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Assessment of predator and parasitoid control of bark beetles

H.A. Moeck and L. Safranyik

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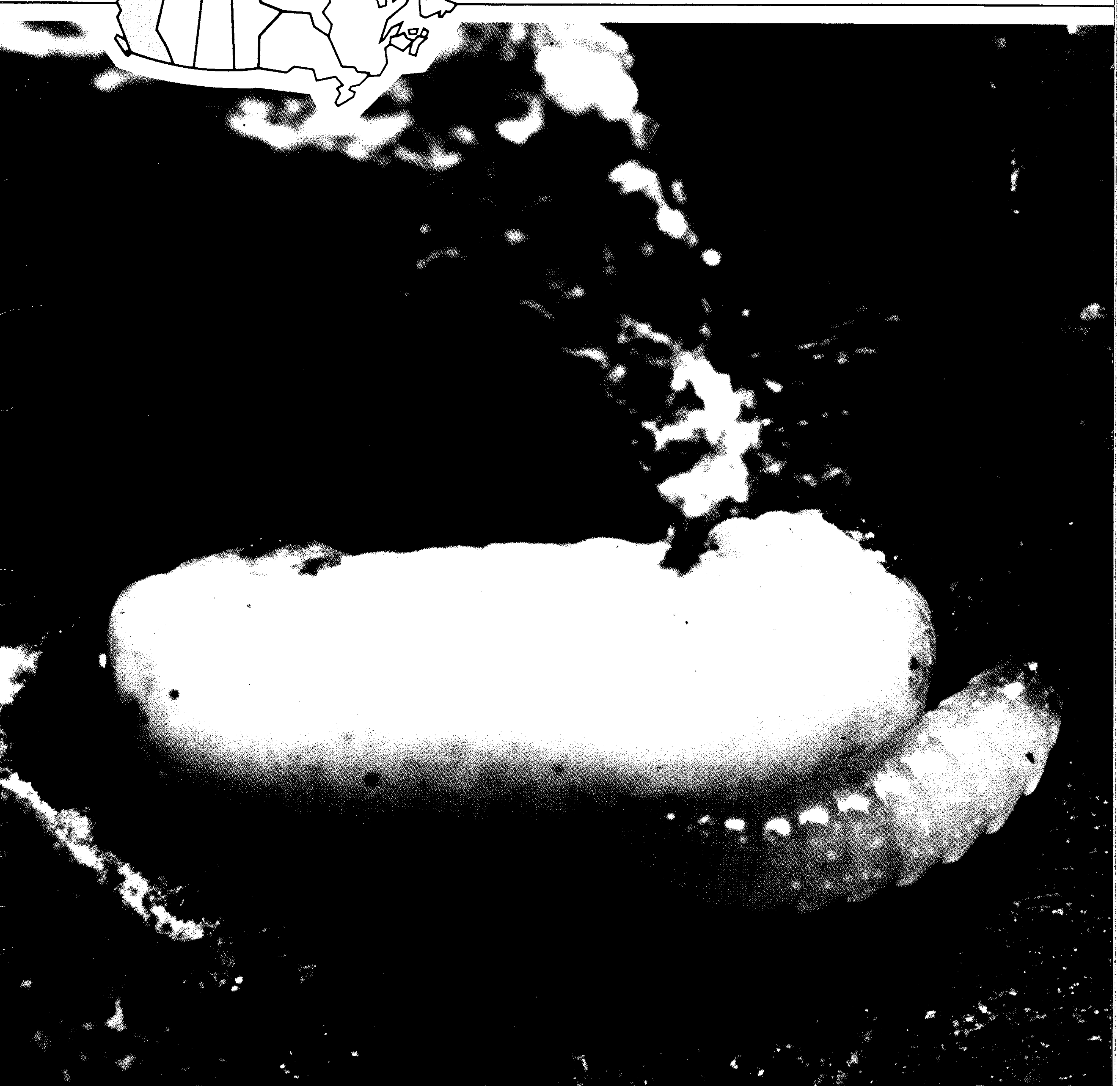

Cover: *Coeloides* sp. (Hymenoptera: Braconidae) larva on *Dendroctonus ponderosae* larva; Riske Creek, B.C.

Photo: H.A. Moeck

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Preface

This paper has been prepared in response to recommendation No. 27, "That predator-parasitoid control of bark beetles be assessed by PFRC," made by M.A. Hulme in the report *Biological Control in the Canadian Forestry Service*, Department of the Environment, Canadian Forestry Service, Report DPC-X-11, 45 pp., 1982.

The natural enemies of bark beetles include vertebrates (birds, mammals, reptiles, amphibians, fish), arthropods (insects, spiders, mites, pseudoscorpions, centipedes), nematodes, and micro-organisms (bacteria, fungi, protozoa, microsporidia, and possibly viruses) (Chamberlin 1939; Dahlsten 1982). Only the vertebrates and arthropods are considered here.

Acknowledgement

We wish to thank Drs. R. Alfaro, M.A. Hulme, I. Otvos and H.S. Whitney, Pacific Forest Research Centre, for reviewing the manuscript.

Abstract

The literature on predators, parasitoids, and competitors of bark beetles was reviewed, and the potential use of these organisms for applied biological control of bark beetles was assessed, in order to provide guidelines for initial investigations in the Canadian Forestry Service of applied biological control of bark beetles using these organisms.

Applied biological control using predators, parasitoids, and competitors has the potential of supplementing existing forest management strategies for reduction of losses from bark beetles. This involves the reduction of beetle numbers directly by use of predators and parasitoids, or indirectly through reduction of their food supply by use of interspecific competitors. The main recommendations for initial research in Canada on applied biological control using predators and parasitoids of bark beetles are: 1) the target bark beetle pest should be the mountain pine beetle, *Dendroctonus ponderosae*; 2) the candidate natural enemies to be used should be native Cleridae beetles; and 3) the tactic to be employed should be inundative releases of clerids against low outbreak levels of mountain pine beetle populations. This tactic appears to be the most amenable to immediate experimental evaluation and operational trials.

Résumé

On a étudié les publications qui traitent des prédateurs, des "parasitoïdes" et des compétiteurs des scolytes et évalué la possibilité d'utiliser ces organismes dans la lutte biologique contre les scolytes en vue d'orienter les travaux initiaux au Service canadien des forêts dans ce domaine.

Ces moyens de lutte biologique pourraient s'ajouter aux stratégies déjà employées en gestion forestière pour atténuer les ravages que causent les scolytes. Il s'agit de faire baisser le nombre de ces insectes, soit directement en ayant recours à des prédateurs et à des "parasitoïdes", ou indirectement en privant ces ravageurs d'une partie de leurs ressources alimentaires qu'ils devront partager avec des compétiteurs interspécifiques. Parmi les principales recommandations applicables à la recherche préliminaire sur cette forme de lutte biologique au Canada, il convient de mentionner: 1) le choix du dendroctone du pin ponderosa, (*Dendroctonus ponderosae*) comme espèce de scolyte ravageur à combattre; 2) le recours à des coléoptères indigènes de la famille des Cleridae, comme ennemis naturels des scolytes; et 3) l'emploi d'une stratégie qui consisterait à relâcher un grand nombre de clérides lorsque les populations de dendroctones sont à des niveaux peu élévés. Une telle stratégie semble le plus susceptible de permettre l'évaluation immédiate de ces moyens de lutte en conditions expérimentales et réelles.

Introduction

Bark beetles (Coleoptera: Scolytidae) are the most destructive insect pests in coniferous forests of North America (Furniss and Carolin 1977; Wood 1982). During periodic outbreaks large numbers of mature trees are killed, particularly by several species in the genus *Dendroctonus*. Although much has been learned over the years about the beetles' biology, population dynamics and interactions with their respective host trees, and effective management strategies to reduce tree losses have been developed, application of these strategies is often limited by economic constraints, and by operational problems relating to the vast areas of stands that may become susceptible to bark beetle attack at the same time. If incipient (spot) bark beetle infestations proceed unchecked, in a few years they usually become so large that control by any means becomes impractical. For this reason, control concepts developed to date have focused on long-term strategies aimed at preventing and reducing the frequency and impact of bark beetle outbreaks. The control strategies are a) silvicultural treatment of susceptible stands, and b) immediate control of spot infestations by use of various mechanical and chemical means.

