

Mountain Pine Beetle Offspring Characteristics Associated with Females Producing First and Second Broods, Male Presence, and Egg Gallery Length

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ABSTRACT Three groups of mountain pine beetles, *Dendroctonus ponderosae* Hopkins, were placed in fresh lodgepole pine, *Pinus contorta* Douglas var. *latifolia* Engelmann, billets and allowed to construct egg galleries. Group I consisted of reemerged females that had previously made egg galleries in the field; group II consisted of new females allowed to mate, then males were removed; and group III consisted of new females with males present throughout gallery construction. Offspring from these rearings were compared by gallery section for brood production, rate of emergence, size, and sex ratio. Reemerged females were as successful in establishing galleries as new females but produced significantly fewer beetles than new females with males present. Offspring of new females emerged at a faster rate than those of reemerged females. Offspring from reemerged females were larger than those of group II females, but not those from group III females. Sex ratios were not significantly different among offspring of the three groups.

KEY WORDS Insecta, *Dendroctonus ponderosae*, *Pinus contorta*, phenology

AS A FIRST STEP in understanding recruitment and reproductive effort of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, a laboratory study was conducted to assess the effects of females producing first and second broods and male presence on egg gallery length and characteristics of offspring. Reemerging female bark beetles (those making a second gallery) affect population dynamics of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, because of the large number of parents constructing a second gallery (Wagner et al. 1981). Little attention has been given to reemerging mountain pine beetles because second flights are infrequent. However, these flights do occur when seasonal temperatures are warmer than average (Reid 1962a). When fall temperatures are unseasonably warm, mountain pine beetles may reemerge and make a second egg gallery; or when winter temperatures are moderate, surviving mountain pine beetles may emerge in the spring and infest live trees. Such phenomena may become more widespread if global temperatures increase.

Egg gallery length of mountain pine beetles generally ranges from 10 to 122 cm in natural infestations and is strongly influenced by the presence of unused phloem and temperature (Amman & Cole 1983). Under laboratory conditions where fresh phloem was provided for oviposition, some females constructed galleries >127 cm long (Reid 1962b). However, these are extremes; average egg gallery length is usually 15-30 cm (Amman & Cole 1983).

The role of male mountain pine beetles following mating is usually limited to moving boring frass (which the female dislodges) to the bottom of the

gallery (Reid 1958). This enables the female to make an egg gallery faster than in the absence of the male (Rasmussen 1974).

Mountain pine beetle sex ratios range from an average of about two females per male (Reid 1958) to almost total females (Cole et al. 1976). Any factor that stresses the population reduces male survival. Some examples observed in laboratory studies are crowding, thin phloem (Amman & Cole 1983), and length of cold storage (Watson 1971, Safranyik 1976). In field studies, excessive drying or a combination of drying and thin phloem (Cole et al. 1976) were factors. These differences led to speculation about the effect male presence (mating several times during gallery construction) or male absence (mating only once and abandoning the gallery) would have on the sex ratio of the resulting offspring. The objective of our study was to assess the effects of females producing first and second broods; male presence; and gallery length on number, size, sex ratio, and rate of emergence of offspring.

Materials and Methods

To obtain beetles, logs were cut from a naturally infested lodgepole pine 30 cm diameter at breast height (dbh) in an area with a high population of beetles and transported to our laboratory in Ogden. The ends were coated with hot paraffin to prevent rapid drying. A portion of the logs was stored for 6 wk at 2°C until larvae in the remaining logs stored at room temperature (22-27°C) had completed development and started to emerge. At that time,

