STUDIES ON THE BIOLOGY OF THE
MOUNTAIN PINE BEETLE, *DENDROCTONUS MONTICOLAE* HOPK.

by

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2) crowding
3) predators and parasites

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3) predators and parasites
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(Note: This figure also represents actual life cycle as it occurred in the experimental area - 1956.)

APPENDICES

1. INTRODUCTION

Studies on the biology of the mountain pine beetle in 1956 were a continuation of those initiated in 1955. The objectives of the study remain as originally drawn up. The initial objective is to determine as many of the factors as posssible which influence survival and to assess the effectiveness of these factors both working singly and in combination with each other. The final objective, which is a long term one, is a more complete understanding of the conditions which lead to population increase and decrease.

During the 1956 season, two study areas were established. One of the areas was on the eastern slope of Steamboat Mountain approximately 19 miles north of Invermere, B.C. The other was in the Francis Creek region, 12 miles north west of this village. The two regions were approximately 10 miles apart and separated by the 1500 foot Steamboat Mountain massive. Both regions have had a history of bark beetle activity. The activity of the population in the Steamboat region has decreased considerably in the last few years. The population in the Francis Creek region has also declined from earlier years but is still quite active. It is probable that the populations in both areas have been reduced in recent years due to lack of host trees of sufficient size and in sufficient numbers. The populations in both areas were found to be comparable in respect to periods of emergence and attack, sex ratio, predators and parasites.

2. EMERGENCE AND ATTACK - 1956: SPRING, SUMMER, FALL

Emergence and attack data was obtained from caged and exposed logs.

Butt logs from 1955 infested trees were placed in cages on May 24. These logs were obtained from the Steamboat and Francis Creek area. Five logs from each area were used. Emergence from these logs is shown in Figs. 1 and 2. Emergence was almost simultaneous from logs in both areas. The emergence of adults in 1955 is also shown in Fig. 1. There is approximately 3 weeks difference between peak dates of emergence.

The period of attack closely parallels the time of emergence. Data on attack were obtained from the exposed logs which were set up at the Steamboat Mtn. site and the Francis Creek site. Twelve exposed logs, ranging in diameter from 5 to 12 inches, and 5 feet in height were set up in each area on June 15. They were secured in a vertical position and placed in 2 rows. Prior to setting up these logs, periodic inspection was made of a number of trap trees felled in the area. Strikes were marked and recorded as they appeared on the exposed logs. No strikes were observed on the trap trees prior to when they were first observed on the exposed logs. The exposed logs were not put up earlier than mid June because of the very early flight of *Ips oregoni* (Eichh.). This species flies much earlier in the experimental region than does *D. monticolae*. Hence logs set up too early become saturated with *Ips*.

The attack period in the Francis Creek area is illustrated in Fig. 3. Evidence of the first brood flight was recorded from July 5 to July 18. The much reduced second flight, by these same adults, occurred from July 24 to August 2. The flights described so far have been those occurring in the wild population.

In 1955 a number of logs were placed in cages and were allowed to

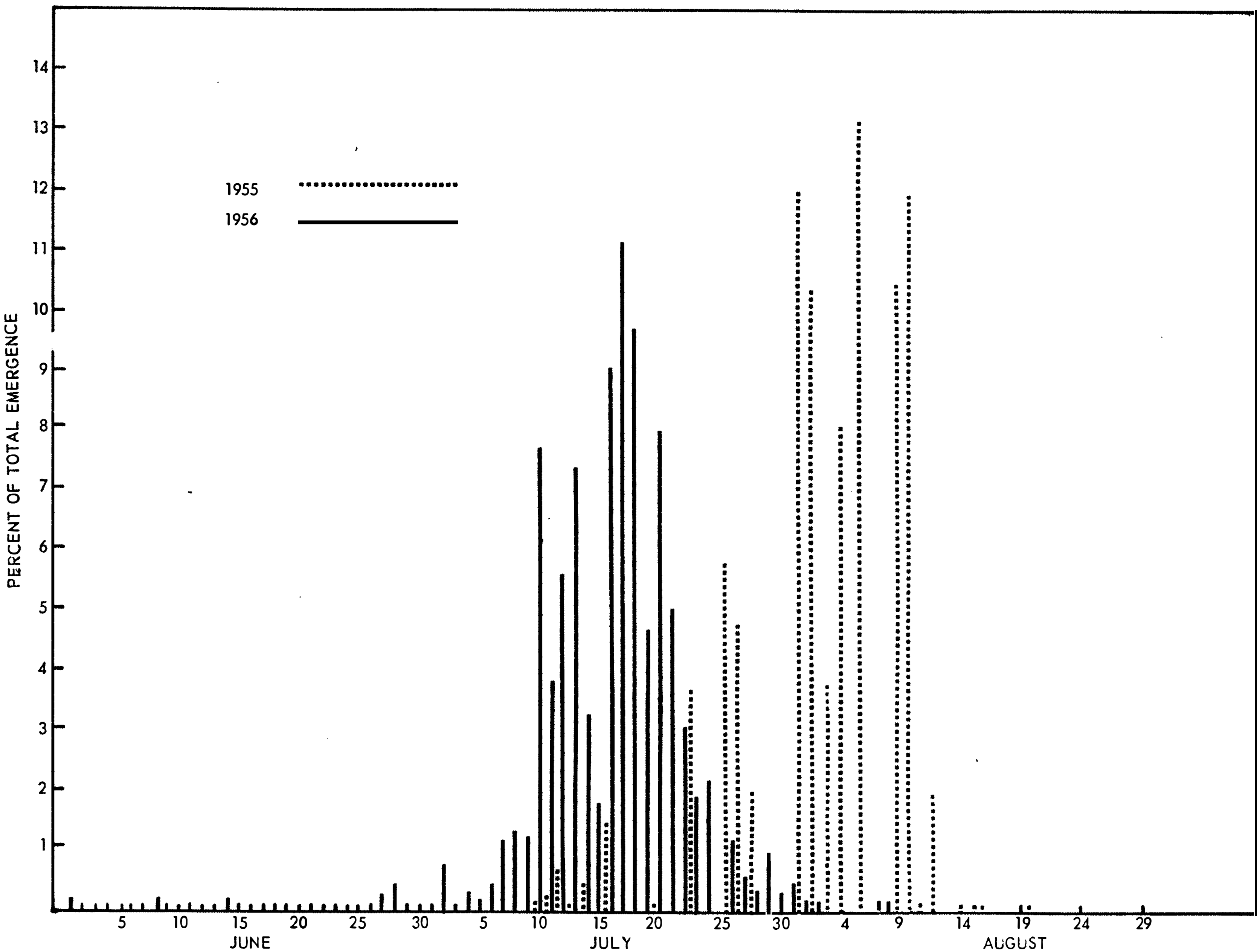

Fig. 1. Emergence of D. monticolae. Steamboat Mtn., B.C. 1955 and 1956.

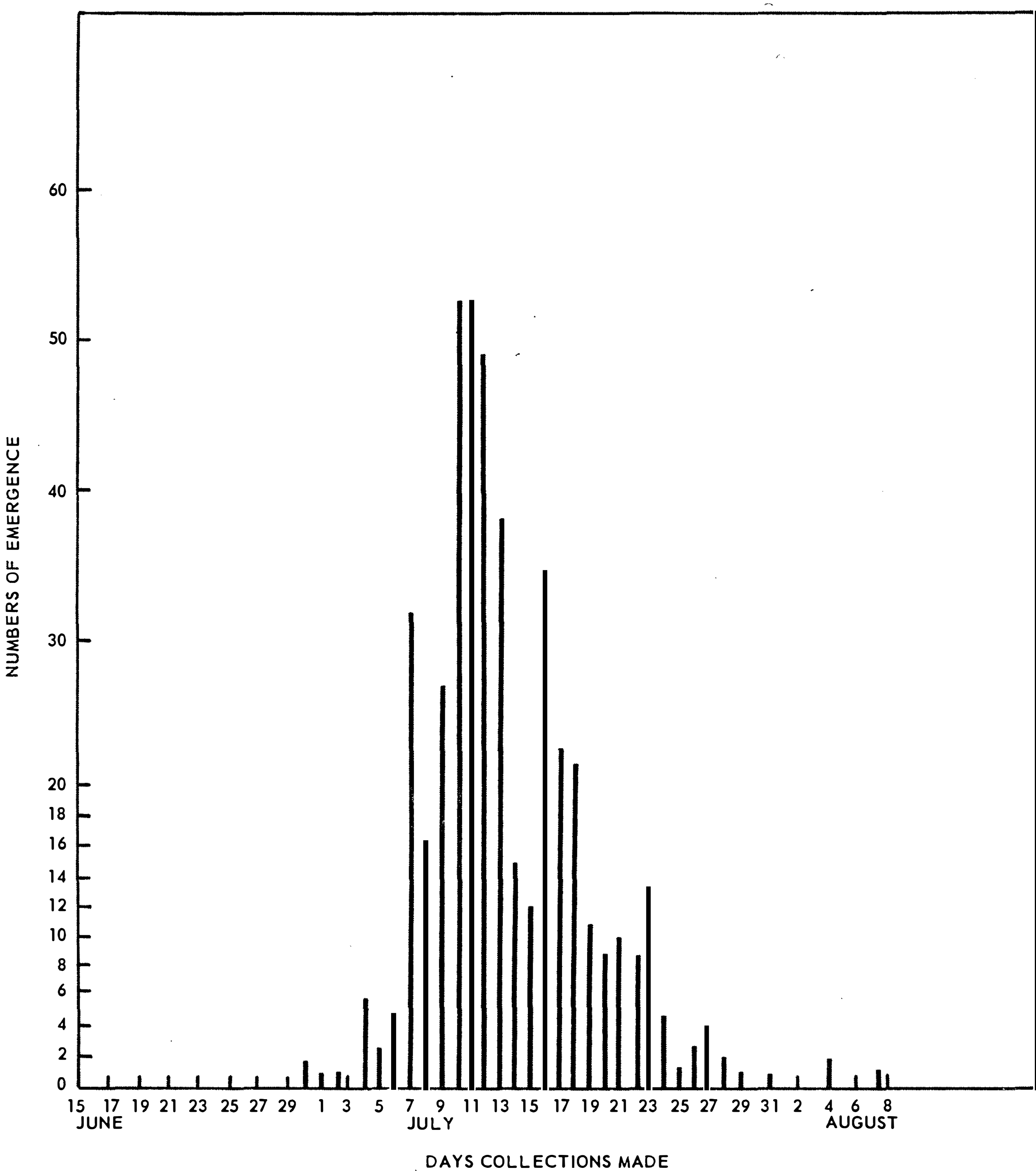

Fig. 2. Emergence of D. monticolae. Francis Creek area, B.C. 1956.

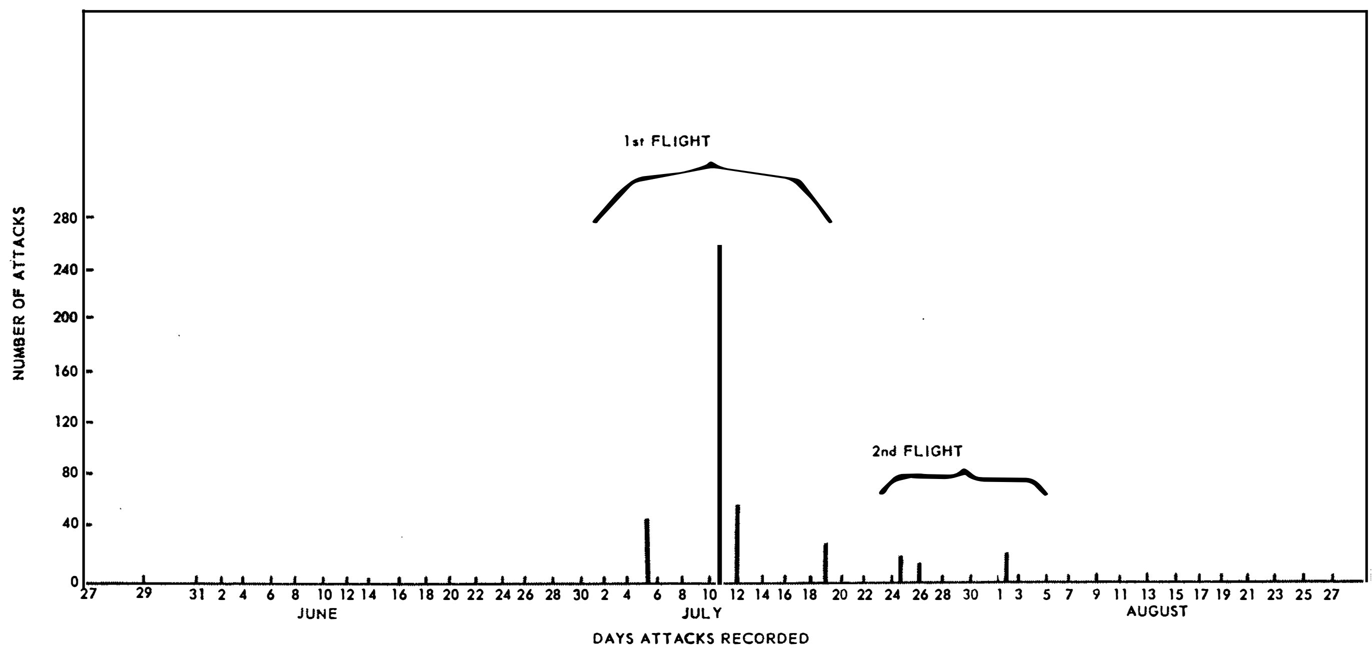

Fig. 3. Flight periods of D. monticolae. Francis Creek, B.C. 1956.

become infested by young adults. Many of these logs were infested in 1955 at the time the wild population was making its first flight. Most of these logs were debarked during the 1955 season, but some overwintered and the progeny were allowed to emerge (Fig. 4). This emergence took place mainly in May, 1956. In Fig. 4 there is also illustrated emergence in July. This latter emergence occurred because in 1955, many of the parent beetles, after having established one brood in July and early August, emerged in late August and established a second brood in the same log.

A number of caged logs were known to contain only second broods, established in late August, 1955. The emergence from one of these logs in 1956, is shown in Fig. 5. Note that this emergence coincides with the emergence in the wild population, and also that in the wild population, the flight as seen in caged logs in May, 1956 (Fig. 4) does not occur.

The emergence of young adults in 1956, from broods established earlier that same year is shown in Fig. 6. These young adults are survivors of the first broods established in early July (Fig. 2), by the wild populations.

Summary of emergence data is as follows:

1. The main emergence period in the wild population occurred from 2 to 3 weeks earlier in 1956, than in 1955.

2. The second flight by these same adults is not nearly so apparent as the first flight.

3. In caged logs, first broods established in 1955 emerged in May of 1956. This flight did not occur in the wild population.

4. In caged logs, second broods established in 1955 emerged in early July 1956. This flight coincided with the main flight in the wild population. There is evidence therefore that the main flight in the wild population is composed of survivors of the second broods established the previous year.

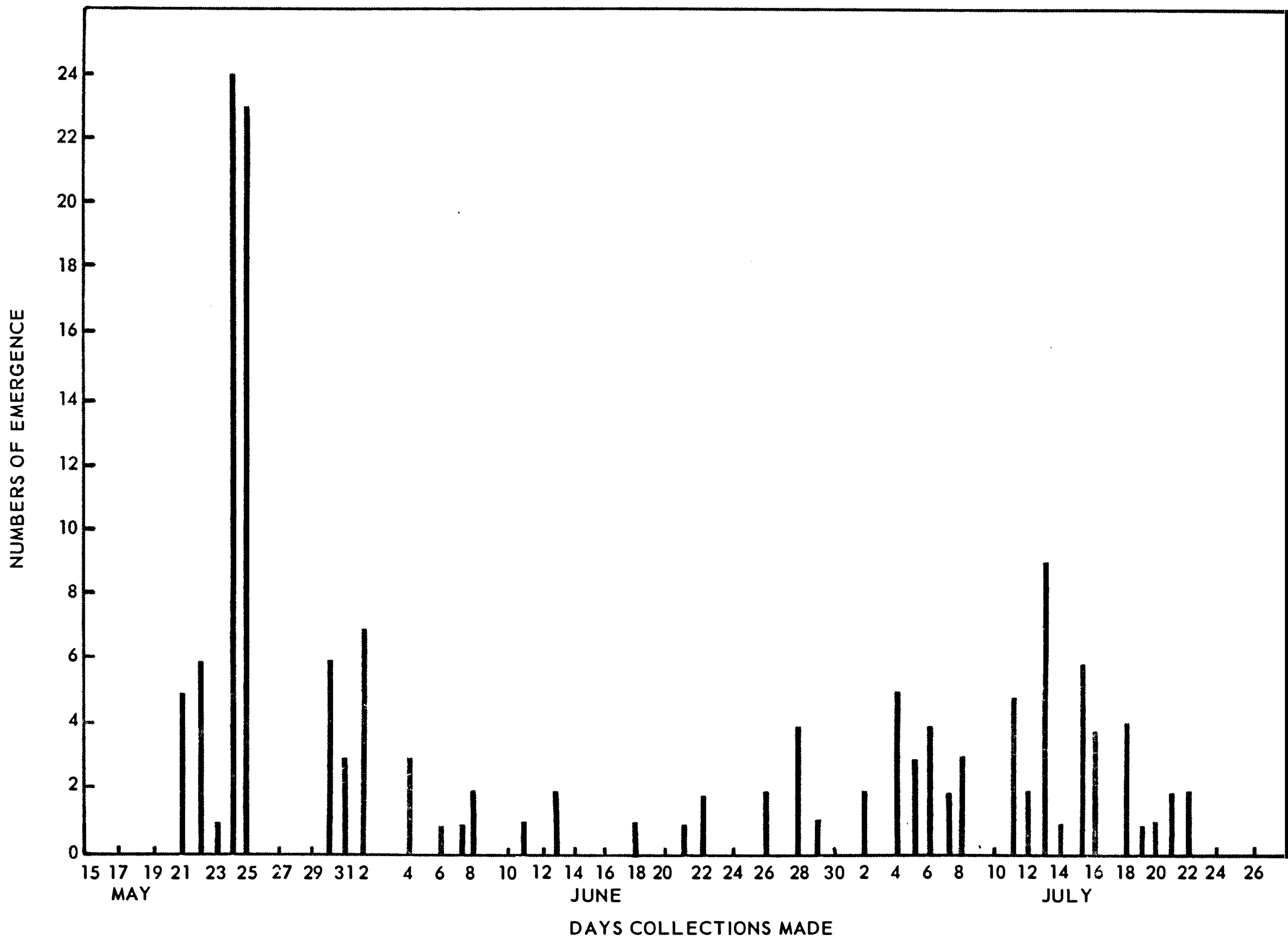

Fig. 4. Emergence of *D. monticolae*, 1956. Invermere, B.C. Log A4. (Log contained 1st and 2nd caged broods established in 1955).

