Retention of External and Internal Markers by Southern Pine Beetles (Coleoptera: Scolytidae) During Gallery Construction'

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Abstract   If retained, markers used in mark-release-recapture studies of bark beetle dispersal could provide valuable tools in the determination of post-dispersal fate. Retention of the internal marker rubidium (Rb) and of the external marker fluorescent powder during egg gallery construction, oviposition, and feeding were quantified at intervals from *0* to 96 h by allowing marked Southern pine beetles, *Dendroctonus frontalis* Zimmermann, to carry out these activities in untreated host material. Significant differences in Rb concentrations were found between fed and unfed Rb-marked beetles at all intervals after 12 h. Unfed Rb-marked beetles were detectable at all intervals, whereas reliable detection of fed Rb-marked beetles declined with time. Over 90% of fed southern pine beetle marked with fluorescent powder were detectably marked after 96 h, while less than 50% of the Rb-marked beetles were detectable after 72 h. Neither marking technique adversely affected the gallery length or number of eggs produced by marked beetles compared to unmarked beetles allowed to excavate for 96 h. Practical aspects of both techniques are considered.

Key Words   Southern pine beetle, mark-recapture, fluorescent dyes, rubidium

Intraforest movement of bark beetles has received considerable attention because of its integral role in the dynamics of these economically and ecologically important forest denizens (e.g., Burnell 1977, Botterweg 1982, Helland 1983, Anderbrandt 1985, Salom and McLean 1989, Polymenopoulos and Long 1990, Turchin and Thoeny 1993, Turchin and Odendaal 1996). Our knowledge of bark beetle dispersal has expanded, in part, due to advances in techniques for marking these relatively small, highly mobile insects. Both internal and external markers have been successfully used in mark-release-recapture studies of scolytid dispersal. The most common external marking technique uses fluorescent powder (Botterweg 1982, Anderbrandt 1985, Salom and McLean 1989, Turchin and Thoeny 1993, Turchin and Odendaal 1996) applied to the bark of infested host material, from which adult beetles become marked as they emerge. Internal marking with elemental enhancement, where insects become marked as they ingest host material with augmented levels of relatively rare heavy metal elements (e.g., rubidium, cesium, strontium), has become an accepted method of marking phytophagous insects (Berry et al. 1972, reviewed in Akey et al. 1991), including bark beetles (e.g., Thoeny et al. 1992, Turchin and Thoeny 1993, reviewed in Fleischer et al. 1991). Both techniques are relatively non-invasive and

each has advantages depending on the objectives of a particular experiment. A limitation inherent to both of these marking methods is a potential lack of permanency; external markers can be dislodged and elemental markers can be metabolically re-placed (Van Steenwyk 1991).

Most field studies have examined patterns of or factors influencing dispersal, not the ultimate fate of dispersing beetles (e.g., Botterweg 1982, Salom and McLean 1989, Turchin and Thoeny 1993). Information about the fate of post-dispersal beetles is lacking in part due to the intractability of these relatively small insects as they enter the subcortical tissues of prospective hosts. The rate at which beetles lose an external marker such as fluorescent powder through gallery construction (i.e., abraded) or an internal marker such as rubidium (Rb) through oviposition or feeding on untreated host materials (i.e., chemical replacement of Rb by K) is important to quantify so that their post-dispersal success can be determined. The retention of a marker by bark beetles that are constructing ovipositional galleries is essential for studying the ability of dispersing individuals to colonize a new host and reproduce. Thoeny et al. (1992) reported no significant loss of fluorescent powder or Rb in southern pine beetles, *Dendroctonus frontalis* Zimmermann, that had been marked, released, and recap-tured after flights of relatively short duration (and before they fed on untreated host material). However, when Rb-enhanced southern pine beetles were allowed to feed on untreated host material for 48 h in a laboratory study, less than one-fourth (23.8%) retained enough Rb for them to be considered marked (Thoeny et al. 1992). While effects of fluorescent powder on survival (longevity) and flight behavior have been examined (Cook and Hain 1992, McMullen et al. 1988), to our knowledge, no other attempts have been made to quantify the loss of experimental markers as a result of gallery construction in untreated host material. The purpose of this study was to quantify the loss of the internal marker (Rb) when southern pine beetles were allowed to feed on untreated host material over time and also to determine if the external marker (fluorescent powder) is retained during gallery construction. A comparison between the two techniques is presented.

