SPECIAL TECHNOLOGY DEVELOPMENT PROPOSAL

PROJECT STATUS:
New, not previously funded.

PROJECT NUMBER:
R2 – 2002 – 01

PROJECT TITLE:
Development of mass rearing techniques for clerid beetles (Coleoptera:Cleridae) and assessment of the impact of field release on bark beetle populations

EXPECTED PROJECT DURATION:
The project will be conducted over a two-year period. The primary goals for the first year are to refine mass rearing techniques of clerid beetles and develop a laboratory colony and testing experimental design for assessing impacts in the field. The second year will use lab-reared colonies to determine the impact of inundative releases of clerid beetles upon caged bark beetle populations infesting standing host trees in the field.

EXPECTED COMPLETION DATE OF THE PROJECT:
The project is will be completed by the end of FY-2004.

SUBJECTS:

Subject Area	Percentage
1. Total Suppression/Prevention Technology	**100**
a. Total Biological Control	
iv. Other (Predators)	
2. Survey and Monitoring Technology	
3. Assessment Technology	
4. Social Values	
5. Technology Transfer Innovations	
6. Other	
	100

STATUS OF SUBJECT SPECIES:
Both the target insect (bark beetles) and the bio-control agent (clerid beetles) are native insects.

PROJECT OBJECTIVE:
This project seeks to utilize recent advances in insect rearing techniques to test the potential for large scale field releases of clerid beetles in order to reduce stand-level bark

beetle caused mortality. The project will refine and apply these techniques to produce large numbers of clerid beetles which will then be placed in field cages to determine the effect on bark beetle brood production in infested host trees.

BRIEF DESCRIPTION OF PROJECT:
This project has two goals: 1) perfecting artificial diets and rearing techniques for clerid beetles and 2) field testing of augmentative biological control by placing large numbers of laboratory produced clerid eggs on bark beetle infested trees. These studies will occur in two locales, one portion will take place near Salida, Colorado where we will mass rear *Enoclerus lecontei* to treat an ongoing infestation of mountain pine beetle (*Dendroctonus ponderosae*). The other portion of the study will focus on producing large numbers of *Thanasimus dubius* for the purpose of treating infestations of southern pine beetle (*Dendroctonus frontalis*). The site of the southern pine beetle aspect of the study will be determined in the spring when the more transient populations of southern pine beetle become evident. Various factors which affect production of insects will be examined in the lab. At least three previously developed diet formulations will be compared and insect handling methods designed to reduce cannibalism and other density induced mortality will be refined. Field application of laboratory produced clerids will be different for the univoltine mountain pine beetle versus the multivoltine southern pine beetle. However, in both cases, bark beetle infested host trees will have cages attached in which differing levels of the predatory clerid eggs will be introduced. The effect of clerid predation will be determined by comparing bark beetle emergence from the treated and control tree sections.

FHP LEAD CONTACT:
Tom Eager, USDA-Forest Service, FHP-Region 2, Gunnison, CO
(970) 641-0471, teager@fs.fed.us

FHP LEAD INVOLVEMENT:
Dr. Eager will act as the overall administrator of the project. He will also supervise the establishment of the mountain pine beetle study site and the Colorado laboratory and rearing facility as well as the direction of field personnel at the Colorado site.

PRINCIPAL INVESTIGATORS:
John Reeve, Southern Illinois University, Department of Biology,
(618) 453-6670, jreeve@zoology.siu.edu

Brian Strom, Southern Research Station, Pineville, LA
(318) 473-7235, bstrom@fs.fed.us

PRINCIPAL INVESTIGATORS INVOLVEMENT:
Dr. Reeve will provide the primary technical direction for the project. Dr. Reeve has completed numerous studies on the laboratory rearing and field analysis of clerid beetle impacts. He will oversee the southern pine beetle study site as well as provide direction for laboratories at both of the study sites.

Dr. Strom has extensive experience in working with southern pine beetle and assessing the ecological implications of bark beetle activity. He will provide direction in all aspects of the study, particularly in the design and implementation of the field studies.