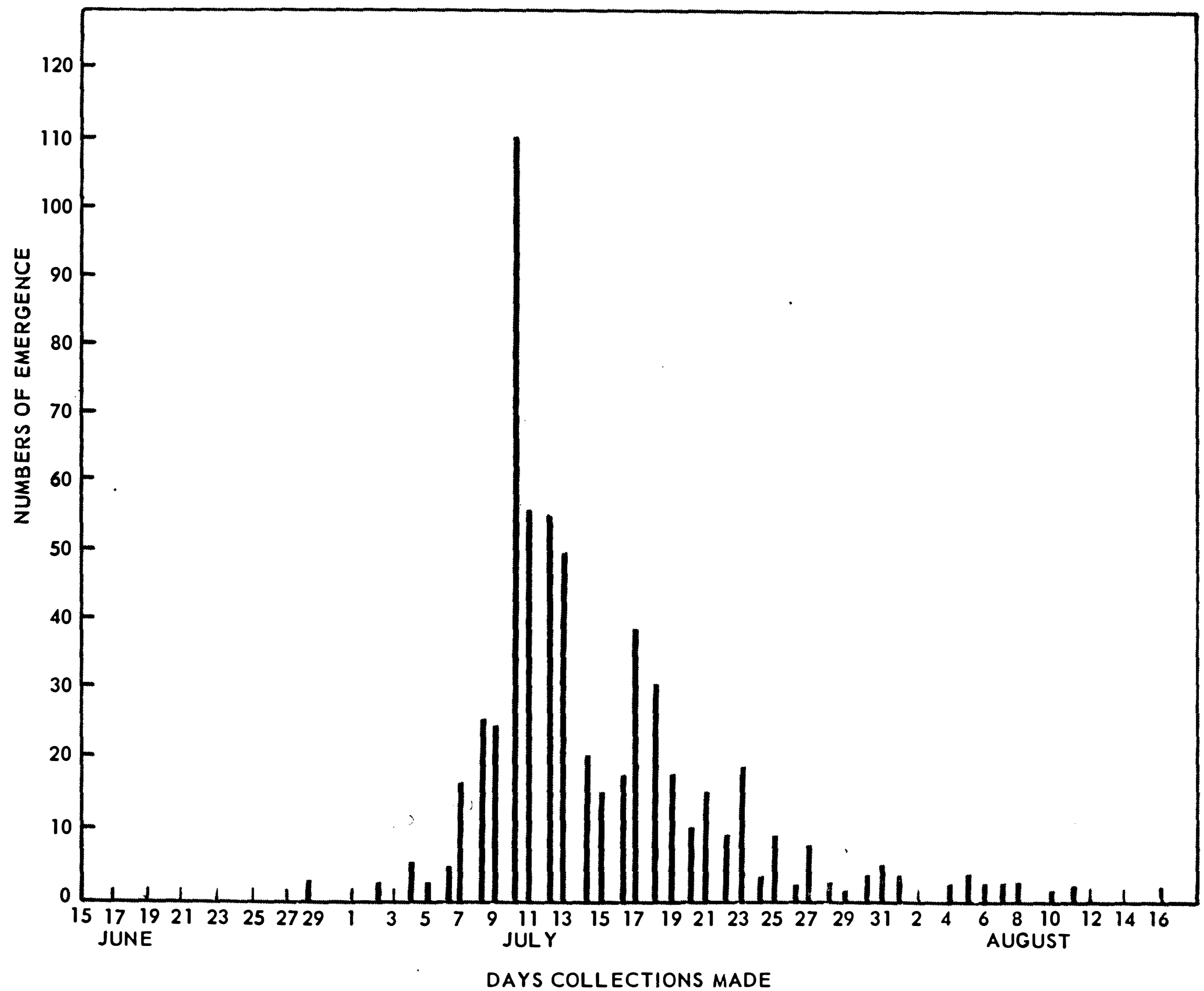

Fig. 5. Emergence of D. monticolae 1956. Log B4. Invermere, B.C. (Log contained 2nd broods established in 1955.

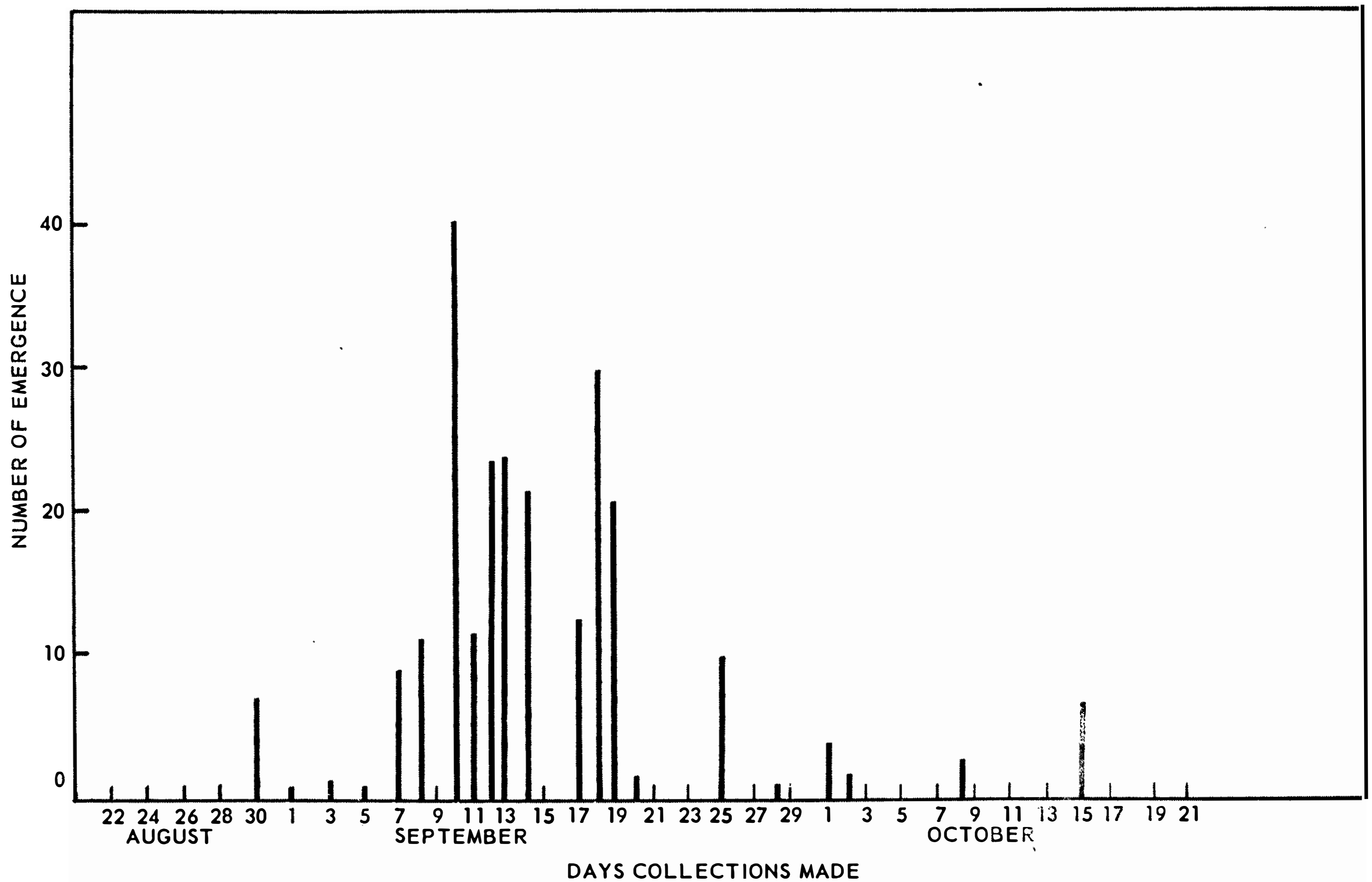

Fig. 6. Emergence of broods established in early July, 1956. (Total emergence from 7 exposed logs containing 450 broods).

5. Some survivors of first broods established in early July 1956, by the wild population, matured and emerged in September of 1956.

3. OBSERVATIONS ON MATING AND OVIPOSITION

Several attempts were made to observe behaviour of the beetles within their galleries. The apparatus used in these investigations was constructed as follows: Sheets of fresh, inner bark, measuring 4 ins. by 10 ins. by 1/8 ins., were placed between two sheets of glass of slightly larger dimension. The bark was sealed in with wax so that the entire apparatus was air tight. An artificial gallery was made by forcing a nail of 1/8 ins. diameter, through the wax and for a short distance into the bottom of the sheet of bark. A young mature female was allowed to enter this gallery, which she generally did quite willingly providing the apparatus was held in a vertical position. Upon entering, she always moved to the upper end of the artificial gallery and in a short time commenced to extend it upwards. After the female commenced tunnelling, the male was allowed to enter the gallery. In most cases he made his way up the gallery until his progress was barred by the female. The male commonly commenced to stridulate when he contracted the female.

Several of these cases were set up, some being more successful than others. It is important that the bark be of the proper thickness, and smooth, especially on the moist surface. If the bark is properly sealed in, it would remain fresh and palatable to the beetles for periods up to three weeks.

Mating was observed only once and egg laying only once. An almost continuous watch has to be maintained if these two activities are to be observed. Unfortunately neither the time nor labour was available to record their activity throughout the day. The mating and egg laying were observed during a continuous four hour watch. Mating took place $1\frac{1}{2}$ hours following release of the male into the gallery.

Another female, laid three eggs after a continuous tunnelling period of 3 hours. She laid one egg, and 15 minutes later laid 2 more. The oviposition was very rapid. Eggs seem to be ejected rather than carefully laid. The eggs were deposited in egg nitches which the female had previously constructed. The upper end of the gallery was approximately 1/4 inch ahead of the last egg nitch. The female under observation did not deliberately pack frass and boring dust around the newly laid eggs. However, in her movements up and down the gallery, loose boring dust within the gallery lodged in the egg nitch. Her passing back and forth soon packed this dust into the egg nitch and thus formed what is termed the egg nitch plug.

While the female invariably maintains her position ahead of the male, she assists in moving the boring dust down the gallery. She does this by using her body as a plow, and backing down forcing the loose boring dust down the gallery. She continues down the gallery, in this manner until she bumps into some obstruction, commonly, but not always, the male. The male in the meantime is performing a similar operation, pushing the loose boring dust farther down. Boring dust is only ejected from the entry hole during the first few inches of gallery construction. The female continues to the upper end and commences tunnelling once more.

It is uncommon to find the male and female together at the upper end of the gallery after a period of 2 or 3 weeks following gallery establishment. After this period, there is generally a considerable length of packed boring dust between the male and female. In most cases the male has left the gallery. In the observation apparatus, only a few males were able to keep the tunnel free of boring dust between themselves and the females. As was mentioned earlier, when the female feels an obstruction, even a larger than usual mass of boring dust, she stops her backward and downward movement, and moves up again. A plug of boring dust soon forms, which is packed more solidly every time the female backs into it. It is unlikely that the male will succeed in coming in contact with that female again. Under natural conditions the male commonly leaves the gallery. Under the artificial conditions described here, the males began constructing side galleries as they were unable to escape through the glass.

It is not known whether the female makes a definite effort to seal off the male, but while laying eggs the female does appear to be antagonistic towards the male.

Egg laying was observed to occur within two days following the release of the female and male in the gallery.

In summary therefore, results of this investigation were as follows:

1. Sexually mature young adults readily enter artificial galleries.
2. Mating can occur within $1\frac{1}{2}$ hours after the male enters the gallery.
3. Eggs are ejected rapidly in oviposition. Three eggs were laid within 15 minutes of each other after a 3 hour interval in which the female extended the gallery but did not lay any eggs.
4. Egg nitch plugs are formed by movement of the female up and down in the gallery. In so doing she forces loose bits of boring dust into the egg nitches. The eggs are thereby firmly packed in.

5. While the female is laying eggs she appears to be antagonistic towards the male.
6. The male commonly becomes sealed off from the female by packed boring dust in the gallery.

4. CHARACTERISTICS OF THE EGG GALLERY

The technique used to study this problem involved galleries established in 1956 in both caged and exposed logs. These galleries were debarked at intervals throughout the season, in the following manner:

1. The outer bark was carefully removed, thereby exposing the full length of the gallery but leaving the inner bark undisturbed.
2. The entire gallery, starting at the entry hole, was marked off into one inch segments.
3. The hatched and unhatched eggs were recorded for every inch of gallery.
4. The position of the female and male was recorded.
5. The survival of larvae and causes of mortality were recorded. This was possible only for periods up to 3 weeks following establishment of the gallery. After this time the deteriorated conditions of the original egg gallery made it impossible to identify specific causes of mortality.

Results discussed in this section and the following two sections were obtained in large part from these debarking operations. Appendix I, II and III contain summaries of the results. Appendix I and II contain records from galleries in which either no females were found, or the female had ceased laying eggs. These galleries are considered to be complete. Appendix III contains records from galleries in which the female only, or the male and female were present in the gallery and the female was still laying eggs and extending her gallery at the time of debarking. These galleries are considered to be incomplete. All adults were dissected later.

A common pattern in egg laying is evident, regardless of the length of the gallery. Three completed gallery lengths are illustrated graphically in Fig. 7. In this figure, eggs laid in each successive inch of the gallery have been averaged and the averages plotted. In Fig. 7 are averages of 12 completed galleries each 7 inches long, 4 completed galleries each 12 inches long, and 3 completed galleries, each 18 inches long.

Few eggs, if any, are laid in the first inch of gallery, but the number of eggs per inch increases rapidly thereafter. A maximum number of eggs per inch occurs in the 4th inch for completed galleries of 7 inches total length. The number of eggs per inch thereafter decreases sharply to the 6 inch mark. No eggs were laid in the 7th or last inch of gallery. A similar pattern occurs in galleries 12 inches in length. Galleries longer than 12 inches show considerable fluctuation over their total length but in the first few inches and the last few inches the pattern is similar to that in the shorter galleries. These three lengths are illustrated graphically to show this pattern. All lengths show a similar pattern as can be seen in the record of individual galleries summarized in Appendices I, II, III.

It appears therefore that short egg galleries, even as short as 5 inches, cannot be considered abandoned in the sense of a sudden exit by the female. The egg laying pattern is of course only a reflection of the activity of the female. Cessation of egg laying appears to be predetermined. In the 7 inch completed galleries illustrated in Fig. 7, the slowing down of egg laying commences at the 4 inch mark even though the total gallery length is ultimately 7 inches. All completed galleries show a similar pattern.

Incompleted galleries are summarized in Appendix III. These galleries are considered incomplete because they contained females which were laying eggs up to the time the gallery was exposed. It is noted that all these incompleted galleries are much longer than completed galleries. This is because the adults have remained working in these galleries for a much longer period, extending the gallery and laying eggs. Two incomplete galleries, one 21 inches long, and one 29 inches long, have been graphed out in Fig. 8 and Fig. 9 to illustrate the extreme fluctuations which occur in these long galleries. The 18 inch galleries in Fig. 7 illustrate this effect to some degree but in the process of averaging 3 of these galleries, some smoothing occurred.

5. INTERNAL CHANGES IN THE ADULT FEMALE ASSOCIATED WITH FLIGHT AND EGG GALLERY CONSTRUCTION

The egg laying pattern in galleries of various lengths, was described in the previous section. It is intended in this section to discuss the gross internal changes which take place within the female and relate these changes to the egg laying pattern.

Chapman (1955) has illustrated in some detail the changes which occur in the wing muscles, fat bodies and reproductive organs of the ambrosia beetle <u>Trypodendron</u> <u>lineatum</u> (Oliv.) during flying and non-flying periods. His observations on the ambrosia beetle to a very large extent can be used to

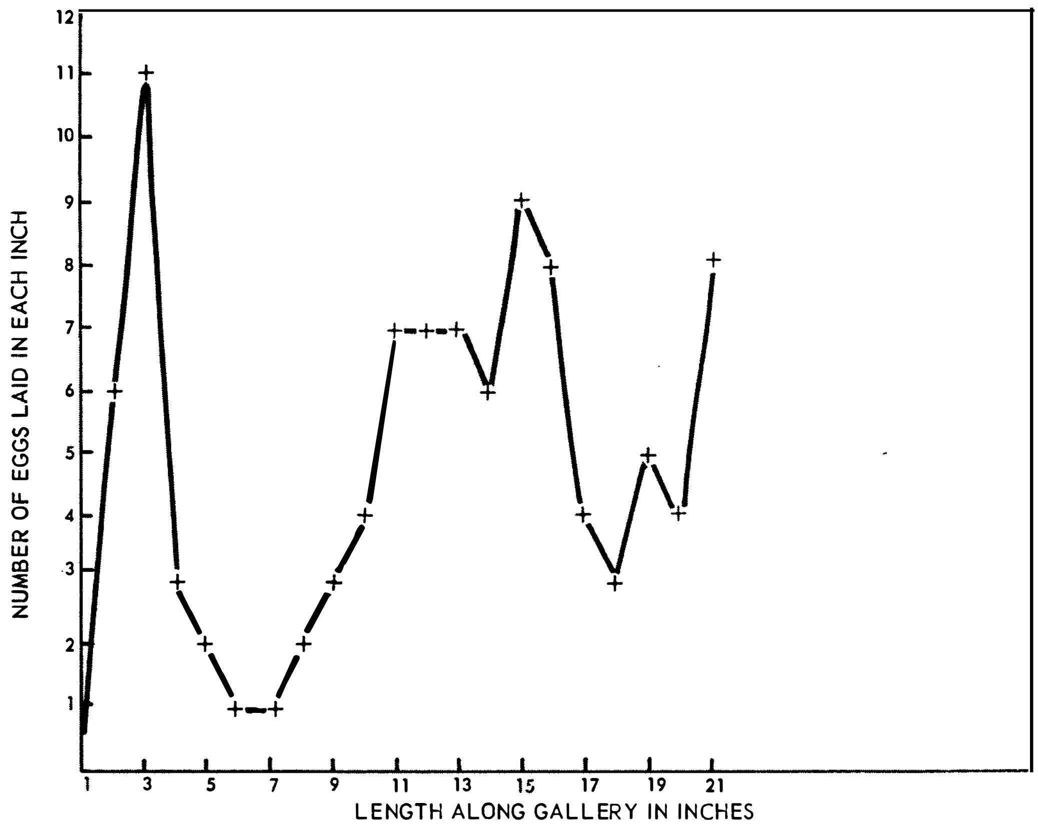

Fig. 8. Eggs laid each successive inch of gallery. (This gallery was 21 inches in length when it was exposed and was still being extended).

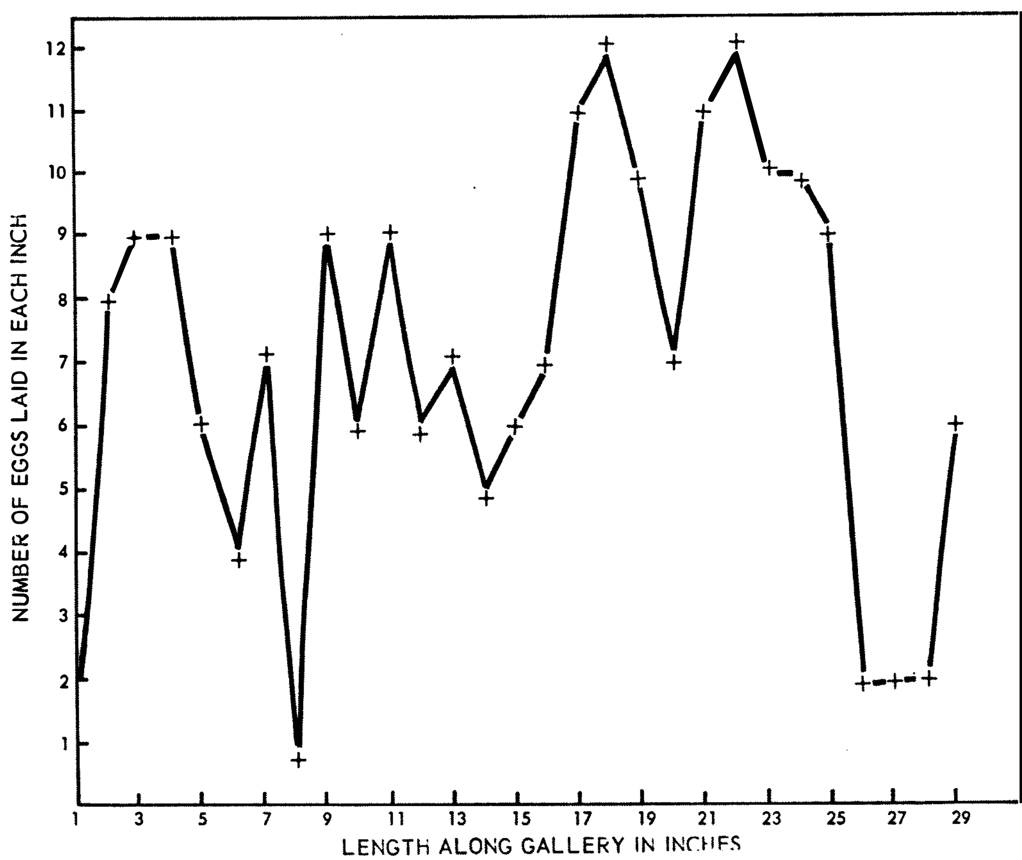

Fig. 9. Eggs laid each successive inch of gallery. (This gallery was 29 inches in length when it was exposed and was still being extended).

describe similar changes in the mountain pine beetle.