Materials and Methods

Bolt preparation. For both the rubidium and fluorescent powder study, pine bolts were prepared similarly. Loblolly pines, *Pinus taeda* L., approximately 25 cm in di-ameter at breast height growing on the Catahoula Ranger District, Kisatchie National Forest, LA, were felled and the boles cut into 60-cm length bolts. Bolts were obtained on 14 August 1993 for the rubidium study, on 15 March 1994 for the fluorescent powder study, and on 5 May 1995 for the combined study. Immediately after cutting, bolts were transported to our laboratory at the Alexandria Forestry Center, Pineville, LA, where bolts were coated on each end with hot paraffin (S & A Wax, Strohmeyer & Arpe Co., Milburn, NJ) to reduce loss of moisture. Test arenas were established the following day by partitioning each bolt into 10 x 10 cm (for the rubidium and powder studies) or 15 x 15 cm (for the combined study) squares with longitudinal and latitu-dinal cuts using a hand-held circular saw. Larger test areas were used in the com-bined study to accommodate greater gallery lengths anticipated at 96 h. Cuts ex-tended through the phloem to the sapwood to enhance our ability to find and extract feeding beetles. All cuts were coated with paraffin to reduce desiccation of phloem.

A pair (female and male) of southern pine beetles was randomly assigned and introduced into the center of each square by making a round hole through the bark to

the sapwood with a cork borer (no. = 30.8 mm diam). Beetles were placed in "0" size gelatin capsules (Frontier Cooperative Herbs, Norway, IA), and the capsule was inserted into the hole. The capsule was secured with a sewing pin and care was taken not to insert the capsule too far into the hole; if the capsule is placed against the sapwood, beetles are unable to leave the capsule to enter the phloem tissue. Beetles were later extracted from host material by carefully removing thin layers of the outer bark with a knife. Upon extraction of feeding beetles, gallery lengths (mm) were measured using a map measurer. Gallery lengths were attributed to pairs because both beetles in a pair contribute to gallery construction. In the fluorescent powder and combined experiments, the number of egg niches in the gallery was recorded.

Rubidium study. The Rb content of host trees was augmented using a stem-well infusion (approximately 50 g per tree) technique modified from Thoeny et al. (1992). These trees were then baited with southern pine beetle aggregation pheromone to promote attack (Turchin and Thoeny 1993). When successfully attacked trees contained beetles in the pupal/callow adult stage, infested bark was removed and placed in rearing cans (Thatcher and Pickard 1964). Newly-emerged southern pine beetles were collected daily from rearing cans for use in the study. After collection, beetles were refrigerated long enough to slow activity and allow accurate sexing with a dissecting scope. Forty beetles of each sex were used as control and 40 of each sex were used as "test" beetles for a total of 160 beetles.

Treatments consisted of: (1) fed-marked beetles that were placed on bolts (see above) and allowed to excavate galleries in untreated host material for one of four time intervals (4, 12, 24, 48 h) and (2) unfed-marked beetles that were held in the laboratory for the same time intervals in covered 125-ml plastic (polypropylene) containers filled with tissue paper to reduce contact among individuals. In this initial rubidium study, 48 h was selected as the maximum time because Thoeny et al. (1992) determined that over 75% of marked beetles feeding on an unaugmented host lost their marker by this time. At each time interval, 10 southern pine beetle pairs were selected at random for extraction; 10 unfed pairs were also selected at random as controls. All beetles were sexed, placed individually into gelatin capsules, and frozen for future analysis of Rb content.