COOPERATORS:

Steve Clarke, USDA-Forest Service, FHP Region 8, Lufkin, TX
(936) 639-8646; sclarke@fs.fed.us

Richard Nathanson, Albany Bug Co. An LLC partnership between BioLogixs, Inc. and Oregon Freeze Dry Inc. Albany OR
(541) 924-0600, rnathanson@biologixs.com

COOPERATOR INVOLVEMENT:

Dr. Clarke has worked extensively with southern pine beetle and has also worked with clerid beetles on several studies. He will serve as an adviser/consultant on this project.

Mr. Nathanson is the Technical Officer for Albany Bug Company, a LLC partnership between BioLogixs Inc., and Oregon Freeze Dry, a private company that produces mass-reared predatory insects for agricultural settings. He has a background in forest entomology and was instrumental in the development of artificial diets and insect handling techniques for producing beneficial insects. He will also serve in an advisory/consultant role.

JUSTIFICATION:

Bark beetles pose a serious recurring threat to conifer forests throughout North America. Outbreaks of southern pine beetle (*Dendroctonus frontalis*) are now occurring in many southeastern states, for example, while mountain pine beetle outbreaks are present at several locales throughout the Rocky Mountain Region, including the Salida outbreak, Vail Colorado and the Black Hills. Although debate continues on the causes of bark beetle outbreaks, studies of southern and western pine beetle (*D. frontalis* and *D. brevicomis*) indicate that natural enemies are key in outbreak collapse (Berryman 1970, Turchin *et al*. 1999). Clerid beetles have been identified as a major source of bark beetle mortality from natural enemies in both these systems (Berryman 1970, Reeve 1997, Reeve and Turchin *in press*), and cause significant mortality for other bark beetle species (Mills 1985, Weslien and Regnander 1992, Weslien 1994, Schroeder and Weslien 1994). Although clerid beetles are often abundant during outbreak collapse, they are typically sparse at the beginning of an outbreak, presumably because their life cycle is longer than their prey and some time is required for a numerical response to occur (Billings 1988, Schroeder 1998, Turchin *et al*. 1999, Reeve 2000). Thus, there are circumstances where the biological control provided by clerids could be improved by augmenting their populations, especially at the beginning of outbreaks and in specific locations where rapid control is desired.

URGENCY:

Bark beetles continue to be one of the biggest problems confronting forest managers. Not only do these insects cause huge commercial losses of timber and other forest

products, they also derail long term management objectives which in turn affect other forest values including recreation, wildlife, etc. Due to the explosive nature of bark beetle population growth, the most effective control of bark beetles is accomplished by early initiation of control activity. Early treatment of bark beetle populations include techniques such as sanitation/salvage to reduce beetle numbers and the application of chemical pesticides to protect individual trees. However, the negative impacts which are perceived to accompany these methods have left forest managers seeking additional modes of control that are more environmentally benign. Previous attempts to utilize clerids (long known as an important natural control of bark beetles) were stymied by the need for repeated handling of the insects that raised costs to prohibitive levels. However, recent developments in commercial production of beneficial insects and the development of artificial diets have resulted in the potential to rear these insects on an economically viable basis. The growing societal concern regarding the adverse environmental effects of other bark beetle control techniques has only increased the desire for effective biological controls.

NATIONAL FHP TECHNOLOGY DEVELOPMENT PRIORITIES:

Priority 1: __X__ Priority 2: _ Priority 3:___ Priority 4: ___

The proposed project fits into the first of the four priorities.

- Develop or refine biocontrol methods for established pest species.

STDP TECHNICAL COMMITTEES PRIORITIES:

Priority 1: ___ Priority 2: ___ Priority 3: ___ Priority 4: ___
Priority 5: ___ Priority 6: ___ Priority 7: ___ Priority 8: X

The proposed project fits into the eighth committee priority.

- Development of guidelines and/or techniques for surveying and monitoring of non-target species. These guidelines or techniques should be directly related to actions taken through various Forest Health Protection activities such as prevention, detection, evaluation, suppression, or eradication of native or exotic species.
    - This project seeks to develop techniques to increase the impact of clerid beetles upon bark beetle populations. In order to accomplish this it will be necessary to assess field populations of clerid beetles under varied management conditions. It is evident that these monitoring techniques would be applied to bark beetle populations under evaluation and/or suppression.