A large number of dissections were made of female mountain pine beetles during the past season. These dissections are described in Appendices IV to XI. Listed below are descriptions and summaries of the data in these appendices.

Appendix IV - Summarizes dissections made of young adults which were captured on the walls of cages, shortly after they had emerged from logs. They are progeny of broods established in the late summer of 1955.

The gross internal condition of insects at this period of their life cycle was as follows:

1. The wing muscles were massive and capable of supporting the female in flight.
2. The fat bodies were abundant.
3. The reproductive organs were reduced. They showed no history of egg laying.

Appendix V - Summarizes dissections of females known to be laying viable eggs at time of debarking. These females had been in their galleries for periods of 7 to 16 days.

The gross internal condition of females at this stage of their life cycle was as follows:

1. The wing muscles had degenerated to the extent where they were barely visible.
2. The fat bodies were common in females which had been in egg galleries for up to a week but considerably less than those

described in Appendix 4. Fat bodies were scarce in females after 2 weeks of gallery construction.

3. The reproductive organs were fully extended, ovarioles functioning normally, each of which contained immature oocytes.

Appendix VI - Summarizes dissections of females taken from completed galleries. These females had ceased egg laying. They would very shortly have left the gallery to establish their second brood. Viable eggs had been laid.

The internal conditions here resembled very much the condition of the young flying adults immediately following their emergence from their brood log.

1. The wing muscles were massive and appeared capable of sustaining the female in flight, which they would have required to do very shortly had not the gallery been exposed when it was.

2. The fat bodies were abundant.

The reproductive organs were reduced, in particular the 4 ovarioles which no longer contained oocytes of any size. Reproductive organs showed signs of egg production. In particular corpora lutea were conspicuous.

Appendix VII - This appendix summarizes dissections of young females which, following their emergence from their brood logs in July, 1956, were placed in jelly jars and fed on old bark for intervals ranging from 2 to 10 days.

There were no significant internal difference observed in females kept for 2, 4, 6, 8, 10 days after emergence. The wing muscles were massive, fat bodies were generally common to abundant, and reproductive organs were reduced.

Appendix VIII - Females with the same history as those described in Appendix VII except that they were fed on fresh inner bark.

During the 10 days, some females showed internal changes but in general, their condition was similar to those described in Appendix VII.

It should be noted here, that females described in Appendices VII and VIII had not been allowed to mate. They were not able to tunnel into the bark supplied as food as this bark was in very small pieces. They were subjected to natural light conditions.

Appendix IX - Summarizes dissections of young unmated females which entered fresh slabs of bark via artificially constructed tunnels. They were allowed to remain in these galleries for 7 days. The results are different from those reported in the two preceding appendices.

1. The wing muscles ranged from massive to mainly degenerated.
2. The fat bodies were abundant in all adults.
3. The reproductive organs ranged from reduced and non-functional to enlarged and containing mature oocytes.

It is possible that absence of light and certain tactile stimuli associated with tunnelling may be important in hastening the changes which are associated with egg production.

Appendix X - Summarizes dissections of unmated females which were removed after they had been in galleries for 55 days. The experimental design concerning these females was such that it is known they were unmated. The behaviour of these beetles will be discussed in more detail in the next section.

1. The wing muscles in all these females had degenerated.

2. The fat bodies were mainly abundant.

3. The reproductive organs varied from reduced and non-functioning to enlarged and mature. Only one female had laid any eggs, and these were not viable. Most had mature enlarged reproductive organs but had not laid any eggs.

In several of these females, yellowish 'yolk-like' masses were formed at the bottom end of the ovarioles. These may have been degenerated mature oocytes.

Appendix XI - Summarizes dissections of mated females which were made after cold weather had commenced. All these females had been mated and had established broods. They were taken from their galleries in early October. Egg laying had ceased due to cold weather.

1. The wing muscles remained in the degenerative condition.

2. The fat bodies ranged from common to abundant.

3. The reproductive organs were reduced in size and non-functioning.

It is evident that these overwintering females had not ceased egg laying in anticipation of another flight because wing muscles remained in a condition which would not support flight. The increased volume of fat bodies, as compared to the volume observed in the female at the height of their egg laying period, may be tied in some way to cold weather acclimatization.

The association between internal changes within the female and her behaviour within the gallery can now be postulated. This association is visualized diagramatically in Fig. 10 using for an example, a 7 inch completed egg gallery. Young females, upon emerging from their brood logs in July, have massive flying muscles, very conspicuous fat bodies, and reproductive organs complete but reduced in size and non functioning. These conditions remain for periods up to at least 10 days providing the female does not mate or establish a gallery. In most cases galleries are established within the same day of emergence. As illustrated in Fig. 7, few if any eggs are laid in the first inch of gallery. Once the gallery is established many significant changes take place within the female beetle. After mating has occurred (generally during the excavation of the first inch of the gallery), the wing muscles undergo a rapid degeneration and the reproductive organs, especially the ovarioles, begin a rapid development. Egg production commences and a few eggs are laid in the 2nd inch of gallery. Fat bodies become less abundant also, while the ovarioles produce eggs at an increasing rate. Wing muscles have been reduced to an insignificant size by the time the gallery is 3 inches long. Egg laying reaches a peak in the 7 inch completed galleries at the 4 inch mark (See Fig. 7). Egg production declines rapidly while the fat bodies begin once more to accumulate inside the female. Likewise wing muscles commence to build up. By the 6 inch mark egg production has ceased, reproductive organs and especially ovarioles have been greatly reduced in size, wing muscles are massive and capable of sustaining the female in flight, and the body is packed with fat bodies. At the 7 inch mark the gallery is complete, and the female bores her way out from the gallery and commences another flight. If very fortunate, she is able to successfully establish another gallery, mate, and continue egg laying until stopped by cool fall weather. Her internal conditions at this stage were described earlier in the discussion of Appendix XI.

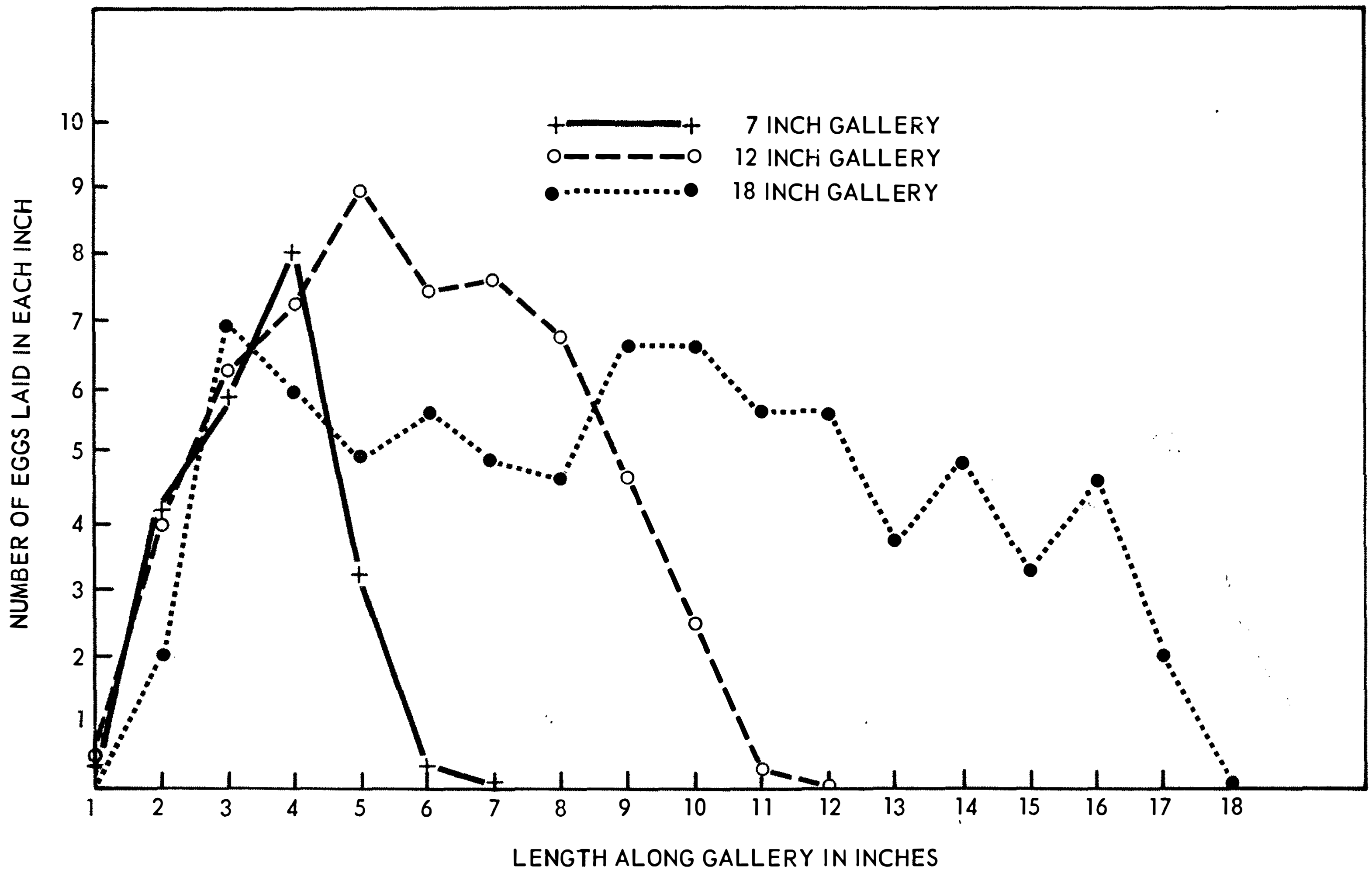

Fig. 7. Eggs laid each successive inch of completed gallery. 7 inch, 12 inch, 18 inch galleries illustrated.

6. NOTES ON THE RELATIONSHIP BETWEEN THE SEX RATIO OF THE POPULATION AND EGG GALLERY BEHAVIOUR OF THE FEMALE

During the course of debarking logs to examine egg galleries in the latter part of the 1955 season, the very long galleries frequently were observed to contain both the male and female beetle. They were galleries which had been established during the main beetle flight.

TABLE I - Averages of Gallery Lengths - 1955-1956 (From Appendix XXII)

Type of Gallery	Nos. of Galleries	Mean Length (ins.)	Standard Deviation
No adults when gallery exposed	124	9.9	5.6
Only female in gallery when exposed	117	12.2	6.8
Male and female in gallery when exposed	56	18.2	6.4

Table I contains a summary of gallery lengths recorded in 1955 and 1956. Three classes of gallery are compared in this table; i.e. galleries in which no males or females were found, galleries in which only females were found, and galleries in which both male and female were found. Galleries in which the males remained with the females were significantly longer than galleries containing only females. Galleries without adults were known to have been completed early in the season. The majority of galleries containing only females would have been completed in a short time if debarking had been delayed. The frequency distribution of gallery lengths are tabulated in Appendix XXII.

In other words, four phases are associated with every completed gallery; 1) Female iniates gallery; 2) she is joined by the male; 3) the male leaves; 4) the female leaves. These four phases can be interpreted from Table II which summarizes the percentage of adults found in the galleries within short periods following the attack. All the galleries in these exposed logs contained broods, indicating that the females had been mated. Within slightly over two weeks, 21% of the females had completed short galleries and then left, 42% of the females were alone in their galleries, and only 37% of the females were still accompanied by the males. By 3 weeks, 72% of the galleries were completed and by 4 weeks 90% were completed. No quantitative data is available to indicate at what precise time the majority of males leave their first gallery. Observations on caged logs suggest that it is within 2 or 3 days. It is important that males do leave their first galleries early because in the experimental area the sex ratio is around 0.43. Therefore, the males probably mate with at least 2 females each in separate galleries.

TABLE II - Showing Percentage of Galleries containing adults - Galleries established July 8 - 11, 1956. Logs debarked at indicated dates.

Log	Nos. of Galleries	Date of Debarking	% galleries with males and females	% galleries with only females	% galleries with no adults
1	43	July 25 to Aug. 2	37	42	21
2	36	July 27 to Aug. 7	6	22	72
3	62	Aug. 8 to Aug. 10	1	9	90

It is the belief of the writer that the presence or absence of the male determines in large part the length of the egg gallery and the number of egg galleries established throughout the season by each female. An experiment was carried out during the 1956 season which was designed to supply evidence to support this.

Ten logs, 3 feet in height and 9 - 11 inches in diameter, were secured in a vertical position within separate cages. Into each cage (1 - 10), were released 10 unmated but sexually mature female bark-beetles. At the same time the following numbers of males were released in cages 2 to 9: Cage 2 - 1 male; cage 3 - 2 males; cage 4 - 4 males; cage 5 - 6 males; cage 6 - 8 males; cage 7 - 10 males; cage 8 - 12 males; cage 9 - 14 males. These logs were examined at close intervals throughout the summer and each new strike was marked and recorded. The time of release, time strikes were established, time of debarking and information concerning each gallery are summarized in Appendices XII to XXI.

It should be noted that the original sex ratios were altered by the time the logs were debarked in the fall. This was due to the high mortality rate and deaths unequally distributed between males and females. In the appendices are given the estimated sex ratios which were believed to be effective rather than the sex ratio calculated from released beetles. Dead adults were collected as they appeared on the floors of the cages. Some of the beetles were missing and the date of their disappearance can only be guessed.

Logs in cages 2 to 8 and cage 10 were not debarked until the fall, allowing beetles over 50 days for gallery establishment.

Logs in cages 1 to 9 were debarked earlier. These results will be discussed first.

The log in cage 1 was debarked after 15 days. Unmated females had constructed one gallery each. The longest was 4 inches. No eggs had been laid.

Cage 9 log was debarked after 16 days. Mated females had constructed galleries up to 11 inches in length in this 16 day interval. Broods were established in 6 of the 11 galleries. All but one surviving female had been mated. This beetle was not at all active when removed from the 1 inch long gallery. Reasons for its behaviour were not discovered. Note the increased rate of gallery construction exhibited by mated females compared to unmated females.

Logs in cages 1 - 8 and 10 were debarked in September, In cage 10, in which, 10 females but no males had been released, unmated females constructed up to 3 galleries apiece before the log was debarked. These beetles were released later than the others and hence could not take advantage of the extremely warm July weather. Their first galleries ranged from 1 - 6 inches in length and averaged 3.5 inches. Their second galleries ranged from 3 - 9 inches in length and averaged 6.6 inches. Some were in the process of extending their third gallery when the log was debarked. Several eggs were laid by one female in this cage but none of them was viable.

It was observed in all cages where unmated females existed, that gallery behaviour of these females was characteristic, i.e. they were slow in extending their galleries, their galleries commonly wandered whereas the mated females constructed essentially straight egg galleries. The unmated females keep their first and sometimes second galleries free of boring dust, thus facilitating the entry of the males. Galleries containing unmated females can frequently be classified as such by observing the continual dribble of boring dust from the entry holes.

In cage 2, the estimated sex ratio was 0.14, and the single male mated 2 females. Unmated females constructed up to 4 galleries each. These galleries got progressively longer. The 3rd and 4th galleries constructed by unmated females were generally plugged with boring dust. Egg nitches were sometimes constructed. No eggs were laid however by unmated females in this experiment. The average length of gallery constructed by unmated females was 2 inches. The single male mated with one female on July 9 and with one female August 6.

The sex ratio in cage 3 was estimated to be 0.20. Seven of the 16 galleries contained broods. Some females were not mated in their 1st galleries but were mated in their 2nd galleries. Two males mated with the 6 females which established broods. The average length of gallery constructed by unmated females was 3 inches, and of mated females was 13 inches.

In cage 4, all the surviving females were mated. The estimated sex ratio was 0.40 (The sex ratio in the wild population in 1955 and 1956 was 0.43).

In cage 5 all but one gallery contained broods. The estimated sex ratio in this cage was 0.37. Heavy brood mortality occurred in this log due to the galleries being concentrated on one aspect. These galleries constructed by mated females averaged 12 inches in length.

In cage 6 all the galleries but one contained broods. The one female which did not establish a brood, nevertheless extended her gallery a total length of 18 inches. She probably mated but, for some unknown reason, was incapable of laying eggs. The sex ratio in this cage was estimated to be 0.80.

In cages 7 and 8, the sex ratio's were estimated to be 1. All galleries contained broods. The galleries were in most cases exceptionally long.

The data summarized in Appendices XII to XXI, is interpreted to indicate the following:

1. Unmated females can construct at least 4 separate galleries during one season. All these galleries are shorter than average egg galleries but can reach lengths up to 9 inches. The later galleries are longer than the first. The first galleries are frequently kept clean of boring dust.

2. The rate of gallery extension is much faster among mated females than among unmated females.

3. One male commonly mates with 2 females. Less commonly, single males are able to mate with 3 females.

4. A sex ratio of 0.40 can result in all the females being mated.

5. Some mated females constructed up to two galleries and established broods in each.

6. In cages where the sex ratio is 1.0, the average gallery length is longer than in cages where the sex ratio is less than 1.0. It is not known if the two factors are related.

In order to synthesize what has been discussed in this and early sections, a review of the main conclusions is pertinent.

1. Observations of males and females in egg galleries suggest that once mating has occurred, the female frequently blocks the gallery with

boring dust, which prevents the male from remaining with her. The male, if unable to keep up with the female, will bore its way out of the gallery. It is known that in wild populations and caged populations, the male leaves the gallery before the female.

2. In short galleries there is a definite egg laying pattern; the number of eggs laid per inch rising to a peak then declining rapidly. In long galleries there is a series of fluctuations, each fluctuation resembling to some degree that described for the short galleries.

3. There are pronounced internal changes which take place within the female and these can be related to the egg laying capacity which in turn is merely a reflection of ovariole activity. These relationships are more apparent in short completed galleries.

4. Galleries containing males and females are extended to greater lengths than galleries containing just females. This is because the females remain for a longer period in the gallery if males are present.

5. The presence of the male stimulates the female into immediate gallery extension. Fertilization does not appear essential for activation of the reproductive system in all females. From information available to date, however, fertilization seems to be essential for production of viable eggs. While it appears that the presence of the male greatly hastens the activation of reproductive organs, it is not known if this is due entirely to fertilization or not. However, once mating has taken place, egg laying and all the associated internal changes soon follow. In the absence of the male, some females appear capable of a partial reproductive system development but only after a lengthy period.

