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Crowding Effects Among Single-Age Larvae of the Mountain Pine Beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae)^{1,2}

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ABSTRACT

An experiment was conducted to determine the effect of crowding on: larval and adult survival; larval stadia duration; sex ratio of adults; reproductive capacity of adult female *Dendroctonus ponderosae* Hopkins.

To investigate distribution of the effect of crowding within a single age group, newly hatched larvae were used. The responses of these larvae and subsequent adults were observed after exposure to densities of 1, 3, 6, and 9 larvae (or adults) per unit of food supply for each of 3 time intervals.

Survival of 1st-stage larvae increased as crowding increased. Survival at the adult stage increased in Crowd 3, decreased in Crowd 9, and was not consistent in Crowd 6 as crowding duration lengthened. The rate of survival decreased as either crowding level increased or duration of crowding lengthened. Crowding influenced the rate of larval development, which in turn influenced sex ratio; i.e., as the 3rd and 4th larval stadia became shorter, more females and fewer males survived. Thus, the theoretical ratio of 1:1 shifted in favor of the female. The reproductive capacity of the female adult decreased as larval crowding increased. There was an apparent feeding stimulus through association that resulted in greater than 60% successful establishment of 1st-stage larvae when crowded.

Population dynamics of insects is usually concerned with increment and decrement of the population. Numerically, a population is based on amount of natality and mortality, but functionally it is an integration of all interactions of factors which contribute to a particular density level. Factors causing changes in populations are numerous—their interactions myriad. Age-specific performance and behavioral reactions of a species under appropriate sets of conditions need to be known. Factors that affect the density of a population can be classified according to the manner in which they function with regard to populations of different densities. The intensity of these factors must be calculated within factor-units and not on the strength of the population. Crowding in any population, and particularly within populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, plays an important role as related to

food and habitat. Crowding affects both age-specific fecundity rates and age-specific mortality rates.

The term crowding was selected for use rather than competition simply because it describes the experimental condition. Competition has come to have several meanings in animal ecology (Andrewartha and Birch 1954, Birch 1957, Park 1941). Some of these meanings are so ambiguous that the word has largely lost its usefulness as a scientific term. In any case, it is not my intent to provide argument for any particular definition, but to provide a basis for differentiating crowding and competition. Crowding in this usage is simply the association of individuals at several numerical levels within a defined volume of food and habitat. Density is used to relate the actual number of individuals to unit volume of food and habitat.

This study is part of a unit designed to develop the mensurational aspects of forest insect populations. Results of studies on the influences of stand density, habitat type, elevation, and stand structure all have

¹ Received for publication 8 Nov. 1971.

² Based upon a thesis submitted to the Graduate School of North Carolina State University in partial fulfillment of the requirements for the Ph.D. degree in Entomology.

Table 1.—Design for determining effect of crowding on single-age larvae of the mountain pine beetle.

Crowd level (larvae/food unit)	No. larval stadia crowded before separation	No. food units/crowded duration	Total no. larvae/crowded duration
Crowd 3	1	20	60
	1-2	25	75
	1-2-3	25	75
	1-2-3-4	30	90
Crowd 1 (check)	1-2-3-4	24	24
Crowd 6	1	20	120
	1-2	25	150
	1-2-3	25	150
	1-2-3-4	30	180
Crowd 1 (check)	1-2-3-4	24	24
Crowd 9	1	20	180
	1-2	25	225
	1-2-3	25	225
	1-2-3-4	30	270
Crowd 1 (check)	1-2-3-4	24	24

shown that food quantity and distribution within a stand are apparently the regulatory factors acting upon mountain pine beetle populations. Studies are now needed to determine the behavioral reactions and performance of the insect itself. Crowding, then, is one more factor in determining the population dynamics of the mountain pine beetle.

There have been numerous studies on the biological effects of crowding within insect populations. Studies on several species of blowflies (Ulyett 1950), *Drosophila* (Bakker 1961, Chiang and Hodson 1950, Mishima 1964, Sokoloff 1955, Pearl and Parker 1922), and *Tribolium* spp., (Park 1932, 1938, 1941, 1948, 1954, 1957; Park et al. 1939; Park and Lloyd 1955; Birch et al. 1951; MacLagan and Dunn 1935; Crombie 1942, 1944, 1945, 1946; MacLagan 1932) have all produced results showing the effects of crowding on rate of growth in size, fecundity, population density, and sex ratio.

These and other experiments of this era that dealt with the effect of crowding upon survival, fecundity, and speed of development were, in most cases, studies dealing with interspecific crowding (or competition). Very few of these studies dealt specifically with intraspecific crowding.

