’) and platypodids (‘pinhole borers’) together (usually as two families), because of their morphological, ecological, and behavioral similarity; they co-occur in the same logs, have similar tunnel systems, and create similar economic problems for the timber industry. Systematists disagree as to whether these taxa should be considered as families (see, for example, Browne 1961; S. L. Wood 1975, 1978, 1982, 1990, 1992; Mertens 1978; Brearley 1992) or as sub-families of Curculionidae (Crowson 1948; Kuschel 1990, 1996; Lawrence and Newton 1996). Until recently, there has been a consensus that, together, the two groups form a monophyletic lineage of highly specialized weevils, either inside or outside the Curculionidae. However, recent studies (see, for example, Crowson et al. 1992; Thompson 1992; Kuschel 1995; Lyal 1995; Lyal and King 1996). There is now a consensus among these four studies that at least teclorids can be readily placed within the Curculionidae, near the Curculioninae; there is no support in these analyses for considering them as a separate family. The phylogenetic placement of Platypodidae is much less clear; none of these studies presents unique, shared derived character states which link platypodids unequivocally with teclorids, or with any other weevil group. Although the exact relationships among curculionids, teclorids and platypodids are thus uncertain, we will follow a long tradition in forest entomology and discuss teclorids and platypodids together in this chapter; we will also continue to use ‘teclorids’ and ‘platypodids’ to refer to these groups, while we await the results of more detailed morphological and biochemical data, on their phylogenetic relationships.

Feeding ecology

Teclorid and platypoid beetles exhibit considerable variability in feeding systems and social behavior. Almost all teclorid and pinhole species breed in tissues of woody plants, mostly in the inner bark (‘bark beetles’), in the initial stage of rot. Most species breed in tunnel systems in dead inner bark, but some, such as Lixus fasciatus, Pachycentrus rufipennis, and Toxostoma pineorum, are also associated with the various breeding habitats have evolved independently on multiple occasions (see, for example, S. L. Wood 1982; Kuschel 1995; Brearley 1992). The current, widely used ecological designations ‘bark beetle’ and ‘ambrosia beetle’ refer broadly to larval feeding habits. In the former, larvae usually feed directly on the plants in which they are embedded; in the latter, they feed exclusively on microorganisms (predominantly fungi, including ambrosia) growing on tunnel walls within plant tissue.

The ambrosia beetles depend upon their highly nutritious symbionts and do not feed directly on the wood (see, for example, Norris and Baker 1975; Norris 1975; Brearley 1988). For the sake of simplicity, we will refer to the food of ambrosia beetles as ‘the ambrosia fungus’. However, the presence of several microbial species may be essential for the successful reproduction of a given beetle species, as there is usually an entire microbial community (fungi and bacteria) with its own succession associated with ambrosia beetle (Fleming and Norris 1985; Brearley 1989). The fungus-growing habit has evolved at least eight times, once in the ancestor to the platypodids and at least seven times in the teclorids (S. L. Wood 1982; Kuschel 1983; Brearley 1989). Many taxa designated as ambrosia beetles are true fungus-growing insects, and possess a wide array of pouches, pores, and cistidioid invaginations (mycangii) for carrying, processing, and nourishing their ‘starch cultures’ (Bura 1963; Ersievski-Gromov 1929, 1964, 1967; Kohn 1979; Norris 1975, 1979; Nakahimasa 1973; reviewed in Brearley 1989).

Those wood-feeding taxa that do not cultivate microorganism communities are usually lumped with bark beetles, although the more technical term ‘symbiophagy’ is also used. In more general discussions, species with other habits, such as breeding in pine cones, pith, seeds and woody fruits, or herbaceous plants, are also commonly lumped with bark beetles. Most bark beetle species breed in the inner bark or outer sapwood tissues of dead trees. We will refer to these phloemphagous species as ‘true bark beetles’ when we wish to distinguish them from species breeding in sapwood and heartwood, pith, seeds and fruits, or other plant tissues.

For the 1329 ambrosia species from North and Central America whose larval feeding habits could be categorized
Bark and ambrosia beetle social behavior

An important feature of scolytid and platypodid biology is a variety of mating systems. Ambrosia beetles are a notable exception to the usual insects (reviewed in Kirkendall 1983, see also Atkinson and Eichho 1984). It is unusual for males to remain with ovipositing females during most or all of the oviposition period (see, for example, Kirkendall 1983, Table 2). Although egg tunnel systems usually are constructed by one female ("monogamous" species), in a variety of unrelated lineages "harem polygyny" has evolved, in which several to many females are associated with each successful male (Kirkendall 1983, Table 3). Brother-sister inbreeding has evolved numerous times, and is perhaps the dominant mating system in tropical regions (Kirkendall 1983, Table 7, Fig. 73).

The mating systems terminology used here differs from usage in the social insect literature. "Monogamous" denotes a breeding unit for an outbreeding species with one female, with or without an accompanying male. "Polygynous" refers to a breeding unit with two or more females; no polygynous species are known in which the male does not stay for at least several days, and usually males remain with their mates for several weeks or more. Species in which breeding units include a variable number of females have been termed "harem polygynous," while those with regular brother-sister mating, where one or a few males inseminate many sisters, have been called "inbreeding polygynous" (Kirkendall 1983).

Mating systems

In most bark and ambrosia beetles, a single female is usually referred to as "galleries," "egg galleries," or "tunnels," and a harem of polygynous species, the collective work of the males mated to a single male is referred to as a "galley system," "tunnel system," or "nest." It is important to emphasize that these nests are normally isolated from the external environment, accessible only through the entrance tunnels, i.e., in some species, through secondary holes often termed "ventilation holes."

Mating location

Mating location in most scolytids and platypodids is accomplished by long-range pheromone attraction. Although the (long-range) pheromone-producing sex is constant within a species and usually within a genus, it varies at higher taxonomic levels. Females are the pheromone producers in most monogamous species, and males the producing sex in all harem polygynous species (Kirkendall 1983; Kirkendall 1983) has argued that male pheromone production in monogamous groups is usually found in taxa derived from harem polygynous lineages.

In those species not using long distance pheromonal attraction, males and females are attracted by host odors (see, for example, Rudinsky 1969; Lyttens et al. 1988, Yosha 1989, Eichho et al. 1993). In both pheromone-producing and non-producing species, copulation may take place at overwintering sites or, more commonly (in those taxa in which maturation feeding in fresh tissue is a part of the life cycle), at maturation feeding sites, prior to the normal breeding activities (see, for example, Spessivtseff 1921; Fisher 1931; Barret 1974; Rudinsky et al. 1979, Mendel 1983; Jann and Leuerer 1998).

Prolonged contact between females and offspring

Overlap between parents and their brood is unusual in insects, although it has evolved in many orders (Wilson 1975). However, it is the norm in bark and ambrosia beetles, arising naturally from their regulating habits of females, and in many cases males, reside in the gallery system. Neither sex need leave the nest for food.
<table>
<thead>
<tr>
<th>Type of care</th>
<th>Possible effects</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs placed in special nests</td>
<td>Spaces our larvae: gives them a starting orientation, keeps them out of way of</td>
<td>Most bark beetles, carabid and obscurus ambrosia beetles</td>
</tr>
<tr>
<td></td>
<td>adults</td>
<td></td>
</tr>
<tr>
<td>Egg mass covered over by froth or single or</td>
<td>Protection against mixed species; Protection against coniferous or parasitic</td>
<td>Most bark beetles, carabid and syrphidae ambrosia beetles</td>
</tr>
<tr>
<td>clumped eggs (not in niches) covered over by</td>
<td>species; Protection against other predators or parasites; Protection against</td>
<td></td>
</tr>
<tr>
<td>froth</td>
<td>destruction</td>
<td></td>
</tr>
<tr>
<td>Eggs use 6 initials, 'tended' by female,</td>
<td>Protection from microorganisms</td>
<td>Observed in Xyleborus</td>
</tr>
<tr>
<td>moved if female disturbed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs as larvae moved from emergence, falling out</td>
<td>Accidental loss of offspring avoided</td>
<td>Platypusidae, Xyleborus</td>
</tr>
<tr>
<td>of tunnel</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Termination of larvacity</td>
<td>Pushing larvae into fresh food source;</td>
<td>Xyleborus, Trypodendron, Neureuter</td>
</tr>
<tr>
<td></td>
<td>removing food, removing litter</td>
<td></td>
</tr>
</tbody>
</table>

Female care is difficult to observe directly. True bark beetles can be observed through a Plexiglas or plastic "roof" (see, for example, Reid 1965 Figs. 1, 2), but behavior of ambrosia beetles can only be observed by allowing the beetles to nest in artificial medium in glass vases or jars (see, for example, Norris 1977). As with bark beetles, brief glances are afforded when gallery systems are carefully and laboriously exposed, but these are in effect one-time inspections. None the less, most of what we know about behavior of ambrosia beetles (and everything about behavior of phytophagous) has been gleaned together from such observations.

We discuss first the effect of type of breeding substrate on contact between parents and offspring. We then discuss, separately for bark and ambrosia beetles, what parent females might or must not be able to do for offspring during the oviposition period (types of care given to offspring are summarized in Table 9-1) and why they might remain in the gallery system after egg-laying is completed. Some of these arguments apply equally well to male presence, but males will be treated explicitly in the next section.

Breeding habits and family cohesion

Differences in breeding habits have important consequences for the evolution of social behavior. Larvae of most true bark beetles, for example, tunnel independently through the thin layer of inner bark and even sproutwood, and the larval tunnels gradually diverge. Their larval mines are packed tightly with froth. Consequently, there can be no physical contact between such larvae and their parents. Furthermore, most bark beetles usually breed in aggregations, and larvae may be in closer proximity to unrelated larvae than to siblings (see Kirkendall 1989).

Conversely, ambrosia beetle larvae do not tunnel as they feed, though in some groups they construct their own enclosed ventilated feeding chambers and in some platypusidae (see below) lateral larval extend the parenal tunnel systems. The result is that siblings are potentially in close contact with each other, either all the larvae of a single family or (in more extensive tunnel systems) contemporaneous batches of larvae. The entire set of siblings is potentially directly affected by parental actions. Consequently, the potential for the evolution of certain forms of social behavior is much greater for ambrosia than bark beetles.

