FEMALE SIZE AND EGG PRODUCTION OF THE MOUNTAIN PINE BEETLE, *DENDROCTONUS PONDEROSAE* HOPKINS

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TABLE OF CONTENTS

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ABSTRACT

The relations of number, size and hatchability of eggs to female size were studied for the mountain pine beetle. Number of eggs laid, dry weight and cross-sectional area of eggs increased with female size. Egg hatchability was statistically independent of egg size, although consistently high for the largest females tested. Differences in female size and egg laying behavior was found between two widely separated populations. These results appear to be relevant to construction of indices for predicting population fluctuation.

INTRODUCTION

Quantitative relationships between body size and fecundity have been demonstrated for several defoliating insects (Prebble, 1941; Miller, 1957; Cook, 1961; Campbell, 1962; Drooz, 1965; Heron, 1966). The purpose of this investigation was to determine whether a relationship of this type exists for the mountain pine beetle (*Dendroctonus ponderosae* Hopk.). Female size, total number of eggs laid, egg size and egg hatchability were considered.

The studies were conducted during 1967 and 1968. The source of beetles and host material (lodgepole pine, *Pinus contorta* var. *latifolia* Engelman) for laboratory experiments was an outbreak in a small area near Canal Flats, in southeastern British Columbia. Field studies were done near Canal Flats and at Invermere, approximately 65 miles distant. Maximum-minimum August temperatures approximate 23 - 9°C at the Canal Flats area and 29 - 1°C at the Invermere area. Biology and behavior of the mountain pine beetle are reported elsewhere (Evenden, Bedard and Stubble, 1943; Reid 1962 a, b; Reid, 1963; Reid, Whitney and Watson, 1967).

METHODS

Female Size

Size of females from the two infestation areas was determined by measuring their pronotal widths to the nearest 0.05 mm with an ocular micrometer. The beetles measured were taken from galleries that had been newly established on the basal 6 feet of the host tree during the main flight period in July 1967. Dry weight was determined for 50 females from each study area by placing each beetle in an open gelatine capsule at 70°C for a minimum of 16 hours before weighing. Additional drying resulted in insignificant weight changes. The beetles weighed represented the size range found in the outbreak area.

Egg Production

The influence of the host material was minimized by using a single tree in each experiment. Slabs approximately 13 x 33 x 4 cm were cut from freshly felled lodgepole pine. The exposed s urfaces of the slabs were dipped in molten paraffin to delay desiccation. Each slab was infested with a pair of beetles of which the pronotal width of the female was known and placed in an individual rearing tube like those described by Lanier and Wood (1968). The tubes were screened at one end and transferred to a rearing room at 21±3°C and 55±10% relative humidity.

The number of eggs laid per female relative fecundity) under the conditions of this experiment was determined by analysing 25 completed galleries from which the female had emerged. Gallery length was measured to the nearest centimeter and the egg niches were counted. Since the mountain pine beetle rarely deposits more than one egg in each niche or rarely leaves a niche blank, this count was considered to be a close approximation of total eggs in each gallery.

To assess the relations between female size, egg size and egg hatchability, 35 slabs were opened 2 weeks following infestation and the first 13 to 20 eggs were removed and their length and width measured to the nearest 0.03 mm. The eggs were immediately transferred to special petri dishes described by Reid and Gates (1968), and placed in a growth chamber at 24°C and near 100% relative humidity. The eggs were checked daily over a period of 14 days or until 100% hatch occurred. Under the experimental conditions used, all viable eggs hatched within 14 days. As eggs hatched, the larvae were removed from the dishes to prevent contamination. The cross-sectional area, through the long axis of each egg was approximated using the formula: $a = dl - 0.785\ d^2$ where $\underline{a}$ is the cross-sectional area, $\underline{d}$ the diameter and $\underline{l}$ the length of the egg.

The relation between dry weight of eggs and female size was determined by drying the first 20 eggs laid by each of 20 females a minimum of 12 hours at 70°C and weighing them in aggregate. Additional drying resulted in insignificant weight changes. The first 20 eggs laid were used to standarize comparisons.

