BIOLOGY OF *GNATHOTRICHUS RETUSUS* AND BEHAVIOURAL RESPONSES OF *G. RETUSUS* AND *G. SULCATUS* TO SEMIOCHEMICALS

by

YONGBIAO LIU

B. Agri., Beijing Forestry University, 1982

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The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date: December, 1986
Abstract

*Gnathotrichus retusus* is primarily univoltine with a minor fraction of the population taking more than one year to complete the life cycle. From the spring to the summer, the development of brood from egg to adult took about 40 days or more in Douglas-fir logs. Brood production was significantly related to the gallery length. Boring activities were not consistently related with temperature, shifting from shallow sapwood to deep sapwood over time. Fungal staining was usually limited to the wood near the gallery entrance, and became darker in colour over time beginning in June. Abandonment of some galleries mainly occurred in June and July by females, and was probably induced by high temperatures.

*G. retusus* preferred Douglas-fir stumps to western hemlock stumps, but both host tree species were equally suitable for *G. retusus* brood development. Significant differences were found among individual Douglas-fir and western hemlock stumps in attack density and brood production. Within a stump, attack density and brood production for Douglas-fir, and attack density for western hemlock increased from the stump top to the bottom.

*G. retusus* emergence from Douglas-fir and western hemlock stumps and *G. retusus* and *G. sulcatus* flights began in late April when the daily maximum temperature reached 13.5°C, and peaked in late May. Brood emergence of *G. retusus* ceased, with rare exception, in late June. *G.
retusus had only one big peak flight while G. sulcatus had a small second peak flight in late July. Seasonal flights ceased in October when weekly mean maximum temperatures dropped below 15°C. Brood emergence, seasonal flights, and the sex ratios of brood ready to emerge and captured flying beetles were positively correlated with maximum temperature.

G. retusus had a bimodal diurnal flight rhythm: a very small morning flight and a much larger dusk flight. Light intensity seemed to be a major stimulus in initiating the flight. However, diurnal flight might also be influenced by both temperature and relative humidity.

Both G. retusus and G. sulcatus of both sexes responded significantly to ethanol or their own aggregation pheromones, (+)-sulcatol and (±)-sulcatol respectively, and ethanol was a synergist of (+)-sulcatol for G. retusus of both sexes. Alpha-pinene was neither a primary host attractant nor a synergist of aggregation pheromones. The sex ratios (female/male) of both species increased significantly from less than one for host chemicals alone to above one for treatments including aggregation pheromones. The sex ratio of G. sulcatus increased with increases in release rates of (±)-sulcatol.
Acknowledgements

I wish to express my deepest gratitude to the following persons and organizations with whose contribution this thesis becomes reality. Dr. J.A. McLean, my supervisor, for great enthusiasm to introduce me to this topic, firm guidance, valuable suggestions and advice, and tremendous help; my committee members, Drs. M.B. Isman, T.L. Shore, B.J. van der Kamp for their care and helpful suggestions and advice; J. Northrop, M. Putland, N. Ryant for their help in the field and laboratory work; and the Government of the People's Republic of China for financial support.

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1. INTRODUCTION

Ambrosia beetles consist of many members of the family Scolytidae and all members of the family Platypodidae. The total number of species is well above 1000, with nearly 400 species identified on the America continent (Wood 1982). Ambrosia beetles are so named as both adults and larvae feed on ambrosia fungi (Chamberlin 1939).

In coastal British Columbia (B.C.), five ambrosia beetle species are known: *Trypodendron lineatum* Oliver, *Gnathotrichus sulcatus* LeConte, *G. retusus* LeConte, *Xyleborus saxeseni* Ratz, and *Platyapus wilsoni* Swaine (Johnson 1958; McMullan 1956; Prebble and Graham 1957). Ambrosia beetle damage includes the black stain around galleries, which is probably caused by symbiotic ambrosia fungi (Fisher et al. 1953), and the pinholes themselves. The damage is mainly aesthetic resulting from the black fungal staining rather than any reduction in the physical strength of the wood.

The problem caused by ambrosia beetles to the B.C. forest industry has been recognized since 1928 when portions of some shipments of lumber from British Columbia to Australia were ordered destroyed on arrival under quarantine regulations because of the presence of live ambrosia beetles (Graham and Boyes 1950). From that date, ambrosia beetles have continued to cause economic losses due to inspection costs, fumigation, closing of foreign markets, downgrading of lumber, and volume and time losses at the headsaw in a
sawmill if a clear face was required on the lumber (Graham and Boyes 1950; McMullan 1956). In late 1940's, it was estimated that about 25% of the lumber volume produced in coastal British Columbia contained worm-holes excavated by ambrosia beetles, and 11% was downgraded (McBride 1950). A similar situation existed in late 1950's, and the average loss per M fbm was C$6.00 due to the downgrading (McBride and Kinghorn 1960). In 1975-76, the annual loss owing to ambrosia beetle damage in B.C. was estimated by Western Forest Products Laboratory, Vancouver, B.C. to be C$7 million (Nijholt 1978). In 1980-81, ambrosia beetle downgrading of sawlogs processed through the Vancouver log market was estimated to be C$63.7 million (McLean 1985).