Very few crowding experiments, per se, have been done with species of bark beetles. Those who have dealt with this factor have done so from an intraspecific approach and have measured rather gross factors, i.e., brood production (fecundity) decreased with density and maximum number of progeny was related to gallery densities of *Blastophagus piniperda* L. (Nuorteva 1954, and the Engelmann spruce bark beetle, *Dendroctonus engelmanni* Hopkins, Knight 1958). McMullen and Atkins (1961) stated that competition within Douglas-fir beetle, *D. pseudotsuga* Hopkins, broods acts as a regulating feature to keep

the population in check—as the population increases, attack density increases, and brood survival decreases. This last-mentioned relationship was found to be true also for the mountain pine beetle (Cole 1962). Schmitz and Rudinsky (1968) also concluded that intraspecific competition was an important natural regulation of the Douglas-fir beetle.

Andersen (1960), summarizing recorded experiments, indicated that the factors studied are generally related linearly to density:

Death rate—linearly related to initial density.

Fecundity—linearly related to the reciprocal of density.

Sex ratio—proportion of females may be linearly related to density.

Developmental rate—can be dependent or independent of density.

Straight-line relationships do not seem probable in biological processes. For instance, if the interim death rate is linearly related to initial density, changes in the structure of the population as a result of mortality apparently are not taken into consideration. On the other hand, if the ultimate death rate is linearly related to initial density, we would be assuming that such changes in the interim structure of the population did not have any effect on the ultimate death rate.

Experimental Design

The experiment was conducted to determine whether crowding affects larval and adult survival, duration of larval stadia, sex ratio of adults, or reproductive capacity of the adult female beetle.

To investigate the effect of crowding over time within a single age group, newly hatched larvae were first crowded at varying degrees and later separated and allowed to feed singly upon an excess of food. Four levels of crowding were used; each level had 1, 3, 6, and 9 larvae per unit of food. With the exception of Crowd 1, the larvae in each of these crowdings were separated at the end of the 1st, 2nd, 3rd, and 4th stadia. Crowd 1 was used as the control for differences in effects due to crowding (Table 1).

The food unit, containing the required number of larvae, served as the experimental unit. Variation caused by food quality was reduced in the experiment by homogenizing enough phloem at one time for the duration of the experiment. No more than one egg from the same female was placed in the same experimental unit, and one egg from each of the females served for each of the check units.

The responses to be determined were measured every 4 days. All rearings, those actually used and those in reserve, for any one crowd level, were started the same day and kept under identical conditions.

Materials and Methods

An oligidic diet (Bedard 1966) was placed in plastic rearing chambers containing the larvae. These chambers were constructed of 2.54-cm clear plexiglass (Fig. 1) and each contained 3.61 cm³ of food.

The rearing chambers were placed in a sealed desiccator at 75% RH and the desiccators were placed in a growth chamber at 24°C.

Early in the experiment it became apparent that ventilation of the food units was necessary to: (1) stimulate feeding; (2) provide oxygen; and (3) allow a slight rate of drying, simulating natural conditions. These food units were placed longitudinally on their edges in the desiccators. This position aided successful establishment and feeding by the larvae.

Within 48 hr of hatch, the larvae were systematically selected for assignment to food units. A starting niche for each larva was punched out of the medium using a large hypodermic needle (no. 13) equipped with a plunger for cleaning. Positioning of larvae in the food unit simulated their natural position. Thus, each larva began the feeding period under similar environmental conditions.

All larvae in the food units were inspected for survival or establishment at 24- and 48-hr intervals after placement in the desiccators within the growth chamber. Dead larvae found during the examinations were replaced with larvae from reserve rearings obtained under similar growth conditions. The requirements for crowding level, single age, and systematic selection were maintained during these replacements.

Larvae deaths were recorded at the time of the survival examinations as being due to (1) crowding influence, (2) bacteria and/or fungi, (3) "entomocide." ("Entomocide" is defined as the act of one larva killing another but not necessarily as a cannibalistic act for food.)

Larvae were moved from the crowded to the isolated, or single feeding condition with a fresh food supply, when $\frac{2}{3}$ of the larvae in a given food unit had molted to the next stadium. Artificial niches and air pockets were constructed for the isolated larvae. This separation procedure was repeated after each stadium until pupation.

