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Biology of the Mountain Pine Beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay Region of British Columbia II. Behaviour in the Host, Fecundity, and Internal Changes in the Female[1]

By R. W. Reid

Forest Entomology and Pathology Laboratory, Calgary, Alberta

Introduction

This paper deals with the influence of bark moisture and temperature on the behaviour of the egg-laying female within the host. Fecundity of the insect will be discussed, as well as internal changes associated with the behavioural pattern. The life-cycle, brood development, and time of flight was described in Part I of the present series. The behaviour during mating, egg laying, and gallery construction were described earlier (Reid 1958b).

Influence of Tree Moisture

A laboratory technique was developed whereby moisture and temperature could be altered in the immediate environment of the insect. Strips of bark, two by twelve inches, were peeled from fresh logs and subdivided into two, four, and six-inch lengths. The moisture content of the inner bark was calculated on the oven-dry weight (o.d.w.) basis, using one-half inch square samples, at the time the plates were constructed. A notch one-eighth inch wide by one-half inch long was made in one end of the bark strip which was then placed between two pieces of one-eighth inch clear Lucite plastic. The sides were sealed with waterproof tape to prevent loss of moisture. The completed unit is referred to as an observation plate. To restrict loss of moisture from the bark during construction of the plates, the work was done in a high humidity atmosphere.

The observation plates were placed in an upright position with the elongated notch at the bottom. A pair of beetles in the flying condition was introduced, the female first, into the elongated notch of each plate. They were observed through the plastic during gallery construction (Fig. 1).

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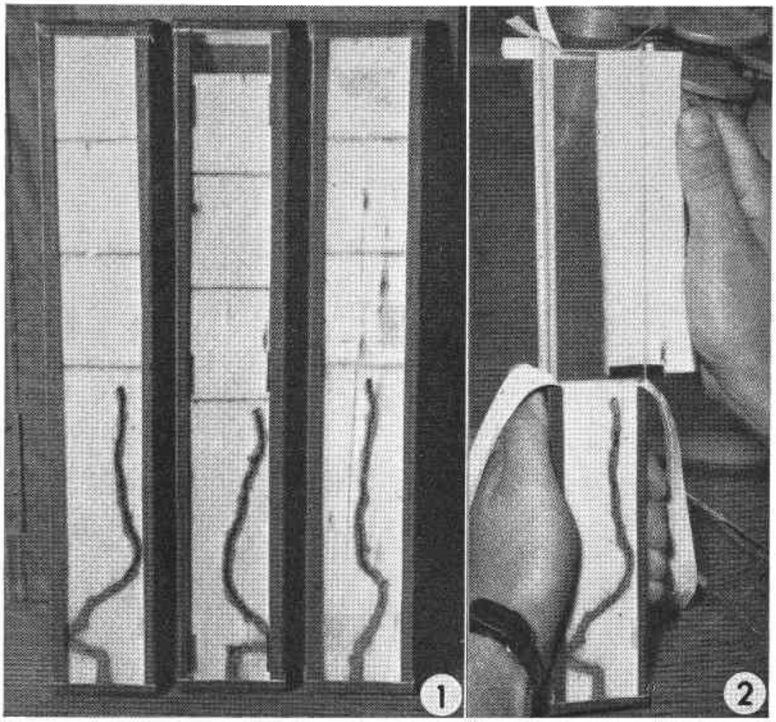

Fig. 1. Completed observation plates containing egg-laying beetles.
Fig. 2. Inserting bark of lower moisture content into observation plate.

The females were allowed to construct egg galleries six to ten inches long in the moist bark. Sections of bark immediately above this were exchanged with others of known moisture content to test the influence of moisture content upon beetle behaviour. The bark was removed by slitting the tape on both sides of the plate and pulling the bark out through the slit. This was replaced (Fig. 2) by a strip of bark which had been collected and wrapped in aluminum foil at the time of plate construction. Both strips were taken from the same log and adjacent to each other. The moisture content of the replacement bark was lowered by removing the foil and exposing it to dry to a predetermined weight. Waterproof tape was inserted between the bark strips to prevent exchange of moisture. A narrow opening directly in line with the egg gallery was left free of tape to permit the entry of beetles into the replacement bark. Adults for testing and samples for moisture determination were removed through small windows cut in the plastic with a hand drill and dental burr.