Egg Distribution

To compare the distribution of eggs within galleries between the two study areas, the infested portion of trees was divided vertically into thirds and a maximum of five complete galleries was analyzed from each section. Total gallery length and number of eggs in each centimeter of parent gallery were determined for 95 galleries in seven trees from the Invermere infestation and 25 galleries in two trees from the Canal Flats infestation. For each population, number of eggs in each consecutive centimeter of gallery, excluding the last 2 cm, was averaged over all galleries until a minimum of six galle ries were contributing to the mean. The last 2 cm of each gallery were not used because they seldom contained eggs.

RESULTS

Female Size

Pronotal width distribution of 589 females from Canal Flats and 858 females from Invermere are compared in Fig. 1. Mean pronotal widths for the two populations, 2.08 and 1.94 mm respectively, were significantly different ($p<0.001$).

An analysis of covariance showed significant differences between both the slopes and intercepts of the regressions of dry weight on pronotal width for each population (Fig.2, Table 1)[2]. Except for

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[2] The covariance analysis (Table 1) and classical least-squares fitting of the regression lines (Fig.2) are permissible only if the x-variable was measured without error or where errors in x are sufficiently small to be ignored when compared with errors in y (Acton, 1959. p.129). Although the x variable was measured with error, the estimate of error in y was 95 and 49 times as great as that in x for the Canal Flats and Invermere data respectively. (The error variances were calculated from formulae given by Wald (1940). Fitting of the regression lines by the method of Wald (1940) gives the following equations: Canal Flats: $y = -12.56 + 7.65x$; Invermere: $y = -8.58 + 6.14x$. The slopes an d intercepts of these equations agree closely with those given in Fig.2.