Applied biological control of bark beetles as an alternative or supplementary control strategy has received very little attention. The impact of natural enemies on bark beetle populations is largely unknown. This is especially true in Canada, where gathering of data on predators and parasitoids has usually been incidental to studies on bark beetle population dynamics, and bark beetle population manipulation attempts with trap trees and behavioural chemicals (L. Safranyik, unpubl. data; Dyer 1973; Dyer *et al.* 1975; L.H. McMullen, Pacific Forest Research Centre, pers. comm). More intensive investigations on predators and parasitoids were conducted in Alberta by R.W. Reid (1954, 1963).

Instances of attempts at applied biological control of bark beetles with predators and parasitoids are few in number, even on a world-wide basis; in Canada only two attempts have been reported. The following assessment of the potential for using predators and parasitoids for biological control of bark beetles is therefore based largely on foreign literature.

The objectives of this review were the following: a) to examine the role of predators, parasitoids and competitors in the population dynamics of bark beetles; b) to appraise the potentials of predators, parasitoids and competitors for applied biological control of bark beetles; and c) to recommend approaches for initial investigations in the Canadian Forestry Service of applied biological control of bark beetles using predators and parasitoids.

General Literature Review

Although the organisms associated with bark beetles have been studied for well over 100 years, there exist no general reviews, summaries, or bibliographies of the world literature on this topic. A thorough treatment of the subject was presented by Chamberlin (1939) for North American bark beetles but it is seriously out of date, especially from the taxonomic viewpoint. A recent paper of similar scope (Dahlsten 1982) presents an overview of natural enemies of bark beetles. However, much of the information given deals with research in California; other areas of North America and the Old World are not covered as well. Kolomietz and Bogdanova (1980) wrote an excellent book on parasitoids and predators of xylophagous insects (including bark beetles) of Siberia. Unfortunately, this book remains untranslated from the Russian. Since all scientific names are in the English script, the appendix which lists hosts and their respective associates is of immediate use. Vertebrate predators, mites, nematodes and micro-organisms are not covered. The literature review of the natural enemies of bark beetles by Mills (1983) is a very useful recent work but treats mainly the scolytids of conifers in Europe; treatment of the North American literature is very brief. The short paper by Stevens (1981) is only a very general treatment of this topic. However, since biological control deals with specific organisms under specific conditions, important exceptions can be found for almost every generalization made in the paper. Review papers dealing with the broader topics of population dynamics of bark beetles (Coulson 1979) and biological control of forest insects (Turnock *et al.* 1976; Ryan 1979) rarely mention natural enemies and bark beetles, respectively.

The world literature on natural enemies and other associates of bark beetles is extensive and very scattered. Taxonomic papers on associates contain information on host bark beetle associations; papers on specific bark beetles often contain lists of associates, perhaps with information on biologies and impact, and the papers dealing with specific associates range from brief scientific notes to comprehensive monographs. A review of all this information is a very time-consuming, yet highly important task. The following summary and recommendations are based on a critical review of selected contributions in the available literature.

Vertebrate Predators

Class Aves — Birds

Piciformes: Picidae — Woodpeckers

Woodpeckers are thought to be one of the most important biotic mortality agents of bark beetles (Dahlsten 1982). They have been most studied as predators of species of *Dendroctonus*, especially of *D. rufipennis* (Kirby) (spruce beetle), *D. brevicomis* (LeConte) (western pine beetle), *D. ponderosae* Hopkins (mountain pine beetle), and *D. frontalis* Zimmermann (southern pine beetle). Old World literature on the subject is sparse.

Woodpeckers, by their mode of searching for bark beetle and other subcortical prey on infested trees, create the most conspicuous evidence of predation. All the outer bark, and sometimes even the inner bark, may be stripped from infested portions of bark beetle-infested trees. Besides consuming bark beetle brood, woodpeckers also indirectly kill the insects by dislodging them from the tree and reducing the survival rate of insects remaining on the tree (desiccation, increased parasitism and predation) (Otvos 1979).

Woodpeckers exhibit a limited direct density dependent response to increasing bark beetle populations. At low spruce beetle population levels woodpeckers remove only a small proportion of the beetles. As beetle populations increase, woodpeckers feed more on bark beetle brood in relation to other food (a functional response), and woodpeckers also congregate in the area of infestation, resulting in greater spruce beetle mortality (a numerical response by migration). Increased nesting populations of woodpeckers in the vicinity of spruce beetle outbreaks have been found (a numerical response by reproduction) (Baldwin 1968). In large-scale bark beetle outbreaks woodpeckers are not sufficiently abundant to bring the outbreak under control.

Woodpecker populations may be limited by availability of food during non-outbreak periods, suitable roosting and nesting sites (snags of a suitable size and condition for cavity construction) and their own territorial requirements during the breeding season (estimated at up to 160 hectares for the pileated woodpecker, *Dryocopus pileatus* Linnaeus (Kroll *et al.* 1980)).

Negative aspects of woodpecker activity are the consumption of insect parasitoids and predators of bark beetles (Massey and Wygant 1954; Miller and Keen 1960; Hanson 1937), transmission of tree diseases (Ostry *et al.* 1982) and damage to wooden power poles (Otvos 1979).

A number of recommendations have been made with regard to enhancement of woodpecker populations, the most common being the provision of adequate numbers of snags suitable as nesting sites (Bull and Meslow 1977; Evans and Conner 1979; Kroll *et al.* 1980). Snag management may be the cheapest option, because it involves the modification of existing forestry practices and use of existing natural nesting sites. Costs involved could be those incurred identifying and marking suitable snags, and in killing suitable trees where no snags are available. Currently, guidelines are being developed by the U.S. Forest Service (Coulson and Stark 1982) and the B.C. Ministry of Forests, Kamloops Forest District (J.P Weinard,[1] communication to I. Otvos, Pacific Forest Research Centre) for management of snags for conservation and enhancement of cavity nesting birds.

It may be possible to provide artificial nests (Semenov 1956; Evans and Conner 1979; Gary and Morris 1980), but this method of woodpecker population enhancement would be very expensive and of doubtful practicality in the vast North American boreal forests (Otvos 1979).

Woodpecker food supplies may be enhanced by girdling some trees to increase populations of secondary stem insects, by culturing and dispersing other insects attractive to woodpeckers (Koplin 1972), and by "high-stumping" during cutting operations to provide additional feeding sites (termites and carpenter ants). However, in many situations, regulations, economics and equipment limitations prevent high-stumping for large numbers of trees (Kroll *et al.* 1980). Since woodpeckers supplement their insect diet with fruits, nuts and berries of wild plants throughout the year but primarily in the summer and fall, leaving these plants after harvesting would favor woodpeckers. However, such an approach would discourage tree establishment and survival on many sites (Kroll *et al.* 1980).

Other suggested tactics that would favor woodpeckers are reducing the size of clearcuts, making clearcuts long and narrow rather than square to reduce the impact on woodpeckers, leaving some mature forest suitable as woodpecker habitat, and lengthening the rotation age to provide trees of adequate size for nesting purposes (Kroll *et al.* 1980). These tactics would be expensive to implement, and may in some cases be counter-productive; the older the trees, the greater the risk of bark beetle infestations.

The efficacy of woodpecker population enhancement for bark beetle control has not been evaluated. An assessment would be technically challenging, since the birds can range over a large area (Bent 1939) and data would have to be collected over a period covering several bark beetle outbreaks.

Passeriformes — Perching Birds

Birds in 11 families have been recorded as preying on bark beetles, primarily during the short period of bark beetle emergence, flight, and attack on trees. Included among these are tree creepers, chickadees, nuthatches, flycatchers, swallows, tanagers, finches, thrushes, jays, wrens, kinglets, and warblers (Dahlsten 1982; Otvos 1969, 1979; Baldwin 1968; Stallcup 1963). Being general insectivores, these birds probably also consume insect predators and parasitoids of bark beetles (Otvos 1979). This impact, which has not been assessed, must be balanced against the birds' consumption of bark beetles. Thus, at this stage, the total impact of bird predation is not known. However, since any mortality agent that acts on the pre-ovipositing female bark beetle is proportionally more important than one which acts on any of the earlier brood stages, the "in-flight" mortality effected by these birds is probably significant (Blackman 1931).