SCOPE OF APPLICATIONS:

The proposed line of work would take place in at least two FS Regions (Regions 2 and 8). However, the techniques developed by the project would be applicable in bark beetle systems throughout the world.

RESEARCH BASIS:

There is considerable evidence that natural enemies, and in particular clerid beetles, are important sources of mortality for bark beetles when abundant (Berryman 1970, Mills

1985, Weslien and Regnander 1992, Weslien 1994, Schroeder and Weslien 1994, Reeve 1997, Turchin *et al*. 1999, Reeve and Turchin *in press*). Biological control by clerids might be improved, however, by augmenting natural populations of these predators in the initial phases of an outbreak when they are sparse, and at locations where more rapid control is desired. There are several problems that must be overcome to implement such a control strategy, common to any system where augmentative biological control is contemplated using predators (King 1993, Van Dreische and Bellows 1998). One critical need is for a low cost artificial diet for clerid larvae, because it is impractical to rear more than small numbers on their natural prey. An artificial diet is unnecessary for adult clerids, however, because these can be inexpensively fed using the factitious prey *Callosobruchus maculatus*, the cowpea weevil (Nebeker *et al*. 1980, see also below). Another potential problem arises from the fact that clerid larvae are highly cannibalistic, and so must be individually confined and reared. For this reason, methods of repeatedly feeding large numbers of individual larvae must also be developed. The magnitude of this problem would be reduced if a diet with a long shelf-life was developed, so that each larvae need be fed only a few times (ideally once) during development. Finally, methods of releasing predators should be developed to target specific trees under bark beetle attack. These releases could be coordinated with semiochemical treatments designed to disrupt infestation growth (e.g. verbenone).

We have already made some progress along these lines. An artificial diet for clerid larvae has been used to rear *Thanasimus dubius*, a predator of *D. frontalis*, for many generations in the laboratory (J. D. Reeve, M. G. Rojas, and J. A. Morales, unpublished data). The diet is primarily composed of veal baby food, eggs, baby formula, sucrose, and various protein extracts, plus small amounts of pure vitamins, cholesterol, ergosterol, and amino acids. In our initial experiments, we dispensed the diet in Parafilm sandwiches, and replaced the diet once a day. Water was provided on a small piece of cellulose sponge. The larvae were held in 50 cm Gelman culture dishes lined with tissue. Table 1 compares the survival and development time of larvae reared on the diet with larvae reared using *Ips grandicollis*, a natural prey species for *T. dubius* (data from Lawson and Morgan 1992). Adults reared on the artificial diet were fed either *I. grandicollis* or cowpea weevils as prey, and their performance compared with adults reared on and then fed natural prey. In general, larval survival and development rates were similar for the artificial diet vs. natural prey, and adult longevity and fecundity were better on the artificial diet. The performance of adults fed cowpea weevils was actually superior to that obtained using natural prey.

We also conducted experiments where *T. dubius* was reared in larger numbers using insect trays obtained from Bioserv, Inc. The cells in the trays were filled with a small amount of coarsely ground pine bark, to provide a substrate for the larvae to crawl and hide. The diet was dispensed in Parafilm capsules, changed three times per week, while the adult predators were fed cowpea weevils *ad libitum*. Small amounts of water were provided by lightly misting the trays with a sprayer. Maintaining this culture required approximately eight hours per week. The aggregate performance of *T. dubius* reared using this method is shown in Table 2. Our results indicate that high values of R_0 can be obtained using this rearing procedure, and sufficient eggs were produced to permit

augmentative field tests on a small scale (see proposed studies below). The relatively low survival rate and R_0 for the second generation seemed to occur when we inadvertently increased the amount of water sprayed on the trays. The main bottleneck in this rearing method is the need to individually feed the larval clerids three times per week – this process must be made faster and easier, and the shelf life of the diet extended to reduce the number of feedings.

