INFLUENCE OF COMPETITION ON SIZE, BROOD PRODUCTION AND SEX RATIO IN SPRUCE BEETLES (COLEOPTERA: SCOLYTIDAE)

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ABSTRACT

In spruce beetles, *Dendroctonus rufipennis* Kirby, the effects of intraspecific competition on reproductive biology were studied in the laboratory at constant temperature. The factors were: egg gallery length, brood production per female, adult size in the broods, and sex ratio of the young spruce beetles, using egg gallery spacings of 1, 3, 6, 9 and 12 per 30 cm. All variables except sex ratio were significantly and inversely related to gallery spacing. The results indicate that density-dependent compensatory processes operate in spruce beetle populations during gallery construction and brood development.

RÉSUMÉ

Les effets de la compétition intraspécifique sur la reproduction chez le dendroctone de l'épinette (*Dendroctonus rufipennis* Kirby) ont été étudiés en laboratoire à température constante. Les facteurs considérés ont été la longueur des galeries de ponte, le nombre d'oeufs produits par femelle, la taille des adultes obtenus et le rapport des sexes chez les jeunes dendroctones, pour des densités des galeries de ponte de 1, 3, 6, 9 et 12 par 30 cm. Toutes les variables, exception faite du rapport des sexes, étaient inversement reliées de façon significative à la densité des galeries. Il semblerait d'après les résultats obtenus que chez les populations de dendroctones de lépinette il y ait compensation en fonction de la densité au cours de la construction des galeries, de la production des oeufs et du développement.

INTRODUCTION

Previous work on the population dynamics of several bark beetle species demonstrated that the density of emerged adults is strongly related to attack density (Amman 1972, 1976; Berryman and Pienaar 1973; Cole 1962, 1973; McMullen and Atkins 1961; Reid 1963). The nature of this relationship is such that maximum production usually occurs at intermediate attack densities because either egg production or survival from egg to adult or both of these factors are functions of attack density (Berryman 1974). Egg production in bark beetles can be affected through the inhibitory effect of attack density on the length of egg galleries or the number of eggs laid per unit length of egg gallery or both, as has been shown by several workers. Attack density may also affect the size of brood adults (Amman 1976) and thus the fecundity of female beetles (Cole 1973; Reid 1963; McGhehey 1971).

For the spruce beetle, *Dendroctonus rufipennis* Kirby, Thomson and Sahota (1981) showed that competition effects among parent beetles during egg gallery establishment increased with gallery accumulation and resulted in subsequent reduction in gallery length and oviposition.

Berryman (1974), using data derived from Knight (1958, 1969), suggested that the relationship between attack and emergence density for the spruce beetle is non-linear and characteristic of populations in which survival is density dependent. The objectives of this research were to examine the effect of the density of spruce beetle attack on the length of egg galleries, numbers of adults produced per egg gallery, and the size and sex ratio of the brood adults in the laboratory at constant temperature and food quality.

MATERIALS AND METHODS

Adult spruce beetles were collected in bark slabs from their overwintering sites on windfallen spruce logs, *Picea glauca* Moench, Voss, and stumps near Hixon, B.C. in early May, 1981. The bark slabs containing beetles were transported in plastic bags to the cold storage facilities in the laboratory in Victoria, B.C., where they were kept at -5°C until needed. A single tree was felled in mid-June, cut into bolts of approximately 50-cm, and transported to the laboratory where both ends of each bolt were sealed with hot paraffin to prevent desiccation.

Bark slabs containing adult beetles were removed from storage July 3, placed in cages at room temperature, and the insects were allowed to emerge. Emerged insects were collected twice daily, sexed and placed on moist paper towelling in jars which were stored at 5°C. Males and females were kept separate to facilitate further handling. On July 8, female beetles were placed in a large cage for a day of flight exercise and conditioning before being placed on brood logs. The males were exercised 24 hours later.