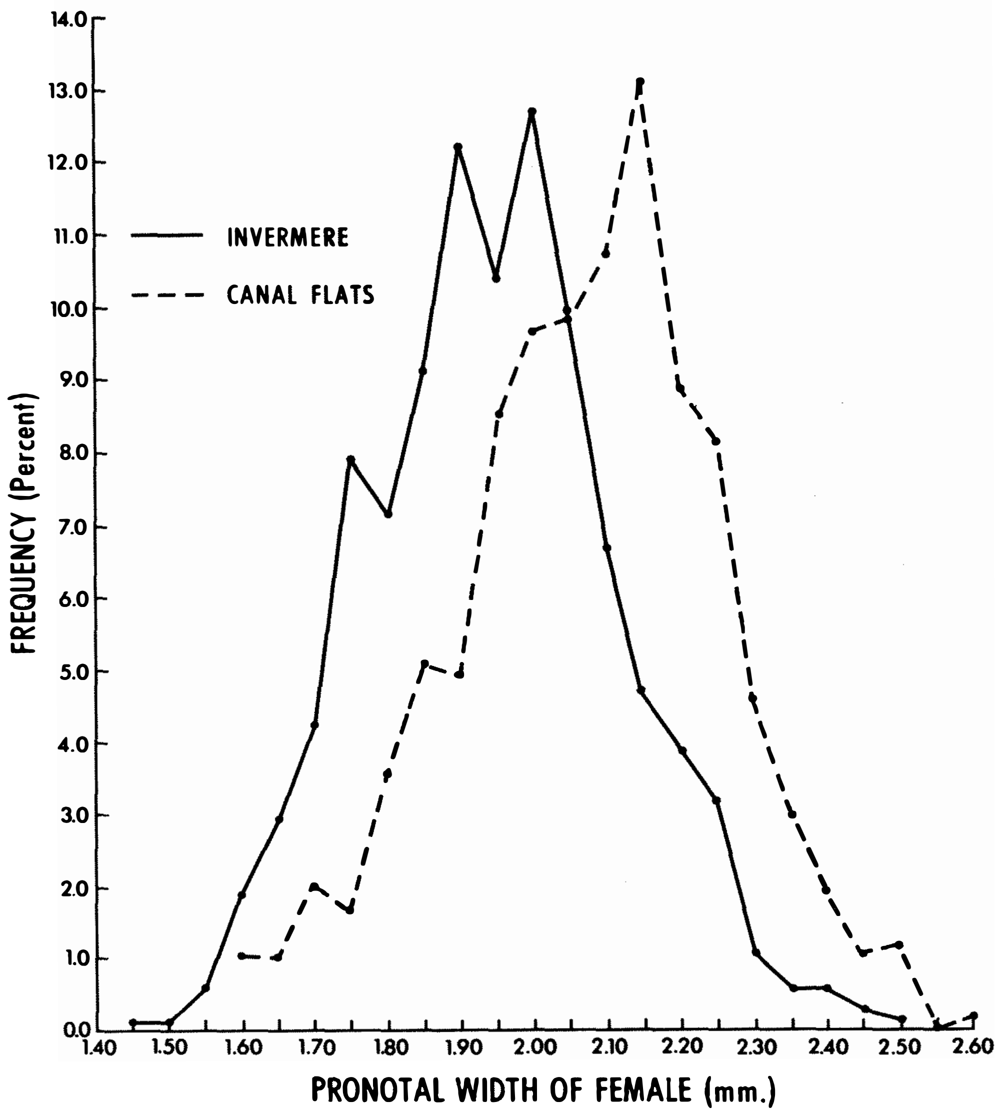

Fig. 1. Pronotal width distribution of female mountain pine beetles from two populations.

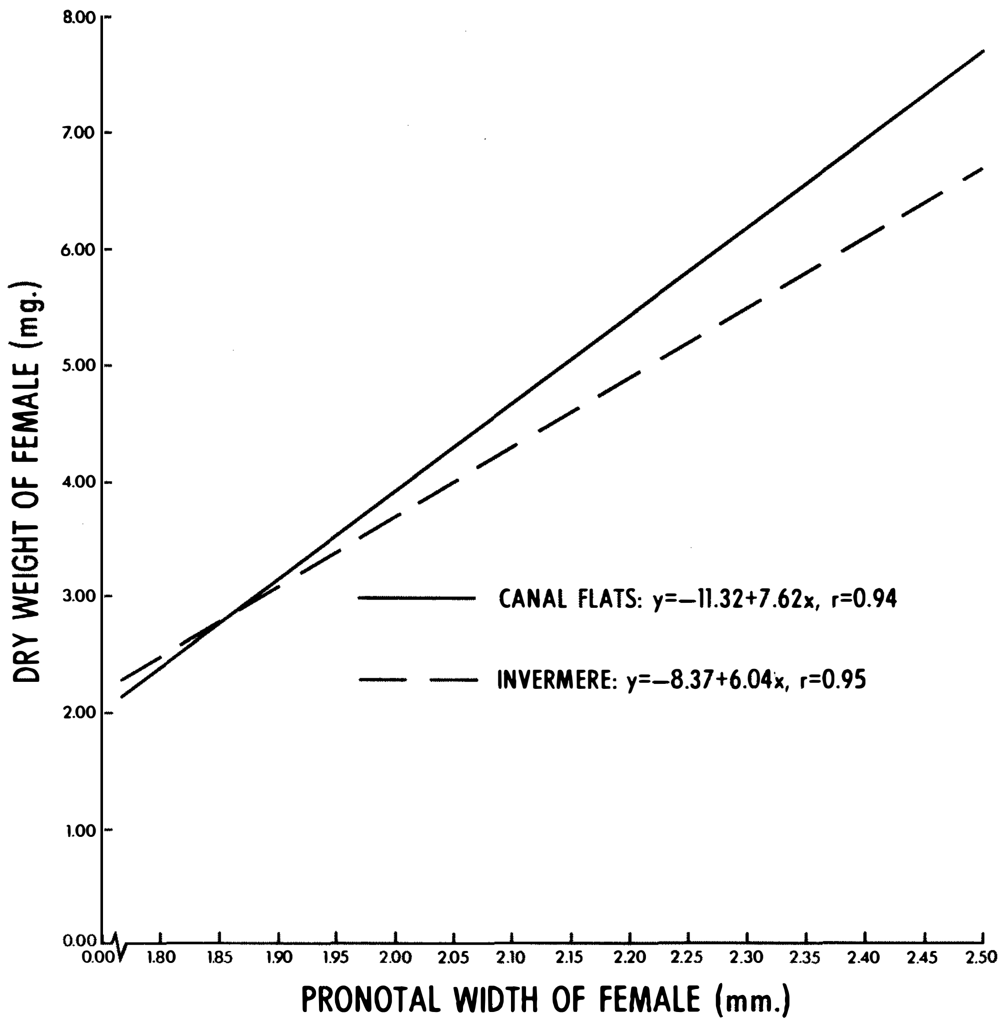

Fig. 2. Regression of female dry weight on female pronotal width for two populations of the mountain pine beetle.

the smallest females, beetles from the Canal Flats population were larger and proportionally heavier than beetles from the Invermere population.