Spatial clustering of larvae also commonly results from breeding in seeds or in pit. Sibling larvae remain in "social" close contact, although they may tunnel individually, and many will be close to their parents. As with ambrosia beetles, they need deeper in the resource to be largely protected from the community of natural enemies preying upon true bark beetles. In pit, extensive movement within the nest may or may not be possible, depending on the shape of the gallery with respect to beetle diameter; regardless, the actions of a given individual will potentially affect one or many family members. Thus, with respect to factors important for the evolution of social
behavior path- and seed-breeding species are more similar to ambrosia beetles than to the true bark beetles from which they are derived.

Prolonged female-offspring contact in bark beetles

Females of most bark beetles by many or all of their eggs in one egg gallery. Eggs are laid singly or in small batches, and are relatively large with respect to the female's body size, being produced by arboreally selected species. The ratio of egg length to female body length varies from 1:8 the smallest we could find, for Scolytus multistriatus: Kruyt 1916 to 1:4 or larger in a number of species (e.g. Trypodendron populivorus and Pityogenes chalcographus, Perty 1977; Xyleborus affinis, Rooper et al. 1980). Prolonging a clutch of such large eggs requires feeding during the extended oviposition period, leading to more efficient oviposition with early-produced offspring. While parents are present, what behaviors increase egg and larval survivorship, and are the effects on offspring fitness due to adaptive behaviors or incidental effects of "normal" oviposition behavior? Which, if any, female bark beetle behaviors qualify as parental investments, i.e. do certain behaviors help current offspring or the egg or female's future reproduction?

In those species with independent larval mines, care of eggs or larvae is restricted to any general protection offered by the female's presence. Ovipositing females of most species keep the egg galleries clean, and presumably offer some defense against intruding predators or parasitoids, though not against parasitoids ovipositing through the bark, or predators which do not come through the entrance to a defending female's egg tunnel. Diseased or dead adults are assembled, which may prevent further spread of pathogen within the gallery system (though it is not clear whether anesthetizing is the work of the female or the male).

When males are absent, females may also block entrances before oviposition is finished, either with their bodies (Phloeocharius demeassus, Mikkendorf 1984; Hylobius abietis, Beaver 1986) or with a hardened plug (Cryida thoracica, Beaver 1974; Pityogenes chalcographus, Debyry and Kreisendahl 1962). Hard plugs are also found in a few species with male residence, as in Xylosandrus turris (Laurent and L. B. Kittredge, unpublished observation) and Camponotus rufipes (Beaver 1972), and some Deuteroscolytus taxa block the gallery entrance with resin-laden frass (see, for example, Stackman 1973). Possible benefits to blocking during oviposition are illustrated by two Xyloxyrus species in which males do not stay with females after copulation. Females of Eustenocerus laetator (Hightower, Elaphidi- daceae) will visit a Xyloxyrus female at the far end of the egg tunnel, then dash in and oviposit into S. laevis eggs (Beaver 1967). Exostemus sanguinus apparently attacks S. merinu eggs in a similar fashion (Yates 1984).

Female presence after oviposition can represent maternal care if females can block out potential predators or parasitoids whose offspring follow larval mines away from egg tunnels (e.g. Rhamphognathus, Davis and Franklin 1980). However, female residence after cessation of oviposition could have two other explanations: (1) females remain to feed and regenerate flight muscles; (2) females use the egg tunnel as a safe place to overwinter. Both behaviors are commonly reported for scolytids.

Blocking the entrance during or after oviposition has been reported for a number of species, and in the entrance has been reported for a number of species. For a number of outbreeding monogamous species, for example, males leave after oviposition but female stay (e.g. Cones- torus gemine, Chambers and Atkinson 1954). Males do not stay at all, in tunnel systems of Scolytus merinu, females usually die in the entrance (92% of 130 galleries had a dead female) (Yates 1984).

Prolonged female-offspring contact in ambrosia beetles

Adult presence in an ambrosia-beetle gallery normally sought to occupy a wider variety of habitats than the presence of a parent in a bark-beetle gallery. Maternal activity is critical for maintaining an appropriate rate of food production: cropping the fungal or yeast mass on tunnel walls keeps the tunnel system from being overgrown, as has been shown experimentally for Xyloxyrus affinis (Rooper et al. 1980) and X. xanthesoma (King- قول and Norris 1977) and has often been inferred from field or laboratory observations (see, for example, Heukelbach 1987; Barnes 1993). In addition, Xyloxyrus females have been observed to assist newly emerging larvae from the eggs, to push eggs and young larvae onto food, and to tend both young and older larvae (French and Rooper 1975; Kingsepp and Norris 1977; Rooper et al. 1980). Trypodendron limacinum eggs are laid in tunnel-wall niches, and the larva gradually expand these niches into small tubes; females keep the egg galleries open by cropping the ambrosia growth, and remove larval excreta; the presence of females leads to death of the
Table 9-2. Reproductive behavior of *Eusimulium* species

<table>
<thead>
<tr>
<th>Season</th>
<th>Both sexes</th>
<th>Female only</th>
<th>Male only</th>
<th>Neither present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female, no eggs</td>
<td>7</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Swarming, some eggs</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fall, end of breeding</td>
<td>7</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Spring, larvae killed</td>
<td>23</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

* Reproduction in *Eusimulium* and *C. fumes* on the E.S. George Reserve, Wausaukee Co., Michigan. These previously unreported observations were made between 1975 and 1980 by S.B. For the fall data, only the two females that were alive were counted; these were the two shortest galleries.

* Swarming of reproductive cycle—usually started by eggs laid; some eggs laid all eggs laid, and of breeding; all bred now the next spring.

offspring (reviewed for this species in Beavers 1988). Finally, *Xiphophorus* females either are blind and weakened, poorly, or entomb them in a short branched tunnel (Gould 1941; Norris 1979).

The most striking care thus far detailed remains that in the *archipeta* species *Amphorura* entailed by Hubbard (1937) and Deane and Gilliland (1939). According to Hub- bard, female of *M. archezus* first prepare a bed of wood chips which they introduce with the ambrosia fungus; chips are later placed in the kitchen (callistus) along with each egg. Females seal each candle with a plug of ambrosia fungus. After hatching, the larvae crop the ambrosia from the chips and French plug, and periodically perforate the plug in order to expel waste. The mothers repeatedly remove refuse from the fungus bed, seal, and renew and renew the food plug. According to Hub bard (1937, p. 27), "The mother boles is in constant attendance upon her young during the period of their development, and guards them with jealous care." Deane and Gilliland report similar habits, for *Xiphophorus* species of *Amphorura*, as well as for species of the closely related genus *Cicindela*. For both genera, the fungi are said to occur in pitch-pine, in the runnels, where they are tamed successively.

Female blocking after the conclusion of viviparity should be especially effective in these *xiphophorus* breeding vs. ambrosia beetles in sawdust, or breeding in seeds. First, in these taxa, offspring remain in close proximity to their mother. Second, access of natural enemies is limited. When the runnels systems are in sick sawdust, ambrosia breeding or in sawdust seeds, where breeding units are usually isolated and the one entrance hole will be the only hole heading under the surface for the major rearing unit, they cannot move readily from runway systems to tunnels system as they can in inner bark. Blocking the tunnel entrance would exclude predators and possibly help regula- te microclimate, and might have a greater effect on offering insulation in such species that have specific breeding in large aggregations. It would be interesting to know if the incidence of preovipositional entrance blocking is higher for pitch- and shell-boring species and for ambrosia beetles than for species breeding in inner bark.

Preovipositional blocking may be widespread in ambrosia beetles; in some cases, this includes blocking both during and after oviposition. It has been mentioned for *Sagatia minima* (Beavers 1981), *Xiphophorus siamensis* (Braun- tey 1947; Malicky 1971), *Eusimulium stenomelle* (Kasachwan 1963), *Trypodendron persianum*, *Xiphophorus amedi*, and *S. asiaticus* (Kirkendall 1984). Female preovipositional blocking has also been observed in pitch-boring species, such as *Hypohenus distans* (Kirkendall 1984) and the ambrosia beetles *Sagatia minima* (Beavers 1984) and *Hypohenus distans* (Beavers 1984).

PROLONGED MALE RESIDENCY

Males remain in tunnel systems with females for at least some days or weeks, in most Silvina Old and Protodipteridae (Kirkendall 1983). In at least,2 genera both sexes degenerate- ate without mating to a non-functional condition at the end of breeding, which restricts male mating behavior (see for example, Roberts 1941, references in Barten 1974 and Lugger 1987). Males die with females in some taxa (e.g. *Chimixis averaux* (Table 9-2); see Kof ifer- dahl 1981), and in other species they may remain in their breeding system after females have left (discussed.
below, and see Table 6-2 and Kirkendall 1963). In plasmodids, the commitment of males to their original
united region may often be total; it is apparently
assumed that both parents break of terminal segments
shortly, thereby rendering them incapable of taking over
their gall region systems (Bresnan 1977, Brown 1963, b).
Roberts 1954; Hayes et al. 1976; Milligan 1976; Now and
Simmons 1972).
Such male fidelity is extremely unusual in insects: male
association with females, seldom extends beyond a few
hours, or perhaps a few days, pre- or postcopulatory guard-
ing (Chapman and Alcock 1983; Zeh and Smith 1985).
In this section, we will discuss the primary hypotheses for
prolonged male copulatory residence - mate attract-
ing, mate guarding, increased offspring survivorship,
increased offspring number - followed by a summary of
empirical evidence, and finally a discussion of the alter-
atives to male residency.

Male residence and mate attraction

Males may stay with the first female because of the poten-
tial for attracting additional mates. Many acridoids, and all
tropical phytophagous, are monogamous, and normally only
one female or egg tunnel is found in these species; the
possibility that later-birthing females copulate with stran-
geld males but do not eclose their tunnel systems has not
been carefully ruled, but it is unlikely that this can be a
significant benefit to male residence. In various poly-
ygamous species, male attractiveness may be a factor in male
residence for only a brief period. At least it is temporary,
and the different species, colonization of a given resource unit
is highly synchronous, weather permitting (Boyraz 1982; Casden 1979; Reid and Rauberg 1999);
or exceptions, see Kirkendall 1963, Gutierrez and Atkin-
s 1994; Yates 1986). The result is that few new females
arrive after the first few days of gallery initiation in such
species.