In preparation for analysis of Rb content, beetles (fed and unfed) were oven dried at 70" C for 24 h and weighed. Beetles were then individually placed in 13 x 100 mm disposable flint glass culture tubes (Fisher Chemical, Pittsburgh, PA), into which 0.2 ml reagent grade nitric acid (Baker Chemical, Phillipsburg, NJ) was added. Beetles were allowed to digest in the nitric acid overnight (-16 h) at room temperature (-24" C). The next day, culture tubes containing the partially digested beetles were placed in a boiling water bath for 20 min to complete digestion. The nitric acid-beetle solution was then poured into 14-ml graduated polypropylene centrifuges tubes (Falcon Labware, Oxnard, CA) that had been acid-washed (soaked overnight in 3% hydrochloric acid solution to remove potential Rb contamination). Distilled deionized water was then added to the dilute nitric acid-beetle solution until the final volume was 2.0 ml. Samples were analyzed for Rb content on a Perkin-Elmer 2100 atomic absorption spectrophotometer (AAS), using a HGA 700 graphite furnace (Perkin-Elmer, Norwalk, CT). Operating conditions followed Hayes and Claussen (1988).

Fluorescent powder study. Bolts infested with southern pine beetles were coated (approximately 1.1 kg per tree) with fluorescent powder (Day-Glo Color Corporation, Cleveland, OH) using a garden duster (Dustin Mizer, R. J. Winmore, Inc., Sioux Falls, SD) and then placed in rearing cans (Thatcher and Pickard 1964).

Beetles were self-marked with fluorescent powder when they emerged, crawled on bolts, and expanded their wings in preparation for flight. These beetles were collected and examined under a black light to ensure that their exoskeleton had been marked. A beetle was considered marked when the fluorescent powder could be easily detected (without the aid of a dissecting scope) using a black light. Beetles were sexed as described above. Again, 40 pairs (IO per interval) were used as controls and 40 pairs (10 per interval) as test beetles. Longer time intervals (24 h per interval) than in the rubidium study were used because our preliminary findings suggested that dust particles could be detected for periods in excess of 48 h.

Treatments consisted of: (1) fed-powder-marked beetles that were placed on bolts and allowed to excavate galleries in untreated host material for one of four time intervals (24, 48, 72, 96 h), and (2) unfed-powder-marked beetles that were held for the same time interval in covered containers as described above. At each time interval, 10 southern pine beetle pairs were selected at random for extraction; 10 unfed pairs also were selected at random as controls. Fed and unfed beetles were sexed and examined for fluorescent powder using a black light and dissecting scope.

Combined study. To compare these marking techniques under comparable conditions, a concomitant comparison of Rb- and powder-marked beetles was conducted. Rb- and powder-marked beetles were obtained as described above in the separate studies. Beetles were sexed and pairs introduced into bolts or held in plastic containers as described above. Treatments consisted of: (la) fed-Rb-marked beetles that were placed on untreated bolts and allowed to excavate galleries for one of three time intervals (48, 72, and 96 h), (1 b) fed-powder-marked beetles and (lc) fed-unmarked beetles that were placed on untreated bolts and allowed to excavate for 96 h; (2a) unfed-Rb-marked beetles that were held in plastic containers for the same intervals as in (la). At each time interval, 10 pairs were selected at random for extraction and 10 unfed pairs also selected at random as controls. Additionally, 10 pairs of Rb-marked and 10 pairs of unmarked beetles (obtained from a nearby untreated tree) were frozen immediately upon emergence (0 h) to serve as controls and provide background data on naturally-occurring levels of Rb. Depending on the type of marking, fed and unfed beetles were sexed, placed in gelatin capsules, and then frozen for further analysis of Rb content or examined for powder using dissecting scope under a black (UV) light.

Data analysis. Correlation was used to analyze the relationship between time intervals and gallery length, and the relationship between Rb marker retention and gallery length was analyzed by linear regression (SAS Institute 1988). For the rubidium and combined studies, t-tests were used to compare, by interval, dry weights and Rb concentrations between fed and unfed beetles. Concentration of Rb (ppb) was converted to mg/kg [(ppb + dilution factor)/dry wt] to control for weight differences among individuals and between treatments (i.e., fed and unfed). For the combined study, t-test was used to compare gallery length and egg numbers between marked (with Rb or powder) and unmarked beetles removed at 96 h.

Results and Discussion

Rubidium study. Of the 80 Rb-marked beetles that were introduced into bolts, 46 (23 males, 23 females) were recovered and included in analyses. Thirteen pairs of beetles did not enter the host (i.e., produced no gallery), three additional pairs had only one individual in the gallery upon extraction, and one female was destroyed

during extraction; these beetles were not included in analyses. Gallery length varied from 3.0 to 63.5 mm and was highly dependent on the amount of time spent in the bolt ($R^2 = 0.90$; $P < 0.0001$) (Table 1, Fig. 1).