A second series of experiments was conducted to test further the effect of moisture on the female. Two logs, five feet in length, were obtained from two trees which were similar in appearance, bark characteristics, growth rate, and diameter. The logs were cut into ten pieces, 12 inches long, and most of the outer bark on the upper six inches was removed with a wood rasp. The remaining outer bark on the upper six inches constituted a thin corky layer around the stem. Four holes measuring four inches deep and one inch in diameter were drilled in the outer sapwood of the upper end of each section to increase the rate of moisture loss from the sapwood. Five of the ten sections were waxed at both ends and were placed in close fitting polyethylene envelopes. The logs were

TABLE I
Effects of inner bark moisture on the egg laying behaviour of mountain pine beetles.

Observation Plate	Initial Moisture content (per cent of o.d.w.)	Remarks	Final moisture content (per cent of o.d.w.)	Remarks
1	187	Quickly established egg gallery	155	Egg laying is continued into dryer bark
2	202	"	135	"
3	197	"	125	"
4	165	"	108	"
5	143	"	105	Egg laying ceased in dryer bark. Female altered to flying condition.
6	189	"	100	"
7	202	"	100	"
8	133	"	99	"
9	154	"	93	"
10	180	"	90	"
11	147	"	90	"
12	202	"	80	"

examined 14 days later. The experiments, including observation plates and logs, were both carried out at room temperature.

When confronted in the observation plates, with bark of different moisture contents the females constructed egg galleries when the inner bark moisture was about 133 per cent o.d.w. or more. When moisture content was 105 per cent and less, egg gallery construction ceased (Table I). When egg laying ceased the females changed to the flying condition and flew when subjected to the toss test (Chapman 1955). Five of the females, which had ceased egg laying due to dry bark and had changed to the flying condition, were placed in new observation plates containing inner bark of high moisture content. They all constructed egg galleries and, without mating again, laid viable eggs. When bark moisture was reduced they once more ceased egg laying and changed to the flying condition.

In the experiment where moisture was altered in 12-inch logs (Table II), female beetles in the moist polyethylene-covered sections constructed galleries to the top of the log where they either emerged or continued their gallery construction in a downward direction. Those in the unprotected sections constructed galleries up to the region where the outer bark had been removed, and emerged, or, as in the previous group, turned and continued gallery construction in a downward direction. In all sections the inner bark remained fairly moist despite the fact that much of the outer bark had been removed from the upper six-inch portions of the five exposed sections. These observations and those for the observation plates indicate that when conditions become too dry, the females cease egg-laying, change to the flying condition, and leave their galleries.

Females were allowed to establish galleries in a newly-cut, four-foot, polyethylene-covered log at the same time the experiment with the 12-inch logs was being carried out. One month later the inner bark and outer sapwood were still moist (258 and 125 per cent o.d.w. respectively) and the females were extending galleries that then averaged 34 inches in length. So far as moisture is

TABLE II
Effects of log moisture on the length of egg galleries constructed by the mountain pine beetle*

Log	Total Galleries	Average total length (ins.)	Average length of galleries in upper and lower 6 inch segment of log (ins.)		Final moisture content ln per cent o.d.w. upper half of log	
			lower half	upper half	inner bark	outer sap-wood
1	5	8.6	**8.6	0	154	47
2	3	6.8	5.0	1.8	227	46
3	4	9.0	**9.0	0	127	41
4	2	6.3	6.3	0	242	67
5	5	5.9	5.8	0	171	50
6	5	10.6	5.5	5.1	307	124
7	4	14.0	5.2	8.8	264	129
8	6	8.0	5.1	3.8	309	118
9	7	11.4	6.1	5.3	284	114
10	6	8.1	2.6	5.5	278	100

*Fresh logs 12 inches long, six inches in diameter, and experimentally infested. Logs examined two weeks after they were infested.
**Females turned down when they reached the drier upper six-inch portion.

concerned, and under normal conditions, long egg galleries are constructed when the bark and sapwood of infested trees maintain a high moisture content.