Female beetles were placed in prepared entrance holes punches through the bark about 2 cm from the end of the bolts, and confined to the holes by gelatin capsules (Lanier and Wood 1968). Entrance holes were punched at even spacing across 30-cm-wide areas of the bark on each of 20 bolts. Five spacings were created providing densities of: 1, 3, 6, 9, and 12 attacks per 30 cm strip of bark. The boundaries of the 30 cm-wide strips were defined by two vertical grooves cut through the bark with a chainsaw, and sealed with hot paraffin. The bolts were assigned at random to the five density treatments, 4 bolts per treatment. When space allowed, more than one replicate/bolt was prepared, allowing extra replicates of the low-density treatments on the same bolt. After 24 hours, males were placed in all galleries where frass indicated boring activity. Females not boring were replaced. All galleries had a pair of insects after 5 days. Only adults capable of flying or climbing easily to the top of the exercise cage were used, in order to minimize the use of injured insects.

All bolts were left undisturbed in a rearing room at 21 ± 1 °C until September 12, when examinations showed that brood devlopment was complete. All bolts were peeled between Septembr 24 and October 13. The galleries that produced brood were counted on each sample strip and the length of each of these was measured to the nearest millimetre. The numbers of adult beetles were tallied separately for each 30 cm bark strip in each bolt. All beetles were sexed and the width of the prothorax of 20 randomly chosen beetles of each sex from each density treatment was measured to the nearest 0.03 mm with an ocular micrometer wedge. The effects of gallery spacing on average egg gallery length, density of brood adults, sex ratio and adults size were determined by regression analysis. These variables were averaged within bolts, the experimental units, prior to analysis.

RESULTS AND DISCUSSION

The average length of the egg gallery, average number of brood adults/egg gallery, the average size of both sexes and the percentage of female spruce beetles all decreased with increasing egg gallery density (Table 1).

The average egg gallery length, 21.8 cm at the widest spacing, was in good agreement with that reported by Sahota and Thomson (1979) for the average length of 19.3 cm produced by female spruce beetles in spruce slabs at a constant 21.1 °C. The inverse relationship between attack density and average egg gallery length has been demonstrated by McMullen and Atkins (1961) for *D. pseudotsugae* and by Dudley (1971) for *D. brevicomis*. Thomson and Sahota (1981), studying population quality of the spruce beetle, also found that competition effects among female beetles during egg gallery construction resulted in a reduced rate of gallery production. Besides the reduced boring rate under crowded conditions, female beetles may also have stopped gallery construction and abandoned the galleries rapidly as was found by McMullen and Atkins (1961) for *D. pseudotsugae*. The relationship between mean egg gallery length within bolts (ΥG) and spacing (χ) suggested a curve of the following form: $\Upsilon = A \exp(-B\chi)$; where A = maximum

TABLE 1. Average egg gallery length, average number of brood adults/egg gallery, and the size and sex ratio of brood adults of the spruce beetle produced in spruce bolts in the laboratory at 5 egg gallery spacings.

Variables	Egg galleries/30 cm bark strip				
	1(1)[1]	3(2.1)	6(4.5)	9(7.7)	12(10.0)
No. egg galleries	4	34	24	36	48
% succ. egg galleries	75.0	70.6	75.0	86.1	83.3
Ave. egg gallery length (mm)	21.8 (1.59)[2]	16.4 (1.11)	16.4 (0.84)	14.9 (0.75)	13.4 (0.10)
Ave. no. beetles/gallery	50.3 (19.16)	32.0 (5.40)	28.8 (3.00)	17.8 (2.95)	14.2 (0.85)
Total no. brood adults	155	769	518	552	568
% females	65.2 (5.92)	55.5 (2.20)	55.6 (1.94)	56.1 (2.92)	52.8 (2.21)
Ave. female size (mm)	2.37 (0.02)	2.35 (0.02)	2.30 (0.03)	2.29 (0.03)	2.26 (0.03)
Ave. male size (mm)	2.42 (0.02)	2.37 (0.03)	2.36 (0.03)	2.30 (0.02)	2.33 (0.03)

[1] Initial and ( ) successful egg galleries.