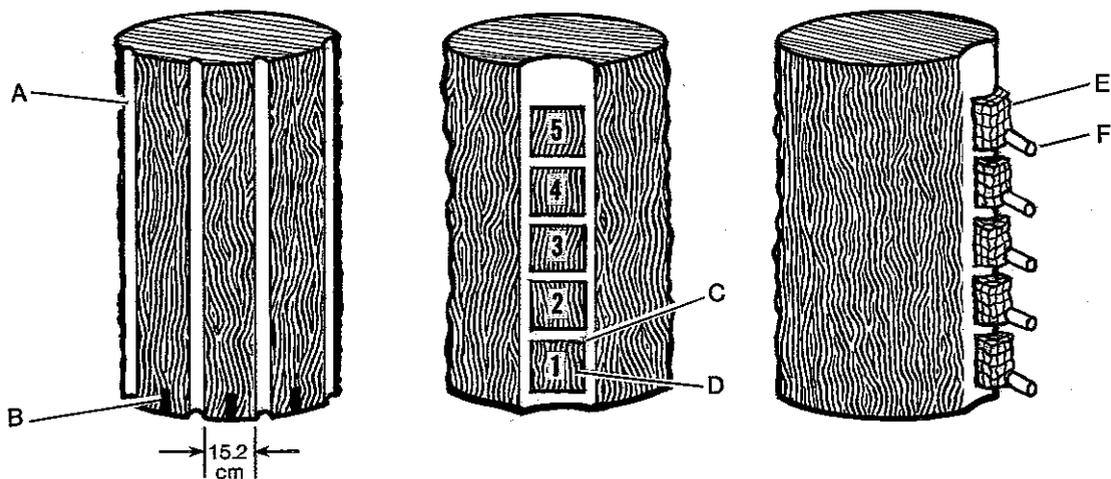


Fig. 1. Illustration of bark strips, sections, and cages with tubes. A, bark removed from 2.5-cm-wide strip between 15.2-cm-wide bark strips; B, beetles placed in bark at base of each strip; C, 2.5-cm-wide strip of bark removed between bark sections; D, 15.2- by 15.2-cm bark section; E, plastic mesh cage over each section; F, collecting tube to capture emerging beetles.

bark was peeled from the logs stored at 2°C, and females were removed for introduction into fresh green logs. Green logs were cut from a single lodgepole pine 41 cm dbh having phloem thickness ranging between 2.3 and 3.0 mm. Three groups of beetles were then placed simultaneously in fresh green lodgepole pine logs in a laboratory study. Group I consisted of females that had made egg galleries in the field. Group II consisted of new females and males (progeny of group I females) reared from logs brought in from the field. Pairs of these group II adults were introduced into fresh lodgepole pine logs and, 4 d later, a flap of bark over each pair was lifted and the male was removed. The bark then was stapled to the log so females would not leave after being disturbed. Group III consisted of new beetles from the same population as group II beetles. These beetles were treated similarly to group II beetles, except males were left with the females throughout egg gallery construction, and the bark covering each pair was not lifted on day 4. Previous studies show females continued to construct gallery and oviposit normally following lifting of the bark, provided bark is subsequently stapled tightly to the wood to prevent rapid drying and escape of females (Logan & Amman 1986).

Green logs 99 cm long were prepared for beetle introduction by subdividing the circumference into 15.2-cm-wide areas of bark with 2.5-cm-wide strips between adjacent areas. Bark was removed from the strips the length of the logs to create a barrier between the 15.2-cm-wide areas (Fig. 1). Exposed wood (where the bark was removed) and the ends of the logs were coated with hot paraffin to prevent rapid drying.

Logs were assigned randomly to each group of beetles. Because of differences in log diameters, the number of 15.2-cm-wide areas infested by each

group also varied as follows: group I, 28; group II, 27; and group III, 23. Beetles were introduced into the center at the base of each bark area (Fig. 1). The logs were kept in a vertical position at temperatures of 22–27°C throughout the experiment.

To determine if offspring characteristics change as galleries lengthen, each strip of bark was subdivided into 15.2-cm sections. Because beetles bore ≈ 15.2 cm or more of egg gallery in a 10-d period (Amman 1972), a 2.5-cm-wide strip of bark was removed horizontally across the 15.2-cm-wide area at ≈ 2 -wk intervals, leaving a bark area of 232 cm² with a single vertical egg gallery in the center. This process was repeated until five of these 232-cm² areas, each progressively higher on the log, were delineated for each boring female (Fig. 1). Each time bare wood was exposed, it was coated with hot paraffin to prevent rapid drying. A plastic screen cage (32 by 32 mesh/2.5 cm²) then was stapled over each 232-cm² area. A plastic tube was attached to the bottom of the cage to catch emerging beetles (Fig. 1).