Male residence as mate-guarding

Comparison between males for access to females is often
fierce in bark beetles (Kirkendall 1983). Males that have been
stored mostly or entirely under the bark can usually resist
challenges from other males (see, for example, Ooster and
is only be important as long as rival males are still on the
bark; this seems to be the case for only a relatively short
period, however, at least in those bark and ambrosia beetles
for which the colonization process has been carefully
studied. However, although pheromone production by
females of *T. piniperda* is drastically reduced by
removal of a male, production begins again (Klimaszewicz et al. 1986). If this capability is widespread in female-colonizing species (which category includes the vast majority of selected phytophagous
larvae), then male residency may be favored as mate-
guarding, as long as there is a good probability that an
abandoned female can still produce pheromone and attract
a new male. It is likely that the 'capability is lost as females begin ovipositing, at least a few frequency of solitary-
breeding females are usually found in such species, and
this frequency increases over time (see, for example,
McQuistan and Atkas 1979, 1982; Borden 1989; Sizemore
1973).

As mentioned above, colonization of a given resource
unit is frequently highly synchronous. Consequently,
male are attracted to an active breeding site for only a
short period of time, under favorable weather conditions
for only a week or less. Where local colonization is synchro-
nous, defense against cuckoldry cannot be a benefit for
more than the first few days (see, for example, Reid and
Rauberg 1994).

Male residence and offspring survivorship

Blocking out prenursery, parasitic, inquilines, and
other species

An obvious potential function of burrow-blocking is exclu-
ding predators, parasites, inquilines, or competing species.
The efficacy of prolonged burrow-blocking in this regard has not
yet been investigated in detail for any bark beetle. How-
However, Reid and Rauberg (1994) found that removal of
the pine males for only three or four days led to a major
increase in the occurrence in their initial try of two species
of beetle that prey on eggs and larva. The effects of blocking
on parasitic or burrow-inquilines (Hymenoptera: Leptopon-
quilines) Nautmann-Etienne (1973) of ambrosia beetles (a) has
never been measured; there are few natural enemies of ambrosia
beetles, but most of those that do occur are highly specialized for the task, often with elaborate exten-
sions of the pronotum, biventral (frontal), or mandibles,
which is not the way they would be especially useful for
preying and puncturing (see drawings of *Cryptolestes*
in Whitehead 1983, and of *Cryptolestes* (a Cylindroctorus
Globiformis) in Nautmann-Etienne 1973), and specially
shaped, smooth, external characters of the hind-most which would appear to aid in preventing burrow residents from backward digging processes. Naupactus-Euusurus 1928 and durations cited above. These mentioned burrows are most often from the families Heterobasalia, Ompolidae, and Coitus.


Cerastes under the bark are apparently the extremely viscaseous reasons for subterranean and subaquatic insects. Encouraging the enzyme work in time-consuming and risks; a surprising individual is a visible to have definite and equal extraction. Blocking the ventral antennae shapes themselves also serve to keep up other species feeding very thinly under the bark. There are numerous observations of one species either occasionally or regularly using the opening for each egg laying of another as a nesting point for their own egg galleries (see, for example, schwart 1918; Chantos 1962; Stewart 1945; and L. S. Wood 1937). Random and Kamil 1974, Wood 1962; two studies reported that the including Cerastes reduced breeding seasons of the host species (tolpa, cunea, 1970). If by species, Kripps (1952) through uncorrectable but all comprehension and egg destruction. In addition, mongrelization gain are occasionally found during an existence with pairs of the same species (e.g., Calpophora, musca, Hedderick 1950. 

Hypophyes jules, Blackmore 1949. In studies, Cohn et al. 1962. Although it is possible in these cases that this interspecific growth-management would lead to increased competition (which work) imply a benefit for burrowing-biology, this subject has not been studied.

Burrowing-ant species females (contour of barometric) 

Burrowing-blowing species males can control the number of burrow-gaining access to the burrowing system. It remains to be established, however, whether mongrelization prevents tolerant in tows that include several females, or because subsequent females choose not to exist systems in which one female is already present. For burrow-plant species, studies have shown that males in barrows by parasitic-moles and five alleles enter to subsidize females, once they have acquired their normal complement (Bordogna 1967). Swedih and Radinsky 1951, and the 1 pin males with three or four females are much more uncommon in females. Voices of Polybiini systems with four burrow-harvest predators may resemble those of the same individuals when naupactid (James et al. 1994). In allophorus males with three or more females again synthesizing the same component is unusual (Vite et al. 1972). All of these suggest the powerful possibility that males behave some burrow-polyhedral species attempt to form lines since there is a way to copulate two females (see Kisker 1963) an extremely unusual insect-mating phenomenon which deserves more interest.

Concluding remarks

Several descriptions have suggested that blocking in of resistant burrows 1982; Hughes 1965; Cadmus 1958, Kalkos 1959. Bever 1948. Amphipterygids retain high moisture content in the soil and in the absence in their 1965; Bever 1948, Bever 1946, and the surrounding archit and attack details. Dendroctonus is at high altitude, and mating in the northern 1948; 1949. In several polyhedral, during the mass period of lar- 

differentiation, males plug the extract with long cylinders of wood debris; these are rapidly replaced if they are insufficiently removed (Kev 1972; Man|| 1973). In Polybiini species, the male uses his body in combination with a wire or fibers to fill together with egg (Kalkos 1972). Males of the amorphous leaf bee Polybia longipes were observed to make rapid cutting movements with the abdomen, latter period in Kalkos 1959 as possibly assisting the mate.

Keeping larvae and eggs in gallery systems

Nobles, 1965, but the typical polyhedral place egg in spatial voids or cells; (Typical Polybiini refers to the monogamous amorphous beetle that move up the bulk of the form Sufnis, reported planted in Wood 1965). In numerous time and Puertosolomento, by Thompson (1925). In Polybiini- 

taceae, Stenoten beetles frequently move about in the tunnel system, and soon they may discover a burrow bearing towards the entrance, they risk entrapment. With the aid of a silk thread, they make Polybiini colo- 

dents are removed. Reference to his observation on three Polybiini species in New Zealand, Mitzelfeldt (1979) remarks similarly that if the nest is low the larvae may fall from the entrance. In cultures taken with females of Polybiini often an interesting species, with no adult male present in the nest, but were occasionally found on the surface in the culture medium (Bogert et al. 1960). Thus, for both of symbiotic beetle species in which eggs and larvae are
Table 9.1: The effect of male presence on offspring production and survival rate in and around brooding hosts.

For most data sets, only these means were published (in measures of variation, or raw data, were given).

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>a</th>
<th>No. of eggs</th>
<th>Tunnel length (mm)</th>
<th>Eggs traits</th>
<th>Breeding situation, source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hylastes cellulosae</td>
<td>Male present</td>
<td>49</td>
<td>—</td>
<td>28.4</td>
<td>—</td>
<td>From legs colonized during a phenomone study, egg tunnels were dissected and analyzed (8.5 days after initial colonization of the legs; NE: 0.0 for both, Redfors and York 1975)</td>
</tr>
<tr>
<td>Scytis multiplana</td>
<td>Male present</td>
<td>72</td>
<td>—</td>
<td>35.1</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>S. multiplana</td>
<td>Male present</td>
<td>120</td>
<td>64.5</td>
<td>27.8</td>
<td>2.5</td>
<td>Introduced population; Connecticut.Pairs or females alone were allowed to colonize freshly cut log sections (Walsh 1982)*</td>
</tr>
<tr>
<td>Nosties conicus</td>
<td>Male present</td>
<td>7</td>
<td>51.9</td>
<td>38.7</td>
<td>1.2</td>
<td>From naturally occurring tunnel systems in trees colonized for tests by Redfors and York (1986, Table 3)</td>
</tr>
<tr>
<td>N. conicus</td>
<td>Male present</td>
<td>66</td>
<td>50.0</td>
<td>60.8</td>
<td>0.96</td>
<td>—</td>
</tr>
<tr>
<td>Trypodendron lacustre</td>
<td>Male absent</td>
<td>105</td>
<td>64.6</td>
<td>60.0</td>
<td>0.47</td>
<td>Females were confined on logs, single or with males (Hap- mar 1959)*</td>
</tr>
<tr>
<td>T. lacustre</td>
<td>With male</td>
<td>120</td>
<td>57.0</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>T. lacustre</td>
<td>Female alone</td>
<td>30</td>
<td>9.5</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

* No difference in egg hatch. Banko and Laniot (1974) asked found males in dissected galleries, in New York. Chapman (1989) noted found males affect oviposition has not been observed (England no data).
not confined in any way, resistance-blocking may prevent accidental loss of offspring.

In one species of Phycocystis, Callicorex, males have evolved an intricate solution to this problem, summarized by Bowles (1961a, p. 221).

The female is deep-bodied, in front, and the internal seer is entered and incubated so that it can be used as a young female. As the mother lays her eggs, she pica them up with her snout and places them in the hollow of her head, where the abdomen and the head are at more freely in the tunnel without danger to them.

Male residence and number of offspring produced

Available data on female reproductive success with and without males present reveal no consistent pattern among monogamous and most polygamous species. In females by more eggs per female, more adult offspring with males present than with males absent (Tables 9.3, 9.4, 9.5). However, experimental manipulation is necessary, since male absence could be related to the female quality, perhaps males do not stay long with sick or fat females. Data in Tables 9.3, 9.4, 9.5 for Sallyus canaliculatus and Campsaria species could be confounded in this way.

There is also a tendency in bigamous and harems polygamous species for females to have fewer eggs, in proportion to the number of other females with which they mate and share the service of a male (Fig. 9.6). For the two species in which this is not true, Polydora lamarckii and Physopanthenidae, it is interesting to note that they have higher average baram sizes than the other species in this figure, perhaps because in these species male help can be more easily obtained than in others.

It is not known why fewer eggs are laid when males are absent (when such is the case), as why in some bigamous or harems polygamous species fewer eggs are laid in larger than smaller harem sizes. These data support the hypothesis, however, that the male helps females during egg tunnel extrusion, by keeping the egg tunnel free of refuse, in a significant factor in determining the size in which females are deposit eggs (see, for example, Reisch and Richard, 1994; G. H. Pfleider and L. R. Kirkendall, manuscript in preparation).