Among the five ambrosia beetles in the coastal areas of British Columbia, *Gnathotrichus retusus* and *G. sulcatus* together are a distant second in importance to *Trypodendron lineatum* (Furniss and Carolin 1977). Among the three important species, *G. retusus* has received the least attention. The knowledge of its biology and behaviour are very limited compared with that of the other two species.

*G. retusus* is distributed in southern British Columbia, the western United States and probably into Mexico. Its host spectrum probably includes all conifers in its range (Bright 1976).

The biology of *G. retusus* is similar to that of *G. sulcatus* (Doane and Gilliland 1929; Prebble and Graham 1957), and the two species have often been treated jointly
in relevant literature. *Gnathotrichus* beetles attack "green" wood, after death or injuring of the tree, or after felling and bucking into logs. They also attack freshly sawn lumber in mill yards and the exposed surface of logs floating in water (McLean and Borden 1975a, 1977a; Prebble and Graham 1957). Douglas-fir (D-f) logs felled from one month up to 14 months and western hemlock (WH) logs felled from one month up to 18 months may be subject to attack by *Gnathotrichus* beetles (Mathers 1935; Prebble and Graham 1957). A few attacks have been found even within a week of felling (Mathers 1935).

The penetration of galleries is restricted by the depth of sapwood in D-f but not in WH. The deepest gallery penetration is 8.1 cm in D-f logs and 13.5 cm in WH logs. A completed *Gnathotrichus* gallery system may consist of up to six transverse galleries at various depths, each essentially concentrated within an annual ring. The maximum total length of a gallery system can reach 73.7 cm (Prebble and Graham 1957). The average diameter of a *Gnathotrichus* gallery is 1.32 mm (Johnson 1958).

*Gnathotrichus* species have no true diapause; all stages of their life cycle can be found during the year, and they overwinter in the host material in all stages (Chamberlin 1939; Doane et al. 1936; Prebble and Graham 1957). The flight of *G. retusus* beetles begins in April and occurs continuously until September (Mathers 1935) or October to November (Daterman et al. 1965; Lindgren and Borden 1983;
McLean and Borden 1977b; Shore 1982; Shore and McLean 1985). One single flight peak in May and June was recorded with the aggregation pheromone baited traps (Lindgren and Borden 1983; McLean and Borden 1977b; Shore and McLean 1985), which suggests that *G. retusus* is univoltine. However, evidence for the existence of two generations has been found (Chamberlin 1939; Daterman *et al.* 1965, Doane and Gilliland 1929). According to Daterman *et al.* (1965), *G. retusus* beetles may fly as late as November 1st and gallery initiation may occur in mid-October. Two flight peaks, the first definite peak between mid-May and early June and a second less evident peak in July, were also reported (Daterman *et al.* 1965).

Attacks by *G. retusus* start in the spring when brood emerge from galleries, disperse, and infest new host material. The emergence of *G. retusus* from host material seems to be governed by daylight since it begins at noon and increases in intensity between 1600h and 1800h. No emergence takes place in the forenoon even when subcortical and air temperatures are favorable (20-21.1°C) for emergence of other scolytids. The lowest subcortical temperature at which *Gnathotrichus* species was observed to emerge was 17.8°C (Rudinsky and Daterman 1964).

The dispersal flight of *G. retusus* beetles depends upon an interaction of temperature and light intensity. A temperature of 14.4°C is necessary to initiate flight, and the flight ceases at 15.6°C and below. Within this
temperature range light intensity above 10.8 Watts/m\(^2\) (100 ft-c\(^1\)) is required for the beetles to start flying, but they stop flying shortly before total darkness. A light intensity of 10.8 to 21.5 Watts/m\(^2\) seems optimal for the beetle flight, while temperatures between 18.3°C and 22.2°C seem to be the most favorable. Temperatures above 26.1°C inhibit *G. retusus* flight (Rudinsky and Schneider 1969), and a maximum of 26.7°C for *Gnathotrichus* flight was established by Rudinsky and Daterman (1964).

*Gnathotrichus* beetles have two flight peaks in a day; a morning flight and an evening flight. The morning flight has a low temperature threshold of 14.4°C and a low threshold light intensity of 16.1 Watts/m\(^2\), and an upper limit for light intensity of about 215.3 Watts/m\(^2\). The evening flight is much greater than the morning flight and begins when evening light intensity falls below 215.3 Watts/m\(^2\). A small number of beetles could be collected between 1000h and 1500h (Rudinsky and Schneider 1969).