No recommendations have been presented for enhancing populations of these birds for the purpose of bark beetle control.

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Class Mammalia — Mammals

Insectivora, Rodentia, Chiroptera — Shrews, Rodents, Bats

Miscellaneous small mammals consume bark beetles, particularly in overwintering sites at the bases of infested trees and in the duff (Mills 1983; Chamberlin 1939; Dahlsten 1982). The impact of this predation has not been assessed, but it probably is not very great.

Although shrews have been successfully introduced into Newfoundland to prey on larch sawfly cocoons in the duff (Turnock *et al.* 1976), a similar program against bark beetles would not be reasonable for two reasons: a) most pest bark beetle species spend no part of their life cycle in the duff, and so would escape this predation, and b) shrews already exist in areas where bark beetles are a problem.

Miscellaneous Vertebrate Classes

Lizards, frogs, toads and fish occasionally consume bark beetles that stray into the aquatic habitat during dispersal, but their value in this regard is limited (Chamberlin 1939; Otvos 1977). From a practical standpoint these predators need not be considered further because they do not actively seek out bark beetles for consumption.

Invertebrate Predators

Class Insecta — Insects

Coleoptera: Cleridae — Checkered Beetles

The checkered beetles or clerids prey both as adults and as larvae on the adults and brood of various bark beetle species. At certain times and in certain places they can be abundant and exert a considerable influence on bark beetle populations.

Adult clerids are attracted by pheromones emitted by bark beetles during the attack phase (Dahlsten 1982), and so aggregate on trees with abundant prey. This is a numerical response of the predators to the prey, but this lasts only as long as pheromone is emitted. A numerical response of clerids by reproduction was observed by Dixon and Payne (1979); greater numbers were found in a 10-year-old infestation of southern pine beetle than in a 1-year-old infestation.

The impact of adult clerid predation on attacking adult bark beetles is difficult to measure. Estimates range from less than 1% in the mountain pine beetle (Schmid 1970), to 4% in the spruce beetle (Dyer *et al.* 1975). Based on cage tests, Thatcher and Pickard (1966) estimated that 15 clerids per 100 southern pine beetles would be needed to prevent attacks on caged bolts. In the field, however, it is unlikely that clerids prevent successful bark beetle attack on a given tree.

When fed bark beetles *ad libidum* in the laboratory, clerids have a high fecundity. Over 1000 eggs were laid by one female over a period of many months (Berryman 1966). Clerid longevity and fecundity in the field are not known.

Clerid larvae are general predators in the bark of infested trees, and are capable of mining through the bark to find their prey. Consumption of bark beetle brood in laboratory tests ranges from 5 to 50 per clerid larva, depending on clerid species and prey size (Berryman 1966, 1967; Reid 1954; Schmid 1970; Thatcher and Pickard 1966). Cannibalism tends to regulate clerid larval numbers in the bark (Berryman 1967).

Some clerids pupate in cells in the outer bark of infested trees, whereas others migrate to the base of the infested tree to pupate near the ground. Clerid emergence frequently occurs after bark beetles have emerged. These factors have important implications for clerid conservation to be discussed later.

Adult clerids are prey for birds and spiders. Immature clerids are eaten by members of their own kind, by other insect predator species, and by woodpeckers. Parasitism of larvae and adults by Diptera and Hymenoptera has been recorded (Hopkins 1899; Schimitschek 1936; Turnbow and Franklin 1979).

Thanasimus formicarius (Linnaeus), a clerid from Germany released against the southern pine beetle in the eastern United States in 1882 and 1883 failed to get established (Hopkins 1899; Dowden 1962); the effort was deemed adequate (Turnock *et al.* 1976) but reasons for the failure are not known. This effort was the first importation of a predator into North America for the biological control of a forest insect.

In 1909, *T. formicarius* was imported from England into Sri Lanka against the shot hole borer of tea, *Xyleborus fornicatus* Eichhoff, but the clerid larvae were too large to live in the galleries of the shot hole borer (Austin 1956). The clerid did not become established (Clausen 1978).

In 1976, *T. formicarius* from Austria was sent to New Zealand by the Commonwealth Institute of Biological Control for release against the introduced bark beetles *Hylastes ater* Paykull and *Hylurgus ligniperda* Fabricius. Adults surplus to rearing needs were released in 1977 and 1978; no recoveries were made to date, but it is too early to say whether they have or have not become established. The releases were perhaps made at the wrong time of the year, in light of the fact that the seasons are reversed from those in the northern hemisphere where the clerids originated. Doubts were also expressed about the predator's ability, even if it did become established, to affect populations of the bark beetle *H. ater*, in view of the large numbers present in any new clearcut (Milligan 1978; Zondag 1979).

Clerid larvae of some species migrate to the bases of infested trees prior to pupation. In order to conserve clerid populations, Berryman (1967) recommended that stumps and surrounding litter not be sprayed with insecticide during chemical control operations against the western pine beetle, or that high stumps be left, or that the basal 2-3 m of standing trees be left untreated. However, since downward migration of clerid larvae occurs just before western pine beetle emergence, very little time is available to control the bark beetles without inflicting heavy losses on clerid populations — an operationally impractical situation.

Since clerids do not emerge from infested trees until after the bark beetles are gone, Moore (1972) recommended that salvage crews leave trees already vacated by southern pine beetles long enough for the clerids to mature and emerge. Thatcher and Pickard (1966) recommended that trees just vacated by southern pine beetles not be treated by control crews. These recommendations have not been incorporated into bark beetle control procedures, nor has their utility and value been properly evaluated with field trials.

Certain control procedures using bark beetle pheromones can be very destructive to clerid populations. Dyer (1973) and Dyer *et al.* (1975) caught up to 2.45 clerids for every spruce beetle on pheromone-baited poisoned trees, and therefore recommended that such trap trees not be used for spruce beetle control because of their negative impact on clerid populations. Scandinavian pipe traps used in mass trapping of *Ips typographus* Linnaeus caught very few clerids (Lie and Bakke 1981), indicating that proper selection and design of the type of trap can reduce the impact on benefical insects to a negligible level.

Clerids can be reared in the laboratory, but with varying degrees of success, depending on methods and species used. Costs of rearing clerids have not been determined, but are substantial. Although adult clerids can eat a variety of insects (Cowan and Nagel 1965; Mizell and Nebeker 1982), bark beetles are the preferred prey. The prey has to be living, and within a certain size range. Clerids fed cowpea weevils were 62% less fecund than those fed southern pine beetles (Mizell and Nebeker 1982). Adult clerids can be maintained in groups, but will kill each other if too crowded. Larvae, on the other hand, are cannibalistic, and must therefore be reared in individual containers. As for the adults, larval food must be living, and of appropriate size range for the various stadia. Attempts to find larval food other than bark beetle eggs, larvae, pupae, and tenerals have had minimal success (Cowan and Nagel 1965; Struble 1942). Much research is needed if cheap alternative food sources for clerid rearing are to be discovered. The problem of larval cannibalism also must be overcome.

Clerid pupation either occurs readily or not at all in the laboratory, depending on species used. A prepupal period of up to one year in some species creates a rearing problem.

Oviposition in the laboratory occurs readily and eggs can be easily collected (Berryman 1967; Struble 1942).

Field release of clerids in bark beetle outbreak areas where natural predator densities are low has been suggested (Berryman 1967; Struble 1942), but so far this has not been done.

Coleoptera: Trogositidae — Trogositid Beetles

Like clerids, the trogositids prey both as adults and as larvae on the adults and brood of various bark beetle species, as well as on other bark and wood-inhabiting insects. They are not as common as the clerids (Berryman 1967), and for that reason are not nearly as intensively studied.

Adult trogositids are attracted by certain bark beetle pheromones and host tree volatiles (Bedard *et al.* 1969), enabling them to find high prey densities (numerical response by aggregation).

In the laboratory, adult trogositids could kill up to 15 bark beetles per day and eat many of them (Struble 1942). With a lifespan of up to 8 months in the laboratory, the theoretical consumption rate is very high. The impact of adult trogositid predation on bark beetles has not been assessed in the field.