General considerations of male residence

Experime ntal evidence

Two studies of harems polygamous species in the fryli have specifically addressed the question of long male residence (i.e. longer than a few days). In one breed in weakly and recently dead plankton makes sex with females for several weeks. Reisch and Richard (1994) found the hypothesis that male residence (1) attracts more females; (2) is a form of nest-guarding; (3) leads to a higher reproductive rate of females; and (4) increases mortality of offspring from predation or parasitism. The rate attachment and nest-guarding hypotheses were clearly rejected; prolonged male residence did not increase the number of times they acquired, and experimentally reduced males were not replaced after the short colonization period had ended. after three or four days, the male had laid 10% fewer eggs in systems from which the male had been removed. In addition, two-thirds of these systems had at least one pericarps present, whereas only 10% of systems with males present had pericarps. G. H. Pfleider and L. R. Kirkendall (manuscript in preparation) tested hypotheses 1-5 for a common European harems polygamous basking shrimp in dead scrap, Physopanthenidae. In field experiments, males were removed from every other galley; in laboratory experiments, males of two, three, and five females were established; after which the males were removed from half the systems. As in the fry, hypotheses 1 and 2 were rejected.
Females with males present laid significantly more eggs than females in systems where males had been removed; the difference arose both because females left systems earlier when a male was not present, and because they laid slightly but significantly more eggs when males were present.

Cheap, multifunctional defense

Removal in the tunnel system entrance requires neither exceptional morphological modifications nor major change in pre-existing behaviors, and can be done with little or no energetic expenditure beyond that of normal metabolism. Feeding, however, presents a problem, and presumably usually requires leaving the entrance for a short period of time. There is a certain risk of mortality to guarding individuals from predators or parasitoids (see, for example, Beaver 1986), but often this same mortality might have been incurred by males as blocking the entrance. If the predator or parasitoid entered the tunnel system, burrow defense is also multifunctional, regardless of the context in which it may have been employed, most of all of the possible functions discussed above may be served simultaneously.

Offering in tunnel systems are much easier to protect than exposed patches of eggs or larvae. The entryway is only slightly larger than the beetle; this close fit, coupled with male ability to wedge themselves firmly in place, makes pushing or pulling males from their guarding position difficult. Blocking out intruders, then, does not require complex behavior.

The value of entrance-blocking will be reduced or negated, however, if the entrance is not the only hole in the outside. Holes from egg tunnels on the surface occur in a variety of species, although their taxonomic distribution has not been reviewed. These holes are additional points of entry for intruders, including clerid larvae (Ber-ryman 1986) and torymid parasitoids (Dox and Franklin 1988).

Alternatives to fidelity

Males of perhaps most scolytids and platypodids may be committed to the local resource unit, and platypodids may be confined to their original tunnel system, by slowly reversible (wing-muscle jerparination) or irreversible (loss of tarsi) morphological changes, which occur shortly after mating. At least theoretically, though, or before their
change, have taken place, the alternative is mating with a female (a group of females is to seek further mating opportunities. In species with relatively synchronized breeding, this alternative may disappear after only a few days, at least in the current resource unit and perhaps in neighboring units as well. Finding other mates will then require leaving the immediate area, if for period of copulation has ended. Males do not usually leave for more than a minute or two with females in a few species; in other species, males may continue searching for females at night, and eventually stay with one female (Kirkendall 1985). In most monogamous species, at least some mated but unpaired females are found; the extent to which this is due to (a) male departure, (b) unassisted, unpaired females establishing a new egg-tunnel, or (c) predation, has not been quantified.

The general costs and benefits of searching vs. staying have more recently been discussed by Leeb and Smith (1985), Yamamoto (1986) and Akre (1990). Important parameters include the operational sex ratio (OSR), female receptivity to other males, search time and mortality. Costs of searching for further matings, the capacity for nestling care, nest-scaping patterns, and the strategies pursued by rival males (see also Akre 1994, Table 2).

The most important problem faced by males in finding additional breeding sites. Each and elchoesthesia beetle populations are generally thought to be limited by availability of suitable breeding material (e.g., mowers, 1982), and mortality during the season for new beetles is thought to be 50% for beetles (Klein et al. 1977, Pope et al. 1982). Cuckoo and Frenette (1981, 1983) have estimated that the average life span of a beetle is only one or two days in the breeding season (Pope et al. 1980). Freely feeding males (i.e., those which are not restricted in space and time, and which are of an appropriate quality for a relatively short period. Species breeding in dense forests likely have specific requirements with respect to one or two factors such as host sexes, material distance, host moisture content, temperature conditions, presence or absence of certain fungi. etc. demands which further reduces the spectrum of available breeding material. Species calving in wood are much less specialized with respect to host species (Blower 1954, Uccellari 1975, Akimov and Equiluz 1988), but may still have preferences with respect to host material (e.g., moisture content), and other physical and toxic factors.

Summary: why do males stay?

The available evidence leads us to the following conclusions. Nesting males is probably the correct primar function of male presence in only a few myrmicid species: particularly those in which males leave before egglaying begins. However, it may well have been the initial advantage to remain with females Reid and Rotheier (1994) point out that mate-guarding terms to have pre

cutting copulation care by males in other species (see kirk

""
occurs within populations in many monogamous species. The genetics of sociality and sociability, and parasitism plus competition, would seem to be the best studied clades for detailed examination and comparative studies of the evolutionary ecology of mate residence; each contains a wide range of male behaviors and of mating systems (see, for example, Bohm 1976, S. L. Wood 1982, Kirkendall 1983, 1984, L. R. Kirkendall, personal observations, Askin and Emlen 1985, 1986).

INTERACTIONS AMONG OFFSPRING

Interactions among larvae and parents

Bark and ambrosia beetle larvae can move through tunnels or chew through wood, but are otherwise limited in the possibilities for physical interactions with each other. No special adaptations for larval helping have been found in these beetles, and no dimensions within an isolate outside of slight differences between the sexes are known for larvae of any xylophagous or phytophagous

Last (fifth) instar phytophagous larvae make their way pelvic changes in all species studied, and in most species they also extend the branch tunnels which they used as larvae (see, for example, Table 9-7) prior to pupating. Fifth-instar larvae are equipped with mandibles capable of cleaving wood, unlike the older instars, which can only crop fungi (Bohm 1984a). Apparently, there is little or no such tunneling when the wood has already been invaded by competing fungi (Jimenez 1979). This larval tunneling leads to a rapid expansion of the nest (see, for example, Chapman 1970; Holloway 1973). Some xylophagous ambrosia beetles make large bored chambers (as opposed to only systems of cylindrical tunneling) after larvae appear, at least during the later instars, to anxious in the widening of the tunnel, and for this purpose they have relatively powerful mandibles. . . .'' (Bohm 1984a, p. 10; Hubbard 1987 describes the same, for Xylosandrus morus).

It is not clear whether such lateral tunneling by ambrosia beetles contributes to the success of the family as a whole, or if it primarily advantageous to the individual larva doing the tunneling. However, in Xylosandrus crassiusculus, these larvae form a 'bouquet' passing along wood fibers from larva to larva, out to the female and finally the male, who shoves them up to the entrance tunnel (Taylor 1952). This participation in nest hygiene presumably benefits siblings and parents, possibly at some small cost to the larvae. Roberts (1982) reported that larval larva and young adults of Tryophora puncta perform 'sanitary duties' in older gallery systems, including packing frass and feces into old branch tunnels.

Holloway (1973) suggests that the new branch tunnels contributed by the larva of Platypus cinctus provide more saprophytic sites that would be available in the original nest, and that the additional tunnel length also provides faster ambrosia for larval brood. Tryophora atriplicis females oviposit in such vertical branch tunnels (Roberts 1962a). Brown and Bowers (1984b) observed that the younger larva of Dioryctria brassicae quickly move into these new tunnels, to feed on the fresh fungus Phytopha. In such instances, the branch tunnels may or may not directly benefit the larva making them, but they clearly benefit parents or siblings.

Hubbard, writing generally about North American Platypus species, stated that the older larvae assist in excavating the galleries and furthermore that they 'show evident regard for the eggs and very tender young... . If disturbed, the older larvae will frequently step at the nearest intersecting passage way to let the small fly pass, and show fight to cover their retreat' (Hubbard 1987, p. 15).

In bark beetles, gregarious larvae occur in solitary breeding Dendroctonus species, D. sibiricus, D. punctatus and D. maurus. Larval behavior has only been closely studied in the latter European species, in which larva feed side by side in groups of up to 50 individuals. Larvae actively aggregate in response to larval pheromone, and larva mean in groups have higher survivorship and full mass than isolated larvae (Gregoire 1985, 1988).

Interactions involving adult offspring

Adult offspring helping parents and siblings

The most likely 'helping' behavior to be commonly found among ambrosia beetles is in aiding parent beetles with keeping the tunnel from being overgrown by ambrosia fungi, when these fungi have continued to grow late in the breeding cycle (Hudon 1932). As useful as this behavior might be for the last-developing offspring, particularly if the parents have died or destined, it involves little or no cost to the young adults: the 'helping' apparently involves little more than feeding on the ambrosial growth on the tunnel walls (see discussion of reproductive altruism, below). Nonetheless, this helping behavior is essential for maintaining the normal gallery environments, because in the absence of continual cropping galleries are quickly overgrown by the ambrosial fungi or by contaminants (Hubbard 1986).
It is occasionally reported that daughters have replaced their impaling mothers, in blocking a gallery system (see, for example, viewers 1986), or that they nurse in nest burrows (Roberts 1986). It cannot be determined whether their behavior is a regular occurrence. Both play media species in which helping by progeny has been regarded bred in living trees. In older burrows of Pedunculotarsus, young adults and adult larva larvae participate in 'nest dispatch,' which involves gathering all waste, trash and feces into old branch tunnels that have been vacated; as in the case, the parent male has frequently been seen (Roberts 1986, p. 5). In the second species, Hyalinophanes monyurus, young adult females (that may also be ex- larva larvae) are long-term helpers, which defend the nest area and keep it clean (up to 10) before have been stored in a single nest. In particular, they keep the other storage por- tion free of the polyphemus-tubes known as bones, which, along continuously from the surrounding tree wood (Cain and Simpson 1992; D. S. Kemp, unpublished observations).