Within the experimental area the average gallery length often varies significantly (from six to 16 inches) between trees. Successfully attacked trees dried at different rates due in part to differences in their degree of exposure, their original moisture content, the density and success of the insect attack, crown characteristics, and soil moisture conditions.

The rate at which infested trees deteriorate in terms of inner bark and outer sapwood moisture determines in part the time available to the female for gallery extension, and hence affects the number of eggs laid by each individual.

Studies on infested tree moisture content in relation to insect behaviour were carried out in the field in 1958 concurrently with the laboratory experiments. The moisture of bark and wood from two infested trees was determined at the top of the galleries when female beetles were leaving for their second flight. Overcrowding or pitch flow was not a factor and there was no outward change in the appearance of the bark. The lower five feet of the one tree had sustained 60 attacks, and the other 49. The average moisture content was 124 and 126 per cent o.d.w. for the inner bark, and 62 and 60 per cent o.d.w. for the outer sapwood. It should be noted here that moisture contents of less than 200 and 80 per cent o.d.w. for the inner bark and outer sapwood respectively, have never been observed in living unattacked trees during the summer.

The moisture content of the inner bark in the sample trees at the time of beetle emergence was higher than that recorded in the observation plates and the 12-inch wood sections. However, the moisture content in the outer sapwood of the 12-inch logs and infested trees at the time of beetle emergence was approximately the same and may, under natural conditions, have greater influence.

A low moisture content in the outer sapwood and inner bark within infested trees is likely responsible for the change from egg-laying to flying condition of

TABLE III
Egg-laying activities of mountain pine beetles in relation to bark temperatures

Observation plate	Total elongation of egg gallery in mm. after	
	Seven days	14 days
Temp. 55° F.		
1	125	201
2	115	191
3	115	300
4	101	171
5	119	105
Temp. 45° F.		
6	0	0
7	1	1
8	2	2
9	0	0
10	0	0
Temp. 35° F.		
11	2	6
12	5	6
13	5	5
14	6	12
15	0	5

the beetle (Reid 1958a) and this initiates the second flight. This second flight, as will be demonstrated in a later paper, had a high survival value for the population as a whole in the experimental area.

Influence of Bark Temperature

In the field, oviposition ceases in late October or early November, when freezing temperatures are the rule and the females alter to the overwintering condition.

To test for the possible effects of low temperature on oviposition, 15 observation plates containing moist bark and egg laying adults were acclimatized for two days at 65, 55, 45, and 35° F., plus or minus one degree. The temperature of five plates was then adjusted to 55° F., five to 45° F., and five to 35° F. for two weeks. After this, plates at the 35° temperature were adjusted to 28° F. for one week.

Egg gallery construction and oviposition occurred at 55° F. (Table III). Although egg gallery construction and oviposition ceased at 45° F., the females continued to lengthen their galleries and lay eggs at 35° F., although very slowly. A possible explanation for this lies in the fact that when the plates were originally set up at room temperature the five females which were ultimately placed in the 35° temperature had elongated their galleries more rapidly than the others. By the time their acclimatization was completed, most had galleries nine to ten inches in length. Because there was less room left on these observation plates, they were placed in the lowest temperature. The less vigorous females in the other plates ceased activity at 45°. All beetles at 55°F. and 45°F. remained in the egg laying condition during the full two weeks of the experiment. Two of the five kept at the 35°F. and 28°F. combination changed to the over-wintering condition.

TABLE IV
Size of the mountain pine beetle in relation to the number of eggs laid per day in logs.

*Size class in mm. (width of prothorax)	Number of galleries and number of females measured	Average number of eggs laid per gallery per day
1.54 – 1.69	2	1.94
1.70 – 1.85	16	1.87
1.86 – 2.01	20	2.19
2.02 – 2.17	16	2.21
2.18 – 2.33	20	3.04
2.34 – 2.49	10	3.60
2.50 – 2.65	2	3.35
2.66 – 2.81	1	1.20

* Size determined with binocular microscope and disc micrometer.