In the laboratory, trogositid egg production averaged 111 eggs per female, with a maximum of 581 eggs (Struble 1942). O'Connell (1967) found that the female trogositid *Temnochila chlorodia* (Mannerheim) must feed on adult bark beetles for reproductive maturation. This might be important in mass rearing attempts in which alternate non-bark beetle prey might be used.

Larval trogositids, like the clerids, are voracious feeders capable of tunnelling through intact bark. Cannibalism tends to regulate their numbers in infested trees (Struble 1942).

Pupation occurs *in situ* in the phloem, and does not involve larval migration. The recommendations for conservation of clerids described above therefore do not entirely apply to the trogositids.

Birds are the only known enemies of trogositids.

There are no reported instances of attempted importation of trogositids for control of native or introduced bark beetle species. Their possible utility for bark beetle control should not be discounted, however, because, like the clerids, they prey as adults on attacking bark beetle adults, and larvae can operate in thick-barked trees, where parasitism may be limited. Their wide geographic distribution and host range imply a high degree of adaptability.

Bark beetle control procedures using pheromones can be destructive to trogositid populations. Bedard and Wood (1974) caught 594,000 western pine beetles and 86,000 trogositids, giving a predator:prey ratio of 1:6.9.

This reduction of predator populations could be avoided if an efficacious, non-sticky trap for bark beetles could be developed (Bedard and Wood 1981).

No specific recommendations have been found in the literature for conserving trogositid populations.

Trogositids can be reared in the laboratory (Struble 1942). Larvae are cannibalistic and must be reared individually. The trogositids did better on alternate insect prey species than did the clerids, and appeared to develop normally. Dead insect prey or artificial diets were unsuitable. Struble (1942) determined that 200 man-hours were needed to rear 1000 *T. chlorodia* from eggs to adults, using mountain pine beetle adults and brood as hosts; most of that time was required for rearing and collecting the mountain pine beetles and larvae. Although mass production and improvments in methods of rearing through use of substitute hosts may greatly reduce the cost, it may still be much too high to be practical, mainly because each predator larva must be handled separately (Struble 1942).

Coleoptera: Rhizophagidae — Rhizophagid beetles

The genus *Rhizophagus* is holarctic, most often associated with various bark beetle species. Some consider them to be fungivores, while others ascribe a facultative or obligate predatory role to them. Habits probably vary with species.

Very little information is available on North American species, whereas the European literature on *Rhizophagus* is more voluminous. Unfortunately, much of it is in untranslated Russian works.

Rhizophagus grandis Gyllenhal is the most studied rhizophagid in Europe; it is considered to be an important predator of *Dendroctonus micans* (Kugelmann) (Gøhrn *et al.* 1954; Kobakhidze *et al.* 1973).

In 1933 and 1934, a total of about 800 specimens of an unidentified *Rhizophagus* from England were released in Quebec against the spruce beetle in an outbreak area, but the introduced beetles failed to become established. The failure of the introduction attempt may be related to the host relationships of *Rhizophagus*: the introduced species were obtained from pine-infesting bark beetles other than *Dendroctonus* (Clausen 1978; McGugan and Coppel 1962). Turnock *et al.* (1976) classified the above predator release as a futile colonization attempt, doomed by inadequate selection of natural enemies and poor handling and release techniques. These predator releases were the only ones ever made in Canada against any bark beetle species.

Another futile colonization attempt (Turnock *et al.* 1976) was made against the introduced bark beetle *H. ater* in New Zealand (Miller and Clark 1935; Milligan 1978; Clausen 1978; Zondag 1979).

The most intensive effort expended in the propagation and establishment of a bark beetle predator has been carried out in the district of Georgia in Russia. *Rhizophagus grandis* is reared in numbers on *D. micans* brood in bolts, and released as larvae and adults on spruce trees infested by *D. micans* (Kobakhidze *et al.* 1970). *Dendroctonus micans* differs from the common North American species of *Dendroctonus* in that it attacks a given tree in low numbers, patch-killing the bark; successive attacks over a period of 5 to 8 years are needed to kill the tree. The success of this biological control method with *R. grandis* hinges on this behaviour of *D. micans* — the predator can build up its own population in an infested tree over several years, without having to search out new infested trees annually. North American *Dendroctonus* species apparently escape many of their natural enemies by dispersal to new areas (e.g., Dixon and Payne 1979).

Specimens of *R. grandis* have been sent to the United States on three occasions (1976-78) to be tested against North American *Dendroctonus* species, but none were released (Coulson 1981).

Coleoptera: Miscellaneous families

Many genera and species in 24 beetle families have been found to be associated with various bark beetles. Many species are obligate or facultative predators of bark beetles, whereas others may be competitors for the bark beetle food supply. The biological roles of many other beetles, in relation to the bark beetles with which they are associated, are not known. The abundance and impact on bark beetle populations of most of the species has not been determined. A notable exception is the work of Coulson *et al.* (1976, 1979, 1980) who studied the impact of foraging by *Monochamus* (Cerambycidae) larvae, which resulted in southern pine beetle mortality of 70% in the foraged areas and 15% on a per tree basis. These levels of mortality to the southern pine beetle were considered to have a significant influence on within-generation survival because the effects take place towards the end of the life cycle of the bark beetle.

No attempts or suggestions to import, augment, or conserve any of these miscellaneous coleopterous associates of bark beetles have been reported.

Diptera: Dolichopodidae — Long-legged Flies

Many species of the genus *Medetera* have been reported as predators of bark beetles in North America, Europe and Asia (Dahlsten 1982; Kolomietz and Bogdanova 1980; Mills 1983). Abundance of *Medetera* varies greatly, depending on many factors (e.g., Dixon and Payne 1979; Marsden *et al.* 1981). Adult flies feed on small live insects and mites on the surface of the bark of trees (De Leon 1935a); feeding is necessary for oviposition, presumably because the ovaries of the flies are relatively undeveloped on emergence (Beaver 1966a). Fly larvae feed on eggs and larvae of bark beetles as well as other subcortical insects. All life stages of *Medetera* are preyed upon by other organisms. The fly larvae are also cannibalistic.

Fecundity was estimated at over 100 eggs for *M. nitida* Macquart (Beaver 1966a) and 65 eggs for *M. aldrichii* Wheeler, not counting eggs perhaps laid before the flies were captured, or that could have developed had the flies not been dissected (De Leon 1935a).

In laboratory tests, *M. aldrichii* larvae, on average, required about 15 prey to complete development, but only about 6 when each instar fed exclusively on the largest-sized prey offered (Nagel and Fitzgerald 1975).

Pupation occurs under the bark, near holes made by its prey through which the pupa can move to the bark surface prior to adult eclosion; the adult lacks mouthparts that would enable it to chew its way through the bark (Fitzgerald and Nagel 1970).

Larvae of *Medetera* sp., predacious on *D. micans* in Russia, brought into the United States in 1978 for tests against *Dendroctonus* spp. died in quarantine (Coulson, 1981).

There are no recorded suggestions for conservation or augmentation of dolichopodids for bark beetle control.

Diptera: Lonchaeidae — Lonchaeid Flies

Although many species of *Lonchaea* are reported as associates of bark beetles, their role in the bark habitat is not clear. They have been designated as scavengers, facultative predators, and predators, depending on species. Bedard (1938) considered *L. corticis* Taylor to be the most important predator of the Douglas-fir beetle, *D. pseudotsugae*, since he found *L. corticis* to be more abundant than *Medetera*, while Kline and Rudinsky (1964) consider *L. corticis* larvae to be more scavengers than predators in Douglas-fir beetle galleries. *Lonchaea furnissi* McAlpine, the most studied North American species, associated with the Douglas-fir beetle, was found to be a scavenger (Johnsey *et al.* 1965). In the European and Asian literature various species of *Lonchaea* are considered to be predatory on bark beetle broods, although no definitive studies of larval behaviour and impact seem to have been carried out.

Larvae of *Lonchaea* spp., predacious on Scolytidae (general), *D. micans* and on *Blastophagus piniperda* Linnaeus (Scolytidae) in Russia, which were brought into the United States in 1978 and 1979 for tests against *Dendroctonus* spp. either were dead on arrival or died in quarantine (Coulson, 1981).

There are no recorded suggestions for conservation or augmentation of lonchaeids for bark beetle control.