Two other behaviors of offspring adults are occasion- ally found: entrance to parental tunnels, and 'nesting of the enormous tunnel when a parent breed' cannot do. The former makes more tortuous nest available for entailment growth, which can be beneficial to younger siblings in those species in which larvae move freely through the tunnel system. The latter provides protection from intruders, and possibly helps in regu- lating tunnel climate. It is not clear what events either involves a significant sacrifice of personal fitness for siring.

D. S. Kemp (unpublished observations) found that the second species 'nest' (daughter) females of a mony- ours species show hearty development, ranging from expanding-ontologies with developing societies in the presence of well- developed eggs. Roberts thought it unlikely that the birds' females in T. phaenusa now had entered the gallery system after the original larva had become established (Roberts 1986, p. 33).

Unfortunately, there are no quantitative data on often Roberts encountered more than one adult female in a T. phaenusa gallery system. Not can be seen if sex or not, or if male, whether they can be censured of offspring which have occurred in nests, or females that have crowded or secondarily invaded a nest. If they are not offspring, that is it in fact maybe several species of female breed together, and the species can be considered monyurus (or others; otherwise, conspecific). If they are offspring then especially becomes a possibility. Further work this species could be of great interest with respect the evolution of complex forms of social behavior.

Multiple female in one nest system have been found in these polyphemus species, all of which live in living trees. The second species, H. monyurus, it dis- covered below, is conspecific. In the third species, Phaenusa phaenusa, D. S. Kemp (unpublished observations) found whereas females within a single large, well-established gallery that had crowded throughout the host tree both ver- tically and horizontally, five of the females were di- scerned harboring the same nest system. Three of these females had laid eggs. It is an intriguing possibility, that the original nest system was being expanded by the other females out their initial colonizing phase; regardless, the avian source of these many females, the observer finds the old peters of polyphemus layout behavior: universally linkage monyurus species, for example (Brown 1986).
Table 3.1. Power: factors in the evolution of colonial breeding in Bark and ambrosia beetles

<table>
<thead>
<tr>
<th>Factor</th>
<th>Solitary breeding</th>
<th>Colonial breeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest material availability</td>
<td>abundant</td>
<td>rare, unpredictable</td>
</tr>
<tr>
<td>Nest material size</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>Nest material condition</td>
<td>dead or decaying</td>
<td>alive</td>
</tr>
<tr>
<td>Breeding system</td>
<td>solitary breeding</td>
<td>outstanding with sex pheromones</td>
</tr>
</tbody>
</table>

We will use the term "colonial" in this chapter only to refer to aggregations of breeding females, pairs, or hares. "Colonial" has been used to refer to the gallery system behavior in a single family but we will not use "colonial" or "colonial" in this sense. "Solitary," then, denotes a breeding situation characterized normally by one family unit in a single female, a male-female pair, or a hare (per measure unit). "Solitary" breeding appears to be the derived character state in ambrosia and (if it occurs at all in the group) in platypleurids. In phylogenetic distribution, it is very scanty, and it occurs most often in tribes (Dryococciini, Cryptocciini, Cryptocciini) thought to be highly derived (Wood 1973). Regular solitary breeding is associated with species adapted to the use of lignin-rich (as old growth) trees or other materials of the nest materials. This has led to the use of such a term as "solitary" for breeding in solitary, small groups of individuals. Many solitary breeders are species with regular nesting (Kirkendall 1993).

Colonial breeding characterizes most ambrosia and platypleurid species. Colonial behavior in most species is a result of requirements for a breeding habitat that is of limited and very limited occurrence, but which cannot be monopolized by a single individual. A variety of chemical and acoustic signals evolved at least in part as a result of the competition imposed by group living: one effect is that entrance tunnels are usually found to be more evenly spaced than would be expected from random setting (reviewed by Byers 1988), which is hypothesized to reduce competition between larvae from different broods.

In the following discussion, we emphasize species regularly attacking living tissue ("aggressive" species). These few species are one of a few spectrum; the vast majority exclusively breed in completely dead woody tissues, but it is important to emphasize that many species fall between these two extremes here, for example, Bleschek 1951, Browne 1961, Routledge 1962). Aggressive species are of particular interest in the context of the chapter because they have evolved a strong dependency upon colonial breeding, and thus provide the most logical candidates in a search for behaviors that might be classified as cooperative. Why some colonial species regularly kill trees but must do not act in an interesting question in itself, but beyond the purview of this chapter.

The ecology of solitary vs. colonial breeding

Role of the host plant

The host plant plays a crucial role in the radiation of scolytid behavior along solitary or colonial lines (Table 3-5). Two aspects of the host, its quality as a breeding substrate, and the mechanisms it possesses to defend itself, are often opposing selective pressures. Fresh inner bark, for example, has more favorable carbon-to-nitrogen ratio and mineral content than older tissues, which makes females to be more frequent and produce more eggs in fresher plant tissues (Shirshov 1975; Kirkendall 1983; Haack and Shimoy 1991; Popp 1989; Schubert et al. 1992). However, living inner bark and the outer sapwood may also be actively defended chemically by toxic terpenes and phenols as well as physically by gum, latices or resins (see, for example, Chapman 1974; Raff and Berryman 1983a; Nebecker et al. 1993; Raff 1993; Klepzig et al. 1995), and recently killed tissue will at least initially have dangerous residues of defensive compounds.

The more time has elapsed since killing tissue death, the more available the tissue is to competitors. Thus, a species that can in some way avoid or overcome the defensive system of a living tree will benefit from higher resource quality and lower competition for that resource, than one breeding in dead plant tissues (Ruff and Berryman 1987). Anecdotal arguments apply also to some extent to ambrosia beetles, even though they are usually confined to dead sapwood or heartwood where they may experience
conspicuous competition from vines and other plants (see, for example, Schoenwalder et al. 1995). Their requirement for sustained high humidity is well met by the dead wood within the canopy. Many of these vines that are not being actively defended by the vines that have been killed by fire or other defensive chemicals from the living trees that have successfully propagated. Species must be able to protect their new foliage from the waves of the wind, adjacent undefended trees within a large area.”

Explaining trapping
There are three types of successful trapping material: (1) kill a large host plant; (2) kill only a small part of a large host plant; or (3) kill several small plants; (4) use host defenses, and breed in drying or already dead stems. The first requires cooperation, the latter cooperation that successful trapping for as individuals can only result from group activity. The latter two do not require multiple colonization. Few species possess the ability to kill healthy vines; many vines can kill vines weakened by drought or pathogens attack (see, for example, Blackman 1954; Stevens 1968; Marvin 1999; Hentz 1961; Jordan 1975; Gehot and Cobb 1960; Mason and Hentz 1985; Bora 1987). Larger units of living trees material can occasionally be killed by toxic, constricted colonization. However, a single brood- ing site is far less, a pair, or a group, depending on the spe- cies can kill a small plant in part. In addition, plants that regularly kill (by gnawing) and breed in small vines (Robert 1992; Freeman 1965; Hentz et al. 1975). Cen- trophyllum species breed in gilled zone zones, tips or brood tips (S. L. Wood 1882; Thomas and Bong 1887; Hymenioptera kumana); (the cutie berrry berrys) near green coffee berries and jersey the seed (see, for example, Leffey 1986). In such cases, colonization by groups of individuals is not necessary for the success of individuals. Single family units in vine bark can also utilize their unique local defenses (for example, Dolichosus mimicus, Cer- gonia 1988), or parts of those among beetles breeding in wood (Centrophyllum ceratodeum, and the pine-embedded Dolichos- tus communis; D kilianus, T. carnipes, Dendroctonus noveboracensi- s, P. macer, S. cernuus, S. orichilonis). Nut- er, these entities include, generally, directly entering the heartwood or living trees through snags (S. K. Kent, personal observations). In these cases, too, it is possible to breed in living trees without living being part of a large group.
expanding the efforts of earlier, risk-taking colonists, for example, Mock 1982; we would expect (1) the stronger, and most localized response to be by the opposite-intimate-seeking sex; and (2) the calling set to cease producing pheromone when startled at least, for monogamous species. To the extent that the calling, pheromone-producing set is actively eliciting further colonization, we would expect that set to exhibit the strongest response to the first colonizers, and we would expect that, especially in monogamous species, ceasing of pheromone production by individual beetles would be at least partially related to the exhaustion of host-tree resistance. If early-colonizing females experience further local colonization solely as competitors, then females should stop releasing attractive substances immediately after having secured a mate.

Among non-aggressive aggregating species, there is normally a much weaker opposite-sex than same-sex response to pheromone beetles (Raffa et al. 1983); however, in tree-killing species of Dendroctonus, the same-sex (female-female) response dominates in the early phases of colonization, and only later does the sex ratio of arriving beetles become male-biased (Renwick and Vint 1972; Raffa and Berryman 1983a). Furthermore, in the tree-killing southern pine beetle (D. frontalis), matings do not lead to an abrupt cessation of attraction as found in the less aggressive D. ponderosae (Richardson 1969), and there is relatively little difference in attractiveness of unmated and mated females (Cooper and Vint 1972). Thus, there is substantial support for the view that some bark-beetle behaviors involved with colonization and killing of living trees include an important component of cooperation.

Cooperation and competition during colonization: the costs and benefits of pioneering

Aggregating bark beetles include representatives along the entire continuum of host-material feeders. Those species that colonize dead plants or plant parts do not encounter active host resistance mechanisms, and the amount of residue of defensive chemicals will depend on time since death. High beetle density in such species only increases larval mortality due to competition and resource deterioration. Individuals and species that colonize the stems of living trees, however, enter an environment that will soon become lethal if additional recruits do not arrive (Raffa and Berryman 1983a; Raffa 1981; Raffa and Smalley 1993). During rapid aggregation, each beetle contributes by physically damaging trees, severing root canals, and inoculating the tissue with phytophagous fungi (Berryman 1972; Raffa and Berryman 1983a; Christiansen and Ericsson 1986; Christiansen et al. 1987).