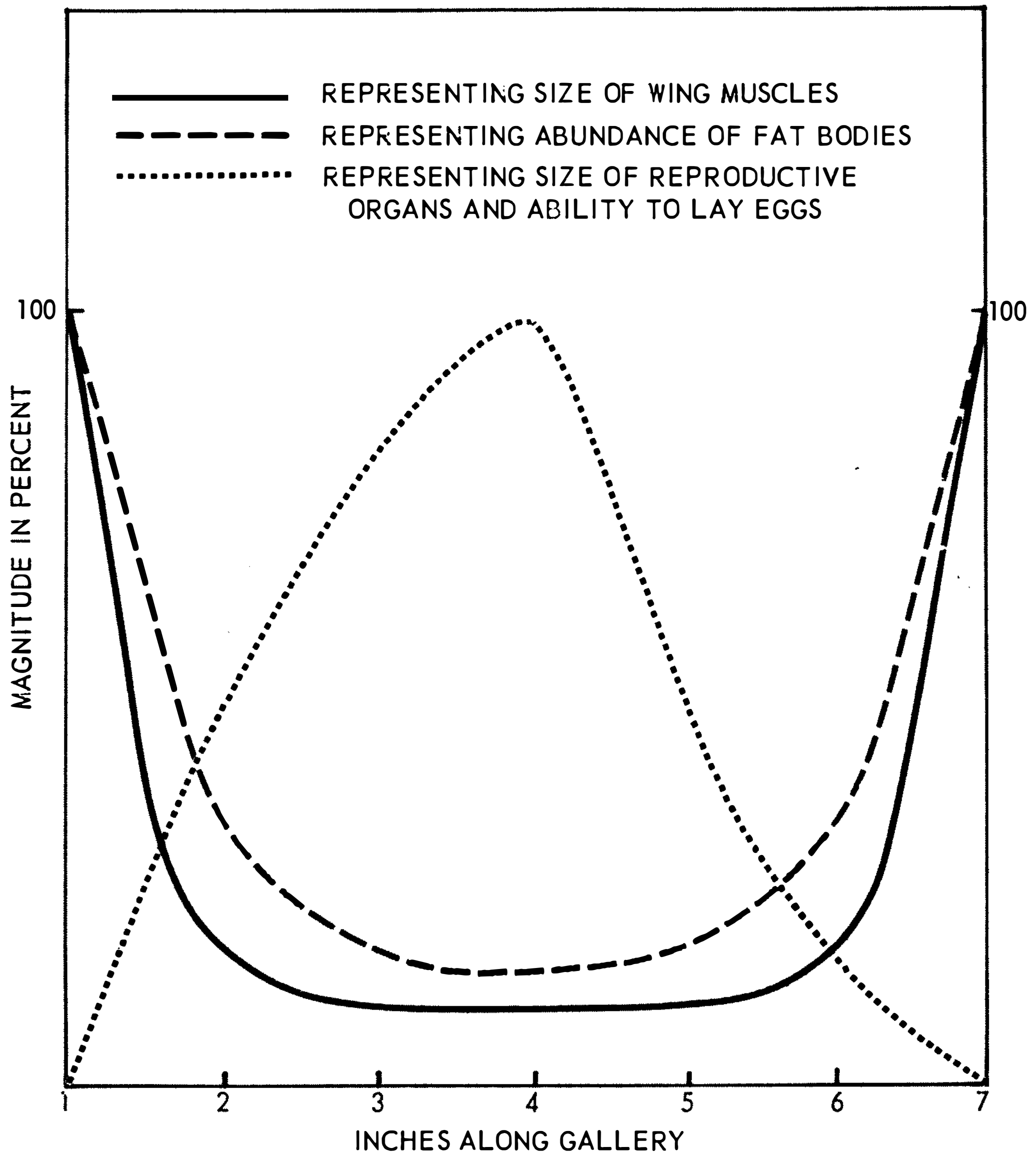

Fig. 10. Illustrating diagramatically the internal changes which occur in a female beetle from the time it commences construction of a 7 inch egg gallery to the time it is ready to abandon the gallery.

The behaviour and internal condition of a hypothetical female will be followed as it constructs a 7 inch brood gallery.

A young female emerged at midday from its brood log, and flew to a fresh log where it succeeded in establishing a gallery. This young female possessed massive flying muscles, its body was packed with fat bodies, and its reproductive system was reduced. By the following day this female had excavated 1 inch of gallery, the boring dust having been forced out the entry hole. The female at this time begins to reduce the rate of gallery extension. Internal conditions i.e. wing muscles, fat body, reproductive organs have not altered appreciably (See Fig. 10 and Sec. 5). At this stage, a male locates the entry hole of the gallery and enters. Mating soon follows. As a result of this mating, changes commence which are described in Section 5. There is a rapid enlargement of reproductive organs, especially ovarioles. Oocytes commence to develop. Fat bodies supply much of the required energy for egg production and hence their abundance decreases. Wing muscles diminish in size. The female commences to elongate the gallery, depositing more and more eggs per inch as the ovarioles increase their output. However, the male has not been able to keep up with the female and by three days the gallery between the two beetles is plugged with boring dust. The male then leaves the gallery. The egg production per inch reaches a peak by the time the gallery is 4 inches in length. Egg production begins to decline and continues to do so for the next several inches. By the time 5 to 6 inches of gallery have been constructed, the female beetle requires to be mated again. This does not occur however as the male, being unable to keep up with the female, left the gallery earlier. Stimulation by the male not being available, certain changes within the female commence, or if they had commenced earlier, are now accellerated. These changes include a shrinking of the reproductive organs and especially the ovariole an accumulation in volume of the fat body, and a vast increase again in the size of the wing muscles. These changes occur while the female is slowly extending her gallery to the 7 inch mark. At this point she is physiologically about in the same condition as when she left her own brood tree. She bores out through the bark and if fortunate, is able to establish a second gallery where the process described above may be repeated.

Longer galleries as shown graphically in Figs. 8 and 9, are originated in the same manner as that described for the 7 inch completed gallery. The males however, remain longer in these galleries. For instance in Fig. 8, the female which constructed the 21 inch gallery, was about to abandon this gallery after 5 inches and probably would have if the male had not remained in the gallery. Mating took place and the female then recommenced egg laying. In this same gallery, it is probable that mating took place again when the gallery was 14 inches long and again when 18 inches long. A similar situation is seen in the 29 inch gallery, Fig. 9. Mating in this gallery appears to have occurred when the gallery was 1, 8, 14, 20, and 26 inches long respectively. In each of these galleries, male and female were together at the upper end and egg laying was continuing at the time they were exposed by debarking.

Because the male can leave the gallery at any time, a wide range of gallery lengths occurs. It is known that gallery lengths will vary directly as the size of the female (Sec. 12). From careful debarking records, as tabulated in Appendices I, II, III, it is believed that a range in gallery length, due mainly to size and vigour of the female, can vary from 5 to 12 inches following the initial mating. However, a small female which normally constructs 5 inches of gallery following mating, would be able to construct a much longer gallery if the male remained with her.

Males are not always found with females in the very long galleries, but if the female is still in the gallery and still laying eggs, then it can be assumed the males left not long before the gallery was examined.

It is apparently common for some young adults of Dendroctonus micans the only European species, to mate in their brood galleries prior to emergence, (Husson and Stauder 1954, reporting on observations by Francke-Grosmann). The writer is fairly certain this does not occur in D. monticolae populations. The possibility of its occurrence however, will be re-investigated in the 1957 season.

7. NEMATODES

An extensive nematode complex is associated with mountain pine beetle galleries. A list of species and where they were found is given in Table III. The identifications were made by Dr. M.A. Khan, Nematode Investigations, Science Service, Ottawa.

Little is known on the biology of many of these nematodes, nor on the effect they have on the mountain pine beetle. It is probable that only a few are directly parasitic. There is a large insect and arachnid fauna associated with mountain pine beetle broods, including many scavenger and phytophagus type feeders. Likely many of the nematodes, listed in the above table, more directly concern these latter forms.

Some specific information is available on Aphelenchoides sp. and Sphaerularia hastata.

TABLE III - Nematodes Associated with Mountain Pine beetle - 1956

Species	Where Found
Sphaerularia hastata Khan	Digestive tract of adults Body cavity of adults Reproductive organs of adults Egg nitches
Sphaerularia sp. (Juvenile stages)	Frass in main gallery
Aphelenchoides tenuidens Thorne 1935	Egg nitch Frass in larval galleries Frass in main gallery
Aphelenchoides brachycephalus Thorne 1935	Egg nitch Frass in larval galleries Frass from main gallery
Aphelenchoides latus Thorne 1935	Frass from main gallery
Aphelenchoides talonus Thorne 1935	Egg nitch Frass from main gallery Frass in larval galleries
Aphelenchoides sp. (Juvenile stage)	Digestive tract of adults
Aphelenchoides sp.	Frass from main gallery
Panagrodontus dentatus Thorne 1935	Egg nitch Frass from main gallery
Diplogaster pinicola Thorne 1935	Frass from main gallery

Aphelenchoides sp. are found moving freely throughout the moist regions of the egg and larval galleries. They attach themselves under the wing pads of pupae, tenerals of all ages, and of adults. They do not appear to mechanically damage their host. They are transported from gallery to gallery by securing themselves to the membraneous wing of adults. Observations reveal that the menatodes invariably attach themselves to one specific area of the of the wing, the jugal fold (as described by Snodgrass p. 237, 1945). When the beetle is in the gallery, the membranous wings are folded under the elytra, the jugal lobe at this time is folded over, along the line of the jugal fold. The nematodes force their way beneath this jugal lobe and secure themselves along the jugal fold, generally in that portion closest to the wing sclerites. Examination of these nematodes under the binocular microscope indicate that they "cement" themselves directly to the wing. They appear to excrete a substance from the region of the head. They attach themselves in a group, and no more than one group has been observed per wing. The effect of this mass of nematodes on the flying ability of the beetle is not known.

Sphaerularia hastata is an important parasite and the discussion which follows refers to this species. Both male and female beetles are parasitized and mortality of the host generally results when these nematodes are numerous. Results of dissections were reported in the 1955 report. A summary of the 1955 conclusions is as follows:

1. 24% of the adults examined in the experimental area were known to contain *S. hastata*. The numbers of nematodes varied from a few per adult to over 3300. When nematodes occurred in numbers over 2000, death generally soon followed.

2. The egg production of infested females was found to be 33% less than egg production by non-infested females. Egg production was reduced because the parasites reduce the vigour of the adults. No mechanical damage to internal organs was observed.

3. The largest percentage of nematodes was found in the body cavity. Very few were found in the digestive tract. None was found in the proventriculus

or ventriculus. A few were found in the mid gut and hind gut. Large numbers of nematode eggs were found in the body cavity of heavily infested adults.

4. From available evidence in 1955, the following life cycle was postulated: bark beetles, tenerals or adults, ingest parent nematodes. These nematodes are known to move freely through the frass and galleries. The ingested nematodes pass through the digestive tract into the upper intestine. They move through the intestinal wall into the abdominal cavity. The time they spend in this region, without reproducing, is not known. Up to this time there is little effect on the host. After a period of time, the female nematodes produce large numbers of eggs, which hatch in the body cavity of the host. This increased parasitism begins to affect the vigour of the host. Eventually the number of nematodes increases to such an extent that the death of the host results. The nematodes force their way out of the carcass, move through the frass, and some are ingested again by other adult bark beetles. The cycle then repeats.

A large number of dissections were made of adult beetles during the 1956 season. Fortunately, electricity was available at the site, permitting binocular microscope examinations of fresh galleries and adult dissections. No quantitative data was collected on the effect of nematodes. However, observations on their method of dispersal, methods of infection, etc. were continued.

Sphaerularia hastata is able to move freely throughout the gallery providing there is a high moisture content. The movement of the nematodes is facilitated by the presence of fungi. When egg galleries have been established for short periods, and larval galleries are being extended, the bark surrounding these galleries frequently supports active infections of fungi. The inner bark shows a definite brown stain resulting from the fungi. The bark fibres appear to be loosened, the region turns rather spongy and loose. Nematodes were observed to move through these areas very easily. They can thereby move from one bark beetle gallery to another, so that a single nematode infested gallery can contaminate many others.

Little was learned this past season on how the beetle becomes infested with S. hastata. As was mentioned earlier however, entrance is probably through the oral cavity of the beetle. Free living stages are very active in the bark of beetle infested trees. It is conceivable that they could find their way deliberately or by chance, to the digestive tract of the adult.

Similar to results of last years dissections, no S. hastata nematodes were found in the proventriculus or ventriculus. A few were found in the hind gut and rectum. Moderate numbers were found in the reproductive organs of females which had been laying eggs immediately prior to their being dissected.

Occasionally, after debarking galleries in which eggs had been laid, it was found that none had hatched and all had collapsed. These collapsed eggs could be easily spotted because the region immediately around the egg nitch was stained a dark blue to black by a fungi infection. Examination of egg nitches containing collapsed eggs in most cases revealed small clusters of nematodes between the collapsed egg corium and the wall of the egg nitch. It was believed at first that the nematodes were responsible for the destruction of the eggs. When close examination was made of freshly laid eggs it was often observed that small numbers of nematodes were either moving over the egg or were between the egg and the egg nitch wall. A number of these eggs, containing nematodes on their outside, were reared through. In no case was an egg deflated as the result of penetration by the nematodes.

A female beetle was dissected which had just previously laid eggs having the nematode associations described above. It was found that the reproducti system contained nematodes, fairly numerous, but not sufficiently abundant to impede oviposition. Within the vagina, nematode larvae and eggs occurred in loose formation. Nematodes were found appressed to the walls of the median oviduct The largest numbers occurred in the bursa copulatrix. Within this organ they were all aligned and in sufficient numbers to give the organ a turgid appearance. It appears very likely therefore that the nematodes associated with the newly hatched eggs were ejected with the egg. Nematodes would have many opportunities to attach themselves to an egg as it moved down the median oviduct to the gonipore and was then ejected.

Concerning the deflated eggs which were mentioned above, it is known that non fertilized eggs deflate soon after oviposition. They appear to have a very fragile corium. It may be that some eggs laid by female beetles which have nematodes in the reproductive system, are not fertilized because the male sperm has been disturbed in some way. These eggs would be oviposited but would be non-viable and soon collapse. Most of the eggs having the nematode associates, hatched and the larvae appeared to behave normally. The nematodes move throughout the larval gallery. While few larval dissection have been made, no evidence has been found to date that these nematodes affect the larvae.

The largest proportion of nematodes are released from the adult when it dies. Heavily infested beetles can frequently be determined as such by their behaviour. Their movements are very lethalgic and they do not attempt to escape when removed from the galleries. If placed on their back, they make no effort to right themselves. There is frequently a noticeable tremor in the antennae and the legs. Several adults, displaying these symptoms, were placed under observation. All died within 4 days. Immediately following death, S. hastata larvae and adults were observed leaving the body of the host. In most cases they appeared to force their way through the sutures, between the sclerotized portions of the abdomen. Within a short time, nematodes appeared in high numbers and moved into the surrounding boring dust and frass of the gallery. The length of time spent in this free state is not known.

8. INSECT PREDATORS AND PARASITES

No specific investigations were carried out during the past season on biologies of predators and parasites. The most important predators were the Diptera as recorded in last years report i.e. Medetera aldrichii Wheel., Medetera viduus Wheel., and Lonchaea sp. watsoni complex; and one hymenopteron, Coeloides dendroctoni Cush.

It was mentioned in last years report dealing with the biologies of the predators and parasites, thatC. dendroctoni, while present in fairly high numbers, was not found to be of great significance. A similar conclusion was arrived at after this season's work.

Cage studies this season have shown that the life cycles of the predators and parasites parallel that of the host. Coeloides and Medetera emerged from 1955 bark beetle infested logs from June 21 to July 19th. They commenced emerging from logs infested early in 1956, on September 10th and continued to October 8th. The emergence is summarized in Appendix XXIII.

While no specific investigation concerning these insects was carried out, critical data on their combined effects were obtained in the course of

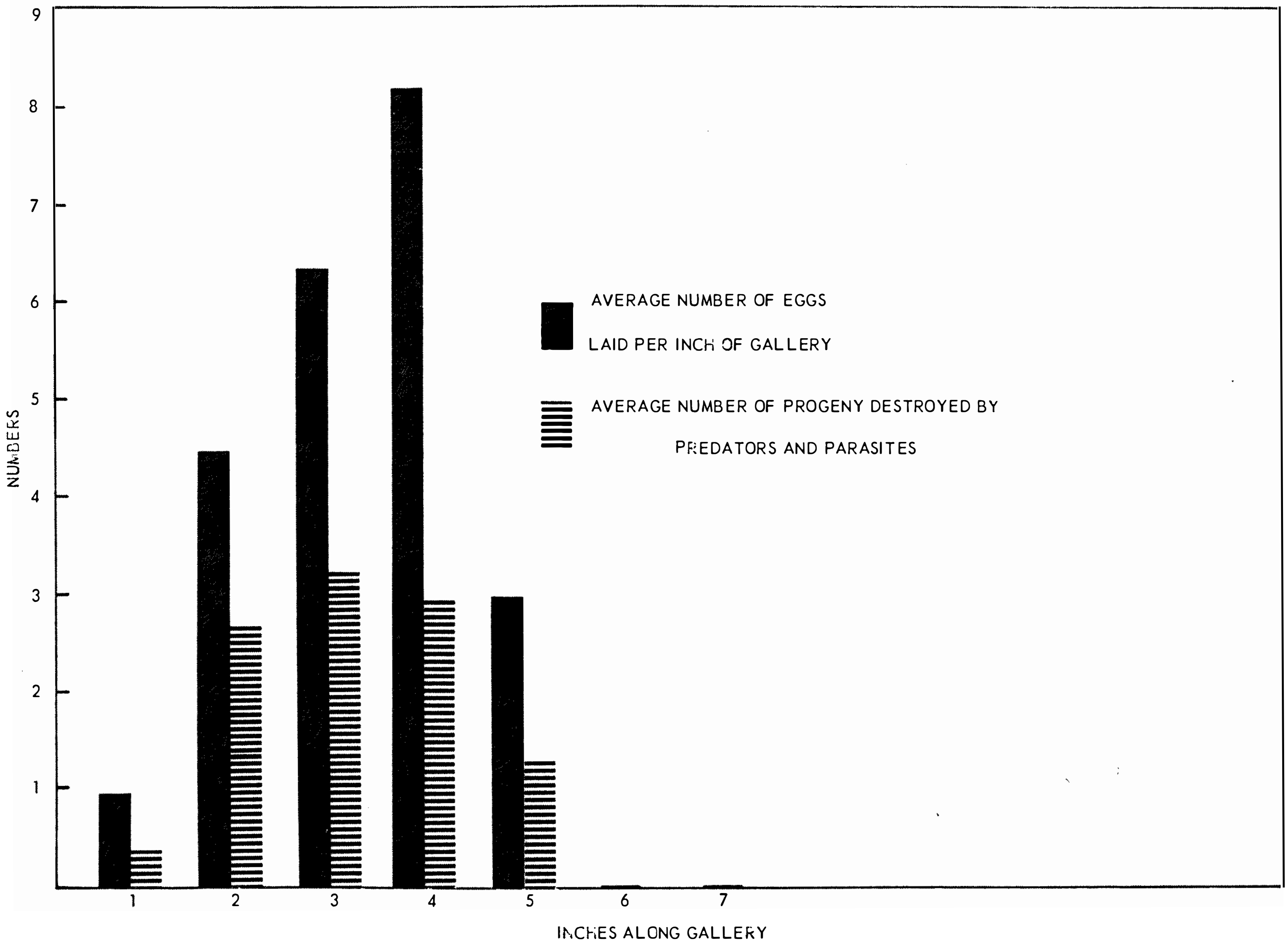

Fig. 11. Illustrating effect of predators and parasites on broods of mountain pine beetle - 1956. (average of 12 completed galleries each 7 inches in length and 2 - 3 weeks old).

debarking exposed logs. Mortality to bark beetle broods by predators and parasites has, of necessity, been grouped. However, the largest percentage of mortality is attributed to larvae of Medetera aldrichii. In Table XII, which summarizes data from debarked logs, specific causes of mortality are not shown after the 3rd week following the time of gallery establishment. The reason is that after this period, larval activity, interference from adjacent galleries, molds and fungi, etc. combine to make causes of individual larval mortality confusing. A similar situation occurred during the 1955 season. It was believed in 1955, that mortality of larvae from predators and parasites, in the exposed logs, would not be much higher than 10 - 12 per gallery. This is now believed to be incorrect. Mortality from predators and parasites (especially M. aldrichii) is believed to be very much higher. Unfortunately no exact figures are available. Accurate data of this type is difficult to obtain as there are so many other variables which will determine the final effect.

However, up to a certain time, following establishment of the gallery, specific information on brood mortality can be determined. The number of predators and parasites responsible for this mortality is seldom available. Techniques used to study gallery patterns were described in Section 4. In a number of these galleries it was possible to determine survivors per inch. The mortality is probably due mainly to larvae of M. aldrichii as this was the most common larva found, other than the host. This mortality is illustrated in Fig. 11. The histogram shows the average number of eggs laid along each inch of a 7 inch completed gallery. (The figures are averages from 12 completed 7 inch galleries). These were established during the first flight of beetles from July 7 to 17. The effect of predators and parasites is considerably less on the second flight but comparable figures are not available. In these completed galleries, mortality of near 50% has occurred in a period of less than 3 weeks. It is apparent that this heavy mortality of broods established by the first flight will greatly influence the time when the first emergence occurs from that brood later in the season.