Beetles were collected daily from the tubes. The length of each beetle (front of the head to the tip of the elytra) was measured with an ocular micrometer in a microscope. Beetle sex was determined using characteristics of the seventh abdominal tergum (Lyon 1958). Bark was peeled from each 232-cm² area after emergence stopped to assure that all beetles had emerged.

Analysis of variance (general linear models procedure [SAS Institute 1987]), χ^2 , and linear regression techniques were used in analyzing data. Tukey's test was used to determine differences among treatment means, and contrast sums of squares (not orthogonal) were used to determine differences in the rate of emergence among groups. Rate of emergence is the percentage of offspring emerging in a

Table 1. Progeny characteristics of reemerged and new female mountain pine beetles associated with egg gallery length

Female group ^a and progeny characteristics	Egg gallery section ^b											
	1		2		3		4		5		All sections	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Group I												
Successful galleries (no.)	25	—	24	—	22	—	16	—	7	—	18.8	—
Progeny production/232 cm ²	16.2	9.8	13.1	9.3	9.9	8.4	7.4	6.2	5.0	5.0	11.7	9.1
Female length, mm	5.19	0.18	5.26	0.18	5.30	0.17	5.33	0.16	5.28	0.19	5.26	0.18
Female progeny, %	73.2	17.6	65.5	24.7	67.6	24.2	59.3	24.5	60.7	34.6	66.8	23.6
50% progeny emergence, d	11.3	1.2	16.3	1.2	25.3	1.2	37.3	1.2	42.0	1.7	26.5	12.2
Group II												
Successful galleries (no.)	21	—	17	—	16	—	13	—	10	—	15.4	—
Progeny production/232 cm ²	12.8	8.6	14.2	9.6	16.0	6.9	10.5	6.4	4.6	4.1	12.4	8.3
Female length, mm	5.07	0.26	5.22	0.22	5.24	0.22	5.24	0.27	5.20	0.25	5.18	0.25
Female progeny, %	75.0	25.6	71.4	20.7	69.7	26.3	65.6	29.5	57.4	38.1	69.5	26.8
50% progeny emergence, d	8.3	0.6	9.3	0.6	15.0	0	23.3	2.3	37.3	1.6	18.7	11.2
Group III												
Successful galleries (no.)	16	—	16	—	13	—	12	—	6	—	12.6	—
Progeny production/232 cm ²	16.7	8.7	19.4	8.8	15.8	9.7	6.7	4.7	10.5	11.0	15.0	9.5
Female length, mm	5.14	0.15	5.24	0.15	5.29	0.16	5.33	0.24	5.13	0.15	5.23	0.18
Female progeny, %	68.3	24.5	61.0	18.7	61.9	21.1	71.9	22.3	62.5	12.7	63.7	20.7
50% progeny emergence, d	8.0	0	8.3	0.6	15.0	0	23.3	5.1	24.0	0	15.7	7.5

^a Group I, reemerged females that previously made an egg gallery; group II, new females with males removed; group III, new females with males present.

^b Each egg gallery section was 15.2 cm long.

given number of days starting with the first offspring emergence from any of the gallery sections. In addition, nonlinear curves were fit (NLIN [SAS Institute 1987]) to the data using a multivariate secant method; this approach is also called the method of false position, or DUD (doesn't use derivatives) (Ralston & Jennrich 1978).

A nonlinear logistic function was fit to emergence data for each of the defined groups by sex and by egg gallery section, which resulted in 45 equations of the form:

$$\hat{y} = \frac{\text{gamma}}{1 + \text{alpha} e^{\text{beta}(x)}}$$

where \hat{y} is percentage beetle emergence; x is days; and alpha, beta, and gamma are equation parameters.

Dummy variables were used to permit testing for differences in alpha, beta, and gamma from group to group (Draper & Smith 1966). The asymptote is equal to gamma. This led to constraints being placed on gamma to assure that the fitted asymptote did not exceed 100%. In most instances, this model performed adequately; however, in three equations, a more realistic model may have been developed. To maintain continuity throughout, we decided to use the same model for all 45 equations.