The evolution of intraspecific cooperation within members of the same sex results in several cooperative mechanisms (Raffa and Berryman 1983a). In acridids, these include: (1) a complex communication system that facilitates sufficiently rapid aggregation to outstrip the dynamic wound responses of host trees (Wood 1972; Raffa and Berryman 1983a, b; Schlyter and Bergerson 1989); (2) association with phytophagous fungi that augment the virulence of each beetle (Whitney 1982); (3) mechanisms for minimizing intraspecific and interspecific exploitation of communication signals (Richardson 1969; Birch et al. 1986a, b; Lantier et al. 1986; Pyne et al. 1984; Raffa and Klepzig 1989; Herms et al. 1993; Raffa 1993a; Raffa and Dahlem 1993); and (4) mechanisms for facilitating synchronous brood emergence (Raffa and Berryman 1978; Benet et al. 1991).

Cooperative attack always includes elements of competition, because the thin phloem layer in which bark beetles breed can support only a fixed number of progeny. Hence, each arriving beetle depletes the available substrate for all other individuals. Soyroids have evolved an array of mechanisms for reducing intraspecific competition, such as the emission of anti-aggregation pheromones (usually terpenes known) and apocarpic acoustic signaling in the form of arcedulation (Richardson 1969; Byers 1984; Byers 1990a). Adjustment of egg clutch size by ovipositing females can also reduce the adverse effects of competition. At high colonization densities, reproductive success is higher for females that deposit only part of the egg load, re-emerge from trees and seek new hosts (Coulson 1979). This behavior is more common among species that colonize healthy trees, and hence rely more heavily on co-specifics for food procurement, than among species that only colonize highly stressed or dying trees (Raffa and Berryman 1987).

Pheromonal communication among tree-killing scolytids (see D. L. Wood, 1982; Ruben 1985; Pyne and Coulson 1980; Raffa et al. 1993) can lead to optimal colonization density for maximal brood per parent through the physiological linkage of beetle communication with host defense physiology (Berryman et al. 1983, 1989; Zhang et al. 1992). That is, beetles are more attractive while trees resist attack, which both increases the likelihood of successful colonization and protects against excessive intraspecific competition (Renwick and Vint 1971; Raffa and Berryman 1983a; Bergersen 1989). The multicomponent, context-dependent
phenotype systems of tree-killing species include incorporation of tree defensive chemicals into phenotype blends as synergistic allelopathic precursors (D. L. Boddie 1982), the leakage of 'unsynergized' phenotype chemicals in may (Buschbom 1960), host defense reaction (Bodeker et al. 1986a) and the successful establishment of 'unsynergized' phenotype-producing fungal chemoautotroph (Buschbom et al. 1979). Responding beetles may differentially in the same phenotype, responding within the path of the phenotype to tree chemistry. The ratio reflects the current status of the colonization attempt. For example, the unmodified MCH, the 'unsynergized' phenotype of L. pendulus, attacks trees when the ratio of MCH to main compounds is low, and refills from when the concentration of resin in the nursery is low (Radoski 1972). Similarly, the effect of the L. pendulus phenotype components sin-bensent and sin-benlate at least in some circumstances are reversed with concentration, acting to increase attraction at low doses but repressing beetle feeding at high doses (Bodeker et al. 1986a). The phylogenetic validity of these communication systems is reinforced by the path to recapture from recognizing specific signals (L) and their lethal production is low under stressed conditions and (2) the late arriving beetles have a low likelihood of success if they try to repair their attacks into alienated semaphored trees (Gore 1967; Gore and Currier 1968; Gaudier et al. 1990; Raffa and Bare- man 1991; Raffa 1988).

Rapid termination of group attack might also reduce the possibility of predators 'identifying' utilizing some members of selected populations. That is, might some individuals respond to pheromone but not signal, and thereby avoid the cues of pheromonal production and lack plant selection, yet benefit from group attack? Most authors believe that such behavior, at least as a generally fixed strategy, would be maladaptive, particularly during periods of low population density (Bargmann et al. 1980; Schuetz and Bargmann 1989). However, a flexible system in which optimal strategies vary with changing conditions might favor some degree of damping (Schuetz and Bargmann 1989). We currently lack the information to evaluate this possibility, but several studies have demonstrated high invertebrate variation in pheromone synthesis (Miller et al. 1988; Seybold et al. 1992; Seybold 1994; Taylor et al. 1994).

Dependence upon group attack to acquire favorable breeding sites also require relatively synchronous generation of adult beetles, particularly in secondary species (Raffa and Bowers 1982). Consistent with this view, some species, such as L. pendulus, appear to have inherent stage-specific temperature thresholds that preclude adult emergence per se regardless of seasonal conditions (Raffa et al. 1994). Interestingly, these are not mass-attacking, tree-killing species in tropical environments for with monophasic diapause may, for example, L. pendulus there is no convenient host and the dominant diapause species occurs at relatively high densities (Raffa 1990).

In summary, research into the consequences of interspecific competition and cooperation for the population dynamics of scolytids has given us fascinating insight into the evolution of their colonial life cycle. Breeding (tree-killing) stage trees appear to acquire a level of cooperation that is essential for insects. Many details are known, the mechanisms of communication, but since they have been gathered largely through observation of and experiments on populations rather than individuals, we cannot be quite of the extent and nature of true cooperation between these beetles, nor do we know in what degree flexibility of the behavioral patterns is conditional as opposed to set in highly polymorphic. Research focused on the cost and benefits of individual options would tell us much about the relative fitness of these complex signaling systems. Specifically, we need a better understanding of the details of the behavior of colonies of individuals which vary widely within the colony organization process, and the effects of colony density and mixing of sex (i.e. males or females) of these individuals as these phenotype and motivational behavior. Much could be learned by studying these behaviors in species that breed in both living and dead trees (heterarchic tree-killers), which includes a much wider range of trees. Finally, the evolution of cooperation in colonial scolytids or platypodids is intricately linked to the evolution of breeding in living or freshly killed trees; comparative research into why to some extent the evolving cooperation will shift to address the interplay between the ecology, physiology and architecture of the host plants, as well as associations with other organisms and the impacts of competitors and natural enemies.

THE EVOLUTION OF REPRODUCTIVE ALTRUISM IN AMEROSIA BEETLES

Insect group behavior is traditionally characterized by overlap of generations, cooperative brood care, and the presence of non-reproductive helpers i.e., for example, the class
Bark and ambrosia beetle social behavior

Bark and ambrosia beetles are social insects. Their nests are usually found in dead or dying trees, where they construct tunnels to protect their larvae. The females and males have different roles in the social structure of the nest. The females are the ones who lay eggs, while the males help in the construction of the tunnels and other nest structures. The larvae, which are the young beetles, live in the gallery and feed on the wood surrounding them. The adults emerge from the nest and fly away, often to find new host trees or to disperse to other areas.

The reproductive systems of these insects are fascinating. The females can lay multiple eggs in a single tunnel, and each egg is protected by a small plug. The males, on the other hand, are smaller in size and play a more passive role. They do not lay eggs but are responsible for helping in the construction of the nest gallery and maintaining the social structure.

The social behavior of these beetles is important for their survival. By living in groups, they can better protect themselves from predators and other threats. The cooperative efforts of the adults in the nest gallery also help in the distribution of food resources, which is crucial for the larval development.

The reproductive behavior of these insects is also unique. The males are attracted to the pheromones released by the females, and the females select a suitable site for laying their eggs. The males play an active role in the construction of the nest gallery, which is essential for the survival of the larvae. The female beetles can lay up to 200 eggs in a single tunnel, and the males help in the maintenance of this gallery, ensuring the survival of the next generation.

In conclusion, the social behavior and reproductive systems of bark and ambrosia beetles are critical for their survival and the health of the host trees. Understanding these behaviors can help in the development of strategies to control their populations and protect the host trees from damage.
females of sibling-interbreeding or mother-sun-interbreeding species, would entail a sequence of changes in the mating behavior for species (such as monogamous polytypids) with complex mate attraction and courtship behavior in which neither sex is normally sexually mature before leaving the nest (see, for example, Roberts 1962). It is not known whether any polytypids accomplish within-clutch matings. For example, it cannot be ruled out that feeding, oviposition males are the source of matings for self-dispersion females of E. manicata that then go on to become new queens. Mature daughters have been found in nests of *Trachymyrmex flaviceps* and *Polyrhachis lamponia*, both of which breed in living trees.

A costless form of helping is blocking the entrance. Feeding and blocking are incompatible, and blocking individuals are also vulnerable to parasites specialized on subterranean ants (see Bucholz 1963, Wilkes 1983). In contrast to parasitism, the risk of predation may not be significantly different for blocking a non-blocking individual; some of the most common queens frequently kill most or all of the breed (Brown 1963b, 1962; Roberts 1962a). If this is the case, then there may be no opportunity for the evolution of physical self-sacrifice (hence sacrifice: Alexander et al. 1991) as a form of altruism in ambrotilis beetles.

**Conditions favoring reproductive altruism**

- **Overlap of generations**: compat between parent and adult offspring — it is common in ambrotilis beetles. Spatial overlap between parents and adult offspring will normally only be likely to species in which larvae do not remain independently away from the egg gallery; ambrotilis beetles, and many species breeding in sand or silt. Temporal overlap will most likely occur when separation extends over a long period when the resource degrades relatively slowly, and when larval development is relatively rapid (Table 9-8).

- **There is generational overlap in many polytypids** (Table 9-5); only one is known not to have overlap, because separation extends over a long period. As a
consequent, emergence from single families can take weeks or months to complete, and females may still be laying eggs when the first natal adult appears, depending on the food production of the tunnels (the stability of the resource). All stages of cytochrome oxidase are occasionally found in a single nest area, for example, Zehntner 1980; Beeson 1993; Khubhani 1995; Schneider 1983. However, the data are too fragmentary to allow any conclusions about how common overlap of generations actually is in this group.

Stability of the host. In the warm, moist climate of tropical rain forests, decay is much faster than in temperate forests (Olson 1978; Lang and Knight 1979). Consequently the dead tree—especially compared with a live tree—is an ephemeral habitat, capable usually of supporting a single generation of bark or ambrosia beetles (Hubbard 1967; Browne 1964a; Beaver 1977, 1984). According to Browne (1964a, p. 41), for example, development in D. pusillius in Malaysia takes only a few weeks, while for the same species in Queensland it requires one year. In Malaysia, the length of the life cycle for most ambrosia beetles is 4–6 weeks (Browne 1964a); 3–6 weeks is considered usual in the tropical forests of Ghana (Jones et al. 1989) (6–12 weeks for phyllophagous colonizingtrunks; Roberts 1961). Temperate ambrosia beetles frequently require one or more years to develop to maturity.