The survival of the first brood in logs protected from predators and parasites (Table XIII) was almost 50% higher than the survival in logs subjected to pressure from predators and parasites (Table XII). This latter table indicates 95% mortality in the first broods by August 23rd. Lethal effects of crowding are apparent in both caged and exposed logs. Similar results were obtained in last year's work, i.e. the survival of the first brood in caged logs was very much higher than brood survival in logs subjected to pressure from predators and parasites.

Seoond broods in exposed logs are not subjected to as much predation and parasitism as first broods. They enter the overwintering stage before adverse effects of crowding become severe (Table XII, log T1).

9. CROWDING

Specific information on the effects of crowding, like the effects of predators and parasites, are not available. It is known, however, that crowding is a very important factor in the environment of the mountain pine beetle broods.

The effects of crowding must be considered from three aspects i.e. 1) crowding between members of the same brood, 2) crowding between members of adjacent broods, 3) crowding from other species. Crowding between members of adjacent broods is believed to be the most important in the experimental area.

The direct effects of crowding on brood survival are known to vary directly with the length of time of brood establishment. The effects of crowding are negligible despite high density of attack, for periods up to 2 weeks following establishment of the galleries, providing all galleries are established within a few days of each other. If the attack period on log or tree extends over a long period, the galleries established in the early stages have a great advantage over those established later. After periods of 2 - 3 weeks, larval galleries of adjacent broods have begun to interfere with each other. Mortality then commences and increases rapidly. There is some evidence to indicate that in the first flight broods, which establish galleries in high density per unit area, mortality from crowding with adjacent broods is responsible for up to 50% mortality. The egg galleries are also of importance in determining this mortality. In the previous section considerable early brood mortality is attributed to predators and parasites. This thinning out of the broods undoubtedly reduces the degree of crowding between larvae. It is apparent that the interactions are very complex.

The direct and indirect effects of crowding plus the effects of predators and parasites are believed to be responsible for the almost complete decimation of the first broods. Even in caged logs, mortality of the first brood is close to 50% by September and this is attributed largely to direct and indirect effects of crowding.

The second broods in caged logs in 1955 suffered less from crowding because cool weather halted development before the galleries were far advanced. Emergence from these logs in 1956 indicated the effects (direct and indirect) of crowding operated mainly during their period of development in 1956.

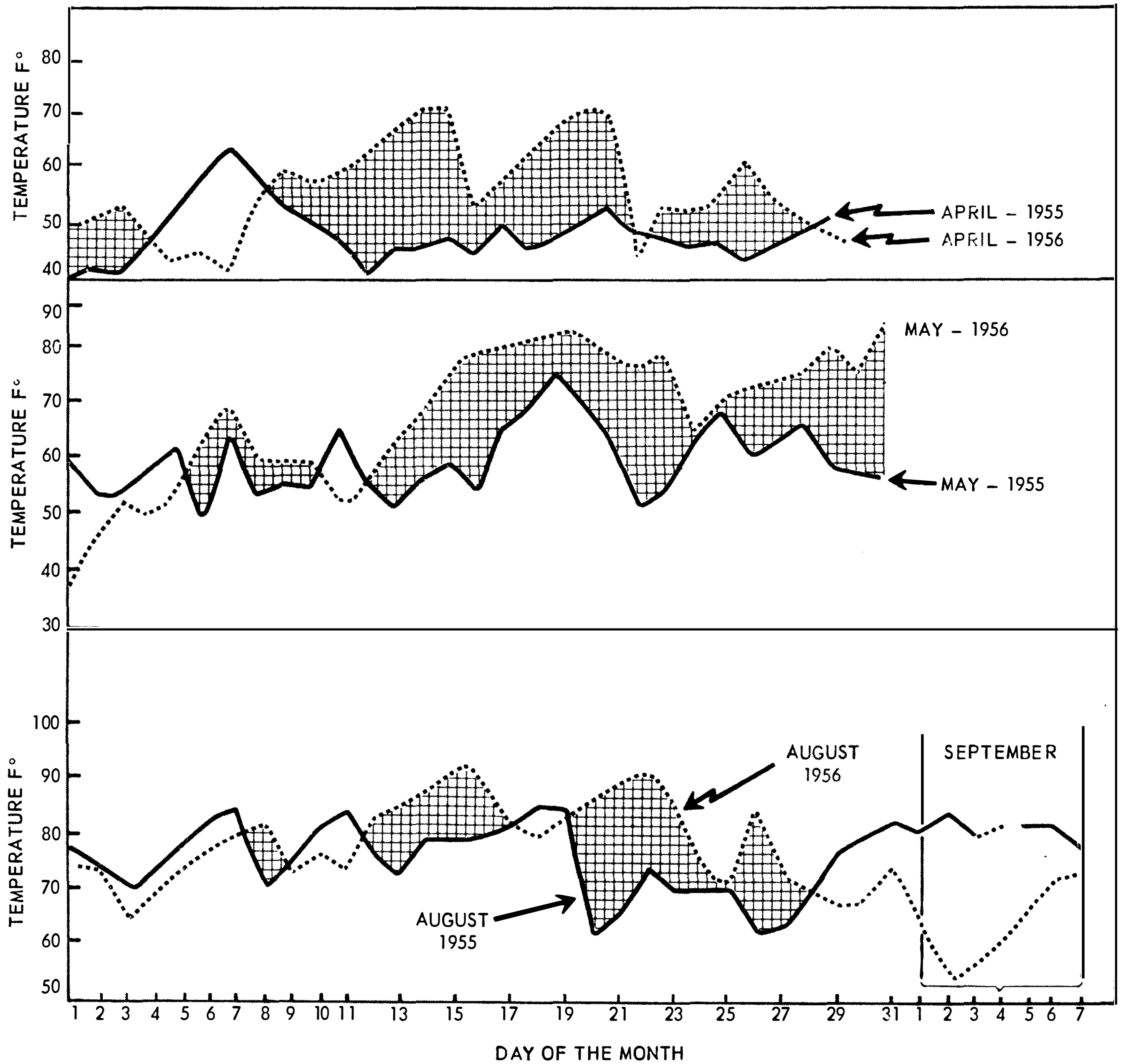

Fig. 12. Comparing maximum and minimum temperatures (F^{O}) for 1955 and 1956. April, May, August, September. Invermere, B.C.

In Table XII, Log T1 contained second broods of the wild population. Up to the sixth of September combined effects of predators and parasites and crowding were responsible for only 31% mortality. These broods were more advanced than the previous years second broods, hence crowding effects were likely more significant before the broods ceased development due to cold weather.

10. TEMPERATURE

Daily maximum and minimum temperatures were recorded in the experimental region from June to October. Temperatures as reported at the Department of Transport Station, Kimberley, B.C. were used for those months for which temperature records were not available in the Invermere region. The weather in both regions is very similar.

Maximum and minimum temperatures for the months June to October 1956 are recorded in Appendix XXIV. Maximum temperatures during April, May, and August in 1955 and 1956 are illustrated in Fig. 12. It was shown in Section 2 that emergence and attack periods of the main flight were almost 3 weeks earlier in 1956, than in 1955. This was probably due to the high daily temperatures in April and May, 1956. Survivors of the overwintering broods commenced development earlier and proceeded at a more rapid rate in 1956 than in 1955. The final result was a much earlier emergence.

Cool weather in late August and early September (Fig. 12) prevented the emergence of survivors from the early July broods (See Fig. 6) until September 7.

An experiment was set up in the fall of 1955 to supply some general information on the winter mortality in broods of the mountain pine beetle.

Two 5 foot logs were secured in an upright position in such a manner that they were above the anticipated snow line. Two 5 foot logs were placed on the ground in a position which would ensure that they would be covered by snow. One of the logs above the snow line and one of the logs below the snow line contained broods established during the first flight of parent adults that previous summer. The other two logs contained second flight broods. All logs had been caged and thus predators and parasites had not affected the broods. In addition, one log containing first flight broods was allowed to overwinter above snow line at the Eisenhower Field Station, Banff National Park.

The snow depth above the logs, in the Invermere area, was 18 inches when measured in March, 1956. All the logs were debarked in May, 1956.

Results of this experiment are shown in Table IV and illustrated in Fig. 13. The number of galleries per log, number of living and dead larvae, pupae, and adults per gallery are shown for logs which overwintered above the snow line and below the snow line.

The broods in "B" logs were second flight galleries and contained large numbers of eggs in the fall of 1955. No eggs survived the winter, either above or below the snow line. Few pupae are generally found in overwintering broods. It will be noted that mortality of broods was for all practical purposes, complete in the logs which overwintered at the Eisenhower Field Station. No winter temperatures are available from the Eisenhower Field Station region so Banff winter temperatures have been substituted. The two sites are only 20 miles apart. The winter temperatures in Banff are known to be less severe than those occurring at the Eisenhower Field Station. Winter temperatures for the Banff area and Invermere area are shown in Table V.

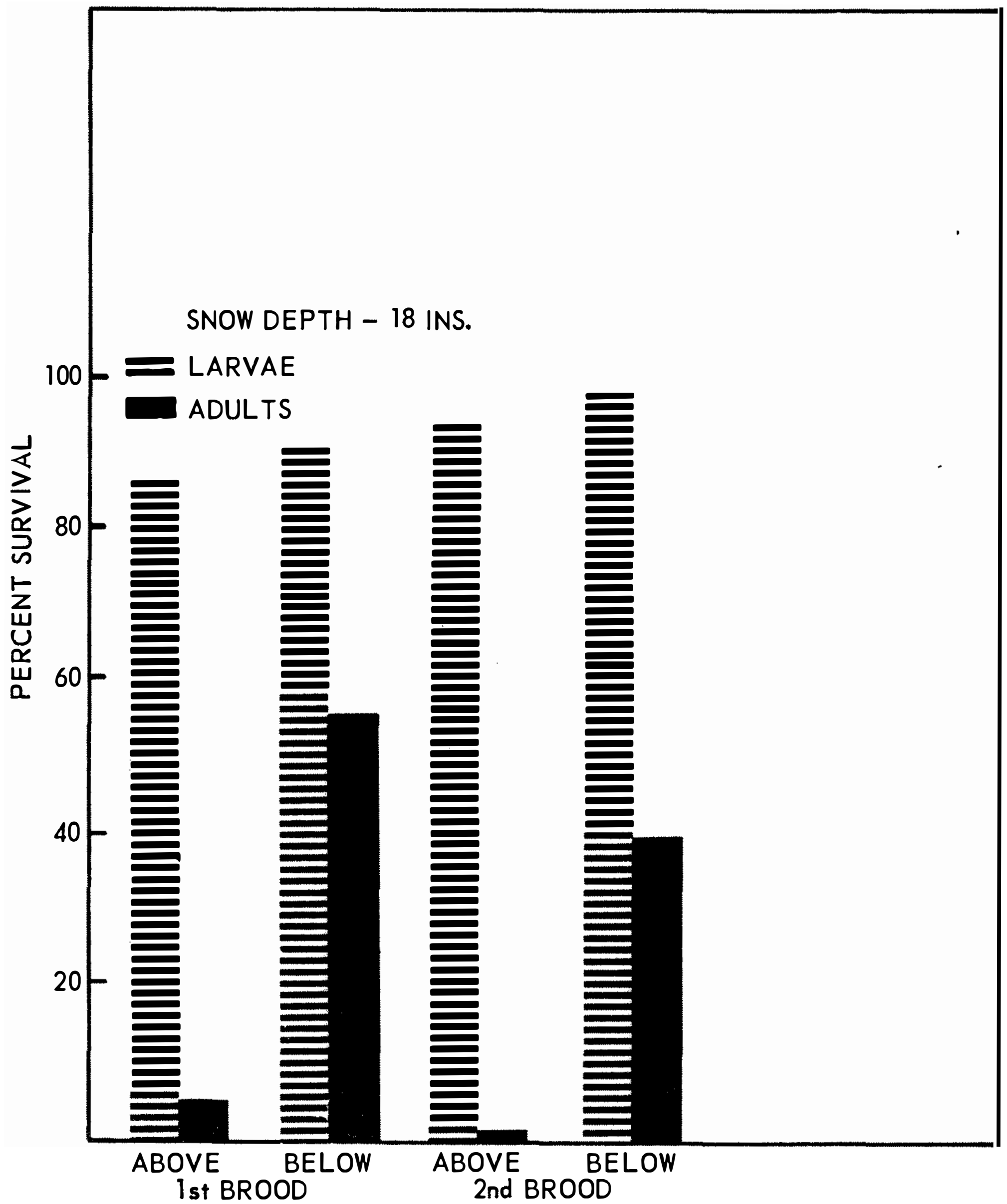

Fig. 13. Histogram illustrating survival of larvae and adults above snow line and below snow line during the winter of 1955-56. Invermere, B.C.

TABLE IV - Summary of results from overwintering mortality study, winter of 1955-1956. 'A' logs contain first broods, 'B' logs contain second broods

Region	Log	Position	Total Galleries	Average per gallery: Larvae alive	Larvae dead	Pupae alive	Pupae dead	Adults alive	Adults dead	Total per gallery
Invermere Region	A10	above snow	63	9.6	1.5	0	0.2	0.2	5.6	17.1
	A12	below snow	64	4.9	0.5	0	0	9.9	7.9	23.2
	B2	above snow	39	38.3	2.3	0	0	0	0.9	41.5
	B3	below snow	58	40.6	1.0	0	0	0.4	0.6	42.6
Eisenhower Region	A9	above snow	88	0.03	15.1	0	0	0	0	15.1

The higher winter mortality at Eisenhower Field Station is attributed to the lower temperatures there as compared to Invermere conditions.

TABLE V - Showing maximum, minimum and mean temperatures (F°), October to March (1955-1956) at Invermere, B.C. and Banff, Alberta.

		Oct.	Nov.	Dec.	Jan.	Feb.	March
Invermere	High	64	43	40	42	40	52
	Low	16	-12	-14	-14	-15	-4
	Mean	43	18	16	19	17	31
Banff	High	67	43	33	40	37	58
	Low	20	-28	-34	-28	-33	-19
	Mean	39	12	9	12	12	26

Larvae appear to be more resistant to low temperatures. In 'B' logs, practically all surviving larvae were in the III or IV instars. Mortality of the pupae was high. Mortality of the adults was very high in those logs which were not protected by snow cover but in those logs which were covered with snow, this varied around 50%. Adults in the 'A' logs were survivors of the 1955 July broods whereas adults in the 'B' logs were parents of those July (first) broods and parents of the broods (second) with which they overwintered.

The effect of winter mortality is apparent in shaping the life cycle as it occurs in the experimental region. Surviving broods in the spring are composed mainly of larvae in their II, III, and IV instar, which were in caged logs. In the wild population, the 1st brood is almost completely destroyed by predators, parasites, competition and finally by low winter temperatures. This will be enlarged upon in a later section.

The important effect of low winter temperatures is to destroy broods at both ends of their development i.e. eggs and I instar larvae and pupae, teneral and callow adults. Therefore larvae of one or two instars comprise the brood in the following spring. In the experimental region the surviving broods in the spring are those of the second attack the previous year and are mainly in the II, III, IV larval instars. This grouping is reflected in the relatively short flight period (Fig. 3).

11. REPRODUCTIVE LIFE SPAN OF THE FEMALE

The average reproductive life span of the female population can only be roughly estimated at this stage. It will vary from year to year depending on the intensity of the environmental pressures. There are three definite periods in the life span of the adult bark beetle in which hazards are at a maximum. These periods are: 1) the interval from the time the young adult leaves its brood tree in July until it has initiated its first successful egg gallery; 2) the interval from the time the adult leaves its first egg gallery and successfully initiates its second egg gallery; 3) the overwintering period. The percentage of parent adults in the wild population which are destroyed during these periods is not known but undoubtedly it is considerable. It is also likely that the percentage survivors during intervals 1 and 2, would vary considerably, depending on the severity of the environmental pressures which operated during the time when these adults were out of the galleries.

Debarking data and general observations in the experimental region suggest that the bulk of the females establish one egg gallery and attempt but are not very successful, in establishing a second egg gallery. Both this season and last season, successful second attacks were much less evident than successful first attacks. In 1956, only 1/12 as many egg galleries were established in exposed logs by the second flight of beetles as by the first flight. It is known that most of the parent beetles left their first egg galleries (Table 11). Just as many logs were available to this second flight as to the first flight. The incidence of attack to standing trees by second flight adults is believed to be somewhat higher than the exposed log data indicates. It is still very low however, compared to the successful attacks of the first flight.

If these observations can be interpreted to indicate a very high adult mortality between the first and second flight, then it is assumed a similar mortality occurs during the interval between emergence from the brood log and the first attack. Adult mortality during the winter is also considerable. This was discussed in Section 10.

Female beetles which succeed in maintaining themselves through these three critical periods have other hazards to face. A small number of adults in caged logs were found to have survived from July, 1955 to July, 1956 and laid viable eggs in this interval, except of course when activity ceased in the fall due to cool weather. The number adults in the 1955 wild population which succeede in living this long was not significant.

If the emerging population in July, 1956 is designated as 1.0, the evidence suggests that the proportion which succeeded in establishing first egg galleries would be in the neighborhood of 0.5, and the proportion which succeeded in establishing second egg galleries would be in the neighborhood of 0.05. The number which would succeed in overwintering is believed to be insignificant. These are only rough estimates but the important fact is that a high mortality occurs in these intervals and likely the percentage of mortality varies from year to year depending on the quality of the environmental pressures. This mortality has a considerable effect on the abundance of the populations but little data is available on this subject.

The reproductive life span of the female beetle in the experimental area can be separated into 3 categories: Potential, Actual, Effective. The number of days associated with each category are summarized in Table VI.

1. Potential Reproductive Life Span - This refers to that period from the time of adult maturity to the time when a natural death from old age occurs. While this is an exceedingly rare phenomenon in nature, data is available which indicates this period can extend from July of one year to July of the next year. Within this interval there would be approximately 180 days when temperatures would be high enough to allow activity by the beetle.

2. Actual Reproductive Life Span - This refers to that period in the first season, when egg laying can take place. Winter temperatures commonly destroy parent adults which have survived up to late fall. Within the experimental area this period commenced at time of parent adult maturity (early July in 1956, and early August in 1955) and extended to mid October. In 1955 this period was 64 days and in 1956 it was 96 days.

3. Effective Reproductive Life Span - Refers to that period within the actual reproductive life span in which egg hatching occurs. It is known that egg laying can take place at temperatures below that at which eggs are able to hatch. Eggs laid after a certain date fail to hatch because temperatures are too low. In 1955, the last egg hatching occurred September 2nd. In 1956 last egg hatching occurred August 22. Adults continued to lay eggs up to October 15 in both years. Eggs laid after the last hatching date do not contribute anything to the level of insect abundance because they are destroyed by low winter temperatures.

TABLE VI - Showing the number of days associated with the three categories of the reproductive life span

	1955	1956
	Total Number of Days	Total Number of Days
Potential Reproductive Life Span	180	180
Actual Reproductive Life Span	64	96
Effective Reproductive Life Span	Time for 1st brood 21	21
	Time for 2nd brood 10	21

In Table VI are summarized the number of days in each category. It will be noted, in this table, that the "effective reproductive life span" is separated into sub categories headed 1) Time for First Brood and, 2) Time for Second Brood. Within the experimental area the first brood is generally established within 21 days after which the parent adults leave and attempt to establish a second egg gallery. This 21 day interval for first brood establishment is determined not so much by temperature as by inherent physiological qualities. Temperature is not the limiting factor in determining size of brood or the number which hatch in this first or early brood. This brood is established and develops under generally favorable climatic conditions. However, evidence is available which suggests that this entire brood is so drastically reduced by predators and parasites, effects of crowding, and low winter temperatures that it later contributes very little to the adult breeding population. Survivors of the second brood seem to be the most important in determining the abundance of the bark beetles in the experimental area.

In Table VI the sub heading, "time for second brood", refers to the number of days which second brood eggs have for hatching. In 1955 the second brood was established around August 24 and the last eggs in these broods hatched September 2nd. Therefore, the number of eggs which hatched, in the second brood was determined within the first 10 days even though egg laying by these same adults, continued into October.

In 1956, the time for establishment of the first brood was approximately 21 days. The second brood in 1956, (and the first brood) was established earlier than in the preceding year. Second broods were established around August 1, 1956 and the eggs in these broods were able to hatch up to August 22. Therefore, the number of eggs which hatched in these second broods was determined within a 21 day interval even though, as in 1955, eggs were laid until mid October.