Attacks by *Gnathotrichus* are commenced by male beetles (Borden 1974), that carry symbiotic fungi cells in their forecoxal cavities (mycetangia) (Farris 1963). The ambrosia fungi are introduced into fungus cavities (mycetangium) at the end of hibernation, nourished by secretions of the cells lining the mycetangium, and begin to grow during the dispersal flight. After a gallery is initiated, the fungus is released (Schneider and Rudinsky 1969). The primary

\[\text{1 Watt/m}^2 = 9.2902 \text{ ft-c}\]
species of fungus which *G. retusus* beetles feed on is *Ambrosiella gnathotrichi* Batra (Batra 1967).

*G. retusus* attacks are characterized by fine white frass on the surface of host materials. The frass production rate by the male beetle prior to pairing with the female is lower than that after pairing. Soon after the male is joined by the female, frass production rises to a peak. When galleries were dissected 9 days after attack, the male was always found to be at the head of the tunnel (Borden and McLean 1979).

Both primary host attractants and beetle-produced secondary attractants are known to be involved in attacks of host material by *Gnathotrichus* beetles. *G. retusus* beetles respond significantly to log odors of D-f, WH, and western white pine (Chapman 1963), while *G. sulcatus* responds positively to sawdust from fresh logs (Borden and Stokkink 1973; McLean 1976).

The production of host attractants is probably caused by anaerobic fermentation in sapwood since anaerobically treated logs are significantly more heavily attacked by ambrosia beetles (Graham 1968). This conclusion was further supported by the investigation by Cade *et al.* (1970) who found that *G. sulcatus* mass attacked water soaked western hemlock logs but made no attacks on unsoaked logs. It was concluded that a primary attractant was present in soaked logs, and the attractant also acted as a boring stimulant.
Gas chromatographic isolation and identification and field bioassays demonstrated that ethanol was a primary host attractant for G. sulcatus (Cade et al. 1970; Moeck 1970), and was induced by anaerobic treatments (Graham 1968; Moeck 1970). The effects of ethanol as a host kairomone were later reported by other authors (Table 1). The tunnelling (feeding) stimulating effect of ethanol was demonstrated in the ambrosia beetle Xyleborus ferrugineus (Norris and Baker 1969). McLean and Borden (1977a) also hypothesized boring stimulation effects of ethanol in G. sulcatus attacks.

Alpha-pinene is another host chemical proposed to be a primary attractant to various bark and ambrosia beetles including G. retusus and G. sulcatus (Rudinsky 1966). However, in Rudinsky's study a-pinene was tested in 95% ethanol solution, and ethanol has since been demonstrated to be a primary attractant to ambrosia beetles but not a-pinene (Table 1). Furthermore, evidence of deterrent effects of a-pinene on boring by Trypodendron lineatum beetles has been found (Werner and Graham 1957).

The existence of secondary attractants have been demonstrated in both G. sulcatus (Borden and Stokkink 1973) and G. retusus (Borden and McLean 1979). G. sulcatus of both sexes were found to be significantly responsive to male frass and guts from males in the log. As both sexes responded positively, the attractant was designated as a population aggregation pheromone (Borden and Stokkink 1973).
Table 1. Summary of effects of α-pinene and ethanol as host kairomones or synergists of aggregation pheromones for *Gnathotrichus* spp.

<table>
<thead>
<tr>
<th></th>
<th><em>G. retusus</em></th>
<th><em>G. sulcatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>KAIROMONE EFFECTS:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>α-pinene</td>
<td>attractive (Rudinsky 1966)</td>
<td>attractive (Rudinsky 1966)</td>
</tr>
<tr>
<td></td>
<td>no attraction (Borden <em>et al.</em> 1980b)</td>
<td>no attraction (Borden 1980b; Lindgren and McLean unpubl.)</td>
</tr>
<tr>
<td>ethanol</td>
<td>no attraction (Borden <em>et al.</em> 1980b)</td>
<td>attractive (Borden <em>et al.</em> 1981a; Cade <em>et al.</em> 1970; Lindgren and McLean unpubl.; McLean 1976; McLean and Borden 1977; Moeck 1970, 1971; Shore and McLean 1983)</td>
</tr>
<tr>
<td>α-pinene+ethanol</td>
<td>attractive (Borden <em>et al.</em> 1981a)</td>
<td>no attraction (Borden <em>et al.</em> 1980b)</td>
</tr>
<tr>
<td></td>
<td>no attraction (Borden <em>et al.</em> 1980b)</td>
<td>no attraction (Borden <em>et al.</em> 1980b)</td>
</tr>
<tr>
<td><strong>SYNERGISM EFFECTS:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>α-pinene</td>
<td>no effects (Borden <em>et al.</em> 1980b)</td>
<td>no effects (Borden <em>et al.</em> 1980b)</td>
</tr>
<tr>
<td>ethanol</td>
<td>both sexes more responsive to (+)-sulcatol plus ethanol than to (+)-sulcatol alone (Borden <em>et al.</em> 1980b)</td>
<td>no effects (Borden <em>et al.</em> 1980b)</td>
</tr>
<tr>
<td>α-pinene+ethanol</td>
<td>synergism effects existed for both sexes (Shore and McLean 1985)</td>
<td>synergism effects existed for both sexes (Shore and McLean 1983)</td>
</tr>
<tr>
<td></td>
<td>males responded more significantly to the ternary mixture than to (+)-sulcatol alone (Borden <em>et al.</em> 1980b)</td>
<td>males responded more significantly to the ternary mixture than to (+)-sulcatol alone (Borden <em>et al.</em> 1980b)</td>
</tr>
</tbody>
</table>
In a later study, *G. retusus* of both sexes also showed positive responses to male frass, gut extracts, and male attacked logs (Borden and McLean 1979). This indicates that male beetles are producers of the attractive agent. However, a rise in attraction of frass following pairing of males and females and significant responses to female-infested logs and paired beetles were reported, and it was suggested that both sexes might be involved in secondary attraction of this species (Borden and McLean 1979).