Thus, tropical phyllophagous have shorter life cycles than temperate representatives, and in the tropical phyllophagous, exceptionally long life cycles occur only in the three species that occasionally (D. annulata; Browne 1962) or regularly complete their life cycle in living trees (see Table 9–7). There are too few data to draw any definite conclusions, but it is interesting to note from Table 9–7 that at life-cycle length increases there seems to be a corresponding increase in the difference between time of first progeny emergence and overall duration of the nest. This pattern suggests that the ratio of larval development time to reproduc- tion period is much larger in temperate species. Thus, with respect to host stability, reproductive altruism is more likely to evolve in species breeding in temperate than tropical regions, and in living trees than dead.

For ambrosia beetles of temperate forests, large logs occasionally support multiple generations if not too densely colonized (Hubbard 1967; Chamberlin 1918; Beeson 1993). In such cases, populations are dense, and tunnels merge. Schneider (1983) cites an example of a wind-thrown Quercus muehlenbergii from Kansas, which was gradually colonized downwards by S. scitula over three years; in the fourth spring the network of tunnels was more than 10 m in extent.

Resource stability. Resource stability allows prolongation of adult life span relative to the developmental period and hence overlap of generations, and increases survivorship of potential help- ers that remain in their natal nest area (see, for example, Alexander et al. 1991). In addition, resource stability can lead to a difference in reproductive rates between (1) reproduction via offspring produced by parents, and (2) off- spring produced by individuals choosing to disperse rather than to help, a difference that will be proportional to the difficulty of finding a mate and of establishing a new nest site.

As in wood-feeding termites and ants, and similar to the situation in nectar-fed wasps, ambrosia beetles live in the safety of extensive tunnel systems, which are surrounded by food. The tunnel systems are potentially long- lived and expandable. However, colonization by ambrosia beetles normally initiates an irreversible succession of wood-feeding organisms (primarily insects, fungi and yeasts, and bacteria) which leads to alterations in the physi- cal and chemical properties of the woody tissue. Locally, the ambrosia fungus exhausts the wood in the area around the initial tunnels, and the mycelia on the tunnels walls gradually cease growing (see, for example, Nord 1972). Con- sequently, if a gallery system cannot be expanded, it must be abandoned. Living vs. dead trees. Overlap of generations in ambrosia beetles requires extended tunnel-system productivity, which will depend upon the densities of both conspecifics and the other organisms exploiting the wood. Finding unexploited wood will frequently be difficult or impossible if colonization density is high. Boring into living rather than dead trees, however, may lead to favorable, low within-tree densities for two reasons: first, the much greater availability of potential hosts should act to spread out populations and lead to lower recruitment during colo- nization; second, colonization of living trees involves high mortality and a high rate of nest failure, further reducing within-tree density. Once colonized, living trees provide a much more stable environment than is possible in dead trees. Although the tissue being utilized is dead, it is protected from insect and microbial attack by the surrounding living sapwood and inner bark (as well as the dead outer bark). Thus,
those families successful in invading a living tree will fre-
quently be able to expand their nest volume without en-
counterin g competition, and the tissue consumed will usu-
yally be fresh.

Breeding exclusively in living trees is known for only a
handful of species: the scolytid *Cerambyx echinatus* (see,
for example, Kahl and Grize 1965; Villeneuve and Grize 1969;
Nord 1972) and *C. funereus* (Bustamante and Akesson 1984),
and the platypodid *Tachypnoeodes lucida* (Robertson 1961),
*Emberopis leegi* (Brown 1964), *Phytoncus massaicus* (Kahle 1973),
*Anoplophora cyanophylla* (Kent and Thompson 1991),
*P. rubrata* (D. S. Kent, unpublished) and *Nannostoma denticulatum* (D. S. Kent, unpublished observa-
tions). Ecological behavior or reproductive breeding has
separately evolved in at least one of these six species. In
addition, *N. angusticollis* regularly breeds in living
*Terminalia macrocarpa* in Ghana (Brown 1964b) and Nigeria (Robert
1968) but also in logs of this and other species (Brown
1968). Published observations are detailed enough to con-
clude that cooperative or nesting behavior does not regu-
larly occur in *C. bimaculatus*, *D. tuberculata*, *A. leegi*, *E. leegi* or *P. massi-
cus*.

Living trees simultaneously provide two of the factors
considered most important in the evolution of reproduc-
tive self-sufficiency: they provide an expandable, defendable
nest site, which is capable of persisting for many genera-
tions, but at the same time they are difficult to colonize and
carry high rates of mortality among colonizing bree-
tles. The combination of a stable breeding site combined
with a high cost to establishing a new nest site clearly favors
remaining "at home", if direct (self) or indirect (through
related reproduction) reproduction is possible.

In outbreeding species in which males (fathers or breedi-
er) are present, the choice for those females not dispersing is
between (1) breeding in the natal nest, which entails close
breeding (presumably leading to fewer and lower quality
offspring due to inbreeding depression), and (2) helping
related females raise offspring. The indirect gains from help-
ing a mother or sister coupled with the advantage of immedi-
ate (if indirect) reproduction over the delay necessary to
attain sexual maturity, may outweigh the genetic cost-of delayed, direct reproduction of inferior, low-quality offspring.

The helping alternative would be further favored in circum-
stances where nest location is difficult or costly.

In inbreeding species, it is difficult to imagine similar
outcomes to indirect reproduction over extending the nest
and reproducing directly. Presumably, when further repro-
duction is indeed possible in the natal nest, non-dispersing
females will not suffer a cost due to inbreeding suppression,
and there would be a time lag due to nest location.

Given the advantages, why have so few species adopted breeding in living trees? Trees have evolved quite effective
and passive defenses against insects and fungi that
attempt to penetrate them (see, for example, Manton et
al. 1989, Blanchette and Rags 1992). The extreme longevity of
these plants (up to several hundred or even a thousand or
more years) access to the success of these defense systems.
Trees must attempt to seal off open holes, to prevent infec-
tion by microorganisms. Perhaps future research will reveal
whether the few beetles species capable of breeding in living
trees share particular behavioral or physiological character-
istics which make this lifestyle possible.

**ANCESTRAL BIOLOGY**

We now turn to the question of the ancestral biology for
the scolytid-platypodid lineage. We will briefly present
the biology of what are considered to be the most "primi-
tive" (pleistosomatid) platypodids, and even more briefly
consider the biology of cosmonotine weevils. We do this
because those groups closest to an ancestor can be in morphol-
yogy might also have retained ancestral behavioral traits, but
we acknowledge that there need be no such correlation.

**Primitive** platypodids

The platypodids discussed in this chapter have been
placed in two main subfamilies, Tesserocerinae and
Platypodinae (Wood 1993). A third subfamily, Wood's Cop-
nosomatinae (six genera), may be polyphyletic (Thompson
1992, Kuschel 1995). Kuschel disperses the four genera
that were available to him for study among the Curculionidae
(Papilioninae, biology unknown), Cassidinae (Papiliona-
tinae), Scolytinae (Curculionidae, biology unknown) and
Platypodinae (Scolytinae). Neither author discusses rela-
tionships of Scolytinae Schell, and nothing has been published on its habits; Thompson agrees with Wood that
**Mesopemus** is a platypodid.

Of the aberrant groups placed with the platypodids —
**Mesopemus**, Schoenastus and (according to Thompson)
Curculionidae and relatives — these are ambrosia beetles, but
all are monogamous and in 15-20 subcortical tunnels
(Wood 1971). As they are "very collapsed, details of their
social behavior are not known. They are clearly quite differ-
ent from normal Platypodinae, however, in both 15-20
tunnel construction and feeding habits. **Mesopemus** (one
species from Panama is monogamous and breeds in dead
inside bark, where the female constructs a stinktype cham-
ber and deposits eggs in clusters, as near the late larval
instar food source in the inner bark (Wood 1963). The
Scutellinae species, morphologically the most primitive pla-
typoid, places its eggs in niches in an irregular egg tunnel,
and larval mines single in the wood of dead beams (Wood
1952a; Stämmen et al. 1985). The mined wood is deeply
stained, possibly by fungal, and the larval mines are much
shorter than in bark- or wood-feeding species not asso-
 ciated with fungi. Camphoriniinae, too, appears to be rela-
tively "primitive." It was placed by Wood in his Scutel-
linidae-Camphoriniinae along with Conococinidae
Blainville (two species breeding in wood) and Cantharidi-
can Schaeffer (three species, habits not known) (Wood
1965). The Characteristics of the genus monogamous and breeds
in outer bark apparently like a typical scolytid bark beetle
(Wood 1953).

Conclusions—Discussion

Conclusions are generally believed to be closely related to bark and ambrosia beetles, as discussed above;
adults usually live and feed inside plant tissues, mainly in
dead and dying trees (Kausch 1951). An important differ-
ence between ambrosias and plantypodids, however, is that adults
periodically return to "brow cleanly on the surface.'
However, bark ambrosias and Plantypodidae have "bark-
beetles-like breeding habits" (Kausch 1964; Rutili 1972;
Wood 1953). Plantypodid parasitoids form resin
chambers in woods similar to those of beerehens scoly-
tids, complete with egg niches and individual larval mines
(Wood 1965).

Conclusion

Regardless of the true relationship of these primitive cur-
ulentional taxa, all resemble typical bark beetles or certain
consortments in their biology, and none are true ambrosia brea-
ting. The typical plantypodids and ambrosias, with their com-
plete social behavior, apparently arose from a more
ambrosial, tunnel-breeding ancestor in which parental
and male residence may or may not have been espe-
cially sophisticated. Originals, parent beetles probably
moved in and out of tunnels, as apparently do certain consor-
tants (Robel, in Kausch 1966); the next step was pro-
longed residence in the coexistence tunnel. Presumably
there was overlap between at least females and juveniles.