[2] Standard error of the mean ($s_{\bar{x}}$).

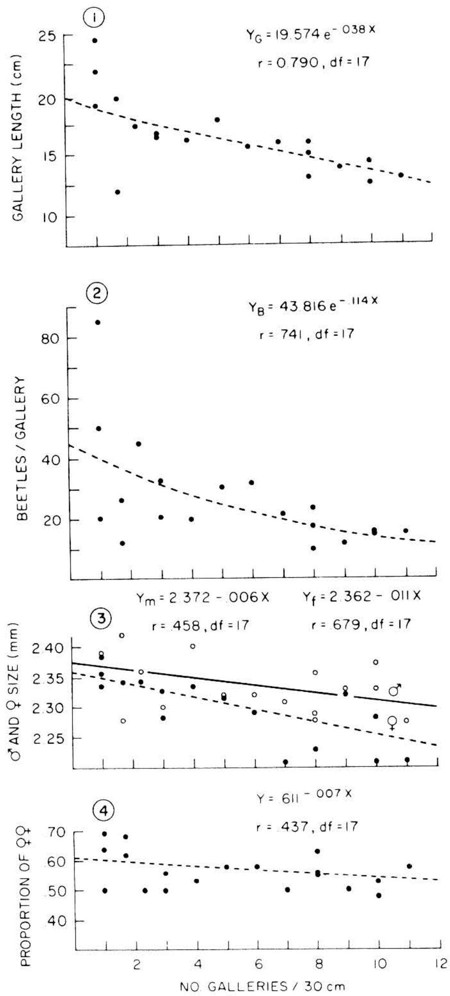

Fig. 1. The relationship between mean egg gallery length by spruce beetle within bolts and egg gallery spacing.

Fig. 2. The relationship between the mean number of spruce beetles per egg gallery within bolts and egg gallery spacing.

Fig. 3. The relationship between mean female (ϒf) and male (ϒm) size within bolts and egg gallery spacing.

Fig. 4. The relationship between the mean proportion of female spruce beetles produced per bolt and egg gallery spacing.

gallery length and b = a rate constant. Least-square fitting of this model to the (ln y, x) data set gave the following equation (Fig. 1): ϒG = 19.574 exp (-0.038 χ); n = 19, r = -0.790. This equation is of the same functional form as was fitted by Coulson *et al.* (1976) to the egg gallery length *vs.* attack density data for *D. frontalis*. By contrast, Dudley (1971) and Saarenmaa (1983) found that egg gallery length decreased linearly on attack density for *D. brevicomis* and *Tomicus piniperda*, respectively, and Berryman and Pienaar (1973) showed that gallery length was directly related to attack density in *Scolytus ventralis*.

The relationship between the mean number of adult beetles per egg gallery within bolts (ϒB) and gallery spacing (χ) was of the same functional form as described earlier for mean egg gallery length. The equation was as follows (Fig. 2): ϒB = 48.816 exp(-0.114 x); n = 19, r = -0.740. Berryman (1976) and Saarenmaa (1983) fitted similar equations to the relationship between brood production per female and attack density for *D. ponderosae* and *T. piniperda*, respectively.

The relationship between egg gallery length and egg gallery spacing does not completely explain the reduction in productivity per female at high density. Thomson and Sahota (1981) showed that the number of eggs/cm of productive gallery is not affected by competition. Therefore the decrease in brood production/cm of gallery with increasing density (YB/YG = 2.238 exp [-0.076X]) must be due to reduced survival. The literature generally supports the view that survival is reduced at high densities, largely through the effects of intraspecific competition (Amman 1972; Berryman 1973, 1974; Cole 1962, 1973; McMullen and Atkins 1961; Reid 1963; Saarenmaa 1983; Schmitz and Rudinsky 1968). Hence, the curve for productivity per female is a function of the relationship between productive egg gallery length, survival from egg to adult and egg gallery spacing.