For *G. sulcatus*, the aggregation pheromone was isolated from boring dust and a benzene extract of male guts and identified to be 6-methyl-5-hepten-2-ol for which the name sulcatol was proposed. In nature, it exists as a racemic mixture of S-(+)-sulcatol and R-(-)-sulcatol enantiomers at the ratio of 65:35, and has been synthesized (Byrne et al. 1974). Both optically pure R-(-)-sulcatol and S-(+)-sulcatol were also synthesized (Johnson and Slessor 1979; Mori 1975; Schuler and Slessor 1977). The two enantiomers act synergistically to elicit a response by *G. sulcatus* beetles (Borden et al. 1976, 1980b).

For *G. retusus*, Borden et al. (1980a) isolated more than 99% optically pure S-(+)-sulcatol from male frass and demonstrated it to be an aggregation pheromone. When more than 2% of R-(-)-sulcatol is present in the pheromone, the response of female *G. retusus* begins to be inhibited, and the response of both sexes is totally inhibited by larger amounts of R-(-)-sulcatol. However, *G. sulcatus* males and
females respond to sulcatol when less than 2% R-(−)-sulcatol is present in the blend. This is considered to be one reason for the lack of response by *G. retusus* to *G. sulcatus* infested logs and (±)-sulcatol baited traps, as well as the existence of cross attraction of *G. retusus* infested logs to *G. sulcatus* (Borden and McLean 1979). Slight cross attractions of *G. sulcatus* and *G. retusus* to each other's aggregation pheromones were later demonstrated (Borden *et al.* 1981).

The successful synthesis of aggregation pheromones of ambrosia beetles has led to the development of present pheromone-based mass trapping systems for ambrosia beetles including *G. retusus* and *G. sulcatus*. Alpha-pinene and ethanol baits are employed as synergists for the aggregation pheromones. These systems have already showed promise in survey and suppression of *G. retusus* and *G. sulcatus* populations (Borden and McLean 1981; Lindgren and Borden 1983; McLean 1980; McLean and Borden 1975b, 1977b, 1979; Shore 1982; Shore and McLean 1985). However, the effects of α-pinene and ethanol as synergists of aggregation pheromones are not consistently agreed on by various authors (Table 1).

A significant shift of sex ratio in favor of male beetles whenever α-pinene and/or ethanol were included with the aggregation pheromones was shown for both *G. sulcatus* (Borden *et al.* 1980b) and *G. retusus* (Shore and McLean 1985). This reflects the importance of host primary attractants (kairomones) to the pioneer sex (male) in both
species of ambrosia beetles.

Based on the above review, there are gaps in our knowledge of *G. retusus* biology, such as that of gallery and brood development and brood production. There are also many contradictory results concerning behavioural responses of the two ambrosia beetles to semiochemicals. To further the knowledge of *G. retusus* biology, and chemical ecology of both ambrosia beetles and to manage them effectively, it is necessary to explore *G. retusus* biology and the behavioural responses of the two *Gnat hotrichus* beetles to semiochemicals further. The objectives of my research were to:

1. Determine attack densities, gallery distributions, gallery structure, brood productions, and brood emergence patterns of *G. retusus* for D-f and WH.
2. Determine the diurnal and seasonal flight patterns as measured by catches in semiochemical baited traps.
3. Evaluate effects of environmental factors on activities of *G. retusus* and *G. sulcatus*.
4. Evaluate the behavioural responses of *G. retusus* and *G. sulcatus* to semiochemicals.
2. MATERIALS AND METHODS

2.1 EXPERIMENTAL SITES AT THE UBC RESEARCH FOREST

Two experimental sites were used at the UBC Research Forest, Maple Ridge, B.C.. The first one was on Road F-3, where the forest is a second growth fire succession stand and composed mainly of Douglas-fir (D-f), *Pseudotsuga menziesii* (Mirb.) Franco, with a minor component of western hemlock (WH), *Tsuga heterophylla* (Raf.) Sarg.. The altitude is about 270m (Fig 1).