As seen today in scolytids and the aforementioned conso-
vents, male residence was presumably favored very early
in the evolution of bark beetle families and plantypod-
dis, for reasons discussed later. Attributes of regular assis-
tiation with fungi and other microorganisms that enrich
the food source would have provided tactual oppor-
tunities for slight changes in behavior that would increase survival and the "beetle" to the parasites,
and could have led repeatedly to the evolution of ambrosia
mutualisms. Moving deep into solid wood provided a rela-
tively safe and stable environment, and possibly a relatively
undereveloped mycorrhizal: the death-wood habitat in tropi-

cal forests is now dominated by ambrosia beetles, in
both numbers of individuals and numbers of species.

DISCUSSION AND SUGGESTIONS FOR FUTURE RESEARCH

Discussion

The unusual richness complexity of bark and ambrosia beetles
their social behavior has been largely from their origination
habitats. Rather than simply laying eggs on plant surfaces or in
crevices or excavations in plant tissues, as so many other
insects (including most weevils), bark and ambrosia beetles
breed in the larval frass medium, laying eggs over a prolonged
period in the same tunnel system. This behavior has
innumerable potential consequences for the development of complete social interac-
tions: 1) the beetle is held hostage from potential predators, parasites, or
parasites, and since the tunnel systems normally have
only one entrance, they are easily defended; 2) they work in
an atmosphere of constant high humidity; and 3) they live
surrounded by their brood. As a consequence of 2) and 3),
they remain in the tunnel system for long periods of

time, in some instances for their entire reproduction.

Thus, in the context of evolution of social behavior, ex-
tensive tunneling into the deep wood was the key
innovation for bark and ambrosia beetles (as well as for
their wood-feeding plantypodid ancestors of termite), tunneling into
food sources laying eggs in tunnels, prolonged presence
of the mother, and related variability in generalistic pre-
ations for both adults and offspring. Tunnels by their very
natures are more easily defended than open surfaces, pro-
viding an opportunity for inexperience parental or sibling
care (tunnel-blasings). This defensibility also car, re
tally favor the evolution of prolonged male residence, probably
initially in a form of mate-guarding, as argued above.
Ambrosia beetles have evolved social behaviors of increasing complexity, including cooperative breeding and communal care. As far as is known, none live in large, socially organized "communities". Ambrosia beetles differ from the other ecologically successful fungus-growing social insects in the ants and termites (see Shelford, 1927, this volume), in one important feature: the ants and termites bring food (honeydew) to the fungus gardens, while the ambrosia beetles bring the fungus to the food (fresh wood). The ants and termite gardens are housed in a structure that is long-lasting, and their food input is renewable. The wood used by a fungus-growing beetle, on the other hand, is locally exhaustible. For species breeding in dead trees, there is also considerable competition with other organisms. This difference may explain why the immense colonies with complex social organizations of the former have not evolved in the latter. Fungus-growing beetles and ants can expand their gardens physically to an impressive extent, and the size of a garden (and hence of the primary food source) is presumably correlated with the numbers of nest laborers and foragers the colony can produce. By contrast, the primary fungus of an ambrosia beetle nest is limited to the wood of the one tree in which it is growing, and in most cases to only a small portion of that tree (within competition with other ambrosia beetles of the same or different species). Consequently the beetles' tunnel systems must be constantly expanded if they are to continue to supply food. Apparently these habitants utter seldom bug for more than one generation; although there are numerous anecdotal reports of species apparently successfully exploiting nests for several generations, for most species this is probably not a regular occurrence. An additional factor limiting fungal growth and hence the number of ambrosia beetles that can be supported in single nests must be the very low nutritional quality of wood, compared with plant materials such as leaves (see, for example, Haack and Slansky 1967, White 1963). As a consequence, the rate of food production for the beetles must be considerably lower than that for fungus-growing ants and termites, and must be a severely limiting factor for colony size in the beetles. The distinction between true bark beetles and ambrosia beetles (plus pit- and wood-borers) would seem to parallel that between precolial and alitruncal birds. The comparisons is best between alitruncal birds and ambrosia beetles, as ambrosia-beeke offspring are apparently dependent upon the activities of their parents for a continual supply of food. Precolial bird offspring could be "handed" and led to good
finding sites and can be actively protected by parents, but bark-beetle offspring can only be defended, since they are in their final instar and the larva of most species tunnel further and further away from their parents with time. Help in the nest has evolved almost exclusively in species (Anderson 1849) and similarly, as we have shown, only ‘structural’ softwids and playpodyids: that is, these species in which larvae are sessile or remain in contact with their parents.

In this discussion, we have so far focussed upon familial interactions. Bark and ambrosia beetles have attracted the interest of researchers, however, largely because of another class of social interaction: their ability to kill large stands of living trees through the coordinated attack of tens of thousands of individuals. Tree-killing is mediated by complex pheromone and intrasocial communication systems, and we argue, is only possible if unrelated beetles cooperate, at least initially, in overcoming tree defenses. ‘Use of the term ‘cooperation’ will be left with a degree of skepticism, owing to earlier interpretations that did not consider selection at the level of the individual. We believe, however, that it might be justified in discussing tree-killing. In fact, a careful re-evaluation of the pheromone and acoustic behaviors of both sexes and of the context-dependent responses to thesesignals might reveal that there is indeed a significant ‘multigene’ selection component (Wilson 1969) to natural selection on some of these behaviors: if x is largely true, for example, that the new generation of colonizers come from trees that have been successfully killed by group action, and the group action has included elements of cooperative behavior.

In his landmark review of insect social behavior, Wilson (1975) was able to cite only two studies involving directly with sociality or playpodyid behavior (Hibbard 1897; Barr 1969), and he relies solely upon Hiaribtiin's classic paper for his discussion of ambrosia-beetle social behavior. However, his review needs updating (Chamberlin 1975; Brown 1981a; Chamberlin 1981). Unfortunately, most useful and playpodyid traits are in the foray and applied entomology literature, much of which is not normally encountered by general biologists.

In this respect, bark and ambrosia beetles make excellent model organisms for investigating a wide range of phenomena in population biology and ecology, and for simultaneously serving both basic and applied research interests (Miller and Sturgis 1986; S. L. Wood 1982; Kalten and Borkent 1982, 1992; Borkent and Ryscatt 1982, 1992; Borkent et al. 1984; 1987).

Suggested for future research

The social behavior of bark and ambrosia beetles stems from having afforded them with dome of evolutionary success; over 5000 species of ambrosia are recognized, plus almost 1500 species of playpodyid (Wood and Bright 1992). Nevertheless, they have received insufficient attention from evolutionary entomologists, and hence many critical details of social behavior have been overlooked or misinterpreted. We are sure that virtually every in-depth study of social behavior will reveal new, often surprising features. In particular, we expect to find further examples of more complex (‘behaved’) forms of social behavior in playpodyid and ambrosia beetles, especially in situations where the resource supply for a family unit can be exploited for several generation. Data exists in known techniques may be acquired, however, given the cryptic lifestyles of these insects.

Research in phylogeny systems would constitute much of our understanding of the evolution of the various forms of behavior in these insects. Bright (1993) has re-surveyed the current situation with respect to current review in taxonomy and systematics, and discussed primarily lower-level phylogenetic analyses; we will focus here on the next for higher-level phylogenetic research. Details of research and synthesis by Stephen Wood and his student Don Briggs have culminated in a series of catalogues and systemic publications treating the higher relationships of scolytids and playpodyid beetles (see, for example, Bright 1988, 1991, 1993, Wood 1978, 1987, 1992, 1993, 1995, 1998, 1999; Wood and Bright 1992). The next step will be a more formal cladistic phylogenetic analysis completing and extending the morphological character set implicit in Wood's (1982) analysis (Wood 1983, 1985), but also including larval characters (Thomas 1965; Laub 1966; Brown 1972), the proventriculus (Naud 1969), intrasocial structures (Barr 1981); Manner 1992, behavior (Wood 1989, Kirkendall 1992; Bright 1990) and biochemical data, such as nuclear and
and DNA sequences (Bregen 1991). Many of the critical phylo-
genetic tracers within the Calyculiidae, for example, have not
been unambiguously resolved (see, for example, S. L. Wood
and Kirkland 1990). The evolutionary validity of social
behavior cannot be assumed until we have more exact,
formal phylogenetic hypotheses. The questions we see as
controlling with respect to higher systematics are the rela-
tionship of scolytids and plant-pollinators to each other and to
other coevolved weeds; the placement of the primitive,
absent taxon placed currently in Conopistognathus by Wood; and
which scolytid taxa are closest to the base of the scolytid tree,
the resolution of these sections of the tree including the
two haplodiploid lineages, Conopothes and the Xylocorisae
(McCoskey in Kirkland 1992).

— Obvious, comprehensive analysis of social behaviors at a low
level (within-nest, within-pan-nest, for example) will also depend upon further phylogenetic study, no scolytids or
plant-pollinators have been subjected to a cladistic
analysis, nor even these most thoroughly investigated taxo-
nomically. Unfortunately, there are very few young researchers
students doing systematic or tarsomic studies on these economically important and biologically fascinating
insects (Brigts 1988). Robust answers to our questions about
the evolution of scale residence, female postcopulati-
onal behavior, cooperative tree colonization, and the evolu-
tion of cooperative or financial reproduction will not be
obtained before this systematic work has been realized.

ACKNOWLEDGMENTS

Thanks Tom Phillips, USDA-ARS, for critiquing an ear-
lier version of this manuscript. Comments by conscien-
tious reviewers, Ian Robertson and John Buslen, and our
several Bernard Camp (all three, Simon Fraser University)
were extremely helpful. This circumscribed collaboration
has not been feasible without the internet, for which
we are enormously grateful.

R.G.K. was supported by the University Of British
Columbia Agricultural and Life Sciences, National Science
Foundation grant DEB-9408254, and USDA Regional Pro-
ject W-147. Logistic support for R.G.K. came from the
University of Bergen Zoological Institute. Research by
D.M. was supported by State Forests of New South Wales.

LITERATURE CITED

Allcock, J. 1992. Natural selection and communication among

- 1994. Phylogenetic associations between males and females in
- 1994. Phylogenetic associations between males and females in
- 1994. Phylogenetic associations between males and females in
- 1994. Phylogenetic associations between males and females in
Bark and ambrosia beetle social behavior


Krysanov, S. A. 2006. Larvae, (larva, larviform) species and the reproduction of the bark beetle (Coleoptera: Buprestidae) in the genera Scolytus and Pissodes. Ent. Exp. 11: 35-45. (Czech with English summary.)