TABLE 1

Comparison of slopes and intercepts of the linear regression equations for dry weight on female pronotal width for the mountain pine beetle.

Source	d.f.	SSy	SSxy	SSx	d.f.	33	MS	F
Canal Flats	49	122.890	14.345	1.881	48	13.491		
Invermere	49	129.661	19.527	3.235	48	11.793		
				Total	96	25.284	0.263	
	Difference for Testing Slopes				1	3.007	3.007	11.433**
	98	252.551	33.872	5.116	97	28.291	0.292	
	Difference for Testing Levels				1	4.325	4.325	14.811**
	99	280.248	36.371	5.342	98	32.616		

** Significant at the 1% level.

Egg Production

Egg density was independent of female size except for the smaller size classes where the gallery length was short (Fig.3A). Eggs per gallery (relative fecundity), gallery length and female pronotal width showed curvilinear relations (Fig.3 B, C). The larger the pronotal width of a female, the greater was its gallery length and number of eggs laid.

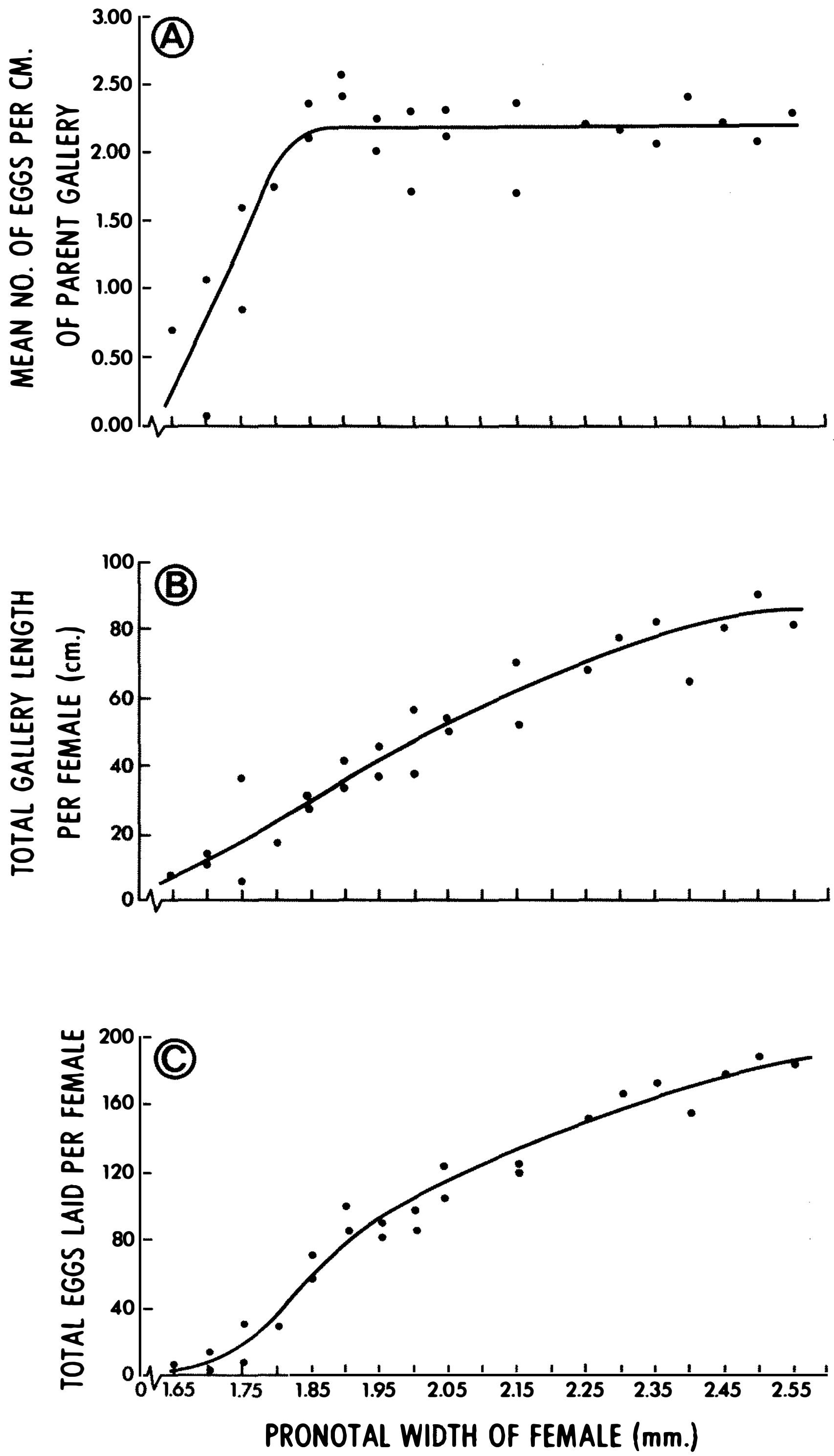

Fig. 3. Relations between egg density (A), total gallery length (B), and total eggs laid (C), to pronotal width for the mountain pine beetle.

The relations between average cross -sectional area of eggs, total dry weight of the first 20 eggs laid and female pronotal width were linear and had significant correlation coefficients (Fig.4 A, B). The larger the female, the larger and heavier were its eggs. There was no apparent relation between egg hatchability and either size of the female or size of the egg. However, the hatchability of eggs produced by the largest females was consistently greater than 80% (Fig.5). Mean per cent hatch for all females was 83.66%. The mean cross-sectional area of the viable and non-viable eggs for all females, 0.457 sq mm and 0.452 sq mm respectively, were not significantly different ($p>0.50$) (Table 2).

TABLE 2

Mean cross-sectional area of viable and non-viable eggs of the mountain pine beetle

Egg type	No. of eggs	Mean cross-sectional area (sq mm)	Standard error	Range
All eggs	635	0.4564	0.0033	0.1863-0.5994
Viable	535	0.4571	0.0038	0.3681-0.5994
Non-viable	100	0.4523	0.0057	0.1863-0.5571