The surviving adult beetles were kept in their respective food units until they had completely hardened or until black. They were then sexed and placed in a refrigerator (4°C) for 1 week. The beetles exposed to this cold period succeeded better than those not exposed to cold in the introduced attacks upon lodgepole pine billets. At the end of the 1-week cold period the female was weighed,

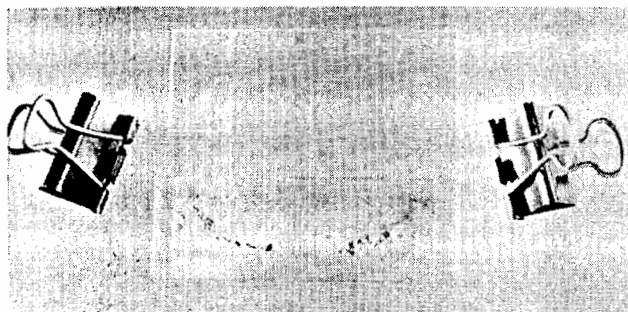


FIG. 1.—The rearing chamber for mountain pine beetle larvae.

Table 2.—Number of experimental units per crowd level at beginning of experiment, at time of separation, and at completion of experiment.

Crowd level	Separation (at stadium)	No. experimental units		
		Beginning (crowded)	Separation (crowded)	Completion (singles)
3	1	20	10	9
	2	25	11	14
	3	25	5	9
	4	30	11	19
Check		24	17	5
6	1	20	11	24
	2	25	10	18
	3	25	7	11
	4	30	4	12
Check		24	17	4
9	1	20	13	30
	2	25	8	11
	3	25	7	8
	4	30	4	2
Check		24	23	2

measured, and introduced into an attack chamber in a green log. Twenty-four hours later the male was weighed, measured, and placed in the attack chamber made for the female. The success of male establishment increased slightly if the male was placed in the chamber in late afternoon.

One week after mating, and once a week thereafter, 2.5-cm square sections of bark were removed from the egg gallery and the eggs counted and removed. The eggs were then placed in petri dishes and incubated. The number of centimeters of gallery constructed before the 1st egg was laid, total centimeters of gallery constructed, total number of eggs laid, and percent of successful hatch were recorded.

Results

The experimental efficiency was based on the 90% confidence level and a coefficient of variation of not more than 20%. The actual number of experimental units are shown in Table 2. The levels of crowding 3, 6, and 9, each with its respective control of Crowd 1, were reared sequentially: i.e., the rearing portion of the experiment using Crowd 3 and its control was completed before Crowd 6 was begun, which in turn was completed before Crowd 9 was begun. Consequently, to account for any differences caused by temporal and/or physiological effects of rearing, all responses for each crowd level were adjusted using the following formula:

$$\frac{A}{B} (Y_{ij}) = \text{Corrected } Y_{ij}$$

where A = average response over all 57 control experimental units, B = average response over all control experimental units within a particular crowd level, Y_{ij} = response for any one experimental unit (i) within a particular crowd level (j), $i = 1 \dots 57$, and $j = 1, 2, 3$.

Table 3.—Percent mortality caused by nonestablishment and bacteria and/or fungi in the early larval stages.

Crowd level	Cause of mortality	
	Nonestablishment	Bacteria and/or fungi
1 (check)	34.33	19.30
3	42.33	13.64
6	13.83	9.89
9	17.81	16.90

Some Responses of Larvae Prior to Separation

There was a thigmotactic requirement that the newly hatched larva must meet before feeding begins. Successful feeding occurred more often than not when the larva formed its own feeding chamber and was completely surrounded by medium. Larval placement and design of the rearing chamber encouraged fulfillment of the thigmotactic requirement.

Feeding and establishment rate of larvae increased when the crowd level increased (Table 3). Even though larvae naturally feed in individual galleries and only chance encounters occur, there is an apparent communication through association that stimulates the early feeding of the larva.

Larval association apparently resulted in dispersal movements based on feeding (constructing galleries) or it caused food and habitat to become more suitable.

The loss of larvae from attack by bacteria and/or fungi was fairly uniform among crowd levels. In spite of precautions, including aseptic techniques and reesterilization of the larvae, some larvae died in the presence of these microorganisms. This cause of mortality occurred sporadically throughout the entire egg and larval populations (Table 3).

During the early stadia, entomocide was expected to increase rather gradually as crowding increased. Increased crowding decreased the amount of food and space per larva. Under the same conditions of increased crowding (= decreased food and space per larva), entomocide was expected to increase rather sharply during the latter stadia. Thus, entomocide was expected to be governed by crowd level and crowding duration. This generally was true by crowd level but was unpredictable for crowding duration (Table 4).