The abundance of the next years breeding stock then is initially determined by temperatures prevailing during the time the second brood is being established. The effective reproductive life span in any year can show considerable flexibility, depending largely on temperatures.

It is believed that larvae from the first instar on can continue development at temperatures below which egg hatching occurs. Once hatching occurs, the broods continue developing until low temperatures finally cause development to stop. This is generally in October in the experimental area. Those portions of broods which succeed in reaching the III or IV instar larval stage have a good chance of overwintering. The eggs do not. It is not all gain however, because if portions of these second broods succeed in developing to pupae or young adults, then these advanced stages have less chance of overwinterin than late larval stages.

12. FECUNDITY OF THE FEMALE BEETLE

There are many factors which affect fecundity of the females. Some are inherent qualities and some are due to the environment. Several environmental effects have been discussed in this report i.e. sex ratio, nematodes, climate. In last years report (Reid, 1955) it was shown that an inherent quality, size, also affected fecundity.

In Table VII is shown a summary of the average number of eggs per inch in galleries of various lengths. (Data from Appendices I and II). There is a trend shown in this table which supports earlier remarks. The increase in numbers of eggs laid per inch of gallery continues up to and including galleries in the 12 inch class. It was stated earlier (Sec. 6) that females, after one mating, can construct up to 12 inches of egg gallery, the differences in size of the female being responsible for the differences in gallery length i.e. the larger the female beetle, the longer the egg gallery will be.

The average lengths of galleries in infested exposed logs and in infested trees are tabulated in Tables VIII and IX. Galleries established after the first flight period and after the second flight period are listed separately. Field observations which indicated that second attack galleries were longer than first attack galleries are supported to some extent in Tables VIII and IX.

It was mentioned earlier that a very high adult mortality is suspected to occur from the time the females leave their first egg gallery until they are successful in establishing their second egg gallery. The longer gallery and hence greater number of eggs laid after the second flight will compensate to some extent for the high adult mortality which occurs during the second flight period.

It is interesting to note that there is an absence of blue stain in the tree attack during the second flight (Table IX).

The highest fecundity was recorded by females within caged logs. For example, in appendices XV to XIX very long gallery lengths and high fecundities are recorded. One female had constructed a gallery of 40 inches, and was still laying eggs at the time of debarking. Females laying over 150 eggs were not uncommon. One female had laid 263 eggs and constructed a 34 inch gallery at the time of debarking, when she was still laying eggs. These high fecundities are associated with males and females which remained in their first egg galleries. They are exceptional cases, however, not the general rule.

It is apparent from data discussed to date, that if the fecundity of the wild populations is being discussed, then gallery lengths on infested trees must be used. For reasons unknown at present, available evidence indicates average gallery lengths on infested trees are shorter than average gallery lengths on exposed logs. Obviously there are other factors affecting gallery lengths, which are not at present known.

TABLE VII - Showing average number of eggs per inch in galleries of various lengths (From Appendix I and II)

Length of Gallery (ins.)	✱ Nos. of Galleries examined	Total eggs	Average per inch $\frac{\text{Total eggs}}{\text{Length X \# of gall.}}$
5	1	5	1
6	2	22	1.8
7	12	263	3.1
8	5	120	3.0
9	2	79	4.4
10	6	279	4.6
12	4	226	4.7
13	4	234	4.5
14	1	61	4.4
15	2	144	4.8
16	2	185	5.8
18	3	231	4.3

Average eggs per inch = 3.8

✱ This distribution of gallery lengths here is not indicative of average length.

TABLE VIII - Mean lengths of egg galleries in exposed logs

	Flight in which galleries estab.	Average length of galleries in ins.	S.D.	Number of galleries
Steamboat Log Deck - 1955	first	11.4	5.5	183
Steamboat Log Deck - 1956	first	9.0	4.8	154
Francis Creek Log Deck - 1956	first	12.1	4.4	131
Francis Creek Log Deck - 1956	second	15.2	8.3	40

TABLE IX - Summary of debarking data taken from 3 butt logs cut from 1956 infested trees. Each log 5' in length. Francis Creek area.

Flight in which brood established	No. of strikes (broods)	Average Length of Galleries in ins.	S.D.	Date of Debarking	Dia. of logs - ins.	Remarks
First flight (established in early July)	132	6.2	2.4	Aug.16	11	90% of parent adults had left their galleries at time of debarking. Adults did not leave because of crowding; no egg galleries ran into each other, no larval galleries were sufficiently extended to run into those of adjacent galleries. The inner bark appeared white moist and soun Blue stain present but had no reached extensive level.
First flight (established in early July)	60	5.2	1.4	Sept.19	11	No parent adults. Much eviden of larval crowding. Very low survival. Extensive blue stain in sapwood.
Second flight (established in late July)	51	11.5	4.5	Sept.19	10	Parent adults in most galleries. Larval development to IV instar. High survival. Little evidence of blue stain.

In Table VII, a general average of 3.8 eggs per inch is given and is considered to be reasonably accurate. Curiously enough, the average eggs per inch as determined from 84 galleries in 1955 was also 3.8 per inch.

13. BROOD DEVELOPMENT AND SURVIVAL

There are no precise data available on the length of time necessary for brood development under varying environmental conditions.

Newly laid eggs were taken from galleries and placed in petri dishes with close to 100% R.H. These eggs were reared through in the laboratory tent. A summary of incubation times is shown in Table XI. Although considerable variation was evident, it was not so pronounced under natural conditions. The average time for eggs to hatch in mid July of this year was estimated at 6 days. Egg viability in the field was known to be much higher than this table would indicate. No eggs laid after August 22 hatched in the laboratory and it seems reasonable that this same situation occurred in the field. Late August and early September temperatures were too low for egg development in 1956 (Fig.12). Eggs laid in this period and even into October proved viable when reared under temperatures of 85° F.

In Table XI are shown summaries of pupal rearings. Prepupal larvae were placed in petri dishes at close to 100% R.H. and the length of time spent in the pupal stage was observed. It appears that high August temperatures considerably shortened the time spent in this stage. Pupal development is able to continue at temperatures below that at which eggs will successfully develop. Few pupae enter the overwintering period. The reason for this is belie to be that prepupal development in the IV instar larvae ceases due to cool

TABLE X - Summary of egg rearings in 1956

T me of Debarking	No. of eggs	Days to hatch	Viability %
June 7	23	4 - 8	40
June 7	14	4 - 8	30
Aug. 18	49	5 - 8	30
July 18	14	6	20
July 20	7	6 - 8	30
Aug. 7	19	5 - 8	80
Aug. 2	9	7 - 8	20
Aug. 2	9	9 - 10	90
Aug. 14	9	6 - 10	30
Aug. 14	17	7 - 9	30
Aug. 6	7	11	30
Aug. 7	10	9 - 10	100
Aug. 22	8		13

TABLE XI - Summary of Pupal Rearings - 1956

No. of Pupae	Period spent in Development	Total T me	Mean Max. Temp. in that period (F^{o})
4	June 26 to July 6	11 days	68^{o}
42	August 16 to August 21	5 - 6 days	87^{o}
15+	September 7 to September 17	10 - 11 days	76^{o}

temperatures but those insects already in the pupal stage are able to continue development to tenerals.

In 1956 close to 60 days were required from the time the brood was established in July until the first young adult emerged. In 1955, the earlier established broods (July 26 - 27) developed to maturity in 60 days. However, the biggest portion of that years broods were established in early August rather than early July as was the case in 1956. Hence the bulk of the early 1955 broods did not have 60 full days during the warm months of July and August. Broods in 1955 were not as far advanced by September as the 1956 broods. In 1956, young adults were fully developed at least one week before the first ones emerged. The cool weather in late August and early September delayed emergence (See Fig. 12 and Fig. 6).

A summary of the results of debarking exposed logs is given in Table XII and of caged logs in Table XIII. Both tables refer to first flight broods except in Table XII where log T1 contains broods established in the second flight (See Fig. 3). Various mortality factors were discussed in earlier sections. It was pointed out that after 3 weeks it was not possible to establish definite causes of mortality for each larva because of the gallery condition. For this reason, unknown mortality causes increase until in logs debarked in September, all mortality causes are grouped under the one heading. This same condition developed in the logs debarked during 1955. Survival of first broods in exposed logs by August 23 of this year was less than 5% and it is strongly suspected that by October it is even less.

Survival of the first broods in caged logs in September was 51% (Table XIII). It is assumed this higher survival in caged logs is due to their being protected from predators and parasites. The mortality in these logs is attributed to direct and indirect effects of crowding.

The second brood, established in the log decks in late July and early August (Fig. 3) showed 69% survival in September (Table XI). It is believed that the second brood, in the field population, is subjected to far less predation and parasitism than occurs in the first brood. What little information is available on emergence and flight periods of predators and parasites (Appendix XXIII) indicates that the largest proportion fly at the same time as the first flight of bark beetles.

It appears likely that when the beetles leave their first galleries and fly to another site, they leave behind them most of the important predators and parasites. Hence the second broods, although fewer in number, are not subjected to the same degree of predation as occurs in the first broods.

In 1956, the second broods were farther advanced towards maturity by September than were second broods in 1955. This is because of the much earlier flight periods in 1956. Whereas in 1955, second broods going into the winter were composed of I, II and III instar larvae, in 1956 they were composed of I, II, III and IV instar larvae, pupae and a few tenerals. The pupae and teneral adults are not likely to survive the winter but the larvae will, providing the winter is no more severe than that of 1955-1956. Winter mortality figures 1956-57 will not be available until overwintering logs are debarked.

Survival and flight periods of young adults in 1956 which were reared in 1955 caged logs are shown in Fig. 4. These adults developed from 1st broods, established toward the end of July, 1955. There were also a number of second

TABLE XII - Summary of exposed log debarking - 1956

	1st Attack							2nd Attack
Log	☆F 5	☆☆ S 11	F 10	S 2	F 1	F 3	S 6	F T1
Date of Debarking	July 25	July 25 - Aug. 7	Aug. 8 - 10	Aug. 13 - 15	Aug. 17	Aug. 23	Sept. 8	Sept. 6
Number of galleries	43	36	62	64	8	11	57	40
Average length of galleries	10.4	7.4	12.4	9.9	10.6	15.3	8.5	15.2
Average eggs per gallery	13	1	1	0	0	0	0	1
Average larvae per gallery	22	8	28	15	23	4	1	33
Average pupae per gallery	0	0	0	2.0	0.3	0	0.68	4
Average tenerals per gallery	0	0	0	0	0	0	1.3	0
Average egg hatch per gallery	31	24	54	53	62	66	?	55
% of galleries with females	77	22	9	2	0	0	0	23
% of galleries with males	35	6	1	0	0	0	0	0
Average mortality due pred. & par./ gallery	8	13	4	?	?	?	?	?
Average unknown mortality/gallery	0.5	3	22	36	39	63	?	17
Average survivors/gallery (all stages)	22.5	8	28	17	23	3	2	38
% survival/gallery (all stages)	73	33	52	32	37	5	?	69

☆ F - from Francis Creek Area

☆☆ S - from Steamboat Mtn. Area

TABLE XIII - Summary of caged log debarking 1956 (all first flight broods)

Log	3A	2A	1A
Date of Debarking	Aug. 17 to 23	Aug. 28 to Sept. 30	Sept. 6
Number of galleries	29	31	24
Average length of galleries	10.7	11.0	9.4
Average eggs per gallery	12	13	4
Average larvae per gallery	20	26	15
Average pupae per gallery	0	0.3	10
Average tenerals per gallery	0	0	2
Average total hatch/gallery	31	44	53
% of galleries with females	48	42	20
% of galleries with males	7	6	0
Average mortality per gallery	11	18	26
Average survival per gallery	20	26	27
% Survival per gallery	65	59	51

broods established in these same logs during mid-August, 1955. This flight in May and early June, as shown in Fig. 4, occurred only in cages containing 1955 caged logs. It does not appear in the wild population for reasons which have been discussed i.e. heavy predation by predators and parasites, severe lethal affects of crowding due to many strikes per square foot of bark and severe winter mortality of the survivors because most went into the overwintering stage as pupae and young adults.

Fig. 5 shows the emergence from a log caged in 1955 which was infested at the time the wild populations were establishing their second broods. A relationship is apparent i.e. emergence occurred from the second brood (caged) logs (Fig. 5) in 1956 at the same time as the main 1956 wild population flight (Fig. 1 and 2).

In 1955 and 1956, there was a very small late flight of young adults. These adults in both years were surviving progeny of the first broods established and their emergence in 1956 is shown in Fig. 6.

Fig. 14 shows diagramatically the life cycle of the female adult bark beetles and the development of progeny in 1955 and 1956. It was the second brood, as illustrated in Fig. 14 which was responsible for the main flight in early July of 1956.

A summary of the discussion in this section is as follows:

(1) In July, egg hatched in 6 days.

(2) In August the pupal period lasted for 5 - 6 days

(3) Broods in 1956 were established 2 - 3 weeks earlier than in 1955. Development from egg to adult took 60 days in both years.

(4) First broods suffered up to 95% mortality by September. This mortality was caused mainly by predators and parasites and the direct and indirect effects of crowding.

(5) A small flight of survivors from the first brood commenced September 7.

(6) The second brood in 1956 went into the winter in all stages from eg to teneral adult. There was a high proportion of III and IV instar larvae. The second brood in 1955 went into the winter in all stages from egg to III instar larvae.

(7) Available evidence suggests that second broods suffer much less

mortality from predators and parasites than first broods.

(8) In the wild population, the main flight of beetles is composed of survivors of the second brood, which were established the preceding season.

14. THE EFFECT OF THE ENVIRONMENTAL PRESSURES ON THE LIFE CYCLE AND ABUNDANCE OF THE MOUNTAIN PINE BEETLE

The life cycle and abundance of the mountain pine beetle is a result of the population response to environmental factors. Little is known of the intrinsic survival quality possessed by individual insects nor how these qualities influence longevity. The overall effects of the most obvious environmental factors, however, can be determined on a quantitative basis: i.e. the variation between insects in their resistance to low lethal temperatures may not be known but the direct reduction in the population due to low lethal temperatures can be adequately estimated by determining percentage survivors.

From the investigations to date, it is apparent that there are four main limiting conditions or environmental pressures which operate in the experimental area. These have been discussed in earlier sections, and are summarized in Table XIV. It should be noted that food is not included. Food is the most important single factor in the insects environment and no extensive increase in numbers can occur unless there is an adequate supply. However, the mere presence of a large food source does not automatically result in a mountain pine beetle outbreak. Other favorable conditions must exist. Within the experimental area, food in the form of large diameter lodgepole pine is available but is not abundant. The stands are mixed, Douglas fir and lodgepole pine being the dominant species. It is likely that in this area food is an important

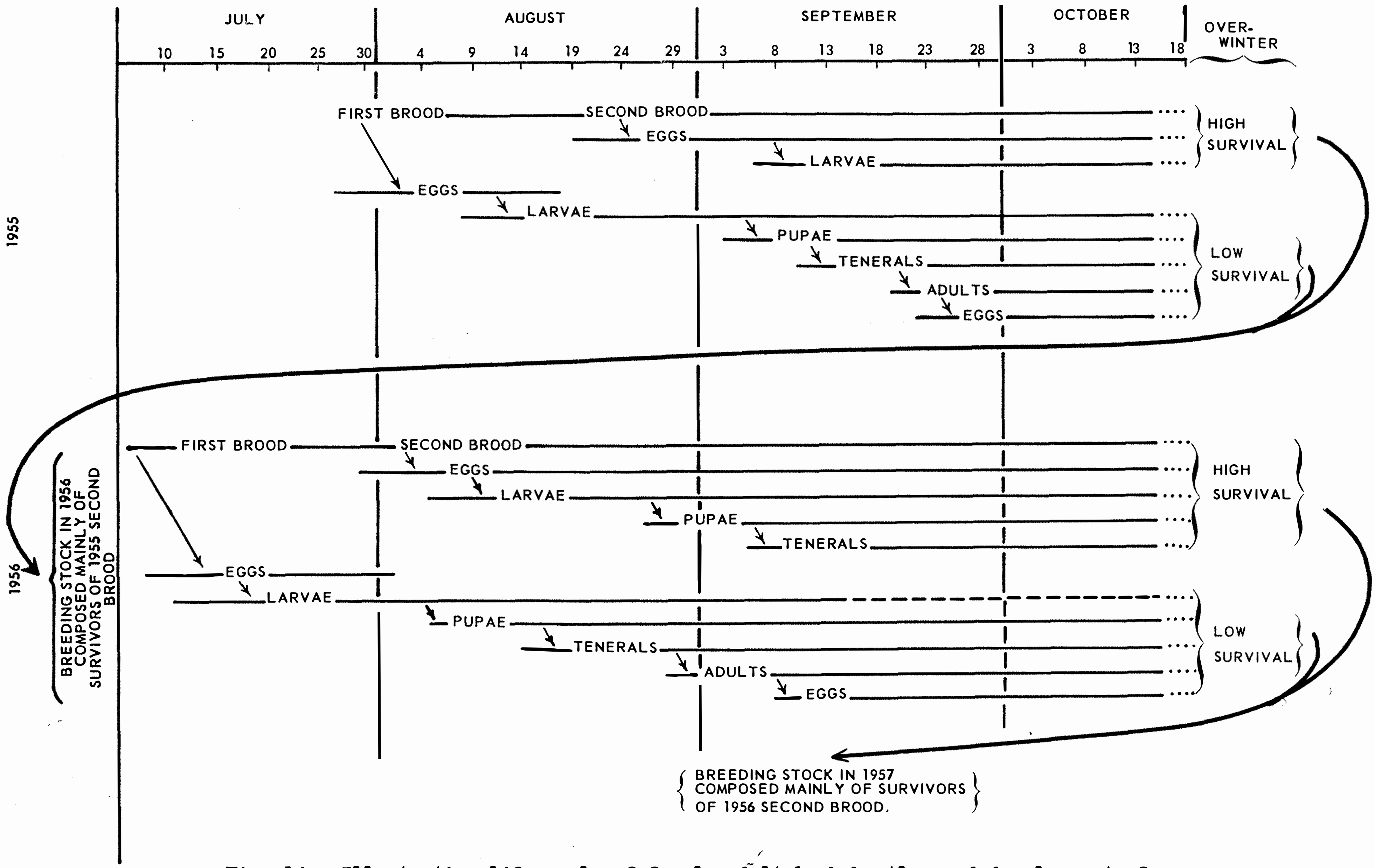

Fig. 14. Illustrating life cycle of female adult bark beetles and development of progeny. 1955 and 1956. Parent adults killed by low temperature in winter. Main portion of flight occurred from July 25 to August 9 in 1955, main portion of flight occurred from July 7 to July 17 in 1956.

limiting factor to further increase in insect abundance. However, even if the population was more abundant than at present, the factors as summarized in Table XIV would still constitute the most important environmental pressures and the life cycle would remain the same for the period under discussion.

It is the intent in this section to illustrate how the life cycle in particular and abundance in general are determined by these four major environmental factors. The effect of each factor is discussed and illustrated separately. The order of their appearance in this theoretical environment is arbitrary. The end effect is the same however, and that is a life cycle and abundance which is a direct reflection of the combined intensities of these environmental factors. These situations described in Figures 15 to 19 are hypothetical. It is not intended that they be regarded as exact descriptions. In particular, Fig. 15 could be represented graphically with much more detail than is evident in Fig. 16, and even Fig. 15 itself, could be drawn out in much more detail. However, these figures are considered to be adequately presented in consideration of the supporting data.