The mean width of the pronotum ($\Upsilon\rho$) decreased directly with egg gallery spacing (χ) for both sexes (Table 1). The regression equations for the females and males, respectively, were $\Upsilon f = 2.362 - 0.010\chi$, ($n = 19, r = -0.679$), and $\Upsilon m = 2.372 - 0.006\chi$, ($n = 19, r = -0.458$) (Fig. 3). Amman (1972) has shown that in *D. ponderosae* the size of the female beetles was directly affected by egg gallery spacing and Saarenmaa (1983) found that the live weight of young *T. piniperda* adults was inversely related to attack density. Fecundity in *D. ponderosae* has been shown to be related to female size (Reid 1963; McGhehey 1971). The existence of such a relationship in the spruce beetle would mean that egg gallery density may also influence brood production in the following generation.

Although the proportion of female beetles tended to decrease directly with decreasing distance between the egg galleries (Table 1), there was not a significant relationship between these two variables (Fig. 4). The overall average female percentage, 55.9, agreed well with those observed in natural populations (Dyer 1973).

Because the larvae tend to mine at right angles to the egg galleries, of any regular spacing of egg galleries for a given density, the arrangement used in this study probably places the most severe competitive stress on the developing broods. However, the gallery arrangement used here also permits unhindered gallery elongation. Hence, the density dependent relationships derived from this study should be compared with relationships based on natural attacks to test their reliability.

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THE APHIDS (HOMOPTERA:APHIDIDAE) OF BRITISH COLUMBIA 13. FURTHER ADDITIONS

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ABSTRACT

Eleven species of aphids and new host records are added to the taxonomic list of the aphids of British Columbia.

INTRODUCTION

Nine previous lists of the aphids of British Columbia (Forbes, Frazer and MacCarthy 1973; Forbes, Frazer and Chan 1974; Forbes and Chan 1976, 1978, 1980, 1981, 1983, 1984; Forbes, Chan and Foottit 1982) recorded 357 species of aphids collected from 787 hosts or in traps and comprises 1485 aphid-host plant associations. The present list adds 11 aphid species (indicated with an asterisk in the list) and 44 aphid-host plant associations to the previous lists. Twenty-three of the new aphid-host plant associations are plant species not in the previous lists. The additions bring the number of known aphid species in British Columbia to 368. Aphids have now been collected from 810 different host plants and the total number of aphid-host plant associations is 1529.

The names of aphids are in conformity with Eastop and Hille Ris Lambers (1976) and are arranged alphabetically by species. Four new collection sites are tabulated in Table 1. The location of each collection site can be determined from Table 1 or from the tables of localities in the previous papers. The reference points are the same as those shown on the map which accompanies the basic list.

TABLE 1. Collection sites of aphids, with airline distances from reference points.

Locality	Reference Point	Dir	Distance km	mi
Mt. Cheam	Vancouver	E	167	104
Pender Island	Victoria	N	43	27
Rock Creek	Kelowna	SE	104	65
Sidney	Victoria	N	27	17

LIST OF SPECIES

ABIETINUM (Walker), ELATOBIUM
Picea sitchensis: Agassiz, May 4/45.

***ACHILLEAE (Koch), UROLEUCON**
Achillea millefolium: Vancouver (UBC), Nov 16/84.

ADIANTI (Oestlund), SITOBION
Athyrium distentifolium var. *americanum:* Vancouver (UBC), Aug 26/83.
Athyrium filix-femina ssp. *cyclosorum:* Vancouver (UBC), Aug 26/83.

AEGOPODII (Scopoli), CAVARIELLA
Angelica genuflexa: Harrison Lake, Aug 20/22.
Daucus carota: Chilliwack, Jun 26/45.

AGATHONICA Hottes, AMPHOROPHORA
Rubus idaeus: Agassiz, Jun 27/40.

ALBIFRONS Essig, MACROSIPHUM
Lupinus sp.: Victoria, May 20/21.

BETAE Doane, PEMPHIGUS

*Aphid species not in the previous lists.