Comparison of dry weights between fed and unfed Rb-marked beetles showed a significant difference after 48 h (t = -2.24; df = 12.5; P = 0.0445). Because of this difference, weight was accounted for when comparing Rb concentration between fed and unfed beetles [i.e., Rb concentration was expressed as Rb (mg)/dry weight (kg)]. Significant differences in Rb concentrations between fed and unfed beetles were found at 24 h (t = 2.99; df = 26.1; P = 0.0049) and 48 h (t = 2.59; df = 26.8; P = 0.0122) (Table 1). No linear relationship was found between marker level (mg/kg Rb) and gallery length ($R^2 = 0.07$; P = 0.08). Despite these differences, all beetles were detectably marked, i.e., Rb concentrations ($\geqslant 4.06$ mg/kg) were consistently above the background levels of local unmarked beetles (see Table 4 and corresponding discussion of marker detection below). In their study, Thoeny et al. (1992) also found a decline in Rb concentration in fed beetles after 48 h; with a detection limit of 30 ppb, Rb levels in <24% of the fed beetles were considered detectable compared with 97% before feeding. In our study, the range of Rb concentrations in the marked group is considerably lower than those repot-ted by Thoeny et al. (1992). The difference is likely to be the result of a difference in uptake by the Rb-treated host; uptake by the phloem can be affected by a number of biological and physical factors.

Fluorescent powder study. Of the 80 powder-marked beetles that were intro-duced into bolts, 47 were recovered (24 males, 23 females) after having initiated gallery construction. Twenty-two beetles were found in the gelatin capsules and 11 others escaped; again, these beetles were not included in further analyses. Recov-ered beetles constructed galleries from 6 to 78 mm in length, again depending on the amount of time they were in the bolt ($R^2 = 0.39$; $P < 0.0001$) (Table 2, Fig. 2). The relationship is not as strong as that found in the rubidium study which may be due to a number of factors such as differences in ambient temperatures and in host material. For each period examined, >90% of the southern pine beetles retained their marker (Table 2, Fig. 2). The fluorescent powder that remained on beetles was most notice-able on the wings and underneath the elytra-areas which are protected by the closed elytra during gallery construction. Heavily-marked specimens were those on which the fluorescent powder was evident on the outer surface of the beetle and

Table 1. Between group comparison of Rb loss over time in **mg/kg between fed and unfed southern pine beetles.**

Hour	No. Unfed	Mean ± SEM mg/kg Rb	No. Fed	Mean ± SEM mg/kg Rb	%Mark Retention	Mean ± SEM gallery length (mm)
4	20	10.00 ± 0.76	16	12.18 ± 1.68	100	4.75 ± 0.64
12	20	12.36 ± 1.37	13	10.48 ± 1.17	100	7.36 ± 1.49
24*	20	15.33 ± 1.39	11	9.81 ± 0.68	100	24.33 ± 2.08
48*	20	15.04 ± 1.83	6	8.32 ± 1.20	100	54.33 ± 4.64