Fecundity

Under natural conditions, females lay only a small fraction of the eggs they are capable of producing. Egg galleries are generally under 12 inches and contain fewer than 75 eggs. In logs, where favourable conditions of moisture, temperature, and density can be sustained, females have excavated galleries up to 60 inches in length; in a gallery 52 inches long, the female had laid 263 viable eggs and was still ovipositing at the time the gallery was examined.

In logs, the average number of eggs laid per inch of gallery was 4.2 (s.d. 0.9) as determined from 84 completed galleries ranging in length from two to 26 inches. A similar average was obtained from infested trees by Richmond (1935). The reduced number of eggs laid at the beginning and at the end of egg galleries resulted in a lower figure per inch in short galleries than in long galleries. The rate of egg laying varied directly with the size of the female (Table IV).

Nematodes sometimes influence the egg-laying ability of females. During 1955, an internal parasite *Stictylus* (*Sphaerularia*) *hastata* Khan, reduced the number of eggs laid by one third (Reid 1958c). Such heavy parasitism by nematodes has not been observed since.

In the wild population the sex ratio is 1:2, males to females, (Reid 1958b). Five different sex ratios were compared to determine their effect upon the fertilization of the females. For each ratio a caged log was populated with 30 females and a specific number of males: 9, 15, 21, 27 and 33. The beetles were released into the cages during the first week of July, 1957, and the logs were examined at the end of September. Each female had established only one egg gallery and had remained in this gallery all summer. Approximately equal numbers of egg galleries were established at each ratio and all contained viable eggs. From this it appears that even when the number of males had been reduced to a ratio near 1:3 all the females were mated.

Males were frequently blocked out by boring dust once the female started to elongate the egg gallery. In contrast, unmated females did not immediately plug their galleries with boring dust and males could readily enter these open galleries and mate with the virgin females. Thus the polygamous habit of the male overcomes the unequal sex ratio.

The possibility of parthenogenetic reproduction was investigated. Twenty-five virgin females were allowed to establish egg galleries. The egg galleries were short and winding, few eggs were laid, and none hatched. These results were in agreement with those of Gibson (1927).

TABLE V
Internal changes in the female mountain pine associated with functional periods of the adult.

Stage of female	Wing muscles	Fat body	Ovar-ioles	Corpora lutea	Sperm-athecia	Ventriculus
	E — enlarged			R — reduced		
Newly emerged (flight)	E	E	R	absent	no sperm	R
Egg-laying	R	R	E	present	contains sperm	E
Second emergence (flight)	E	E	R	present	contains sperm	R
*Unmated in egg gallery	R	R	E	present	no sperm	E
over wintering parent adults	R	E	R	present	contains sperm	R

* After several weeks when males were prevented from entering the gallery to mate with the female

Dissections were made of newly emerged female adults during different periods of their life-cycle, females in various stages of egg gallery establishment, and mated and unmated females before, during, and after over-wintering. Examinations were made of the conditions of the wing muscles, the fat body, and the digestive and reproductive systems. Each stage in the behaviour of the female adult is associated with a characteristic condition of its internal organs (Table V). These, and earlier observations (Reid 1958a) agree in many respects with a report by Chapman (1958) concerning internal changes in the ambrosia beetle, *Trypodendron lineatum* (Olivier).

The relationship between moisture content, egg gallery construction, and internal condition of the beetle are described in the following example, beginning with a young female which has just established a gallery. She possesses massive flying muscles, a greatly expanded fat body, an empty digestive tract and a reduced reproductive system. A day later, after excavating one inch of gallery, the wing muscles, fat body, and reproductive organs have not visibly altered, but the digestive system begins to fill. Following mating, internal changes are accelerated; the fat body and flying muscles are reduced, the reproductive system, especially the ovarioles increase in size; and the digestive tract also increases in size, due to feeding. The female begins to lay eggs and increases the rate of gallery elongation. She deposits more eggs per inch of gallery as the ovarioles increase their output, reaching a peak by the time the gallery is four inches long. After this the ovarioles diminish in size and egg production declines as the gallery is lengthened. In the meantime, the moisture content of the tree is rapidly declining due to disruption of water conductive tissue in the sapwood. When the gallery is five or six inches long, the moisture level of the inner bark and outer