A higher rate of entomocide occurred within Crowd 6 than in Crowd 9, but the reason is not evident. Possibly the greater crowd level of Crowd 9 resulted in less gallery construction and hence fewer encounters. Short larval galleries in dense larval populations and long galleries in sparse larval populations have been observed as being typical in the phloem of lodgepole pine.

Considering only those beetles that survived the larval stages, stadal length was expected to increase (with each larval growth stage) as the crowding level increased. This result could be expected from the decreasing food supply per larva as the larva in-

Table 4.—Percent mortality due to entomocide in the larval stages.

Crowd level	Crowding duration through stages			
	1	2	3	4
Percent.....			
3	6.67	6.78	0	1.39
6	14.02	17.86	7.52	9.82
9	6.78	7.60	5.75	13.56

creased in size. However, stadal length during the pre-separation crowding period decreased with increased crowding during the 1st and 2nd stadia, but increased during the 3rd and 4th stadia (Fig. 2).

Some Responses of Larvae After Separation

Differences within each response (corrected for time) of the mountain pine beetle after separation were considered to be the effect of experimental treatment; i.e., crowd level and crowding duration. The responses were analyzed on the basis that a response was due to release from a particular crowd level after reaching a particular stadia.

Survival from Larval to Adult Stage as Affected by Crowding and Duration of Crowding.—In the analysis of variance, neither differing crowd levels nor crowding durations affected larval survival, but a significant interaction ($P \leq 0.007$) did occur.

As shown in Fig. 3, survival at the lowest crowding level (Crowd 3) increased substantially (about 20%) between Durations 1 and 4. One can only surmise that there is something beneficial about the crowding which develops as the 3 larvae (Crowd 3) grow to larger size within their food unit. Perhaps feeding is stimulated, in a competitive sense, by increasing the number of larvae feeding adjacently.

This beneficial effect of crowding was very large within Duration 1 (Fig. 3), where the survival ranged from 10 to 63% between crowding levels 3 and 9.

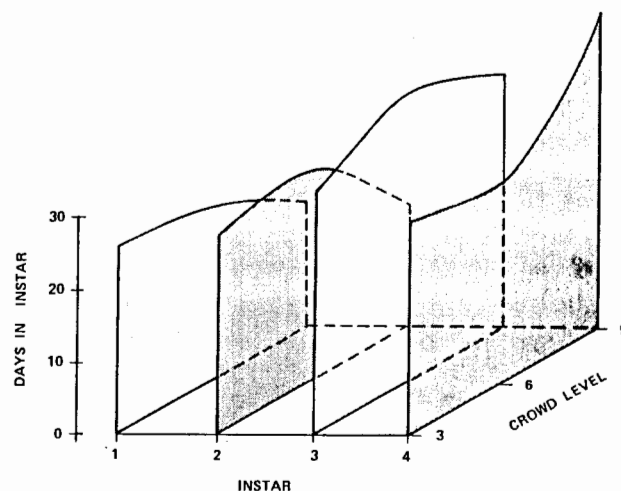


FIG. 2.—Stadal length during pre-separation by crowd level and instar.