*Significant differences in Rb concentration was found between fed and unfed beetles at 24 and 48 h by t-test.
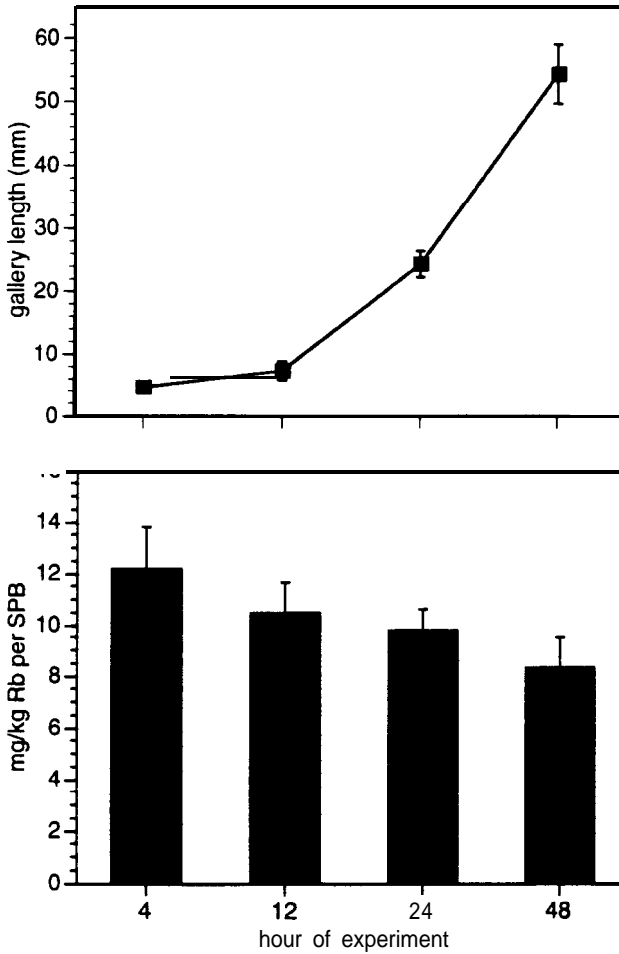
Fig. 1. Mean gallery length (top graph) and Rb concentration (bottom graph) of south-
ern pine beetles allowed to feed on untreated host material for specified
intervals (4, 12, 24, 48 h).

detectable without manipulation under black light; lightly marked specimens were
those which required manipulation under black light to detect the residual powder.
Only three out of the 47 beetles recovered had no fluorescent powder marking. These
beetles had no powder on the wings or underneath the elytra, suggesting that they
may have fallen off the dusted bolt into the collection jar before expanding their wings;
wing expansion on the dusted surface is necessary to mark areas otherwise protected
by elytra. Of the 47 beetles recovered, only 7 beetles retained their marking on their
exoskeleton after extraction from constructed galleries. Egg niches were first ob-
served in galleries at 48 h interval (Table 2), and in all cases were associated with
galleries of ≥ 30 mm.

**Table 2. Gallery construction, egg niche presence/absence and marker reten-
tion by southern pine beetles marked with fluorescent powder.**

Hour	No. Marked	With Niches	No. Unmarked	% Mark Retention	Mean ± SEM (mm) gallery length
24	9	0	1	90	17.10 ± 3.99
48	12	2	1	92	26.29 ± 4.93
72	12	5	0	100	43.83 ± 6.83
96	9	9	0	100	48.00 ± 10.02

Combined study. Of the 60 Rb-marked beetles introduced into bolts, 42 (21 males, 21 females) were recovered. Eleven beetles were found in the gelatin capsule and seven others escaped; these beetles were not included in further analysis. Only when both the male and female were present in the gallery was length and number of eggs included. Gallery length ranged between 9 to 140 mm, and was dependent on the time (r = 0.572, P = 0.0164). Differences in gallery length among studies (e.g., mean gallery length at 48 h = 54, 26, and 42 mm, respectively, Tables l-3) may be due to a number of factors, the most important of which would be differences in host material. Egg numbers ranged from 2 to 21 and was highly correlated with gallery length (r = 0.8665, P= 0.0001), but not with time (r = 0.449, P = 0.0688). Comparison of the fed and unfed beetles again showed a significant difference in weight at all intervals; hence weight was accounted for as described above. Significant differences were found in Rb concentration [Rb (mg)/dry wg (kg)] at all intervals. Rb concentration in fed beetles declined with time (Table 3, Fig. 3), but no linear relationship was found between marker level and gallery length or egg number.