Diptera: Asilidae — Robber Flies

Robber flies have on occasion been observed to capture and consume flying bark beetles (Chamberlin 1918, 1920; Kolomietz and Bogdanova 1980; Mills 1983; Stephen and Dahlsten 1976; Wichmann 1956). Schmid (1969) estimated a predation rate of 1% by *Laphria gilva* (Linnaeus) on an emerging population of mountain pine beetles and suggested that numbers of this predator be supplemented. However, nothing is known of the biology of this species.

Diptera: Miscellaneous Families

Many genera and species in 31 fly families have been reported as associates of various bark beetle species, with about 15 families containing known predators of bark beetles. Very few of these insects have been studied in detail, and the role of many species associated with bark beetles is not known.

There are no reported suggestions or attempts to import, conserve or augment any species of these fly families.

Hymenoptera: Formicidae — Ants

Ants have frequently been recorded as predators or associates of bark beetles but their impact on bark beetle populations has not been assessed. A significant effect should not be expected, since attacking bark beetle adults — the stage most commonly preyed upon by ants — spend very little time on the tree surface. Ant predation on Hymenoptera ovipositing on bark beetle-infested trees has been reported, as well as the destruction of clerid and snakefly larvae (Deyrup 1975; Wichmann 1954).

Neuroptera: Inocellidae and Raphidiidae — Snakeflies

Although snakefly larvae and adults have frequently been reported as predators or associates of bark beetles, their role in bark beetle ecology is poorly documented. Wichmann (1957) considered snakefly larvae to be general predators on the bark surface of infested trees, and thought they may do more harm than good by consuming eggs of clerids and dolichopodids, the larvae of which are better predators of bark beetles.

Hemiptera: Anthocoridae - Flower Bugs

Of the 9 families of Hemiptera reported as predators or associates of bark beetles, the Anthocoridae are by far the most frequently encountered. As a group they are predacious on other arthropods, including bark beetles (Kelton 1978). Since these bugs generally are quite small they can live within the bark beetle galleries.

Both the nymphs and adults feed on all stages of bark beetles, using their piercing mouthparts to suck the juices from their prey. The only two species studied in depth are cannibalistic and territorial (Schmitt 1980; Schmitt and Goyer 1983).

The abundance of anthocorids has been assessed only on trees attacked by southern pine beetle, where one species was found to be the most abundant predator (Linit and Stephen 1983).

Anthocorid importation, conservation or augmentation for bark beetle control has not been considered, although they have been used in agriculture against the pear psylla, *Psylla pyricola* Förster (Hemiptera: Psyllidae) (McMullen 1971). Anthocorids introduced from India and Pakistan against the balsam woolly adelgid in Canada apparently did not become established (Clark *et al.* 1971).

Miscellaneous Orders

Dragonflies (Odonata), as general predators in the forest, capture flying bark beetles during dispersal (Bałazy 1966; L.H. McMullen, Pacific Forest Research Centre, pers. comm.). As indicated previously, predation during bark beetle dispersal is seldom considered, but is an important component, since it acts on the preovipositing female bark beetle.

Bark lice (Psocoptera) prey on bark beetle eggs (Ashraf and Berryman 1969) but their impact has not been assessed.

The role of stoneflies (Plecoptera) found associated with bark beetles is not known.

Class Collembola — Springtails

The role of springtails found associated with bark beetles (Bedard 1938; Dahlsten 1970) is not known.

Class Arachnida — Arachnids

Araneae — Spiders

Many species of spiders are obligate or facultative residents on the bark of living trees (Wunderlich 1982), as well as on dead trees (Bałazy 1966; Howden and Vogt 1951; Massey and Wygant 1954). Attacking and emerging bark beetles are preyed on by these general predators; Reid (1963) observed a *Coriarche* sp. (Thomisidae) preying on emerging mountain pine beetles. Dispersing beetles away from the host tree can also be captured by hunting spiders as well as web-spinning spiders (Jennings and Pase III 1975; Moeck unpublished observations). On the other hand, spiders preying on bark beetle parasites and predators (De Leon 1934a) can have a detrimental effect on beetle control. The impact of spider predation on bark beetle populations has not been assessed.

Pseudoscorpionida — Pseudoscorpions

Pseudoscorpions are small general predators that live on and under the bark of trees, feeding on insect eggs and small insects. They have been reported as predators and associates of bark beetles (Berryman 1970; Chamberlin 1939; Dahlsten 1970; De Leon 1934a; Edson 1978; Kolomietz and Bogdanova 1980; Stephen and Dahlsten 1976). Conflicting statements regarding their abundance have been made. Edson (1978) states that they are encountered only occasionally or rarely, while Berryman (1970) states that they are frequently encountered at the bark-wood interface. DeMars *et al.* (1970) believed that pseudoscorpions, among others, are significant mortality factors in western pine beetle populations.

Acari — Mites

Mites constitute a very diverse group of organisms, occupying a wide variety of habitats. Species in about 60 families have been recorded as associates of bark beetles; many of these are probably incidental associations, since many mite species occupy the bark habitat of healthy trees. Nevertheless, many mite species are close associates of bark beetles, using the beetles for transport (phoresy), and feeding either on bark beetle brood, or on some other component of the bark beetle gallery habitat such as nematodes, other mites, fungi or detritus. Mites that feed on bark beetle brood have been variously designated as parasitic (e.g., Kinn 1971; Lindquist 1969a), predacious (e.g., Dahlsten 1982; Moser 1975), or both (e.g., Mills 1983). In the former case "predacious" is applied to mites which feed on other mites or nematodes. In the present paper, mites which feed on bark beetle brood are considered to be predacious, since they search for the host and the host dies as the result of the feeding process.

As with the insects, few mite species associated with bark beetles have been studied in detail. Important contributions are those of Kinn (1967, 1971, 1980), Lindquist (1969a, b), Lindquist and Bedard (1961), Moser (1975), Moser and Roton (1971) and Moser *et al.* (1971). A brief review of mites with regard to biological control of bark beetles was provided by André (1980).

Mite-bark beetle host relationships can be monospecific (e.g., 17 of 20 *Iponemus* (Tarsonemidae) species and species of *Ips* (Lindquist 1969a)), or very broad (e.g., *Pyemotes giganticus* Cross, Moser and Rack (Pyemotidae) probably phoretic on all scolytids and at least one tenebrionid beetle associate of bark beetles (Moser, 1981)).

All life stages except the adult of bark beetles are preyed upon by mites. Some mites (e.g., *Iponemus* spp.) feed only on eggs, while others (e.g., *Pyemotes* spp.) feed on eggs, larvae and pupae. Some mites contain venom which kills the host even though no feeding may occur (Moser *et al.* 1978).

Mites reproduce by eggs, or live birth of sexually mature males and females. In certain *Pyemotes* spp. the first-born males assist with the birth of subsequently emerging females and immediately mate with them. A hundred or more offspring, mostly females, may be produced by one well-fed female mite (Moser *et al.* 1971, 1978).

The impact of mite predation on bark beetle populations has been assessed only rarely. Estimates of mortality due to mite predation range from less than 1% to more than 90% (Lindquist 1969b).

Moser (1981) assessed the potential of *P. giganticus* from western North American bark beetles as a predator of the southern pine beetle. The mite readily rode the southern pine beetle and other bark beetles, but would not readily attack the immature stages of any bark beetle, either in the laboratory or in its native habitat. He concluded that his findings did not support the release of *P. giganticus* into the field as a biological control agent of the southern pine beetle.

Moser *et al.* (1978) assessed *Pyemotes dryas* (Vitzthum) from Poland as a predator of the southern pine beetle. Although this species is phoretic on a wide range of European bark beetles that attack conifers, it was found not to be phoretic on the southern pine beetle or six other associated beetles. This mite readily consumed brood of the southern pine beetle, but to be useful as a biological control agent, phoresy is essential to get the mite from tree to tree. A study to reprogram the mite species to ride the southern pine beetle or one of its associates is being considered.

Mass rearing of *Pyemotes scolyti*, (Oudemans) using alternate hosts, has been suggested as a possible biological control agent for bark beetles (Weiser 1963, in Mills 1983; Beaver 1967a) but no experiments have been done.