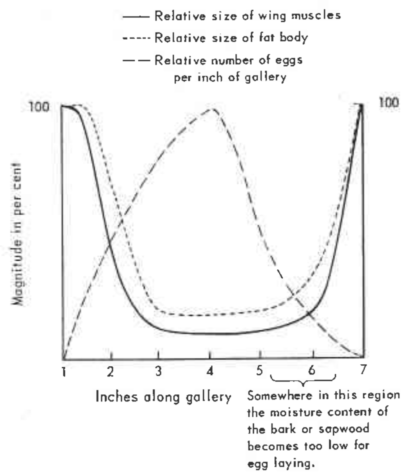

Fig. 3. Internal changes in the female mountain pine beetle associated with gallery excavation and egg laying.

sapwood is sufficiently low to cause a cessation of egg laying; at this time the reproductive system is reduced in size. When the gallery is about seven inches long the insect is once more in the flying condition at which time she mines to the outside, emerges, and attacks a fresh tree. The sequence of internal changes is illustrated diagramatically in Figure 3.

Summary

Female adults of the mountain pine beetle, under the bark of successfully infested trees, are sensitive to the changing environment and react accordingly. Their behaviour in relation to gallery construction, oviposition, and flight preparation are determined in large part by the suitability of moisture and temperature regimes. Oviposition ceases when inner bark and outer sapwood moisture content drops below 105 per cent and 60 per cent o.d.w. respectively. Most females cease egg laying at temperatures of 45° F.

Under continuously favourable conditions of moisture, temperature, and food supply, females have established egg galleries over 50 inches in length and containing more than 200 eggs. Under natural conditions, egg galleries in successfully infested trees are seldom longer than 12 inches and contain fewer than 75 eggs. The significant differences in average gallery lengths between successfully attacked trees are attributed in part to differences in the rate at which trees deteriorate after attack.

Each stage of the life cycle of the adult is associated with a characteristic condition of the internal organs.

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Orientation of the Males of *Aedes aegypti* (L.) (Diptera: Culicidae) to Sound

By G. Wishart, G. R. van Sickle, and D. F. Riordan
Entomology Research Institute for Biological Control, Research Branch
Canada Department of Agriculture, Belleville, Ontario

Many authors noted the attraction of the males of several species of mosquitoes to sound (references summarized by Roth, 1948). The frequencies of sound to which the males respond were investigated by Roth (1948) and the frequencies and intensities by Wishart and Riordan (1959). Tischner (1953) applied electrophysiological methods to the reception of sound in the male of *Anopheles subpictus* Grassi and advanced a theory to explain the ability of the male of this species to orient itself toward the sound source. In his theory he dismissed the use of phase differences between the two receptors because of the relatively small distance between the two antennae and concluded that each is capable of functioning alone by detecting the relationship between the fundamental and the second harmonic in the microphonics produced by the Johnston's organ. He did not demonstrate this by behaviour experiments nor, do we believe, did he produce sufficient electrophysiological evidence. The present paper is a further examination of this subject in the mosquito *Aedes aegypti* (L.), in an attempt to reconcile the data from electrophysiological experiments with those of behaviour in an explanation of the orientation of male mosquitoes towards sound.

The antenna of the *A. aegypti* male is made up of 15 segments, consisting of a narrow first segment, a much enlarged pedicel or second segment, and 13 flagellar segments each bearing numerous fibrils or hairs. The second segment is the Johnston's organ, so called by Child (1894) after Johnston (1855) who first suggested its sensory function. The flagellum is mounted on a circular plate deep in the Johnston's organ. Cells radiate outward both above and below this plate. Vibration of the flagellum is transmitted to this plate and compresses or stretches the attached cells. (Detailed descriptions of this organ are to be found in Child, 1894, Roth, 1948, and Tischner, 1953).

Wever and Bray (1930) demonstrated the presence of electrical potentials of the same frequency as the stimulating sound in the cochlea of the cat and in the tympanal organs of an insect species (1933). Tischner (1953) found similar microphonics in the Johnston's organ of a mosquito and reported that the frequency of the microphonics was doubled at certain frequencies. Pumphrey and