Egg Distribution

Mean gallery length and mean number of eggs laid per centimeter

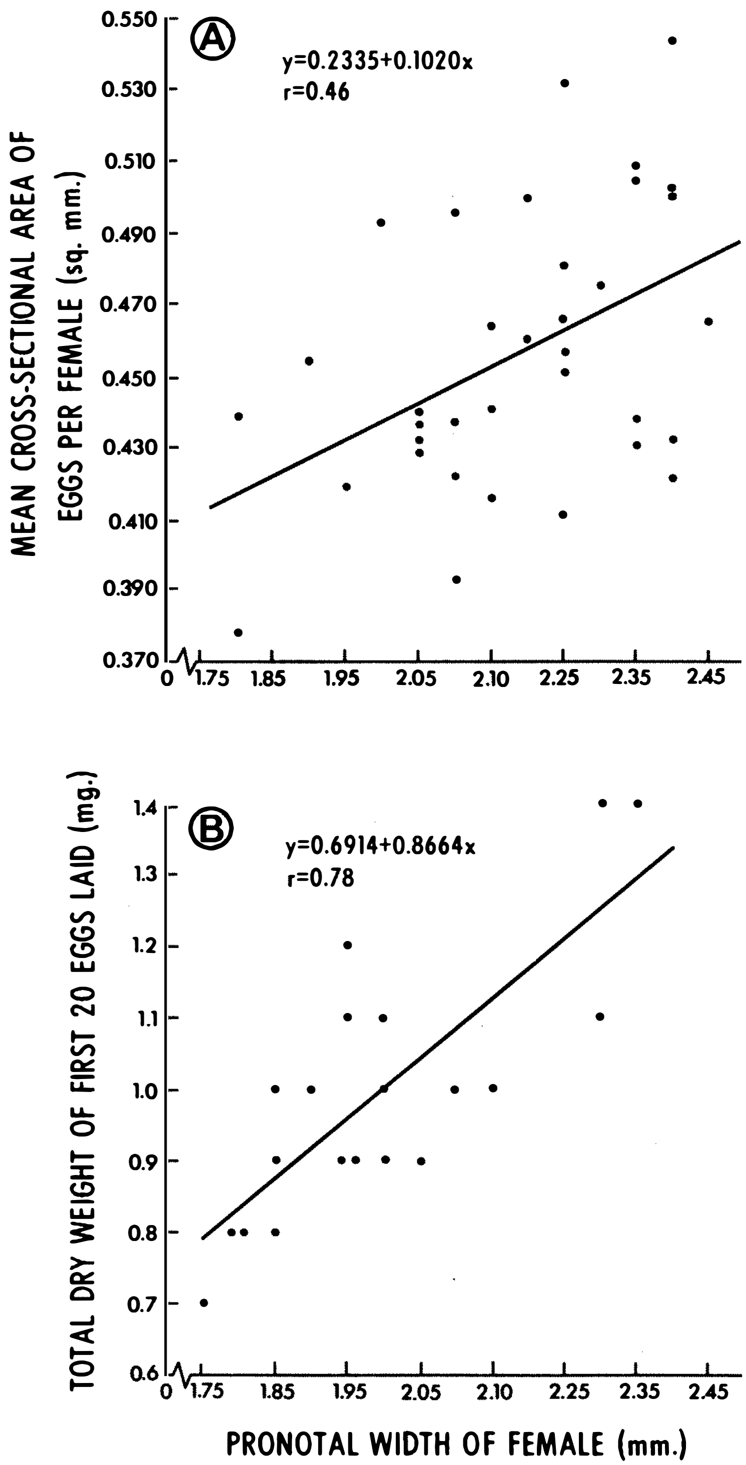

Fig. 4. Regressions of mean cross-sectional area of eggs (A), and total dry weight of eggs (B), on female pronotal width for the mountain pine beetle.

of parent gallery for the Canal Flats and Invermere populations are presented in Table 3. The relations between mean number of eggs laid per centimeter of gallery and consecutive centimeter of gallery length are shown in Fig. 6. Besides exhibiting the higher mean egg density, beetles from Canal Flats reached a peak in egg production in the initial part of the gallery and then showed a steady decline throughout the remaining part of the gallery. Beetles from the Invermere population gradually built up to a level of egg production that was maintained throughout the length of the gallery.

TABLE 3

Mean gallery length (centimeter) and mean number of eggs per centimeter of parent gallery for two populations of the mountain pine beetle

Source	No. of galleries	Mean gallery length ± 1S.E.	Mean no. of eggs/cm ± 1S.E.
Canal Flats	25	23.52 ± 1.88	3.35 ± 0.08
Invermere	95	25.74 ± 1.34	2.36 ± 0.04

DISCUSSION

These results show that major differences in pronotal width and dry weight of females exist between widely separated populations of the mountain pine beetle. Moreover, laboratory experiments

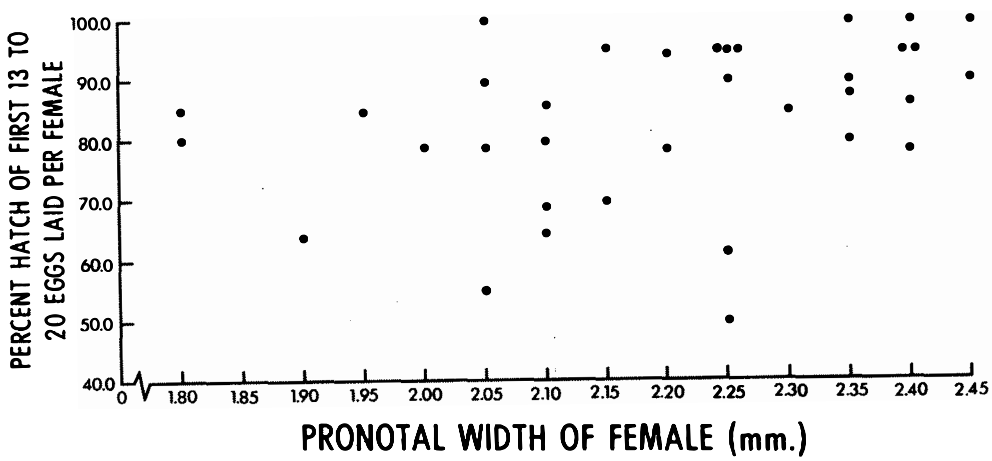

Fig. 5. Relations of percent egg hatch per female to female pronotal width for the mountain pine beetle.