Parasitoids

Class Insecta — Insects

Hymenoptera: Braconidae — Braconid Wasps

The family Braconidae contains the greatest number of genera reported to be parasitoids of bark beetles (Bushing 1965). The genera *Ropalophorus*, *Cosmophorus* and *Cryptoxilos* contain species which are endoparasitoids of adult bark beetles (Bałazy 1966; Bushing 1965; Mills 1983). The remaining genera are all ectoparasitoids of bark beetle larvae, and occasionally of pupae. The parasitoids of larvae oviposit through the bark of infested trees, and are thereby limited by the length of the ovipositor as to the thickness of bark through which they can oviposit. In thick-barked trees oviposition can still occur in bark crevices (Ryan 1962a).

Species of *Coeloides* are some of the most important parasitoids of *Dendroctonus*, and are therefore the most studied (De Leon 1934b, 1935b; Richerson and Borden 1972a, b; Ryan 1962a, b, 1965; Ryan and Rudinsky 1962). Host range is quite broad, including not only bark beetles, but weevils (Curculionidae), flat-headed woodborers (Buprestidae) and round-headed woodborers (Cerambycidae) (Bushing 1965). The genus is holarctic, and taxonomy of nearctic species is well in hand (Mason 1978).

Braconids have been reared in the laboratory using bolts infested with bark beetles. *Coeloides rufovariegatus* (Provancher) (= *C. dendroctoni* Cushman) would not lay eggs on exposed bark beetle larvae (De Leon 1935b), indicating that mass rearing by methods other than using infested bolts may be difficult.

Two braconids, *Dendrosoter protuberans* (Nees) and *Ecphylus sileseacus* Ratzeburg, have been brought into North America against the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham), a vector of the Dutch elm disease. Although a native North American braconid, *Spathius benefactor* Matthews (= *S. canadensis* Ashmead if reared from elm; Matthews 1970, in Peacock 1975) parasitizes the introduced elm bark beetle, it has a negligible effect on beetle populations. Schröder (1974) did not state if *E. sileseacus* was released in North America and it is not listed by Marsh (1979), indicating that it is not established.

Dendrosoter protuberans was obtained from France in 1965 and released against *S. multistriatus*, starting in 1966 (Hostetler and Brewer 1976; Schröder 1974). It is now established in Virginia, Ohio, Michigan, Wisconsin, Missouri and Colorado (Marsh, 1979), and California (Hajek and Dahlsten 1981). It was not intentionally introduced into California, and it apparently arrived there on its own. In some areas it may have displaced the native *S. benefactor* (Peacock 1975). *Dendrosoter protuberans* also attacks the native elm bark beetle, *Hylurgopinus rufipes* (Eichhoff), which is the main vector of Dutch elm disease in Canada, but it did not survive the winter above the snowline in Ontario (Gardiner 1976). The *D. protuberans* used in the above test were obtained from Austria in 1972. Gardiner concluded that *D. protuberans* would not contribute effectively to the control of *H. rufipes* and *S. multistriatus* in central Ontario.

Bark beetles as vectors of the Dutch elm disease represent a special situation, in that a very high degree of control of beetles is needed to prevent inoculation and thus the spread of the disease. In Austria, parasitoids and predators of *S. scolytus* (Fabricius) and *S. multistriatus* were not able to reduce beetle populations to levels where spread of the Dutch elm disease was reduced or stopped (Schröder 1974).

There are no other reports of importation or release of braconids against native or introduced bark beetles.

No suggestions are reported for conservation or augmentation of braconids for bark beetle control.

Hymenoptera: Pteromalidae — Pteromalid Wasps

The family Pteromalidae contains the second-greatest number of genera reported to be parasitoids of bark beetles (Bushing 1965). The genera *Tomicobia* and *Karpinskiella* are strictly endoparasitoids of adult bark beetles (Bařazy 1966; Bedard 1965; Furniss 1968), while the remaining genera are ectoparasitoids of scolytid and of other hymenopteran larvae. Oviposition occurs through the bark, so that ovipositor length becomes limiting on thick-barked trees.

Adult bark beetles parasitized by *Tomicobia* and *Karpinskiella* lay few eggs or none at all (Bedard 1965; Furniss 1968). However, this does not necessarily lead to a reduced beetle population in a given area. Furniss (1968) stated that infestations of the Douglas-fir beetle have been especially intense and long lasting in areas where the parasitoid occurs. Increased parasitism may reduce intraspecific competition and increase the rate of survival of the bark beetle brood. Furniss also found another pteromalid, *Mesopolobus*, to parasitize *Karpinskiella* larvae.

A brief review of pteromalids on European conifer scolytids is provided by Mills (1983). He includes *Roptrocerus* in this family, as does Stevens (1981), but this genus is placed in the Torymidae family (Grissell 1979).

Cheiropachus quadrum (Fabricius) (= *C. colon*) (Linnaeus), supposedly of European origin, has been in North America at least since 1888 (Ashmead 1888), yet adults of this species were imported into the United States in 1964 for release against *S. multistriatus* (Schröder 1974). This pteromalid attacks several species of North American scolytids and a weevil (Bushing 1965). Its effectiveness has not been assessed.

Rhopalicus tutela (Walker) is the only other pteromalid which has been imported and released against bark beetles. In 1975 and 1976, specimens from Europe were liberated in New Zealand against the imported bark beetle *H. ater*, but the parasitoid failed to become established. In Canada, *R. tutela* from England was released in Quebec and Ontario in 1934 against the spruce beetle, but it failed to become established at that time. *R. tutela* had been recorded as a parasitoid of *Pissodes* (Curculionidae) in the northeastern United States as early as 1920, apparently as an accidental introduction (McGugan and Coppel 1962), and is now widely distributed (Mills 1983).

There are no other records of importation and release of pteromalids.

Hymenoptera: Miscellaneous Families

Many species in 13 families of Hymenoptera have been reported as parasitoids of bark beetles (Bushing 1965), although Dahlsten (1982) does not entirely agree with this list. Dahlsten states that ichneumonids probably do not parasitize bark beetles, yet Mills (1983) and Kolomietz and Bogdanova (1980) indicate that four species parasitize *D. micans*, and one species parasitizes *Blastophagus piniperda* Linnaeus.

At least two parasitoid species enter bark beetle galleries to oviposit, thus overcoming the limitation posed by thick bark. *Roptrocerus xylophagorum* (Ratzeburg) (Torymidae), of holarctic distribution, enter the egg galleries and oviposit onto larvae in the larval galleries. This torymid has a very wide host range, including the major *Dendroctonus* species (Bushing 1965; Mills 1983). *Entedon leucogramma* (Ratzeburg) (Eulophidae) is an endoparasitoid of elm *Scolytus* species. It enters the bark beetle galleries and oviposits into the eggs; the parasitoid larvae do not complete development until the scolytid larvae are well grown (Beaver 1966b). *Entedon leucogramma* was introduced into North America from Europe and is now established (Burks 1979; Kennedy 1970; Peacock 1975).

Only two egg parasitoids have been discovered. *Trichogramma semblidis* (Aurivillius) (Trichogrammatidae) parasitizes eggs of *Hylesinus* spp. (=*Leperisinus*) (Michalski and Seniczak 1974; Pedrosa-Macedo 1979), and *Leptoteleia* sp. (Scelionidae) parasitizes eggs of the southern pine beetle (Moore 1972).

Finally, a number of species are hyperparasitoids of bark beetle predators and parasitoids, as well as parasitoids of innocuous associates of bark beetles.

Diptera: Phoridae — Hump-backed Flies

The only non-hymenopterous parasitoid of bark beetles mentioned in the literature is the fly *Megaselia aletiae* (Comstock) (Phoridae), which infests adults of the fir engraver, *Scolytus ventralis* LeConte. Parasitism apparently occurs during flight or attack, and parasitized females excavate normal galleries but lay no eggs. One to two percent of parent females were parasitized, a parasitism rate that was considered to be of minor importance (Ashraf and Berryman 1969; Berryman 1973). *Megaselia* spp. are associated with several *Dendroctonus* species but their role was not determined, or was considered to be secondary (Bedard 1938; Massey 1961; Massey and Wygant 1954; Stephen 1974; Stephen and Dahlsten 1976).