In preliminary studies conducted in Colorado, an artificial diet for predatory insects has been used to successfully rear *Enoclerus lecontei* from the larval stage to adult stage. This commercially available diet (produced by BioLogixs, Inc./Oregon Freeze Dry) has a long shelf-life, yet can be reconstituted on an as-needed basis. The development of this diet, in conjunction with commercial insect handling techniques, are recent developments that have increased the potential for rearing large numbers of predatory insects for the purpose of reducing field populations of pest insect species.

We also have evidence that augmenting clerid populations within an infested tree will reduce bark beetle reproduction. In a laboratory experiment, we colonized logs with three different densities of *Ips grandicollis*, then added various numbers of *T. dubius* eggs to the logs in a two-way factorial design (Reeve and Turchin, *in press*). We then observed the ratio of increase for *Ips* in each log (Fig. 1). As the number of clerid eggs was increased, the ratio of increase significantly declined across all initial *Ips* densities. Similar studies have addressed the impact of adult clerids on adult SPB during the mass attack, and found a significant effect of clerid predation on SPB adults (Reeve 1997). We suggest that augmentation using clerid eggs is the more practical control strategy, however, because these can be directly placed on bark beetle-infested trees. Adult clerids cannot be so accurately targeted because of their high dispersal abilities (Cronin *et al*. 2000).

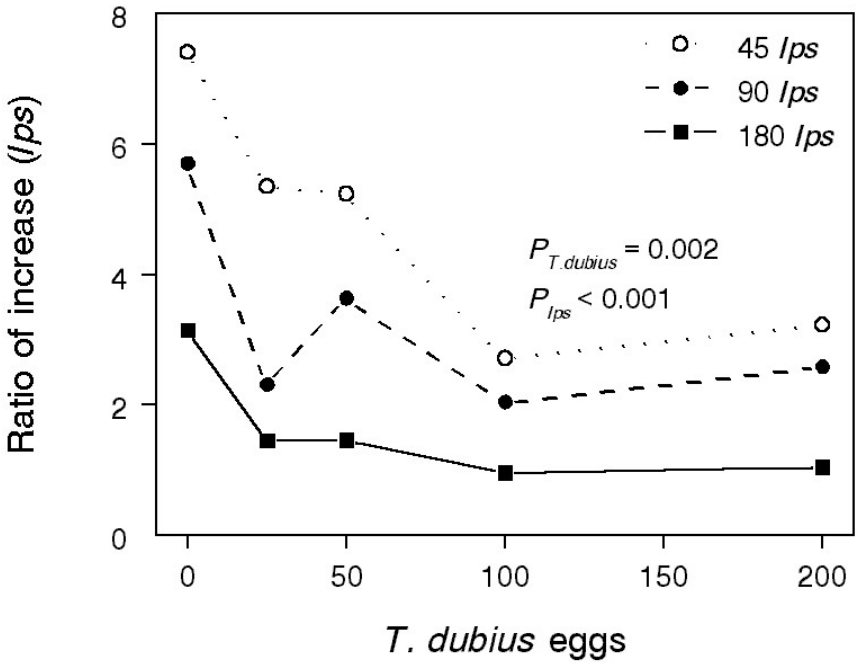
Table 1. Summary of survival rates and mean (± S.E.) adult longevity and fecundity for *T. dubius* reared on artificial diet vs. natural prey. The data for natural prey were extracted from Lawson and Morgan (1992).

	Artificial Diet	Natural Prey
Initial number of eggs	179	-
Prepupae (%survival)	128 (71.5%)	(45.5%)
Adults (%survival)	84 (46.9%)	(32.3)
Larval development time	31.8 ± 0.3 days	41.9 ± 0.6 days
Prepupal development time	73.4 ± 2.8 days	56.4 ± 1.0 days
Adult longevity when fed *Ips* (n = 17)	63.4 ± 6.2 days	50.1 ± 7.1 days
Adult longevity when fed CPW (n = 14)	96.9 ± 9.2 days	-
Adult fecundity when fed *Ips* (n = 17)	205.6 ± 34.2 eggs	123.4 ± 8.2 eggs
Adult fecundity when fed CPW (n = 14)	255.0 ± 38.4 eggs	-

Table 2. Summary of survival rates, total fecundity, and R_0 for *T. dubius* using rearing trays and artificial diet. R_0 was calculated by dividing the total eggs laid by the initial number of eggs in each generation.