An eight hectare clear cut was made in this area in July 1984, and no site preparation or planting was undertaken to the date when experiments were conducted. The site is bordered by forest on its south and west sides and open to old logging sites and F road in its east and north sides respectively. All logs were removed from that area during 1985. Slash and stumps were abundant and left intact.

A preliminary survey conducted in early April 1986 showed heavy attacks of D-f and WH stumps by *G. retusus* which indicated there were abundant beetle resources for various field experiments. The research on *G. retusus* brood emergence, diurnal flight, and behavioural responses to semiochemicals and seasonal flight of *G. retusus* and *G. sulcatus* was carried out in that area in 1986.

In May 1986, a very small second clear cutting was carried out along the south edge of the 1984 logging site. Logs were removed during summer 1986, and slash and stumps
Figure 1. Map of the experimental site at the UBC Research Forest, Maple Ridge, B.C. 1986.

- D-f stump sample.
- WH stump sample.
- trap of *G. retusus* 8x8 LSD experiment.
- *G. retusus* monitoring trap.
- *G. sulcatus* monitoring trap.
- location of the third *G. retusus* diurnal flight monitoring trap and weather recording.
were left intact.

A second experimental site was in the C road area of the UBC Research Forest. Clear cutting was carried out during 1985 and 1986 from north to south on the east side of the road. The stand in that area is composed mainly of D-f and WH. The altitude is about 320m. In August 1985, a field trapping experiment with *G. sulcatus* to test for effects of (±)-sulcatol release rates was carried out in the yarding areas.

2.2 GALLERY AND BROOD DEVELOPMENT

One D-f log, felled in July 1984 and infested by *G. retusus*, was selected in the Road E-3 area of the UBC Research Forest, and cut into approximately ten 1.5 meter long sections in late May 1985. Three sections were taken back to the UBC Campus for detailed observations. The remaining sections were left at the UBC Research Forest. The two ends of each log section were sealed with plastic sheets to slow drying. Every two weeks, four to six log discs about 10 cm thick were sawn from the log sections for gallery dissection beginning on May 31. All *G. retusus* galleries in discs were dissected and gallery maps were drawn at a scale of 1:1. The numbers and positions of egg niches, eggs, larvae, larval niches, pupae, pupal niches, and adults in galleries were recorded. Stain in galleries was also recorded. The lengths of galleries over depths were measured on the maps at 0.5cm intervals. In this way distributions of
gallery length over sapwood depth at different times were obtained.

In July 1985, a second *G. retusus* attacked D-f log (felled in July 1984) was selected and log discs were sawn from the end of the top third and the top of the bottom third of the log in August and early September, 1985. All *G. retusus* galleries in the discs were dissected and gallery maps were drawn at a scale of 1:1. More discs were taken during the fall up to November 1st from the two D-f logs to check gallery and brood development.

Gallery dissection of the first D-f log was done at different times to determine gallery extension pattern and brood development. Maximum temperature records were obtained at the gate of the UBC Research Forest (altitude 146m) and were compared with the gallery extension pattern to reveal any relationship. Mature *G. retusus* galleries in the second D-f were dissected to provide comparative data with mature galleries dissected from the first D-f log. A total of 16 mature galleries were dissected from the two D-f logs (5 from the first and 11 from the second). Detailed gallery maps were drawn as described above and brood were sexed and counted. The relationship between gallery length and brood production was evaluated by regression analysis.
2.3 FRASS PRODUCTION AND GALLERY ABANDONMENT

The three D-f log sections taken back from the UBC Research Forest were set up on the UBC Campus on June 4. The tops were sealed with plastic sheets to reduce water evaporation and the logs were shaded with a piece of plywood to reduce excessive heating. A total of 85 galleries on the three log sections were covered with 5cm plastic petri dishes (Fig 2). The bark was first smoothed with a chisel and a small amount of plasticine (Klean Klay) was inserted between bark and the bottom of the petri dish to ensure a seal. Petri dishes were nailed to the bark, and dish covers were secured with rubber bands stretched between nails inserted on each side of them. A piece of masking tape was used to provide a bridge from the gallery entrance to the bottom of the dish for those beetles which came out of the gallery. At that time, gallery dissection showed that beetles had paired in galleries.