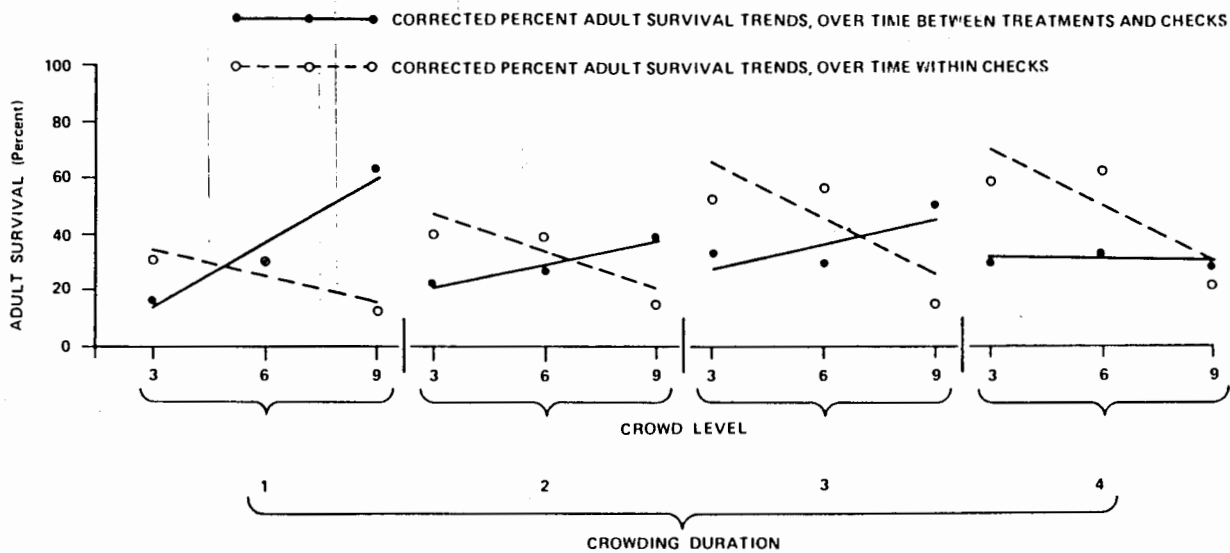


FIG. 3.—Adult survival by crowd level and crowding duration.

As the larvae in the Crowd 9 food units continued to grow, however, they reached a point where limitations in food supply overcame the beneficial effect of social feeding and survival dropped—from 63% in Duration 1, to 31% in Duration 4. Crowd 6 appeared to maintain a more-or-less stable balance between feeding stimulus and competition for food in the food units. There was no appreciable change in Crowd 6 survival by duration.

When postseparation survival curves for crowd levels 3, 6, and 9 were compared (Fig. 4) throughout the period following separation, 2 trends became evident. The final survival of adults tended to increase as crowding duration was extended within Crowd 3, but tended to decrease as a result of extended crowding duration within Crowd 9. Crowd 6 showed a trend similar to Crowd 3. Thus, the longer the larvae were held under Crowd 3 treatment the greater the chance of survival; and conversely, the longer the larvae were held under Crowd 9 treatment the less the chance of survival.

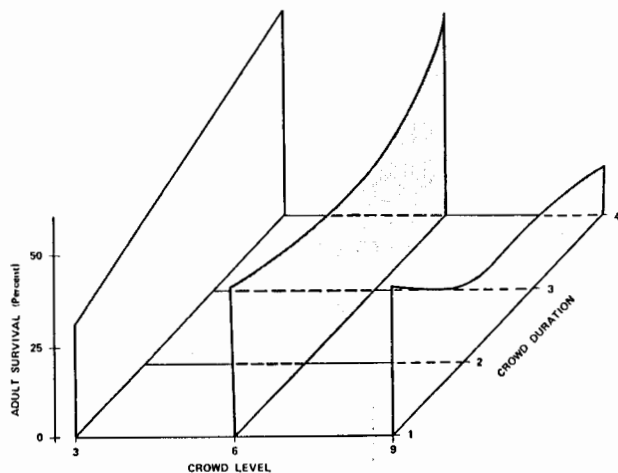


FIG. 4.—Percent of adult survival related to crowd level and crowding duration.

The percent of final survival increased as crowd level increased for the 1st-stadium separation (Crowd Duration 1). However, for the later-stadium separations (Crowd Durations 3 and 4), final survival decreased as crowd level increased (Fig. 4).

Length of Life Stages (Stadial Length) as Affected by Crowding Level and Crowd Duration.—It seems likely that an increase in either crowd level, or crowding duration, or both, would make it more difficult for larvae to obtain food. Plant tissue surrounding larval galleries tends to dry out, and crowding places adjacent galleries in close proximity; thus, larvae might be expected to encounter a substantial proportion of dry, unpalatable food and low feeding efficiency might easily result. Also, there is the offsetting possibility that larval feeding rate is stimulated in the presence of potential competition for food, as under crowding.

The net effect of these factors is unknown in an expectation sense, but the study results here indicate that stadial lengths for the 3rd stadium through the adult stages increase with crowding and that this effect is accentuated with shorter exposures to crowding (Fig. 5).

Using the stadial length of the "no crowd" level as a standard, it is hard to see why stadial lengths increased with decreased exposure to more severe crowding. But no matter what the reason, if this effect is real, it is of interest in understanding the dynamics of beetle populations in an epidemic situation. It appears that crowding larvae lengthens the generation-life year. This result could aid in the explanation for longer-than-usual flight periods during epidemics (high populations) and more consistent and shorter flight periods during endemics (low populations).