	Generation			
	I	II	III	IV
Initial eggs	96	384	256	256
Prepupae (%survival)	68 (70.8%)	172 (44.8%)	190 (74.2%)	200 (78.1%)
Adults (%survival)	59 (61.5%)	139 (36.2%)	158 (61.7%)	163 (63.7%)
Total eggs laid	2,876	6,314	10,870	14,818
R_0	30.0	16.4	42.5	57.9

Figure 1. Effect of predation by larval *T. dubius* on the ratio of increase of *Ips grandicollis*, a surrogate prey, as a function of initial *Ips* densities and the number of predator eggs. *P*-values indicate the effect of predator and prey densities on the ratio of increase using a general linear model.



METHODS:

We divide the proposed research into two areas: (1) modifying the diet and rearing techniques to reduce their cost and improve efficiency, (2) field tests of augmentation using clerid eggs on a small scale. We propose conducting parallel experiments with *T. dubius* and *E. lecontei*, in southern pine beetle and mountain pine beetle systems respectively. Although natural enemies have not been deemed important in *D. ponderosae* dynamics (Raffa 1988), this does not preclude their use as biological control agents. We would expect that the addition of clerid eggs to infested trees would increase

D. ponderosae mortality within the tree, as it does with other clerid species (Berryman 1970, Mills 1985, Weslien and Regnander 1992, Weslien 1994, Schroeder and Weslien 1994, Reeve 1997, Reeve and Turchin *in press*).

Diet and Rearing Efficiency

We will compare the performance of *T. dubius* and *E. lecontei* reared on three different diets: (1) the existing artificial diet for clerid larvae, (2) a simple and low-cost artificial diet developed by Cohen (1998), and (3) natural prey such as *Ips* species. In this last case, we will likely just collect clerid prepupae from infested trees in the field, then rear out the adults in the laboratory. We will use Parafilm capsules to dispense the diet, and insect trays lined with ground bark to enclose the larvae, because these methods have proved effective for rearing *T. dubius* (see above). We will then compare the adult longevity and fecundity, and survivorship from egg to adult, across these three dietary regimes using analysis of variance (ANOVA). Both natural prey and cowpea weevils will be used to feed adult clerids, and their performance on these two prey types will be compared. If the Cohen (1998) diet proves inferior, we will modify its ingredients to more closely resemble the existing (and working) artificial diet, and repeat the experiment. The eggs obtained in these studies will be used in field augmentation experiments (see below).

Oregon Freeze Dry/BioLogixs, Inc. has developed a number of proprietary techniques to mass rear insect predators, including cannibalistic species and predatory beetles, and have solved problems with confining and feeding large numbers of immature predators. We will conduct studies to adapt these methods to rearing clerid beetles. We will measure the fecundity and survival of adults produced using these mass rearing techniques, and compare them with adults reared using our existing method (the Bioserv trays), and with adults reared on natural prey collected from the field.

Field Tests of Augmentation

We will test the efficacy of augmentation with clerid eggs in the field, using cages attached to infested trees. We will locate trees newly attacked by *D. frontalis* or *D. ponderosae*, then attach four 0.5 m cages to each tree within the infested area of the bole. We have successfully used this cage methodology in two preceding studies (Reeve *et al*. 1998, Turchin *et al*. 1999). Briefly, it involves girdling a 0.5 m long area of the bole to the sapwood, then drawing the cage into the girdle and sealing it with caulk. We will then stock the cages on a given tree with four different densities of clerid eggs, namely 0, 100, 200, and 400 eggs per cage. The densities will be randomly assigned to each cage within a tree, and eggs obtained from laboratory cultures of *T. dubius* and *E. lecontei* maintained using our existing artificial diet and rearing methods. For each bark beetle species, we will replicate this procedure on 10 different infested trees. The infested trees will be selected from areas in the early phases of outbreak, when native clerid populations are minimal (the situation of where augmentation is most likely to be useful).