Several methods have been used to establish elemental marker detection levels based on background (naturally occurring) levels of unmarked specimens (see Akey et al. 1991). In one method, marked specimens are those which have Rb concentration (ppb or in our case mg/kg Rb) that exceeds the high-range value of Rb concentrations of a comparable sample of unmarked specimens (e.g., Hayes and Claussen 1988). In the most conservative method, which assumes a normal distribution, the marker detection level is set at three standard deviation units above the mean of a sample of unmarked specimens (Stimmann 1974, Hayes and Claussen 1988). Hereafter, these benchmarks are referred to as the range and Stimmann value (Hayes and Claussen 1988). Typically, the unmarked samples are newly-emerged individuals. We assessed background levels in both newly-emerged beetles (0 h) and in unmarked beetles allowed to excavate/feed for 96 h for comparison. Significantly higher Rb concentrations were found in the unmarked beetles which fed for 96 h than in the unfed (0 h) beetles (t = 8.8304, df = 28, P < 0.01), suggesting that beetles may be acquiring Rb through feeding even on untreated host material. Using the unfed beetles, >75% (79 or 76% exceeded the range or Stimmann value, respectively) of the beetles removed after 48 h retained sufficient Rb to be considered marked. Whereas, using the more appropriate fed sample to set the marker level for beetles retrieved after 48 h of excavation, <50% (41 or 14% exceeded the range or Stimmann value, respectively) were detectably marked (Table 4).
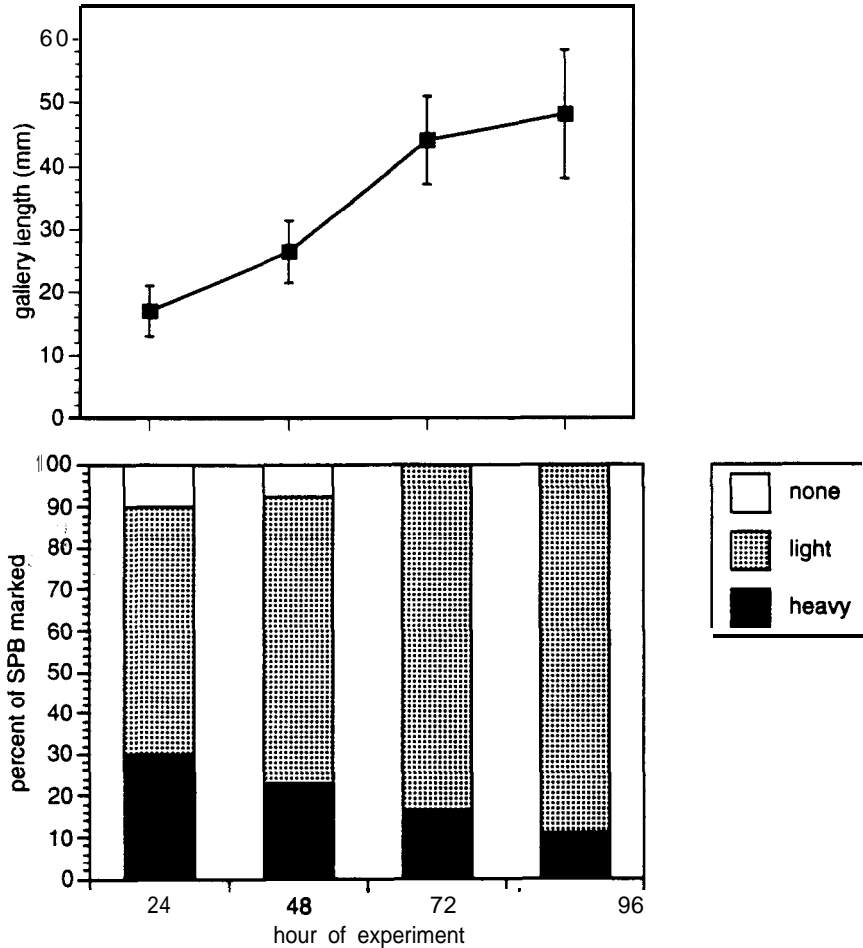
Fig. 2. Mean gallery length (top graph) and fluorescent powder detection (bottom graph) of southern pine beetles allowed to feed on untreated host material for specified intervals (24, 48, 72, 96 h). None = no fluorescent powder visible with blacklight; light = no powder on exoskeleton but powder visible under elytra; heavy = powder visible on exoskeleton.

Of the 20 fluorescent powder-marked beetles introduced into bolts, 16 (8 males, 8 females) were recovered at 96 h; four beetles were found in the gelatin capsule and were not included in further analysis. All recovered beetles were at least lightly (i.e., retained some dust under the elytra) marked. Gallery lengths ranged from 65 to 130 mm, and the number of eggs ranged 4 to 17.