Influence of Larval Crowding on Sex Ratio of Adults.—The sex ratio of the mountain pine beetle usually has been considered as 1:1 (Lanier and Wood 1968). To define the goodness of fit of the

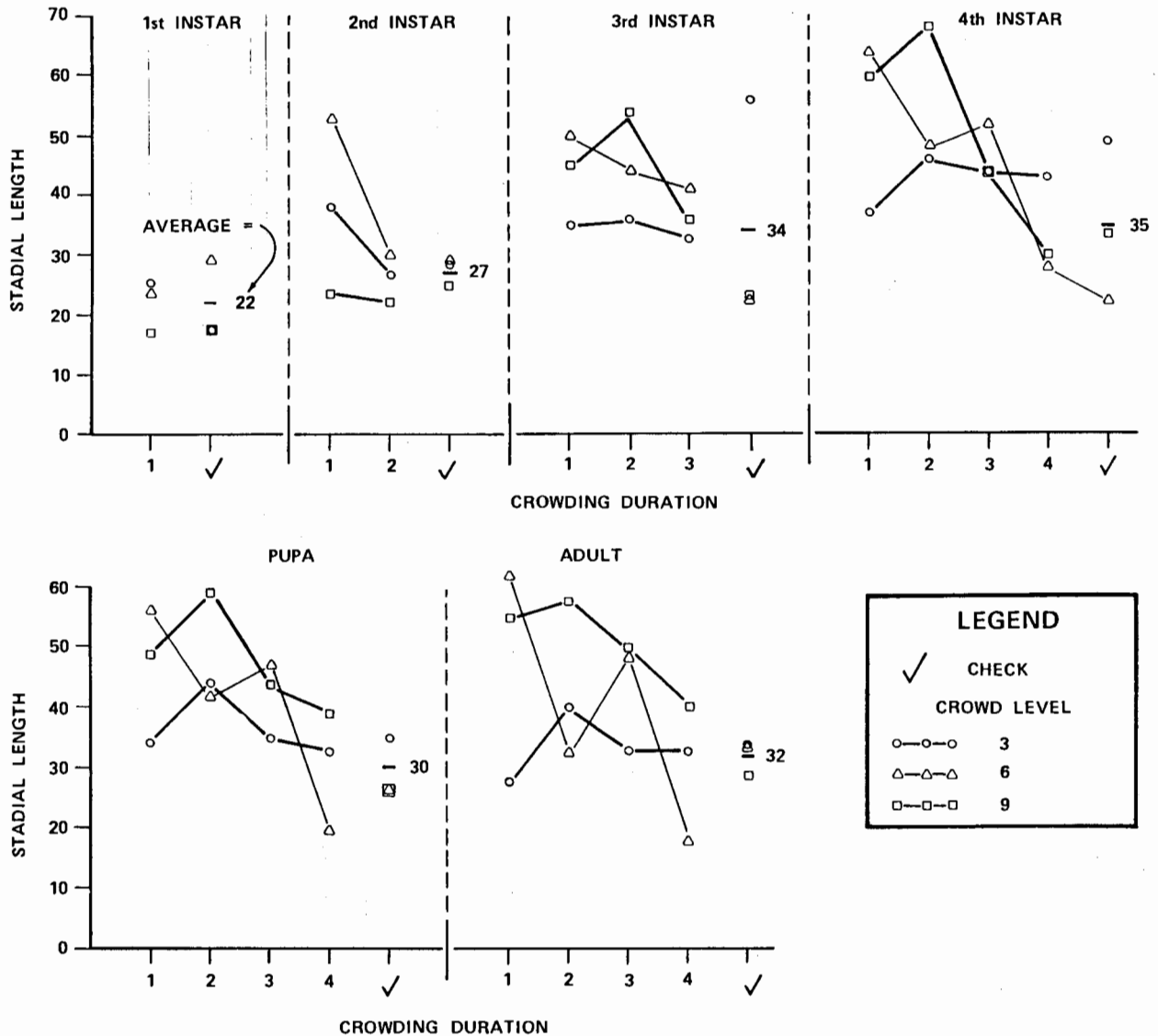


FIG. 5.—Stadia length as related to crowding duration.

observed sex ratios to the theoretical 1:1, a test for heterogeneity χ^2 was made. There was no differential effect on the sex ratio due to either crowd levels or crowding durations. If there were real differences in the sex ratio, then the sample was not large enough to detect these differences. However, the trend between total χ^2 values for crowd levels indicated that crowd levels greater than Crowd 9 might have affected the sex ratio (Table 5). The greater the departure from the expected 1:1 ratio in Crowd 9, as compared with the departure in Crowd 3, the greater the heterogeneity χ^2 would be and the greater the inconsistency of the departure from the expected 1:1 ratio. Based on total χ^2 , the crowding duration became more important as crowd level increased. Reid (1958) reported a 2:1 ($\text{♀}:\text{♂}$) sex ratio, based on mass collection of adults emerging from lodgepole pine in southeastern British Columbia. However, he did not state the conditions of crowding to which the larvae were subjected.