Discussion

Bark Beetle Population Dynamics

Bark beetles, with their associated fungal symbionts and pheromone communication systems, are adapted to finding and breeding in suitable host materials (weakened trees, windfalls, logging residue, etc.). Normally, these suitable host materials occur in low densities, scattered throughout the forest in space and time. Under these conditions beetle populations tend to remain at very low levels owing to the scarcity of breeding sites and the consequent high mortality of the dispersing beetles in search of suitable host material. Hence, during the endemic phase, the beetle population is in a dynamic equilibrium with the population of host trees, and the mortality of the searching beetles is thought to be the key regulating factor (Berryman 1982).

Trees actively resist invasion by bark beetles and their associated fungal symbionts by repelling or killing the attacking beetles and isolating the beetle-introduced blue stain fungi (e.g., Safranyik *et al.* 1974). Thus, the success of host colonization is dependent on sufficient numbers of attacking beetles being attracted to the tree to overwhelm its resistance.At a given level of resistance of the normal healthy tree in the forest, a minimum number of attacks (attack threshold) is required to overcome host resistance. Whether or not the attack threshold will be attained or exceeded depends to a large extent on size of the beetle population. Thus, for a given level of host resistance there exists a population threshold above which there will be sufficient numbers of beetles attracted to the host to overwhelm its defense systems (Berryman 1982).

Epidemics erupt when stands of trees are weakened temporarily (e.g., by drought, defoliation, wind) or permanently (e.g., root disease and senility), or when mass migrations of beetles occur from epidemic areas into areas containing endemic populations. In this regard, the behaviour of bark beetle populations is a reflection of the physiological dynamics of their host trees. Management through silvicultural practices therefore appears to offer the most promise in reducing losses over the long term.

The Role of Predators and Parasitoids

How do other factors such as predators and parasitoids affect the dynamics of the host/bark beetle interaction and bark beetle epidemiology? Singly, and in interaction with other mortality factors, such as interspecific and intraspecific competition, resinosis and diseases, predators and parasitoids act to restrain the potential of bark beetle populations to increase. Thus, predators and parasitoids contribute to the maintenance of bark beetle populations below the epidemic threshold and affect the space-time dynamics of the endemic state. Even though the magnitudes of these effects have not been adequately explored in relation to the destructive bark beetles of North America, some field studies (Beaver 1967b; Bedard 1933, in Amman and Cole 1983; McCambridge and Knight 1972; Williamson and Vité 1971) and modeling work (Stephen 1980, in Berisford 1980) appear to support the general validity of these conclusions.

Strategy and Tactics of Applied Biological Control of Bark Beetles

The strategy of maintaining bark beetle populations below injurious levels using predators, parasitoids, and competitors involves reduction of beetle numbers directly, or indirectly through reduction of their food supply.

Reduction of bark beetle numbers may be achieved by the following tactics: a) importation and inoculative release of exotic predators and parasitoids, b) augmentation of native or exotic predators and parasitoids, c) conservation of predators and parasitoids through manipulation of their environment, and d) inundation through mass rearing or field collection of native or exotic predators and parasitoids. Tactics a) to c) are aimed at achieving long term stability and maintenance of low bark beetle numbers, whereas tactic d) is primarily aimed at immediate reduction of injurious bark beetle population levels.

Indirect reduction of bark beetle populations may be possible by manipulating populations of competitors of the target species, such as innocuous bark beetles and some other bark mining insects.

Generally, the suitability of biological control tactics will depend not only on the biological control agent but also on the target bark beetle species and its population level. Bark beetle species which normally breed in windfall and logging debris (e.g., spruce beetle or Douglas-fir beetle) may require different approaches to biological control than those species that normally breed in standing green trees (e.g., mountain pine beetle or western pine beetle). For example, spruce and Douglas-fir beetles may maintain high population levels without killing trees. Hence, the chance for establishment of introduced predators and parasitoids during non-outbreak periods is increased, because the target pest is easier to find.

Importation and inoculative release of exotic predators and parasitoids is the most commonly used and most successful biological control tactic against epidemic pest populations. Although most successes were achieved against introduced pests, successful introductions against native pests have been reported (Carl 1982). There have been no major biological control programs against native North American bark beetles. There are no logical reasons for this lack of activity because chances for success against bark beetles are potentially as great as against other forest pests (Dahlsten 1982).

Augmentation and conservation of predators and parasitoids have been frequently suggested but to date have not been attempted with bark beetles. The reasons for the lack of operational work in this field include the following: a) lack of understanding of the biology of candidate predators and parasitoids, which is needed to make effective recommendations for their conservation and augmentation; b) a lack of good techniques for rearing predators and parasitoids of bark beetles; c) the published recommendations generally would require forestry practices which may be contrary to sound management, or a level of management currently not practiced; d) even though the notions of conservation and augmentation of predators and parasitoids are logical, it is very difficult to evaluate the biological effectiveness of such programs.

Effective inundative releases of predators and parasitoids can most readily be made only when the host population is small and concentrated (e.g., spot infestations of bark beetles typically associated with incipient outbreaks). This is because the numbers of predators and parasitoids released within the area of control should exceed the number of host insects (Flanders 1949). An essential requirement is the availability of the natural enemy (either through mass rearing or field collection) in sufficient numbers. From the experimental viewpoint, this tactic offers a good possibility for appraisal of efficacy. This tactic has not been tried with bark beetles.

Interspecific competition as an important mortality factor of pest bark beetles has been documented (Dahlsten 1982), but suggestions for manipulating populations of competitors to enhance this mortality have not been made. In view of the large number of competing species associated with destructive bark beetles, an opportunity exists to evaluate the potential of this tactic.

Potential of Predators and Parasitoids for Biological Control of Bark Beetles

Although woodpeckers and passerine birds are important predators of bark beetles, they appear to be least amenable to population manipulation in Canada's vast coniferous forests. Artificial propagation is not practical, and recommendations for bird habitat enhancement would require a level of forest management currently not practiced in most parts of North America.

Vertebrates other than birds are poor candidates for applied biological control of bark beetles, because bark beetles compose only a small part of their diet.

Of the insect predators of bark beetles, those that specialize to a great degree on bark beetles appear to be most suitable for population manipulation. These include clerid and trogositid beetles and dolichopodid flies. The beetles show advantages over flies in the following respects: a) adult predator beetles feed on adult bark beetles, reducing their numbers even before the attack on the tree is completed; b) adult predator beetles have a greater longevity than the flies, so that timing of predator releases would not need to be as precise; c) adult predator beetles appear to have greater fecundity than the flies; d) adult predator beetles are physically more robust than flies, which may make them easier to handle during rearing and release; e) predator beetle larvae require greater amounts of bark beetle food to mature, because they are much larger than mature fly larvae; f) predator beetle larvae are better able to tunnel through unmined bark to find their prey; and g) rearing experiments to date have been more successful with the predator beetles than with the flies. However, adult predator beetles will kill each other if too crowded, as might occur in artifical rearing situations. Also predator beetle larvae remain in attacked trees after the bark beetles have left, increasing their risk of mortality from forestry operations, whereas *Medetera* flies emerge before or during bark beetle emergence. Thirdly, a long prepupal period in some species of predator beetles may create rearing problems.

Insects such as dragonflies and robber flies, that prey only on dispersing or attacking bark beetles, show less promise for population manipulation to effect bark beetle control. Numbers of these predators that would be needed for inundation, the only possible tactic for using this group of predators, to prevent or significantly reduce attack on trees by bark beetles, would probably be quite high, although little information is available on this topic.

Information about other insect associates of bark beetles is so scant that conclusions about their possible use in applied biological control of bark beetles cannot be made.

Of the arachnid predators of bark beetles, mites show greater promise than spiders and pseudoscorpions; spiders catch bark beetles only occasionally, and only during the dispersal and attack phase of the beetles, while pseudoscorpions, although they forage on attacked trees, are not closely tied to bark beetle biology.

Mites have a very short life cycle and can be rapidly produced in huge numbers. Some species predacious on bark beetles readily consume other living food (e.g., *Pyemotes scolyti* can be reared on termites (Weiser 1963; Weiser and Hrdy 1962, in Beaver 1967a)). Inundative releases of these mites could then be made on trees infested with bark beetles. Transport of the mites to new trees would depend on the survival of some brood bark beetles to serve as phoretic hosts.

The prospects for inoculative releases of introduced mite predators of bark beetles are largely unexplored. The specificity of the phoretic habit of mites appears to be the greatest obstacle.