Frass was collected weekly from June 11 to August 20, and kept separate by gallery, dried at 70°C for 24 hours and weighed. Beetles that came out of galleries were identified to species and sex and put back into the galleries. Dead *G. retusus* beetles in petri dishes were replaced with beetles of the same sex immediately after they were found during June in an effort to establish a maximum number of successful galleries. Temperatures (maximum, minimum) in the surrounding area were recorded daily from June 6 to August 13, when frass production almost ceased. Observations were
Figure 2. D-f log set up and installation of petri dishes to monitor *G. retusus* frass production. UBC, Vancouver, B.C. Spring 1985.
made for any trace frass production up to November 1985. Brood were collected in the spring of 1986 when they emerged from galleries.

Gallery abandonment patterns by both sexes of beetles and the frass production pattern were obtained. The temperature record was compared with the frass production pattern to reveal any relationship between them. The log sections were used later to determine the gallery distribution over depth.

2.4 BROOD EMERGENCE FROM DOUGLAS-FIR AND WESTERN HEMLOCK STUMPS AND G. RETUSUS ATTACK AND BROOD PRODUCTION

2.4.1 BROOD EMERGENCE FROM DOUGLAS-FIR AND WESTERN HEMLOCK STUMPS

Eight D-f and four WH stumps were sampled randomly in the F-3 area of the UBC Research Forest. Sixty three Gnat hot r i chus galleries were covered with petri dishes on the D-f stumps on April 10, 1986 and a further 36 were covered on the WH stumps on April 24, 1986 (Table 2). Distances from tops of stumps to gallery entrances covered were measured in order to relate brood productions to gallery positions on stumps.

Brood were collected on a weekly basis until emergence ceased, and brood were identified to species, sexed, and counted. Brood emergence patterns over time were obtained for both D-f and WH stumps, and comparisons were made
Table 2. Distributions of *G. retusus* galleries and attack density sampling units on D-f and WH stumps.

UBC Research Forest, Maple Ridge, B. C. Spring 1986.

<table>
<thead>
<tr>
<th>Stump No.</th>
<th>Diam. (cm)</th>
<th>No. of Galleries&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Attack Density Sampling</th>
<th>Total No.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>E&lt;sup&gt;2&lt;/sup&gt;</td>
<td>S</td>
</tr>
<tr>
<td>D-f stumps:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>41.7</td>
<td>6</td>
<td>3</td>
<td>3</td>
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<tr>
<td>2</td>
<td>36.0</td>
<td>12</td>
<td>4</td>
<td>5</td>
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<td>3</td>
<td>48.9</td>
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<td>5</td>
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<td>4</td>
<td>78.8</td>
<td>7</td>
<td>7</td>
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<td>65.3</td>
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<td>5</td>
<td>5</td>
</tr>
<tr>
<td>6</td>
<td>64.2</td>
<td>11</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>7</td>
<td>54.4</td>
<td>8</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>8</td>
<td>66.0</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SUM</td>
<td></td>
<td>61&lt;sup&gt;3&lt;/sup&gt;</td>
<td>37</td>
<td>38</td>
</tr>
<tr>
<td>WH stumps:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>36.0</td>
<td>12</td>
<td>4</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>47.5</td>
<td>11</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
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<td>3</td>
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<tr>
<td>4</td>
<td>41.9</td>
<td>6</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>SUM</td>
<td></td>
<td>35&lt;sup&gt;4&lt;/sup&gt;</td>
<td>17</td>
<td>9</td>
</tr>
</tbody>
</table>

1. Galleries monitored for brood emergence.
3. Two additional galleries covered produced *G. sulcatus* brood and were excluded.
4. One additional gallery covered produced *G. sulcatus* brood and was excluded.
between brood emergence patterns, pheromone trap catch patterns, and the maximum temperature records at the gate of the UBC Research Forest. The sex ratio of brood ready to emerge at the start of a collecting period\textsuperscript{2} was calculated for all collecting dates and related to beetle emergence and the temperature records.

2.4.2 BROOD PRODUCTION AND ATTACK DENSITY

Unproductive galleries were dissected later to determine if they were \textit{G. retusus} or \textit{G. sulcatus} galleries. Thereby brood distributions were obtained, and the average brood productions of \textit{G. retusus} were estimated for both D-f and WH stumps.

After brood collection from both D-f and WH stumps was terminated, all of the 4 WH stumps and 7 D-f stumps were debarked in order to check attack density on stump surfaces. \textit{Gnathotrichus} attack density was sampled by aspect using a 10 X 10 cm\textsuperscript{2} paper frame. For large surface areas, proportionally more measurements were made (Table 2). The distance from the top of a stump to the centre of the frame was measured for all gallery density sampling measurements in order to evaluate any changes in attack density with

\textit{---}

\textsuperscript{2}MB: No. of males collected at date \textit{n}.
MTR: total male residual in galleries at date \textit{n}.
MTR=grand total of males for all collecting dates - total No. of males emerged before date \textit{n}.
FB: No. of females collected at date \textit{n}.
FTR: total female residual in galleries at date \textit{n}.
FTR=grand total of females for all collecting dates - total No. of females emerged before date \textit{n}.
Sex ratio= FB/FTR : MB/MTR.
positions of sample units on stumps (distances from tops). All *Gnathotrichus* galleries in the frame were counted.