In Fig. 15 is illustrated the egg laying history of a single female and also the periods when these broods will emerge as adults. For example, it is theorized that eggs laid in 1955 during July 15 to July 31, will hatch, develop, and adults emerge in September, 1955, May, 1956, June, 1956. Broods established in August, 1955, will emerge as adults in June, July and August, 1956. Broods established in September, 1955 will emerge as adults in July, August, September of 1956. Broods established in May, 1956, will emerge as adults in July, August, 1956. Broods established in June 1956 will emerge as adults in August, September, 1956. Broods established from July 1st to 15th

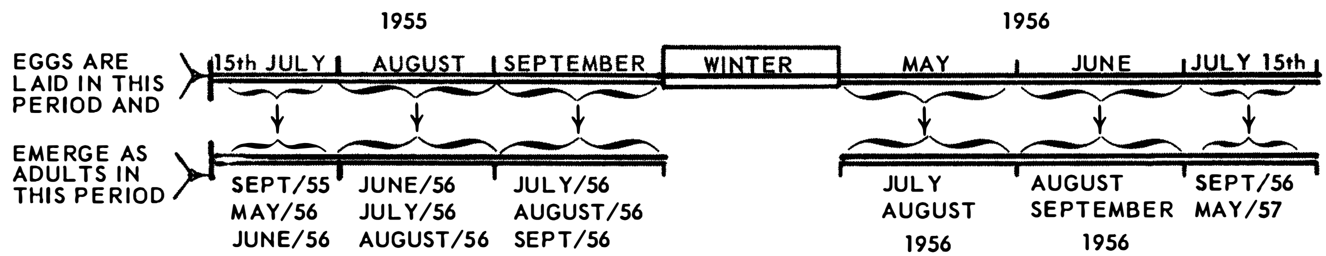

Fig. 15. Showing theoretical egg laying history of a single female commencing July 15, 1955 and continuing to July 15, 1956. No egg laying occurs during the winter. The period when these broods emerge as adults is also indicated.

TABLE XIV - Summary of Important Environmental Factors Operating in the Experimental Region 1955-56

Factor	Result
Cool Weather	- in effect March, April, May, September, October. - causes slowing down and cessation of growth - reduces egg laying and egg hatching
Crowding	- direct effects occur mainly in July, August, September. - direct and indirect effects cause approximately 50% mortality in first broods. Probably less in second broods.
Predators and Parasites	- direct effects occur mainly in July and August. - causing approximately 50% mortality in first broods, probably less in second broods.
Low winter temperatures	- in effect November to February - unless protected by sufficient snow cover - large percentage of adults, pupae, eggs, I instar larvae destroyed. - with snow cover, significant mortality but less than exposed broods.

in 1956 will emerge as adults in September, 1956 and May of 1957. It is assumed that eggs are laid at a constant rate, all eggs are viable, all hatch, all larvae develop and all successfully emerge. The progeny of these emergents do not enter into the discussion. In Fig. 15, this female is considered to lay eggs from July 15, 1955 to July 15, 1956, at which time she dies due to old age (Sec. 11).

In nature, the first contradiction to the hypothetical picture described in Fig. 15, is that the parent female has a much shorter reproductive life span than is indicated in this figure (Sec. 11). The reproductive life span, for purposes here, is considered to extend from July, 1955 to September, 1955. Therefore, in referring back to Fig. 15, this shortened reproductive life span means there are no broods established by this parent female in 1956, and hence no emergents from broods established in 1956. When, in addition to the shortened life span of the parent, cool fall and spring temperatures are allowed to operate in the environment, then emergents of the broods can be visualized as illustrated in Fig. 16. The cool weather, especially in the fall, is effective in reducing size of the broods (Sec. 12), as well as reducing rate of development in the spring and fall (Sec. 13). The rectangles, surrounding these curves, represent the theoretical abundance when no environmental pressures existed.

Figure 17 represents emergence when in addition to reduced life span, and cool weather, the lethal effects of crowding occur. Evidence indicates that this factor causes approximately 50% plus mortality. Mortality resulting from the crowding is apparent in Fig. 17 when this figure is compared to Fig. 16.

When, in addition to reduced life span, cool weather and crowding, the effects of predators and parasites are allowed to operate in this hypothetical environment, then survival is reduced to the level illustrated in Fig. 18. In the experimental area, mortality to first broods from predators and parasites was estimated at close to 50% (Sec. 7, 8, Fig. 11). Mortality in later established broods is not believed to be as high. In comparing September and May emergence therefore in Figures 17 and 18, there is a considerable reduction which can be attributed to the action of predators and parasites. The main July flight is reduced to a lesser degree.

Figure 19 represents emergence in the same brood when the lethal effect of low winter temperatures operates in addition to reduced life span, cool weather, crowding, predators and parasites. Low winter temperatures in 1955-56 caused very heavy mortality among certain overwintering stages (Sec.10). It is evident that some stages are more resistant to low temperatures than others. The somewhat scanty evidence available to date suggests that eggs, I instar larvae, pupae, teneral adults, and mature adults are less resistant to low temperatures than II, III and particularly IV instar larvae. There is therefore a differential mortality attributed to low winter temperatures.

Still in relation to Fig. 19, survivors of broods established in July, 1955 emerge in September, 1955 or overwinter as young adults and tenerals, pupae, and a few IV instar larvae. Winter mortality in all stages except IV instar larvae was very severe, hence the emergence curve in May 1956 is much reduced from that in Fig. 18.

Again in relation to Fig. 19, broods established in August 1955 (Fig. 15) overwintered in the following stages at the indicated percentage:

eggs and I instar larvae (20%); II, III, IV instar larvae (60%); pupae (10%); tenerals and young adults (10%). Broods established in September, 1955, overwintered as follows: eggs (60%); I and II instar larvae (30%); III instar larvae (10%). Mortality in these broods due to low temperatures was complete for eggs and I instar larvae, high among pupae, and teneral adults. Mortality among the II, and particularly the III and IV instars was slight.

The sum total effect of low temperatures to overwintering broods was to reduce their numbers, and by differential mortality (i.e.) heavy mortality in the early and late stages, slight mortality in the in-between stages) reduce the period in which the main flight occurs.

The life cycle and relative abundance which results from all these factors i.e. 1) reduced life span, 2) cool weather, 3) crowding, 4) predators and parasites, 5) low winter temperatures, is shown in Fig. 19.

The actual flight periods, as they occurred in the experimental area in 1956, are also described by Fig. 19.

It should be noted here that the full impact of these factors, acting as controls, are seldom realized. For example, more insects would be destroyed by low temperatures if greater numbers of them had survived depredation by predators. Similarily, more insects would have been destroyed by crowding if cool weather was absent at certain periods. The effectiveness of each factor likely varies in different regions and in different years. However, the writer believes that while certain factors may result in greater mortality than others, they are not necessarily the most important in their influence on the survival of that population. It is likely also that the relative importance of each factor varies in different regions and in the same region in different years.

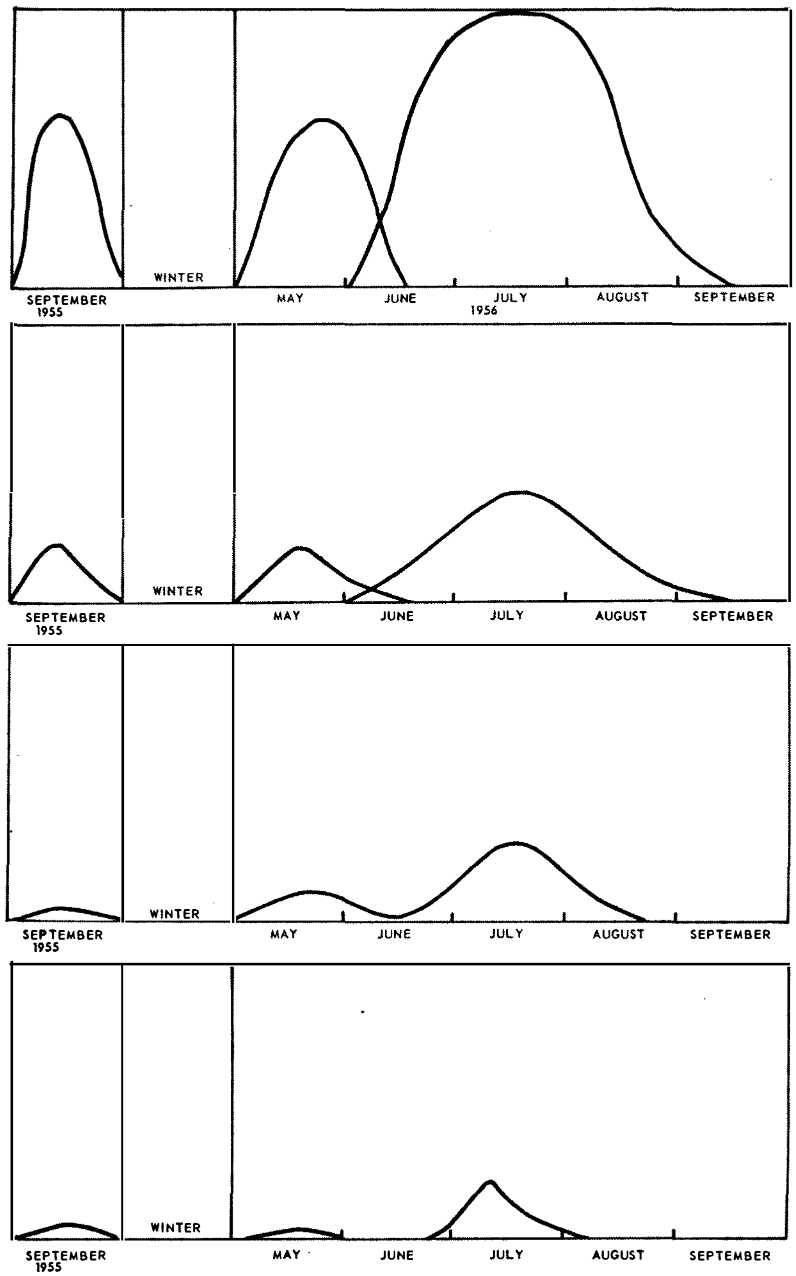

Fig. 16. Illustrating emergence and abundance when the reproductive life span of the female is limited to the period from July to September, and one environmental pressure is allowed to operate: i.e. cool weather in spring and fall. The rectangle represents emergence when no environmental pressures operate.

Fig. 17. Illustrating emergence and abundance when reproductive life span is reduced and the following environmental pressures are allowed to operate: 1) cool weather - 2) crowding.

Fig. 18. Illustrating emergence and abundance when reproductive life span is reduced and the following environmental pressures are allowed to operate: 1) cool weather - 2) crowding - 3) predators and parasites.

Fig. 19. Illustrating emergence and abundance when the reproductive life span is reduced and the following environmental pressures are allowed to operate: 1) cool weather - 2) crowding - 3) predators and parasites - 4) low winter temperatures.

(Note: This figure also represents actual life cycle as it occurred in the experimental area - 1956.)

The one object of the prolific reproductive capacity of these insects is maintenance of a breeding population for the following year. In the case of the mountain pine beetle population in the experimental region during 1955 and 1956 it is believed that the formation of the next years breeding population was initially determined during a relatively brief period in late August and early September. The broods established in this period are subjected to less intensive environmental pressures. It is believed, at this stage of the investigation that an intensive study is warranted into the mechanics of this breeding population i.e. its formation and its survival.

15. SUMMARY AND CONCLUSIONS

1. The bulk of the main flight in the experimental area occurred from July 7 to July 16, 1956. A second flight by these same adults occurred from July 24 to August 5. The number of egg galleries established by the second flight was considerably less than the number established by the first flight. The flights occurred from 2 to 3 weeks earlier in 1956 than in 1955. The reason for this is attributed to the unusually high temperatures in April and May.

2. There were significant differences in emergence from caged logs and from exposed logs in the experimental area. Emergence in 1956 from logs caged in 1955 indicated a definite flight period in May 1956. This flight, from caged logs, was composed of survivors of the first broods established in 1955.

   Survivors of broods established in caged logs during the second flight 1955, emerged in July 1956. It is interpreted from this that the main flight in July by the wild population was composed of survivors of the second flight broods established in 1955.

3. The minimum period for development of broods in 1956 was about 60 days. A large proportion of the first broods in caged logs were able to complete development. In 1955, 60 days was also the minimum time for development but only those relatively few broods in galleries which were established in early July were able to take advantage of the optimum period of growth (July - August).

The minimum incubation period for eggs was 6 days, in July. Viable eggs in 1956 were laid into October but due to cold weather none hatched which were laid after August 22.

The minimum period for pupal development was 5 days, in August. It is suspected that pupae are able to complete development at lower temperatures than those which will permit egg hatching or prepupal development.

4. In the wild population, young adults, survivors of first broods, commenced emerging on September 7. They would have emerged earlier if the weather during late August and early September had been conducive to flight. They continued emerging until October 9. These young adults established egg galleries but due to cold weather, no eggs hatched.

In the wild populations, second flight broods went into the overwintering period as eggs, I to IV instar larvae, a few pupae and a small number of tenerals. The development of these second broods was more advanced in 1956 than in 1955 due to their having an earlier start.

5. First flight broods in caged logs were protected from predators and parasites. Mortality in these broods by September was approximately 50%. This mort-

ality is attributed largely to the direct and indirect effects of crowding.

6. First flight broods in exposed logs were subjected to predator and parasite pressure. Mortality in these logs by September was approximately 95%. This mortality is believed to have been caused by crowding (50%) and the effects of predators and parasites (45%).

7. While only one exposed log containing second flight broods was debarked, these broods showed a survival of 69%. The mortality among these broods is attributed largely to effects (direct and indirect) of crowding. It is believed that the greatest pressure by predators and parasites occurs on the first flight broods.

8. Winter mortality is an important factor in bark beetle abundance. Winter temperatures were lower in the Eisenhower Field Station region (Banff National Park) than they were in the experimental region (East Kootenay). Winter mortality in overwintering broods was complete in logs above snow line at the Eisenhower Field Station. In the experimental area, snow cover of 18 inches gave broods considerable protection. Late larval instars appear to be the most resistant to low winter temperatures. In the experimental area very little mortality occurred in these stages, whether they overwintered in logs above the snow line or below the snow line. No eggs successfully overwintered. Early instar larvae, especially I instar, appear to have suffered severe mortality. Adults suffered heavy winter mortality if they overwintered in logs above the snow line. Mortality in adults was approximately 50% among those which overwintered in logs below the snow line.

9. Winter mortality reduced survivors of the first flight broods to an

insignificant number because most of these entered the overwintering period as young adults.

10. Second flight broods in 1955, overwintered as eggs, I, II, III, and IV instar larvae. Heavy mortality occurred in the egg, and I instar larvae and less in the II instar. The total effect of low winter temperatures on this brood was to reduce the number of stages. The highest percentage of survivors were late instar larvae. This grouping was reflected in the relatively short flight period in July.

11. Parent adults, overwintering with the second flight broods, suffered heavy mortality. Their egg laying potential by spring was not significant.

12. Ten species of nematodes were found associated with the mountain pine beetle broods. Some specific information is known about Sphaerularia hastata and Aphelechoides sp. The former is known to be largely an internal parasite. Heavy infestation by S. hastata reduced fecundity and eventually destroys the adult beetle. They are able to move from gallery to gallery independent of the host. It is suspected they enter the body cavity of the host through the oral cavity. They are most abundant in the body cavity. They are common in the reproductive organs and may cause the female to lay non viable eggs. They have not been found to parasitize eggs, larvae, or pupae.

Aphelenchoides sp. is believed to be non parasitic on bark beetle broods. It is transported from tree to tree by attaching itself along the jugal fold of the membranous wing. They are able to move freely through the bark beetle galleries and to move from gallery to gallery.

13. Bark beetle mating was observed soon after the male entered the gallery, which had been constructed by the female. Eggs are ejected rapidly into egg nitches. The female makes no special effort to construct egg nitch plugs. These are formed as a natural process as the female moves up and down the gallery. In so doing she forces loose bits of boring dust into the egg nitches. In a short time these egg nitches in the sides of the gallery are filled.

The male commonly becomes sealed off from the female by a packed core of boring dust. The male then leaves the gallery.

14. A pattern of egg laying is apparent in the egg galleries. This pattern is believed to be associated with definite gross internal changes which occur in the female as she elongates the gallery and lays eggs. These changes within the female are strongly influenced by mating.

It is interpreted from available evidence that it is the presence of the male which determines the number of galleries established by the female, the number of galleries containing viable eggs, and the length of individual galleries. Unmated females construct up to 4 galleries per season.

15. In caged populations, a sex ratio of 0.4 ($\text{males}_{\text{females}}$) resulted in all the females being mated. In the wild population, having a sex ratio of 0.43, very few galleries were debarked which did not contain viable eggs indicating all females had been mated. One male must mate with at least two females, each in a separate gallery. It is important therefore that the males do not remain long in the first gallery they enter.

16. It is not possible at present to determine the average reproductive life span of the beetles emerging during the main flight because an unknown percentage are destroyed before they succeed in initiating their first gallery. It is suspected that only around 10% - 20% of those which do succeed in establishing a first gallery, are successful in establishing a second gallery. Very few of these beetles succeed in living through the winter.

The average reproductive life span of those which succeed in initiating one egg gallery is estimated near 21 days. The average reproductive life span of those which succeed in establishing a second brood is estimated to extend from the time of emergence to when their last eggs hatch in late August. This period in 1956 would be approximately 42 days. The abundance of the next years breeding stock is initially determined by the number of females which succeed in establishing second egg galleries and by the temperatures prevailing during the time the second brood is being established. The effective reproductive life span in any year can show considerable flexibility, depending largely on temperature.

17. The four environmental factors most important in modifying the life cycle and abundance of the bark beetle on the experimental area are as follows: 1) cool weather, especially in the spring and the fall; 2) the low temperatures in the winter; 3) crowding; 4) predators and parasites.