Comparisons of gallery length and of egg number among Rb- and powder-marked, and unmarked beetles recovered at 96 h showed little differences (Table 5), suggesting that neither of the marking techniques has a detrimental effect on these aspects

Table 3. Between group comparison of Rb loss, gallery length and egg number (mean ± SEM) over time in unfed and fed southern pine beetles.

Hour	No. Unfed	Mean ± SEM mg/kg Fib	No. Fed	Mean ± SEM mg/kg Rb	Mean ± SEM gallery length (mm)	Mean ± SEM egg no.
0	20	0.417 ± 0.06		1.559 ± 0.27		
0	20	33.349 ± 8.76				
48	20	30.883 ± 7.61	8	5.881 ± 2.17	41.5 ± 10.88	1.5 ± 0.830
72	20	58.388 ± 16.38	12	3.057 ± 6.59	76.0 ± 20.38	10.1 ± 1.716
96	20	57.497 ± 14.79	14	2.667 ± 6.43	104.0 ± ii.63	10.9 ± 2.460

of the beetle's reproductive efforts. Cook and Hain (1992) found that powder-marked beetles did not live as long as unmarked beetles when held in unprovisioned containers. Although our experiments were not designed to directly measure differences in survivorship or longevity, we found no difference in survivorship in our studies between either type of marked beetle and unmarked beetles.

In conclusion, both Rb and fluorescent powder are adequate for marking southern pine beetles and are retained during initial gallery construction (24 to 48 h); however, use of fluorescent powder is advisable for studies where post-dispersal fate ≥72 h is to be assessed. In short duration studies, the technique which most adequately meets the objectives of a particular study should be selected. Rb works well as a marker for southern pine beetles because it is an internal marker and neither the treated host nor the beetle marker is affected by weather. Rb-enhancement is lost in feeding southern pine beetles; however, depending on the background level and initial concentration, the marker may be detectable by graphite furnace up to 48 h. Loss of Rb with oviposition should be explored as well as the possible resultant marking of eggs (see Hayes 1991). The major drawback to using Rb as a marking technique in short duration studies is its cost-it is expensive to apply and to detect. When applying 50 g per tree, a rate we commonly use, the cost of Rb alone is over $12.00 per tree. Because the selection of individual host trees by beetles, the timing of beetle attack, and the success of attack (i.e., whether or not brood are produced) are not predictable, a large number of trees must be treated to ensure the availability of a sufficient number of marked insects for recapture experiments to succeed under natural conditions. If it does not interfere with other aspects of the study, the probability of successful infestation can be greatly increased with the use of attractant baits. Once samples are taken, an AAS and graphite furnace are required for analysis and specially trained personnel are needed to prepare the samples and operate the AAS. Analytical costs vary widely, but we estimate the cost of consumables (excluding overhead and labor) to be at least $2.00 per beetle.