Results and Discussion

Egg Gallery Success and Length. The percentages of females constructing a productive egg gallery (egg gallery at least 15 cm long and producing beetle progeny) were as follows: group I, 89.3; group

II, 77.8; and group III, 69.6%. However, these differences were not significant ($F = 1.40$, $df = 2$, $P = 0.28$). Failures usually were associated with females that started a gallery, then died for unknown reasons.

Gallery lengths varied from one to five sections (each 15.2 cm long). The percentages of beetles that made one to five sections of gallery differed significantly among groups ($\chi^2 = 20.8$, $df = 2$, $P = 0.001$). For example, the percentages of beetles that made five sections of gallery were: group I, 28.0; group II, 47.6; and group III, 37.5%. The higher percentages for groups II and III than group I suggest new females are more capable of constructing long galleries than reemerged females.

Number of Offspring. Number of offspring produced was significantly different among groups ($\chi^2 = 26.1$, $df = 2$, $P = 0.001$). Group III females (males present throughout) averaged 15.0/232-cm² area compared with averages of 11.7 and 12.4 for groups I and II, respectively. A significant difference in number of offspring by gallery section also was detected ($\chi^2 = 69.2$, $df = 8$, $P = 0.001$). Linear regression showed a significant decline in offspring with increased gallery length in all groups: group I $r^2 = 0.16$; $df = 1$, 95; $P = 0.005$; $\hat{y} = 19.33 - 3.01(x)$; group II $r^2 = 0.13$; $df = 1$, 67; $P = 0.005$; $\hat{y} = 18.86 - 2.20(x)$; group III $r^2 = 0.16$, $df = 1$, 57; $P = 0.005$; $\hat{y} = 23.03 - 2.77(x)$ (Table 1). The downward trend in production agrees with studies that show fewer eggs are laid per unit of egg gallery as gallery length increases (McCabe 1971, Amman 1972). Groups II and III tended to maintain production, as indicated by offspring emergence,

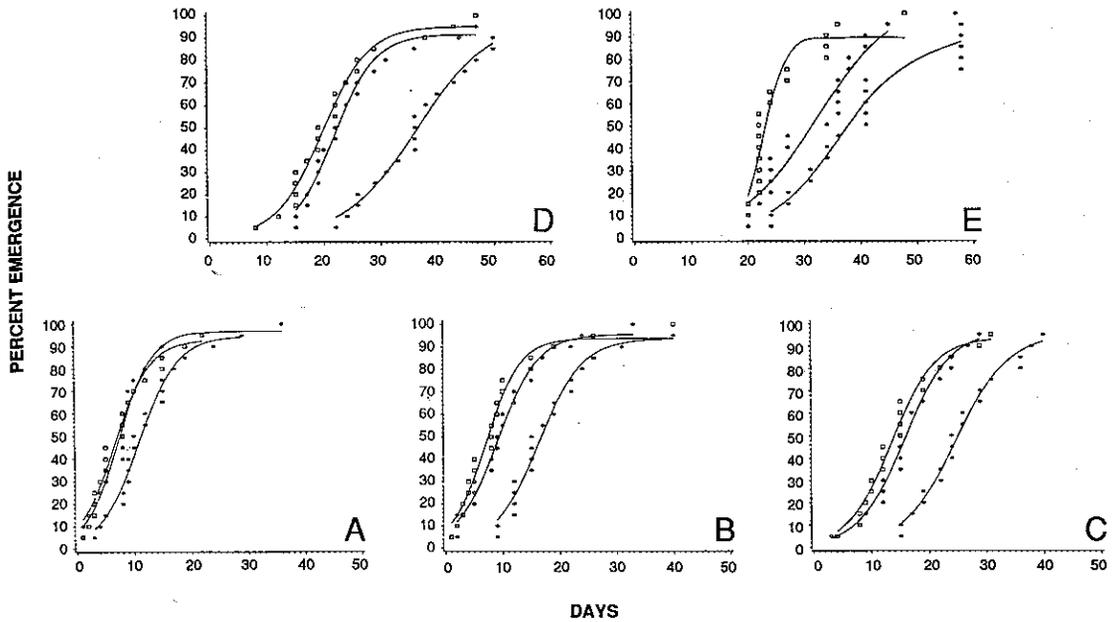


Fig. 2. Sigmoid curves of rate of offspring emergence from gallery sections (section A is closest to the point of parent introduction) for female mountain pine beetles. Group I (star), reemerged females; group II (diamond), new females, males removed; group III (square), new females, males present.