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18. APPENDICES

APPENDIX 1 - Record of Galleries Analysed by inches. All galleries complete.
(1 inch to 9 inch galleries)

Total length of gallery	Inches along gallery								
	1	2	3	4	5	6	7	8	9
	Eggs per inch								
5"	0	2	3	2	0				
6"	0	2	5	2	0	0			
	0	5	5	1	1	1			
7"	0	3	2	6	3	2	0		
	0	0	5	6	4	2	0		
	0	4	10	21	1	0	0		
	0	11	7	9	2	0	0		
	0	4	7	6	1	0	0		
	0	3	1	6	4	1	0		
	4	6	7	8	6	0	0		
	0	7	10	9	8	0	0		
	0	5	8	8	1	0	0		
	0	2	7	6	2	0	0		
	0	0	1	4	2	0	0		
	0	5	5	8	3	0	0		
8"	0	7	6	5	4	3	2	1	
	0	1	5	3	2	0	0	0	
	2	5	5	5	8	6	2	0	
	0	5	10	8	3	2	0	0	
	2	7	8	5	3	0	0	0	
9"	0	5	6	7	7	3	3	5	3
	0	5	8	8	7	6	3	3	0

APPENDIX II - Record of Galleries Analysed by Inches. All galleries complete (10 inch to 18 inch galleries)

Total length of gallery	Inches along gallery																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	Eggs per inch																	
10"	2	7	7	7	3	4	4	1	0	0								
	0	7	11	6	7	6	5	3	3	0								
	5	6	6	10	9	5	5	4	0	0								
	0	5	7	8	6	4	2	2	0	0								
	0	10	15	12	14	7	7	4	3	0								
	0	0	8	6	6	9	6	5	0	0								
12"	0	6	6	5	7	7	7	6	6	7	1	0						
	0	3	5	6	7	5	7	5	0	0	0	0						
	0	3	6	6	8	6	6	4	4	1	0	0						
	2	4	8	12	14	12	11	12	9	2	0	0						
13"	0	6	6	5	7	7	7	6	6	7	1	1	0					
	0	7	7	7	7	5	7	3	2	4	2	0	0					
	1	5	6	4	8	5	8	8	6	3	2	1	1					
	0	7	13	9	6	5	7	7	5	4	3	0	0					
14"	0	4	4	4	7	8	7	8	7	5	4	2	1	0				
15"	0	2	5	7	7	8	7	13	6	7	4	5	6	2	0			
	0	1	4	3	6	12	6	9	6	7	4	3	4	0	0			
16"	0	3	5	7	6	6	9	7	6	7	3	5	2	3	1	0		
	0	4	8	16	7	9	12	4	11	6	10	7	6	7	6	2		
18"	0	1	6	6	6	3	4	2	5	7	5	6	4	6	4	7	3	0
	0	4	9	6	5	6	7	8	10	6	7	5	3	3	2	0	0	0
	0	1	6	6	6	3	4	2	5	7	5	6	4	6	4	7	3	0

APPENDIX III - Record of Galleries - Analysed by Inches - All Galleries incomplete (still being extended at time of debarking)

Total length of gallery	Inches along gallery																																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
	Eggs per inch																																	
9"	0	0	3	7	3	1	4	3	5																									
	0	8	7	4	6	6	3	9	5																									
	2	5	8	12	12	10	4	6	3																									
	0	3	3	5	6	8	6	3	3																									
13"	0	4	4	4	7	4	9	12	8	10	7	7	6																					
14"	0	4	3	9	19	12	9	12	14	12	13	8	12	10																				
	2	3	6	8	9	7	5	5	6	3	3	4	6	3																				
16"	0	5	7	6	6	3	5	2	6	6	5	4	4	5	5	2																		
17"	0	1	6	6	6	3	4	2	5	7	5	6	4	6	4	7	3																	
18"	0	6	14	11	12	13	12	11	11	8	7	9	7	9	5	4	5	4																
	0	1	5	4	1	0	1	0	0	1	2	3	2	4	4	4	7	6																
19"	0	7	15	11	12	13	13	13	14	11	9	9	8	9	7	6	7	7	4															
	0	9	9	11	11	8	5	8	6	6	7	7	8	4	5	3	4	3	6															
20"	2	3	10	5	5	3	6	5	5	4	6	4	4	7	7	6	4	3	3	3														
21"	0	6	11	3	2	1	1	2	3	4	7	7	7	6	9	8	4	3	5	4	8													
27"	0	8	8	2	6	8	8	14	12	13	14	10	8	7	7	8	4	4	7	6	5	5	4	3	2	3	4							
28"	0	6	13	13	11	9	7	10	10	12	10	12	10	7	13	9	9	7	10	9	7	10	5	5	7	7	9	8						
29"	2	8	9	9	6	4	7	1	9	6	9	6	7	5	6	7	11	12	10	7	11	12	10	10	9	2	2	2	6					
34"	0	7	16	10	9	7	6	12	12	8	12	14	4	12	11	9	9	11	8	5	6	5	6	2	3	4	6	7	7	4	3	6	8	7

APPENDIX IV - Summary of Female Dissections - 1956 (These were young unmated adults which were dissected immediately following their emergence)

Log	Date of Emergence	Wing Muscle Condition	Fat Body Condition	Condition of Reproductive Organs & Misc.
B9	July 17	Massive	Conspicuous	Reduced and non-functioning
"	July 15	"	"	"
"	July 11	"	"	"
"	July 11	"	"	"
"	July 11	"	"	"
A6	June 25	"	"	"
"	June 13	"	"	"
"	June 13	"	"	"
"	June 13	"	"	"
"	June 13	"	"	"
"	June 13	"	"	"
S	Sept. 13	"	"	"
"	Sept. 13	"	"	"
"	Sept. 13	"	"	"
"	Sept. 13	"	"	"
"	Sept. 13	"	"	"
F	Sept. 20	"	"	"
"	Sept. 20	"	"	"
"	Sept. 20	"	"	"
"	Sept. 20	"	"	"
S	Sept. 20	"	"	"

APPENDIX V - Summary of Female Dissections - 1956 (These females had been mated and were known to have been laying eggs immediately prior their being dissected)

Log	Length of gallery ins.	Number of days gallery established	Male present	Wing muscle condition	Fat body condition	Condition of Reproductive organs & misc.
X3	9	14	x	Degenerated	Common	Well developed & functioning
X2	9	21	x	"	scarce	"
X10	10	16	x	"	"	"
S8	4	7	x	mainly degenerated	common	"
S7	3	7	x	"	"	"
P1	9	13	x	"	"	"
P6	5	8	x	"	"	"

APPENDIX VI - Summary of Female Dissections 1956 (These mated females had ceased laying eggs sometime before dissection. This was known by the pattern of egg laying in the galleries. These galleries were established during the main flight around July 11, and were debarked from 2 to 3 weeks later).

Log	Gallery	Length of Gallery (ins.)	Male Present	Wing Muscle Condition	Fat Body Condition	Condition of reproductive organs & Misc.
F5	29	16	x	Massive	Abundant	Reduced and non-functioning
"	32	7		"	"	"
"	36	10		"	"	"
"	40	15		"	"	"
S11	1	7		"	"	"
"	4	10		"	"	"
"	6	10		"	"	"
"	13	13		"	"	"
"	24	12		"	"	"

APPENDIX VII - Summary of Female Dissections - 1956 (These young unmated females, immediately after emerging were placed in separate glass containers and were allowed to feed on small pieces of old bark for periods of from 2 to 10 days).

Age in days	Intestinal tract	Wing Muscle condition	Fat Body condition	Condition of reproductive organs and miscellaneous
2	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
4	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
6	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
8	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
10	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"

APPENDIX VIII - Summary of Dissections - 1956 (These young unmated females, immediately after emerging, were placed in separate glass containers and fed on fresh moist bark for periods of from 2 to 10 days).

Age in days	Intestinal tract	Wing Muscle Condition	Fat Body Condition	Condition of reproductive organs and miscellaneous
2	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
4	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	Some increase in size
"	"	"	"	"
"	"	"	"	Reduced and non-functioning
"	"	"	"	"
6	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	Some degeneration	Scarce	"
"	"	Massive	Common	"
"	"	Some degeneration	Scarce	Some increase in size
8	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	Some degeneration	Scarce	"
10	Partially full	Massive	Abundant	Reduced and non-functioning
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"
"	"	"	"	"

APPENDIX IX - Summary of Dissections - 1956 (These unmated females were allowed to establish galleries immediately following their emergence and after 7 days they were removed from their galleries and dissected).

Gallery	Gallery length (ins.)	Numbers of eggs laid	Wing muscle condition	Fat body condition	Conditions of reproductive organs
1	4	9	mainly degenerated	Abundant	Enlarged and functioning. Eggs not viable
2	3	0	"	"	Enlarged but non-functioning
3	3	0	"	"	"
4	3	0	"	"	"
5	1	0	Partially degnerated	"	Slightly enlarged, non-functioning
6	1	0	Massive	"	Reduced and non-functioning
10	3	0	Mainly degenerated	"	Enlarged but non-functioning

APPENDIX X - Summary of Dissections - 1956. (These unmated females were dissected after they had been establishing galleries for 28 days (in log Y11) 55 days (in log Y10). These females were reared separately from pupae. Gallery length refers to the gallery in which the females were located when exposed).

Log	Gallery Length (ins.)	Wing muscle condition	Fat body condition	Condition of reproductive organs
Y11	4	Degenerated	Scarce	Mature but very small
	4	"	"	Enlarged, mature, normal size, but no eggs laid
	6	"	"	"
Y10	9	"	"	Mature, but reduced in size. One oocyte, degenerated in ovariole.
	9	"	Abundant	Enlarged, mature, normal size but no eggs laid
	9	"	"	Mature, normal, one oocyte degenerated in ovariole
	4	"	"	Mature, normal, no eggs laid
	7	"	"	Mature, normal size, several non viable eggs laid
	2	"	"	"

APPENDIX XI - Summary of Dissections - 1956 (These dissections were made in early October. All these parent females established large broods as indicated by length of galleries. Egg laying had ceased due to cool weather. These dissections illustrate to some degree, the condition of females immediately prior to the overwintering period).

Length of Gallery (ins.)	Male Present	Wing Muscle condition	Fat Body condition	Condition of Reproductive organs
31	x (dd)	Degenerated	Abundant	Reduced and non-functioning
42	x	"	"	"
35	x	"	Common	"
16	x	"	Abundant	"
15	x	"	Common	"
24		"	Abundant	"
27		"	Abundant	Reduced and non-functioning but contains 2 mature oocytes
26	x (dd)	"	Common	Reduced and non-functioning
37		"	"	Partially reduced, non-functioning
15		"	?	"
9		"	Abundant	Normal size but non-functioning

APPENDIX XII - Cage 1

10 Females released July 9, 1956 - Log Debarked July 23, 1956
(Log Y1) (no eggs laid)

Date gallery established	Length of Gallery (ins.)	Adult Present Female	Male	Brood (all stages)	Remarks
July 9	3	x			July 5, 1 female dd.
"	4	x			
"	3	x			
"	2	x			
"	4	x			
"	3	x			
"	2	x			
"	7	x			

Average length unmated gallery = 3.5 ins.

Average number of galleries/adult = 1

APPENDIX XIII - Cage 2

9 Females Released with 1 male July 9, 1956 - Log Debarked September, 1956. (Log Y2)

Date Gallery Established	Length of Gallery (ins.)	Adult Present		Brood (all stages)	Remarks
		Female	Male		
July 9	18	1 (dd)		75	July 15 - 1 female dd. July 19 - 1 female dd. July 31 - 2 females dd.
"	1				
"	1				
"	1				
"	3				
"	3				
"	3				
Aug. 6	1				
"	13	1		58	
" ?	2		1		
" 8	1				
"	4	1			
"	5				
" 9	2				
"	4				
"	1				
Aug. 16	2				
"	1	1			
?	1				

Ave. length unmated galleries - 2.1 ins.
Ave. length mated galleries - 15.5 ins.
Seven galleries were established in July, 1 was mated. Five females died.
In August the 4 surviving females constructed 12 galleries, one of which was mated.
Estimated sex ratio = 1/7 = 0.14

APPENDIX XIV - Cage 3

10 Females Released with 2 males July 9, 1956 - Log Debarked September 4, 1956 (Log Y3)

Date Gallery Est.	Length of Gallery (ins.)	Adult Present Female	Male	Brood (all stages)	Remarks
July 9	2				Missing - 2 females 1 mal[e] Sept. 4 - 1 female alive on floor of cage
"	1				
"	13	1		6	
"	17	1		45	
"	1				
"	1				
"	2	1			
"	5				
"	7			19	
"	6				
July 31	3				
	12			30	
Aug. 6	16	1		70	
" 8	13	1	1 (dd)	82	
" 11	1				
" 14	9			39	
"	2	1			

Ave. length unmated gallery - 2.6 ins.
Ave. length mated gallery - 13 ins.
Ten galleries established in early July, of which 2 were mated
In August the 4 surviving females construct 7 galleries of which 4 were mated
Estimated sex ratio = $\left(\frac{\text{males}}{\text{females}}\right) = \frac{2}{10} = 0.2$

APPENDIX XV - Cage 4

10 Females Released with 4 males July 9, 1956 - Log Debarked September 4, 1956. (Log Y4)

Date Gallery Est.	Length of Gallery (ins.)	Adult Present Female	Male	Brood (all stages)	Remarks
July 9	30	1 dd		205	July 15 -
" 12	12		1 dd	75	1 female dd
" 12	9	1 dd		73	Aug. 6 - 1
Aug. 6	19	1	1	120	female dd.
" 6	14	1		35	Sept.4 - 1
					female dd.

Average length mated galleries = 17.2 ins.
All females mated
Estimated sex ratio = $\frac{2}{5} = 0.40$

APPENDIX XVI - Cage 5

10 Females Released with 6 Males July 9, 1956 - Log Debarked September 4, 1956 (Log Y5)

Date Gallery Established	Length of Gallery (ins.)	Adults Present Female	Male	Brood	Remarks
July 9	2				
"	17	1		90	July 15 - 2 females,
"	12			20	and 1 male dead.
"	13	1		30	Aug. 16 - 2 males
"	22	1	1	101	dead (note: these
"	14	1(dd)		80	2 males were both
"	13	1(dd)		90	effective).
"	4	1(dd)		20	
Aug. 6	4	1(dd)		16	
" 8	8			28	

Average length mated galleries = 12 inches
Average length unmated galleries = 2 inches
Eight females establish 1 brood each
Two females establish 2 broods each
Estimated sex ratio = (3/8) = 0.37
Very heavy broad mortality due to grouping of galleries on 1 aspect of log

APPENDIX XVII - Cage 6

10 Females Released with 8 males July 9, 1956 - Log Debarked September 5, 1956. (Log Y6)

Date Gallery Established	Length of Gallery ins.	Adults Present Female	Male	Brood	Remarks
July 9	28	1		181	July 15 - 3 females,
"	34	1	1	263	3 males dead. July
"	28	1	1	245	18 - 1 female dead.
"	19			112	Aug. 15 - 2 males
"	18	1		*	dd. (note: these
Aug. 6	16	1		71	males effective).
Aug. 15	9			40	

Average length of mated galleries = 22 inches
Five females establish 1 brood each
Two females establish 2 broods each
Estimated sex ratio = $(\frac{4}{5})$ = 0.80

* Long, irregular gallery constructed but no eggs laid. On dissection, ovarioles short and thickened, no oocyte differentiation in lower end. Plug of yellow yolk like substance in lower end of ovarioles which may be caused by degeneration of mature oocyte. Spermatheca not enlarged. Fat bodies conspicuous. Wing muscles reduced.

APPENDIX XVIII - Cage 7

10 Females Released with 10 males July 9, 1956
Log Debarked September 11, 1956 (Log Y7)

Date Gallery Established	Length of Gallery (ins.)	Adults Present Female	Adults Present Male	* Brood	Remarks
July 9	1	1 (dd)		325 survivors	July 15 - 1 female,
"	9	1 (dd)			1 male dd. July 18 -
"	12				1 male dead. July 12
"	24	1			1 male dead. Aug. 20
"	36	1			1 male dd.
"	22	1			
"	20	1			

Average length of mated galleries = 20.5 ins. (omit 1" gallery)
Seven females established 1 brood each
Estimated actual sex ratio = 1

* Considerable mortality as all galleries were on 1 aspect of the log

APPENDIX XIX - Cage 8

10 Females Released with 12 Males July 9, 1956 - Log Debarked September 11, 1956. (Log Y8)

Date Gallery Established	Length of Gallery (ins.)	Adults Present Female	Adults Present Male	Brood	Remarks
July 9	11	1 (dd)		676 survivors	July 15 - 5 females,
"	30	1			2 males dead
"	40	1	1		
"	26				
"	42	1			
"	29	1 (dd)			

Average length of mated galleries = 29.6 ins.
Six females established 1 brood each
Estimated sex ratio = 1
* Considerable mortality from crowding

APPENDIX XX - Cage 9

10 Females Released with 14 Males on July 9, 1956
Log Debarked July 24, 1956 (Log Y9)

Date of Gallery Establishment	Length of Gallery (ins.)	Adults Present Female	Male	Brood (all stages)	Remarks
July 9	7	1		26	July 15 - 3 females 3 males dead. July 19 - 1 female, 3 males dead
"	11	1	2	51	
"	1	1			
"	1				
"	7	1		34	
"	6	1	1	18	
"	1	1			
"	5			17	
"	8	1	1	17	
"	1				
"	2				

Average length of mated gallery = 7.3 ins.
Average length of unmated gallery = 1 ins.
Estimated sex ratio = 1
Note: time of 15 days

APPENDIX XXI - Cage 10

10 Unmated Females Released on July 27, 1956 - Log Debarked September 19, 1956 (Log Y10)

Date of Gallery Establishment	Length of Gallery ins.	Adults Present Female	Male	Brood	Remarks
July 27	2				July 31 - 2 females dead. Aug. 9- 1 female dead
"	4				
"	5				
"	1				
"	6				
"	3				
"	3				
"	4				
Aug. 6	3				
Aug. 14	4				
"	9	1			
"	8				
"	9	1			
Aug. 24	4	1			
"	7	1			
"	2	1			

Average length of unmated galleries = 4.6 ins.
Note: 1st Attack in July - average length 3.5 ins. and range 1-6 ins.
2nd Attack in Aug. - " " 6.6 ins. and range 3-9 ins.
3rd Attack in late August, galleries still being elongated.

APPENDIX XXII - Distribution of Gallery Lengths 1955 and 1956 - D. monticolae

Galleries in which no adults were found		Galleries in which only females were found		Galleries in which both male and female were foun	
Length of Gallery - in ins.	Number of gall-eries in this class	Length of Gallery - in ins.	Number of gall-eries in this class	Length of gallery - in ins.	Number of gal eries in this class
1	4	2	1	7	1
2	4	3	2	9	2
3	2	4	3	11	3
4	3	5	4	12	3
5	6	6	11	13	5
6	12	7	13	14	4
7	23	8	9	15	6
8	10	9	9	16	7
9	8	10	6	18	3
10	8	11	7	19	2
11	6	12	7	20	4
12	9	13	5	21	1
13	5	14	7	23	1
14	5	15	2	24	2
15	2	16	2	25	2
16	3	17	2	26	2
17	2	18	6	27	1
18	3	19	3	28	4
19	1	20	2	29	2
21	1	21	2	40	1
22	1	22	5		
23	1	23	1		
24	1	25	1		
26	1	26	1		
27	1	27	1		
29	1	28	1		
31	1	29	1		
		31	2		
		33	1		

APPENDIX XXIII - Summary of Emergence of Predators and Parasites Steamboat and Francis Creek Area - 1956

Emergence from broods established in 1955	*Coeloides dendroctoni*	*Medetera modestus*	*Lonchaea* sp.
June 21	1	2	
25	1	1	
27	1	1	
28		1	
30		1	
July 2		1	
4		1	
6		1	
7		1	
8	1		
9			
11	1		
13	3		
15	1	1	
16			
18			
19		1	
Emerged from 1st flight - 1956			
Sept. 10	1		
12	1	1	
17	3	1	1
18		1	
19		4	
Oct. 8	3 (emerged during Sept. 19 to Oct. 8)	5 (emerged during Sept. 19 to Oct. 8)	

APPENDIX XXIV - Maximum and Minimum Temperatures - Invermere, B.C. - 1956

Day	April Max.	April Min.	May Max.	May Min.	June Max.	June Min.	July Max.	July Min.	Aug. Max.	Aug. Min.	Sept. Max.	Sept. Min.	Oct. Max.	Oct. Min.
1	49	26	37	28	74	53	65	45	75	47	63	42	62	36
2	51	18	46	30	70	52	73	51	74	53	54	33	64	43
3	54	25	53	21	80	42	63	49	64	50	56	38	60	28
4	52	37	50	32	77	50	70	51	70	51	61	27	56	34
5	43	29	54	36	57	44	70	45	75	40	66	26	66	33
6	45	14	65	32	69	42	69	46	77	44	73	30	70	27
7	42	29	70	32	66	43	74	42	81	44	73	38	72	33
8	55	22	60	37	68	40	84	42	83	43	80	37	71	33
9	60	24	60	40	78	44	92	46	73	47	81	39	70	30
10	58	34	60	43	86	43	90	52	77	49	73	43	68	32
11	59	26	52	40	61	47	88	54	74	43	75	39	69	43
12	62	21	54	36	66	30	90	52	84	46	73	35	68	38
13	68	27	64	28	71	42	77	54	85	48	72	42	56	35
14	71	28	67	40	64	50	72	51	88	46	77	49	48	35
15	72	31	75	34	52	49	72	46	94	47	78	44	56	43
16	52	40	80	36	58	50	78	51	90	46	80	41	58	42
17	58	37	80	37	66	48	86	48	82	54	83	42	51	32
18	63	28	82	44	74	47	90	50	80	54	82	38	53	40
19	68	30	83	40	76	44	93	51	83	45	68	43	46	30
20	71	31	83	48	61	47	92	52	88	47	63	40	46	40
21	70	40	78	42	70	40	90	55	90	48	56	38	42	40
22	44	37	76	36	71	39	88	54	93	49	60	28	43	28
23	54	37	79	41	75	46	93	50	86	50	61	38	38	22
24	52	37	63	48	63	48	94	53	74	54	66	41	48	31
25	55	30	70	49	62	37	88	52	72	54	71	53	47	27
26	62	24	73	38	72	50	84	54	85	49	70	44	46	29
27	54	28	74	43	78	47	92	63	72	56	54	33	44	27
28	51	37	75	40	76	48	86	49	70	40	48	38	44	23
29	48	35	80	44	56	42	85	43	67	49	46	36	42	25
30	47	31	75	49	64	44	87	44	68	37			42	33
31			84	42			86	42	75	34			40	27