As the bark beetle brood within each tree approaches emergence, we will fell the trees, remove the areas covered by the cages, and place these logs individually in rearing enclosures. We will also collect four 100 cm^2 bark samples from each log, and use these

to determine beetle attack and egg density, and the densities of competitors such as bluestain fungi and cerambycids. We will then analyze the resulting data as a randomized block design, with brood survival rate or the ratio of increase as dependent variables, and egg density as the treatment and tree the block effect. Attack density, bluestain, etc. will be used as covariates in this analysis, because these often affect brood survival and the ratio of increase (Raffa and Berryman 1983, Coulson *et al*. 1976, Reeve *et al*. 1998).

If successful, our goal of improving the efficiency (and reducing the cost) of mass rearing clerids will facilitate larger augmentation studies. For example, studies testing augmentation over larger spatial scales (entire trees to infestations) may be possible with the greater number of predators reared with improved techiques. Further, if our field studies outlined here demonstrate that augmentation within trees has a meaningful effect on bark beetle populations, then larger studies may be more reasonably pursued and evaluated.

MEASURE OF SUCCESS:
This project seeks to demonstrate the viability of augmentative releases of predators in order to reduce overall bark beetle caused mortality. We would consider this project to be a success by demonstrating: 1) it is possible to produce large numbers of bark beetle predators on an economically viable basis and 2) that augmentative releases of clerid beetles can impact bark beetle populations in the field.

PRODUCTS:
The proposed project would produce:

- Specific guidelines and techniques that can be used to rear large numbers of predatory forest insects on an economically viable basis.
- A demonstration that augmentative releases of bark beetle predators can reduce the size of bark beetle populations and that these reductions can lead to a decrease in host tree mortality.

PUBLICATIONS:
Anticipated publications in will be submitted to mainstream refereed journals such as *Environmental Entomology* for entomology and *The Western Journal of Applied Forestry* for forestry. Results will also be presented at regional forest entomology conferences such as the annual Western Forest Insect Work Conference and also at meetings of national societies. Once suitable techniques have been developed for large-scale rearing of bark beetle predators, technical manuals could be produced that spell out in detail the specific techniques needed to produce large numbers of bark beetle predators.

TECHNOLOGY TRANSFER:
Experiment Station manuals can be developed with which the technical finding of this study can be disseminated to interested parties. In addition, the establishment of field insectaries could serve as focal points for field trips and demonstrations of the technologies that will be developed by this project.

BENEFIT OF THE PROJECT:
If funded, this project will provide an example of how modern insect rearing techniques can be used to produce beneficial insects to be used in a forested setting. Increasing societal concerns over the use of synthetic pesticides as well as silvicultural manipulation of forested stands increases the need for alternative methods of control for undesirable insect species. The economic viability of clerid production is a primary concern of the investigators, the development of control methods that are environmentally and economically sound would be a huge benefit to forest land managers.

LONG TERM BUDGET:
The amount requested from FHP for the two year project is $62,810 ($31,405 per year of the project). The annual contribution from the non-Forest Service cooperators is

FY-2002 BUDGET REQUEST:

	STDP Funding	Contributed funding
Salary		
Graduate Student*	$11,250	
J. Reeve		$23,500
Seasonal Bio-Aide (CO)	4,000	
R. Nathanson		2,000
Supplies & Equipment		
Lab Equipment (SIU)*	1,000	
Lab Equipment (CO)	1,000	
Supplies (SIU)* (Diet Ingredients, trap & cage materials, etc.)	300	
Supplies (CO)	300	
Travel		
S Illinois Personnel*	3,000	
Add'l 4 Project Participants	9,000	
SIU Overhead (10%)	1,555	
Total	$31,405	$25,500

LITERATURE CITED:

Berryman, A.A. (1970) Evaluation of insect predators of the western pine beetle. *Studies on the Population Dynamics of the Western Pine Beetle, Dendroctonus Brevicomis LeConte (Coleoptera: Scolytidae)* (ed. by R.W. Stark and D.L. Dahlsten), pp. 102-112. University of California, Division of Agricultural Sciences.