A simple linear regression was calculated to determine if a relationship existed between stadium duration and sex ratio and, if so, how well the regression fits the data. There was rather poor correlation for the first ($r = 0.2540$) and second ($r = 0.1054$) stadia, but greater correlation occurred for the third and fourth stadia ($r = 0.8110$ and 0.6276 , respectively).

Regression lines fitted for the data of the 3rd and 4th larval stadium (Fig. 6), indicate that the less time the larvae remained in the 3rd and 4th stadia, the greater the chance of obtaining a 1:1 sex ratio. Whether the cause is due to crowding, nutrition, or weather in the field remains to be determined. Nutritional stress caused by crowding is the probable cause.

Oviposition, Egg Viability, Egg Gallery Length, and Adult Size as Affected by Larval Crowding.—The reproductive capacity of the adult female was measured by 3 responses: number of eggs deposited;

Table 5.—Heterogeneity χ^2 for goodness of fit of sex ratios to the theoretical 1:1 by crowd levels and crowding durations.

Crowding duration	Crowd level						Total χ^2	Pooled χ^2	Heterogeneity χ^2
	3		6		9				
	Female	Male	Female	Male	Female	Male			
1	4	5	7	17	14	16	2.2056	1.3413	0.8643
2	6	8	8	10	2	9	2.4813	1.4070	1.0743
3	5	4	7	4	6	2	1.4652	1.1429	.3223
4	10	9	5	7	1	1	.1430	.0152	.1278
Total χ^2	.2804		2.7207		3.2940		6.2951		
Pooled χ^2	.0098		.9308		.2451		.8754		
Heterogeneity χ^2	.2706		1.7899		3.0489		5.4197		

egg hatch; and cm of egg gallery constructed. The number of eggs laid and cm of gallery constructed decreased with increased length of crowding within each of the 3 crowd levels (Fig. 7, 8). Egg hatch showed no apparent trend attributable to crowd level or crowding duration.

Increased crowding tended to decrease the length of stadia duration and total time for the female beetle to reach maturity, as has been noted previously. Adult females from the Crowd 9 level laid fewer eggs and constructed fewer cm of gallery than those females from the Crowd 6 level; Crowd 6 females laid fewer eggs and constructed fewer cm of gallery than the Crowd 3 females even though all 3 types of females had been crowded the same number of days. Both of these responses showed the

same general trend, i.e., the greater the crowd level the less the response (Fig. 7, 8, line 1); and the greater the crowd level the shorter the time interval for female beetles to mature and, thus, the less response (Fig. 7, 8, line 2).

Weight and length of the adult beetle could be expected to be factors in differential egg deposition and gallery construction, and could be affected by crowded rearing. No apparent correlation was found between rearing conditions and the weight and length of the adult beetle.

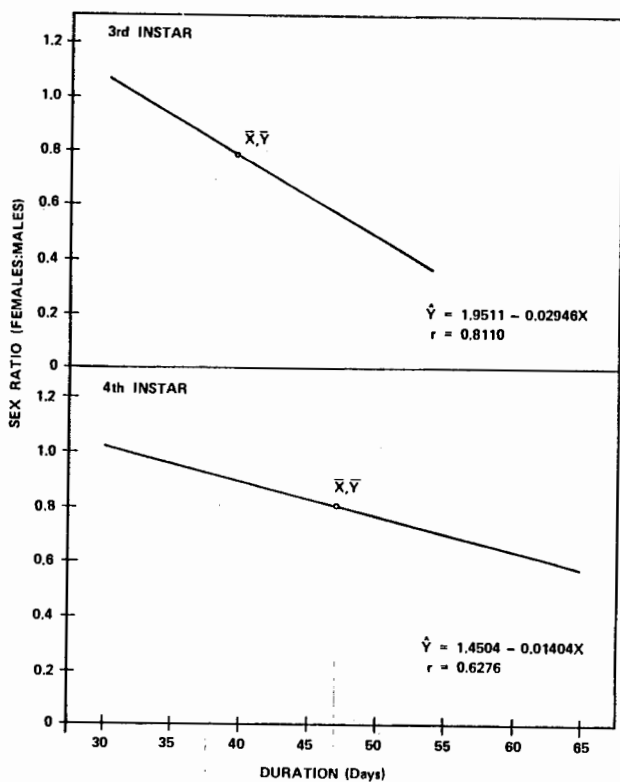


FIG. 6.—Regression of sex ratio on stadia duration for the 3rd- and 4th-larval instars.