for up to 46 cm, whereas offspring emergence, probably the result of low oviposition, declined continually after the first 15.2-cm section of gallery made by group I. In comparison, southern pine beetle females produce more gallery and eggs from second galleries than from first galleries (Wagner et al. 1981).

Results suggest that the number of mountain pine beetle offspring per centimeter of gallery is likely to be greatest when attack density and egg gallery construction interact so that galleries are 15.2–46 cm long. Egg gallery per adult in epidemic populations was within this range, averaging 15–30 cm (Cole et al. 1976).

Rate of Emergence. ANOVA detected a significant difference in the rate of emergence among the three groups, with offspring from group III emerging at a faster rate than groups I and II. For example, the number of days for 50% emergence of females was 26.5 for group I offspring compared with 18.7 for group II offspring and 15.7 for group III offspring ($F = 138.1$; $df = 2, 30$; $P = 0.0001$) (Fig. 2). The rate of emergence differed by section ($F = 371$; $df = 4, 30$; $P = 0.001$). The group \times gallery section interaction for 50% female emergence also was significant ($F = 15.1$; $df = 8, 30$; $P = 0.0001$). Contrast comparisons (not orthogonal) showed group I was different from groups II and III ($F = 304$, $df = 1$, $P = 0.0001$), and group II was different from group III ($F = 22.9$, $df = 1$, $P = 0.0001$). Emergence rates of males and females did not differ ($F = 0.08$; $df = 2, 36$; $P = 0.92$).

The trend for the difference in rate of emergence to increase among groups with increased gallery length is apparent in Fig. 2. We suspect that groups I and II females made egg galleries at a slower rate than group III females. The result would be an ever-increasing time difference between groups I and II on the one hand and group III on the other, from when gallery was constructed and oviposition occurred in succeeding 15.2-cm² areas of bark. The slower rate of gallery construction and oviposition by groups I and II would have the overall effect of delaying brood emergence compared with the faster boring and ovipositing group III.

The faster rate of emergence by offspring of group III than of group II suggests that male presence, resulting in significantly faster gallery construction (Rasmussen 1974) by moving boring frass out of the way of the female into the bottom of the gallery (Reid 1958), had the effect of increasing the rate of offspring emergence. This behavior would appear to give the female, with a male present, an advantage over females without males. Under field conditions, slow gallery construction (and hence oviposition) would result in delayed hatch, or no hatch, because of declining fall temperatures (Logan & Amman 1986). Much of the brood of reemerged females would then enter winter as eggs or small larvae, both of which are highly susceptible to winterkill (Amman 1973, Reid 1962a).

Estimated parameters for rate of beetle emergence (male, female, and both combined) by egg gallery section for all of the various combinations

Table 2. Estimated parameters for sigmoid curves of rate of offspring emergence by gallery section for three groups of parent mountain pine beetles^a