The only successful introduction of parasitoids has been directed against an imported scolytid, *Scolytus multistriatus*, a vector of the Dutch elm disease. Economic control of the target pest species has, however, not yet been achieved by the introduced parasitoids. This instance should perhaps not be used as a model of the potential for biological control, since a very high level of vector control is necessary to stop the spread of the tree disease. What the introduction does show, however, is that the introduced parasitoids transferred to native bark beetles, and that native parasitoids transferred to the introduced bark beetle. Host specificity thus is not very great; indeed, the parasitoids may respond to a greater degree to the host tree genus or species, rather than to the host bark beetle species (Dahlsten 1982).

Parasitoid lists of bark beetles from different parts of the world bear remarkable similarities in terms of the genera represented. Differences are mainly at the species level. Introductions of bark beetle parasitoids from one part of the world to another thus may or may not be successful, depending upon the competitiveness of species already occupying a given ecological niche. Competitive displacement may occur, but this may not necessarily lead to control of the target bark beetle species, due to the complexity of the ecology of a bark beetle-attacked tree.

The potential use of inundative releases of bark beetle parasitoids has not been explored. Mass rearing to date has been achieved only with the use of bark beetle-infested bolts; this is an expensive procedure, as mentioned in connection with the rearing of predators. Parasitoid releases would have to be well synchronized with suitable life stages of the target bark beetles. Territoriality and aggressive behaviour of parasitoid adults of some species has been observed (Dix and Franklin 1974), so that parasitism rates at high parasitoid densities may even be reduced by interference.

Summary and Conclusions

1. Bark beetles (Scolytidae), mainly of the genus *Dendroctonus*, are the most destructive insect pests of conifers in North America. The effectiveness and operational use of existing management strategies to reduce losses are limited by economic and tactical constraints. Hence, supplementary control strategies are required.

2. The key component of bark beetle population dynamics is the interaction of bark beetles with their associated fungal symbionts and the host tree. This interaction determines critical levels (thresholds) of bark beetle populations above which epidemics may develop.

3. Predators and parasitoids of bark beetles contribute to the maintenance of bark beetle populations below the epidemic threshold and affect the space-time dynamics of the endemic state.

4. Applied biological control of bark beetles, although it has received very little attention to date, has the potential of supplementing existing management strategies. Although control of bark beetles by use of predators and parasitoids has been attempted in only a very few instances, mostly resulting in failure, logically and biologically, there is as much chance for success as against other forest pests.

5. The strategy of maintaining bark beetle populations below injurious levels using predators, parasitoids and competitors involves the reduction of beetle numbers directly, or indirectly through reduction of their food supply by interspecific competitors. The tactics of applied biological control with predators and parasitoids are a) importation and inoculative release of exotic predators and parasitoids, b) augmentation of native or exotic predators and parasitoids, c) conservation of predators and parasitoids through manipulation of their environment and d) inundation through mass rearing or field collection of native or exotic predators and parasitoids.

6. Although a large body of literature exists on predators and parasitoids of bark beetles, little of it originated in Canada. Consequently, the identities, biologies, and impact of the predators and parasitoids and other associates of even our most destructive bark beetle species are largely unknown.

7. Woodpeckers and passerine birds are the most important of the known natural enemies, causing the greatest mortality of bark beetles.

8. Woodpeckers consume bark beetles and brood from the bark. Also, disruption of the bark habitat by woodpecker activity results in indirect further mortality of the remaining bark beetle brood. Woodpeckers exhibit both functional and numerical responses to changes in bark beetle population levels above the endemic level. However, they are not abundant enough to prevent epidemics or to bring large epidemics under control. Artificial propagation of woodpeckers is not practical. Woodpecker population enhancement may be accomplished by habitat management to increase nesting sites and non-bark beetle food abundance. However, these recommendations would require a level of forest management currently not practical in most parts of North America.

9. Passerine birds prey on bark beetles during the emergence, dispersal, and attack periods. This predation is opportunistic and of short duration, yet significant because pre-ovipositing female bark beetles are consumed. Enhancement of passerine bird populations for bark beetle control has not been suggested.

10. Other vertebrates, such as shrews, rodents, bats, lizards, frogs, toads, and fish consume bark beetles occasionally, but the impact on beetle populations is probably small. These vertebrates are unlikely candidates for applied biological control of bark beetles.

11. Many species of insects prey on and parasitize bark

beetles. Generic lists from different parts of the world are remarkably similar, differences being mainly at the species level. Some species are holarctic.

12. Checkered beetles (Cleridae), which prey both as adults and as larvae on bark beetles, are the most-studied group, and with the trogositid beetles (Trogositidae) appear to be the best candidates for use in applied biological control of bark beetles. Introduction attempts with clerids against native and introduced bark beetle pests have failed for unknown reasons. Control of bark beetles by conservation and augmentation of clerid and trogositid populations, and inundative releases may be possible.

13. Rhizophagid beetles (Rhizophagidae) have been used successfully against *Dendroctonus micans* in Russia; the unique biology of *D. micans* probably facilitated the success. Rhizophagid introductions from England into Canada and New Zealand against native and introduced bark beetles, respectively, have failed for unknown reasons. Research on biology and habits of native rhizophagids is needed before further attempts at biological control using these beetles are made.

14. Other insect predators associated with bark beetles are inadequately studied to permit an evaluation of their possible utility for biological control of bark beetles.

15. Mites which are predacious on bark beetles have not been adequately studied, but appear to offer possibilities for inundative releases, since some species can be reared in huge numbers on alternate insect prey.

16. Other arachnid predators such as spiders and pseudoscorpions are unlikely candidates for applied biological control of bark beetles, because their biology is largely unknown.

17. Of the parasitoids of bark beetles, braconid wasps (Braconidae) and pteromalid wasps (Pteromalidae) appear to be the most frequently encountered. Species in these two families oviposit through the bark and their effectiveness on thick-barked trees is limited by ovipositor length. A braconid has been successfully introduced into the United States against the imported Dutch elm disease vector *Scolytus multistriatus*, but economic control of this beetle has not yet been achieved.

18. Two European pteromalids have become established in North America, apparently accidentally, but their impact on bark beetle populations has not been assessed. Introductions of one pteromalid into New Zealand against introduced bark beetles failed for unknown reasons.

Recommendations

1. Based on the population dynamics of destructive *Dendroctonus* species in North America, the best long term management strategy for reducing losses appears to be maintenance of stand vigour through forestry practices. Applied biological control to reduce bark beetle numbers has a potential for supplementing this management strategy and should be investigated.

2. The target bark beetle species for initial consideration should be the mountain pine beetle, *Dendroctonus ponderosae.* This species is currently the most damaging bark beetle in mature pine forests of western North America, and also has the potential of becoming a highly destructive pest in the managed pine forests of the future. The large body of literature on its population biology and associated organisms, the simple one-year life cycle, the ease of continuous rearing in the laboratory, and the persistence of populations in readily detectable groups of trees during the endemic phase are important characteristics that will facilitate experimental and operational biological control trials.

3. Based on existing knowledge reviewed, and excluding nematodes and pathogens, native predacious insects and mites appear to be the best candidates for applied biological control. Hence, initial investigations should concentrate on this group of organisms. Predacious vertebrates, although being the most important natural enemies, and parasitoids, are much less amenable to experimental and operational manipulation.

4. Of the possible applied biological control tactics, inundative releases are the most amenable to immediate experimental evaluation and operational trials. The other tactics, namely conservation and augmentation, importation of exotic species, and release of competitors require much greater knowledge of the taxonomy and biologies of the native natural enemies than is currently available.

5. Of the predacious insects, the clerid beetles are the most studied and appear to offer the best potential for inundative releases against low outbreak levels of mountain pine beetle populations. Development of techniques for inundative releases of these predators and evaluation of impacts should receive the highest priority.

6. Concurrently with the above studies, information should be gathered on the taxonomy, biology, and impact of other predators and parasitoids and competitors, both native and exotic, to provide the basic knowledge required for the application of other biological control tactics.

7. Snag management policies for the enhancement of populations of cavity nesting birds developed by the U.S. Forest Service should be reviewed to assess the possiblity of development of a similar

program in Canada, and for providing direct input into the development of regional snag management programs.

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