Fluorescent powder is more expensive (about $20.00 per tree) and labor-intensive to apply; but is easy to detect, requiring no specialized equipment for application and only a black light and dissecting scope for detection. Additionally, personnel require little or no specialized training to employ this marking technique. The cost of detection is, therefore, minimal. A major drawback to the use of fluorescent powder as a
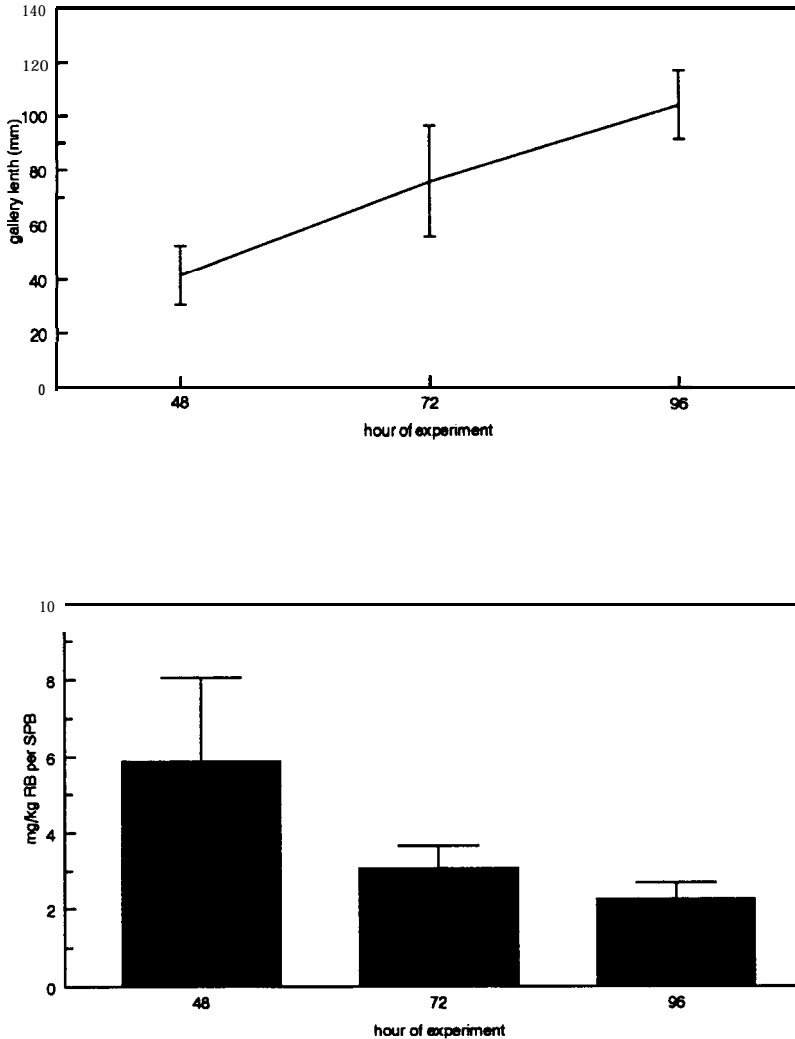
Fig. 3. Mean gallery length (top graph) and Fib concentration (bottom graph) of south-
      ern pine beetles allowed to feed on untreated host material for specified
      intervals (48, 72, 96 h).

marking technique is that, if left unprotected, rain washes it off. However, if protected
from rain, fluorescent powder can stay on the outer bark for several months. Because
there was no apparent decline in the ability to detect fluorescent marking after 4 d (96
h), we feel it is likely that beetles would retain their marker even longer due to the
location of the marking on the wings, which are protected from abrasion and resin by
the elytra. This could be very useful in mark-recapture experiments designed to
investigate beetle success (i.e., egg production) following dispersal episodes. We

Table 4. Percentage of detectable Fib-marked beetles after 48, 72, and 96 h of feeding, based the range or Stimmann value (mean + 3*SD) of un-marked beetles at emergence (0 h) and after feeding (96 h); see text for detailed explanation.

Hour	Marked	No.	Range Rb (mg/kg)	Stimmann value (mg/kg)	% exceeding 0 hr range and (Stimmann value)		% exceeding 96 hr range and (Stimmann value)	
0	no	20	0.02-0.98	1.197				
96	no	10	0.78-3.27	3.917				
48	yes	8	0.04-I 7.72		75.0	(75.0)	62.5	(50.0)
72	yes	12	0.45-7.21		83.3	(75.0)	50.0	(33.0)
96	yes	14	0.47-6.95		78.6	(78.6)	21 .o	(7.0)

Table 5. Summary of performance (mean gallery length and egg no. ± SEM) and detectability of marker after 96 h in unmarked host material of control, powder-, and Fib-marked beetles.

Marker Type	Hours	No.	mg/kg Rb	% marked	mean ± SEM (mm) gallery length	mean ± SEM egg no.
control	0	20	0.417 ± 0.06			
control	96	10	1.559 ± 0.27	0	78.4 ± 8.47	8.0 ± 1.90
Rb	96	14	2.267 ± 0.59	66	104.0 ± 11.63	10.9 ± 2.46
powder	96	16		100	94.9 ± 7.94	9.5 ± 1.69

have successfully employed various tenting techniques to protect the boles of standing trees from rain (e.g., Thoeny et al. 1992, Turchin and Thoeny 1993); however, because it is not reasonably possible to protect boles from all water, weather can still impact the percent of emerging southern pine beetles that are marked.

Acknowledgments

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