Group ^b	Sex ^c	Section	Alpha	Gamma	Beta
1	1	1	28.19	93.22	-0.26
1	1	2	95.98	93.89	-0.26
1	1	3	408.58	97.09	-0.23
1	1	4	194.88	100.55 ^d	-0.14
1	1	5	54.59	101.93 ^d	-0.09
1	2	1	23.83	94.68	-0.29
1	2	2	64.74	93.62	-0.26
1	2	3	195.88	95.42	-0.21
1	2	4	230.73	97.94	-0.16
1	2	5	388.14	90.37	-0.15
1	3	1	22.39	94.34	-0.27
1	3	2	89.57	93.94	-0.27
1	3	3	288.55	97.13	-0.22
1	3	4	239.33	99.69	-0.15
1	3	5	213.94	90.40	-0.13
2	1	1	16.18	93.49	-0.32
2	1	2	45.13*	91.05	-0.39*
2	1	3	49.36	96.43	-0.25
2	1	4	45.52	99.78	-0.16
2	1	5	48.33	99.13	-0.11
2	2	1	11.92	96.80	-0.34
2	2	2	12.36*	95.62	-0.28
2	2	3	49.41	96.40	-0.24
2	2	4	340.67	91.50	-0.27*
2	2	5	140.67	106.48 ^d	-0.14
2	3	1	13.51	94.60	-0.33
2	3	2	17.33*	93.77	-0.31
2	3	3	49.50	94.58	-0.25
2	3	4	108.25	93.93	-0.21
2	3	5	97.27	98.09	-0.13
3	1	1	10.07*	93.43	-0.33
3	1	2	9.08*	93.66	-0.23
3	1	3	22.30	92.91	-0.21
3	1	4	39.16	98.04	-0.13
3	1	5	373,103.60 ^e	90.99	-0.51*
3	2	1	8.42*	93.00	-0.32
3	2	2	10.16*	93.73	-0.33
3	2	3	34.94	93.47	-0.26
3	2	4	114.17	95.16	-0.25*
3	2	5	260,636.34 ^e	88.89	-0.50*
3	3	1	8.94	94.33	-0.31
3	3	2	9.53	93.29	-0.28
3	3	3	28.71*	92.25	-0.24
3	3	4	52.44*	94.66	-0.19*
3	3	5	140,708.47 ^e	91.46	-0.47*

^a*, estimated parameter is significantly different ($P < 0.05$) from that of group 1.

^b Group I, reemerged females; group II, new females, males removed; group III, new females, males present.

^c 1, male; 2, female; 3, both sexes combined.

^d SAS program (NLIN) (SAS Institute 1987) would not converge if gamma was bound ($\text{gamma} \leq 100$). Gammas > 100 are presented only for completeness; emergence exceeding 100% is not biologically feasible.

^e Large values of alpha were achieved for group III and would indicate a different model may be more appropriate. We wanted to maintain continuity throughout; therefore, we chose to use the same model.

are given in Table 2. The sigmoid growth curve provided a good fit in most instances; however, the data from section 5 were more variable, and the sums of squares stabilized at a relatively large number. Section 5 is farthest from the point of introduction of beetles and probably is approaching the upper limits of gallery construction for most beetles.

Size of Beetles. Female offspring were analyzed for size among groups and by section of gallery. Offspring from group I (5.26 mm) were larger ($F = 2.72$; $df = 2, 209$; $P = 0.068$) than offspring from group II (5.18 mm) but not group III (5.23 mm) (Table 1). Size of female offspring also differed by section of gallery ($F = 5.13$; $df = 4, 209$; $P = 0.0006$). Beetles from section 1 were smaller than those from subsequent sections (Tukey's test, $\alpha = 0.05$), except section 5. The interaction of group \times gallery section was not significant ($F = 0.36$; $df = 8, 209$; $P = 0.938$). These differences among beetle groups and gallery sections are small; we have no biological explanation for them. All billets used for rearing beetles came from the same tree; therefore, phloem quantity and quality should have been similar.

Sex Ratio. Sex ratio did not differ among groups. The percentages of female offspring were as follows: group I, 66.8; group II, 69.5; group III, 63.7%. These percentages are similar to the average of 66.7% female in field populations reported by Reid (1962b).

In conclusion, reemerged mountain pine beetles that make a second gallery will produce fewer offspring that will take longer to emerge than will new females making their first egg gallery. Offspring of new females without males present during gallery construction also emerge at a slower rate than offspring of new females with males present. In future studies, our model might be used to predict rate of offspring emergence in relation to gallery length. However, in field populations, output must be interpreted with caution because the temperature threshold for initiation of development differs by beetle stage, thus allowing for late-hatching larvae to catch up partially in development with larvae that hatched earlier (Bentz et al. 1991). The model also could be used to assess effects of competition among offspring of several adjacent galleries because it defines expectation for a single gallery in the absence of competition from offspring of adjacent galleries.

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