The average attack densities and density distributions on both hosts were determined. Comparisons between *G. retusus* brood production and attack density were made for D-f and WH stumps. Comparisons were also made between the two hosts in brood production and attack density.

2.5 **GALLERY DISTRIBUTION AND STRUCTURE**

2.5.1 **DISTRIBUTION IN A DOUGLAS-FIR LOG**

After the brood collection from the D-f logs on the UBC Campus was finished in June 1986, discs were taken from all three log sections. Three discs were taken from the top, middle, and bottom parts of each log section, and each one was dissected radially into 16 parts. The numbers of *Gnathotrichus* galleries on each different radial face were counted and depths from galleries to the cambium and sapwood thicknesses were measured. A frequency distribution of gallery depths and a gallery distribution over percentage depths in sapwood were obtained. Fifteen *G. retusus* galleries used to monitor frass production were dissected to check for gallery development.
2.5.2 DISTRIBUTIONS IN DOUGLAS-FIR AND WESTERN HEMLOCK STUMPS

After attack density measurements on D-f and WH stumps were finished, discs were taken from 4 of the D-f and the 4 WH stumps. All discs were taken from the middle portions of stumps and split radially into 16 even parts. All *Gnathotrichus* galleries on each of the radial faces were counted and distances from gallery holes to the cambium were measured. For D-f stumps, sapwood depths were also measured for each split piece. Two gallery distributions were plotted for D-f stumps, one against depth and the second against percentage depth in sapwood. The gallery distribution over depth in WH stumps were also plotted. Comparisons were made of gallery distributions among the D-f log, D-f stumps, and WH stumps.

2.5.3 GALLERY STRUCTURE

Maps of *G. retusus* galleries in D-f logs were drawn as described in Section 2.2. Mature *G. retusus* galleries were also dissected from both D-f and WH stumps to determine the gallery structure. A general gallery structure model was developed. The D-f and WH stump samples were dissected along growth rings to expose galleries and brood cradles at all depths. The dissection started from the heartwood and progressed toward the cambium in order to measure depths of gallery holes in sapwood. All brood cradles were counted. Distributions of gallery length, pupal niche, and larval
niche over depths, and distributions of pupal and larval
niches per unit gallery length over sapwood depths were
obtained.

2.6 DIURNAL FLIGHT OF G. RETUSUS AND SEASONAL FLIGHT OF G.
RETUSUS AND G. SULCATUS

Four Lindgren multiple-funnel traps (Lindgren 1983)
were set up in the F-3 1984 logging site of the UBC Research
Forest on April 17, 1986 (Fig 3). Two of them were baited
with (+)-sulcatol (10mg/day) and ethanol (100mg/day) to
monitor G. retusus beetle flight, and the other two traps
baited with (±)-sulcatol (5mg/day) and ethanol (100mg/day)
to monitor G. sulcatus beetle flight. The four traps were
set out as two pairs at least 200m apart. Each pair had one
(+)-sulcatol and one (±)-sulcatol baited trap and they were
about 30m apart. Beetles from all four traps were collected
on a weekly basis, and identified to species and sex, and
counted. For large catches, the sex ratio of at least one
hundred beetles was recorded and the numbers of beetles were
estimated volumetrically. The same graduated cylinder was
used, and the graduated cylinder was shaken to let the
volume reading of beetles reach the lowest stable value. The
following formulae were established.

G. retusus: No. of beetles/mL=183.9.

G. sulcatus: No. of beetles/mL=200.3.

On May 27, 1986, a third Lindgren multiple funnel trap
baited with (+)-sulcatol (10mg/day) and ethanol (100mg/day)
Figure 3. Multiple funnel trap set up to monitor ambrosia beetle flight. UBC Research Forest, Maple Ridge, B.C. Spring 1986.
was set up in the same area to monitor *G. retusus* diurnal flight. Pacific daylight saving time was used as the time scale. Beetles from the three (+)-sulcatol baited traps were collected every hour and every half hour during mass flight periods from 0700h to 2100h-2130h when the flight had ceased. Few beetles were found in traps at the 0700h collection thus it was presumed that no flight occurred outside of the observation periods.

Relative humidity was recorded with a hygrothermograph, and air temperature and light intensity were read with a thermometer and a light meter (Sekonic model L-398) respectively at the time of beetle collection. The light intensity readings were converted into Watts/m² with a Quantum light meter (Model L1-185B). Four day observations were made from May 27 to May 30. The environmental conditions for *G. retusus* diurnal flight were evaluated.