Billings, R.F. (1988) Forecasting southern pine beetle infestation trends with pheromone traps. *Integrated Control of Scolytid Bark Beetles* (ed. by T.L. Payne and H. Sarenmaa), pp. 295-306. Virginia Polytechnic Institute and State University, Blacksburg, VA.

Cohen, A.C. & Smith, L.K. (1998) A new concept in artificial diets for *Chrysoperla rufilabris*: the efficacy of solid diets. *Biological Control* , **13,** 49-54.

Coulson, R.N., Mayyasi, A.M., Foltz, J.L., Hain, F.P. & Martin, W.C. (1976) Resource utilization by the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Canadian Entomologist*, **108,** 353-362.

King, E.G. (1993) Augmentation of parasites and predators for suppression of arthropod pests. *Pest Management: Biologically Based Technologies (Proceedings of Beltsville Symposium XVIII, USDA-ARS, Beltsville, MD)* (ed. by R.D. Lumsden and J.L. Vaughn), pp. 90-100. American Chemical Society, Washington, DC.

Lawson, S.A. & Morgan, F.D. (1992) Rearing of two predators, *Thanasimus dubius* and *Temnochila virescens*, for the biological control of *Ips grandicollis* in Australia. *Entomologia experimentalis et applicata*, **65,** 225-233.

Mills, N.J. (1985) Some observations on the role of predation in the natural regulation of *Ips typographus* populations. *Zeitschrift für angewandt Entomologie*, **99,** 209-320.

Nebeker, T.E., Purser, G.C. & Mizell III, R.F. (1980) Collection and maintenance of *Thanasimus dubius* (F.) for biological and behavioral studies. *Journal of the Georgia Entomological Society*, **15,** 406-412.

Raffa, K.F. (1988) The mountain pine beetle in western North America. *Dynamics of Forest Insect Populations: Patterns, Causes, Implications* (ed. by A.A. Berryman), pp. 505-530. Plenum Press, New York, NY.

Raffa, K.F. & Berryman, A.A. (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs*, **53,** 27-49.

Reeve, J.D. Delayed emergence in a bark beetle predator: implications for population dynamics. Agricultural and Forest Entomology . 2000.

Reeve, J.D. (1997) Predation and bark beetle dynamics. *Oecologia*, **112,** 48-54.

Reeve, J.D., Rhodes, D.J. & Turchin, P. (1998) Scramble competition in the southern pine beetle. *Ecological Entomology*, **23,** 433-443.

Reeve, J.D. & Turchin, P. Evidence for predator-prey cycles in a bark beetle. *Population Cycles: Evidence for Trophic Interactions* (ed. by A.A. Berryman), Oxford University Press, New York, NY. *In press*.

Schroeder, L.M. (1999) Prolonged development time of the bark beetle predator *Thanasimus formicarius* (Col.: Cleridae) in relation to its prey species *Tomicus piniperda* (L.) and *Ips typographus* (L.) (Col.: Scolytidae). *Agricultural and Forest Entomology*, **1,** 127-136.

Schroeder, L.M. & Weslien, J. (1994) Interactions between the phloem-feeding species *Tomicus piniperda* (Col.: Scolytidae) and *Acanthocinus aedilis* (Col.: Cerambycidae), and the predator *Thanasimus formicarius* (Col: Cleridae) with special reference to brood production. *Entomophaga*, **39,** 149-157.

Turchin, P., Taylor, A.D. & Reeve, J.D. (1999) Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science*, **285,** 1068-1071.

Van Driesche, R.G. & Bellows, T.S. (1996) *Biological Control*. Chapman & Hall, New York, NY.

Weslien, J. (1994) Interaction within and between species at different densities of the bark beetle *Ips typographus* and its predator *Thanasimus formicarius*. *Entomologia experimentalis et applicata*, **71,** 133-143.

Weslien, J. & Regnander, J. (1992) The influence of natural enemies on brood production in *Ips typographus* (Coleoptera, Scolytidae) with special reference to egg-laying and predation by *Thanasimus formicarius* (L.) (Coleoptera, Cleridae). *Entomophaga*, **37,** 333-342.