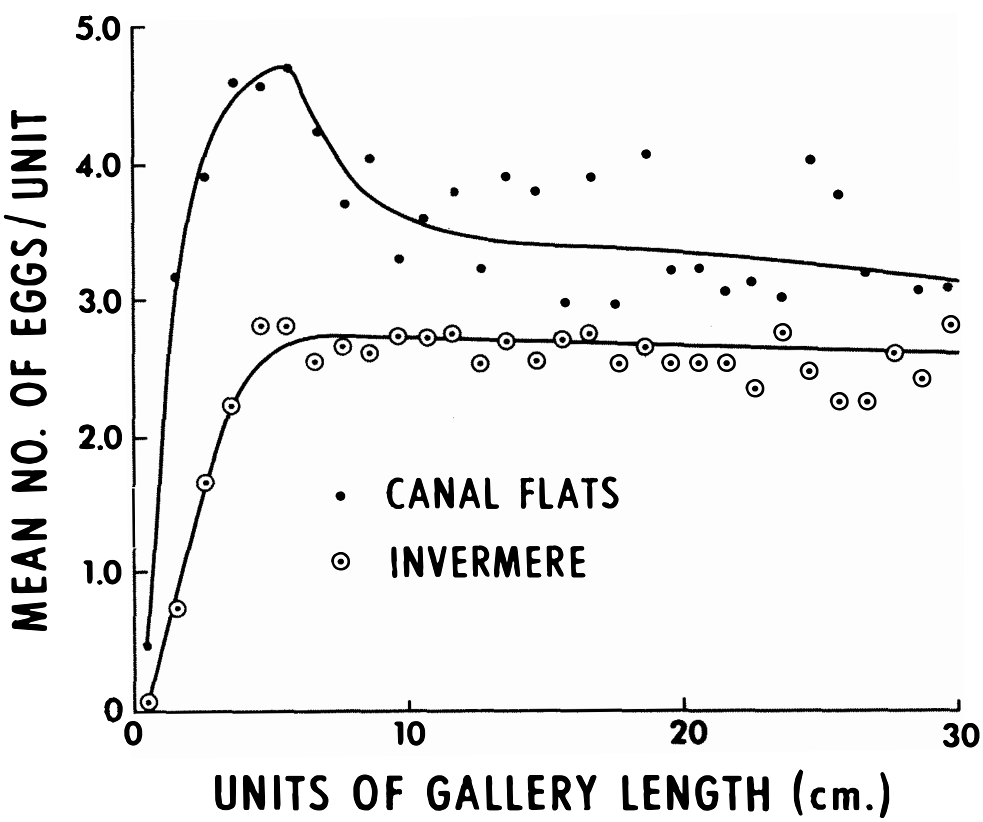

Fig. 6. Mean number of eggs for consecutive cm. of gallery length for two populations of mountain pine beetle.

indicated that fecundity varies directly with the size of the female. Reid (1955, 1962b) found that rates of egg laying and gallery construction increased with female size. Therefore, a change in mean female size may represent a parallel change in fecundity. There is evidence that large shifts in mean size of the female mountain pine beetle do occur periodically. When the Invermere population was reaching its peak during the mid-1950's, Reid (1955) reported the mean pronotal width for emerging females to be 2.23 mm. The population has declined since then (Reid, personal communication) and in 1967, females emerging in the same general area had an average pronotal width of only 1.94 mm.

The data in Fig. 2 show that besides differences in female pronotal width, there can be significant differences in dry weight-pronotal width regressions between populations. A female measuring 2.30 mm, in pronotal width had a mean dry weight of either 6.21 mg. or 5.52 mg., depending upon whether its origin was the Canal Flats or Invermere population. Atkins (1967), working with the Douglas-fir bark beetle, Dendroctonus pseudotsugae Hopk., reported differences in dry weights were a reflection of differences in lipid reserve. He further associated these differences with the propensity of the beetles to respond to host material. The differences in dry weight reported here are apparently reflected in egg laying behaviour and fecundity. Beetles from the population with the greater dry weight laid more eggs per centimeter in the initial part of the gallery. However, since host influences were not considered in this study, it is appreciated this may be a spruious relation.

Under the conditions of this study , hatchability was independent of egg size. This is not to infer survival of newly hatched larvae was independent of egg size. Campbell (1962) reported that with Choristoneura fumiferana (Clem), size of the egg affected not only the ability to survive, but also the growth characteristics of the individual that hatched from it.

While productive potential is related to size, size alone is inadequate for predicting fecundity of a population. Extrinsic factors such as host quality and quantity, competition, and weather are known to influence the number of eggs laid per female per gallery, gallery length, and the number of galleries constructed per female in any given time period. Size appears most useful as an index of the potential of the population to reproduce in a given environment.

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