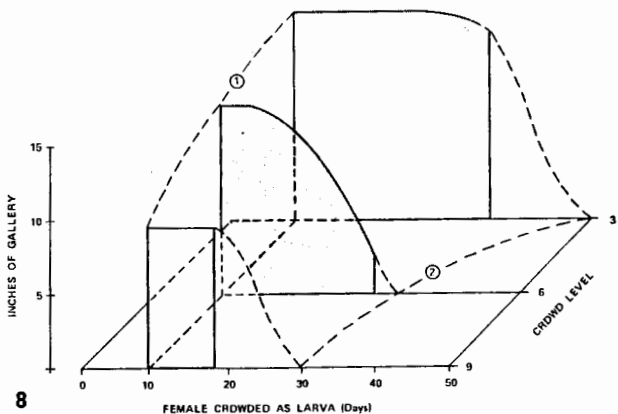
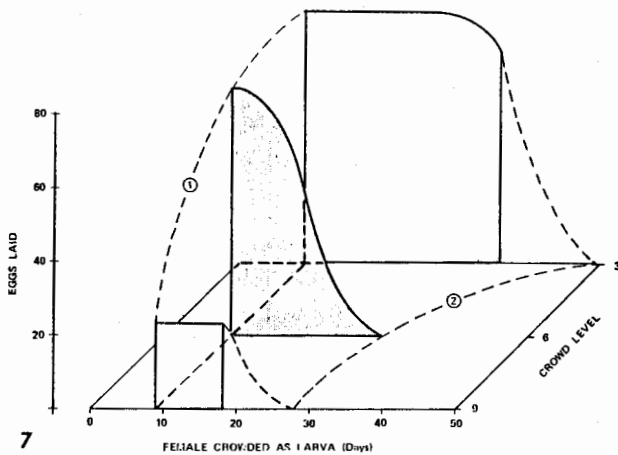


FIG. 7.—Oviposition response of adult female by crowding during larval stages.

FIG. 8.—Length-of-gallery-constructed response of adult female by crowding during larval stages.

Discussion

An endemic infestation of the mountain pine beetle is usually dependent on number of trees infested and population therein. Thus, if the within-tree larval population is of low density one would expect greater survival of adults, a rather uniform rate of development, at least a 1:1 sex ratio (tending toward more males than females), and greater reproductive capacity of adults. Consequently, endemic populations might tend toward life cycles synchronized with the seasons and weather, but with increasing survival and reproductive capacity over succeeding generations until the influence of food becomes effective.

Amman (1969) and Cole and Amman (1969) showed the mountain pine beetle to be grossly governed by food quantity (phloem of lodgepole pine). Cole and Amman (1969) observed that even under endemic conditions the beetle prefers larger-diameter trees which usually have thick phloem. Thus, survival is correlated with food and crowding acts either in a passive or a beneficial role: thus, low-density populations can only increase in numbers over time.

Of interest is consideration of the role of crowding within epidemic populations of the mountain pine beetle. The so-called epidemic period usually spans 6 to 8 years. Each year the thicker-phloem, larger-diameter trees are infested and killed within the residual stands of lodgepole pine (Cole and Amman 1969). The influence of food supply is probably decreasing; crowding is increasing, resulting in increased brood mortality.

The time when the annual flight period occurs is rather consistent within endemic populations, but the greatest fluctuation of time of occurrence and duration of flight has been most evident within epidemic populations. The annual weather pattern during the flight period is usually rather consistent in the Inter-mountain Region and cannot be considered a significant cause of change in the population.

The influence of crowding on stadia duration and subsequent development of the beetle could very well be a leading cause of the variation in time of occurrence and duration of flight within epidemic populations. When crowding interacts with spring weather patterns during the later stadia, greater variation would result.

Within a given small food quantity (thin phloem), crowding probably shortens the developmental period of the larvae. Conversely, within a given large food quantity (thick phloem), crowding is less influential and probably lengthens the developmental period of the larvae. Thus, maturation of the beetle would vary, resulting in variable flight occurrence.

Some possible effects of larval crowding in a natural population of the mountain pine beetle might be summarized as follows:

- (1) Crowding reduces the stadia durations. Shorter stadia durations increase the chance of a 1:1 sex ratio and, thus, the probability of every female being mated increases.

- (2) Increased crowding during the developmental period decreases the reproductive capacity of the female adult.
- (3) Food quantity diminishes as the large trees with thick phloem are killed and the effect of crowding increases, thus a decrease in population results.

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