After the diurnal flight experiment was finished, the third (+)-sulcatol and ethanol baited trap was removed. But the four seasonal monitoring traps were run continuously through September when few beetles were caught in traps. The weather record (maximum temperatures) at the gate of UBC Research Forest was obtained and the possible effects of weather on seasonal flight patterns of the two beetles were evaluated by visual comparison. A comparison between *G. retusus* brood emergence patterns from D-f and WH and its seasonal flight pattern was also made as mentioned in the last chapter.
2.7 EFFECTS OF SEMIOCHEMICALS ON THE BEHAVIOUR OF G. RETUSUS AND G. SULCATUS

2.7.1 EVALUATION OF EFFECTS OF SEMIOCHEMICAL BAIT COMBINATIONS

A $2^3$ factorial experiment was conducted on the UBC Endowment Land Foreshore park above boomed logs in the North Arm of the Fraser River from May to September of 1985 to evaluate G. sulcatus responses to ethanol, $\alpha$-pinene, and $(\pm)$-sulcatol alone or in combination with each other. The design of the experiment was an 8X8 Latin Square Design (LSD). The eight treatments were: control, $\alpha$-pinene (a-P), ethanol (E), a-P+E, $(\pm)$-sulcatol ($(\pm)$-S), a-P+(±)-S, E+(±)-S, and a-P+E+(±)-S.

A second $2^3$ factorial experiment with an 8X8 LSD was carried out in the F-3 area of the UBC Research Forest in May and June of 1986 to evaluate G. retusus responses to $\alpha$-pinene, ethanol, and $(+)$-sulcatol tested alone or in combination. The eight treatments were: control, $\alpha$-pinene, ethanol, a-P+E, $(+)$-sulcatol, a-P+(+)S, E+(+)S, and a-P+E+(+)S.

The release rates of the semiochemicals were:
- $\alpha$-pinene: 20-30 mg/day
- ethanol: 100 mg/day
- $(\pm)$-sulcatol: 5 mg/day
- $(+)$-sulcatol: 10 mg/day
All release devices were supplied by Phero Tech Inc., Vancouver. In each experiment, eight 8-funnel traps were used. Traps were hung from the tops of rebars to keep traps about 50cm above ground. The distance between any two adjacent traps was about 20m to minimize possible interference. All baits were placed at the middle portions of traps.

The two dimensions (row and column) of the LSD were time and trap location. Once any trap caught about one hundred beetles or more, trap locations were re-randomized within the constraints of LSD for the start of the next replication. By the end of the 8 replicates, each trap had been set out in each of the 8 trapping locations. For each treatment, all beetles were identified to species and sex and counted. Analyses of variance were carried out with the UBC-ANOVAR program.

2.7.2 EVALUATION OF EFFECTS OF (±)-SULCATOL RELEASE RATES

A 5X5 LSD experiment with (±)-sulcatol was set out in the C-road area of the UBC Research Forest in August 1985. Five 8-funnel traps were employed, and were set out at 20m spacing near yarding areas. The five treatments tested were: a-pinene+ethanol, a-P+E+(±)-S1, a-P+E+(±)-S2, a-P+E+(±)-S3, and a-P+E+(±)-S4. The release rates of the semiochemicals were:

a-pinene: 20-30 mg/day.
ethanol: 100 mg/day.
(±)-sulcatol 1: 0.5 mg/day.
(±)-sulcatol 2: 1.5 mg/day.
(±)-sulcatol 3: 5 mg/day.
(±)-sulcatol 4: 10 mg/day.

The two dimensions (row and column) of the experiment were time and trap location. Once any trap caught more than one hundred beetles, traps were emptied and re-randomized to start the next replication. For each treatment, all ambrosia beetles were separated by species and sex, and the numbers were counted. The UBC-ANOVAR program was used to analyse the \textit{G. sulcatus} data.
3. RESULTS AND DISCUSSION

3.1 GALLERY AND BROOD DEVELOPMENT

The first six *G. retusus* galleries dissected on May 31, 1985 each contained one male and one female. One egg niche was found and galleries had no second branches and were shallow. The average gallery length was 2.9 ±0.6 (S.E.) cm.

Eggs were found on June 15 in two galleries. Out of 18 galleries dissected, ten galleries had considerable extensions of deep or second shallow gallery branches. Six galleries were noticed to have small black spots on their surface. Larvae were found on June 28 in one of the nine galleries dissected. Meanwhile, a new attack was noticed which had only a 2.5cm long gallery containing one male beetle. More larvae were observed on July 12 in all four galleries dissected; a few eggs were also present. The first teneral adult appeared on July 26. The beetle was light brownish coloured, and a pupal niche was present in the gallery. On August 9, brood were found in all five *G. retusus* galleries.

Eleven mature *G. retusus* galleries were dissected from the second D-f log through August to early September. Two galleries were found to have 4 eggs which were apparently fresh as well as teneral adults in September. In the latest checks in October and November, a few short *G. retusus* galleries with a pair of beetles but without any brood cradles were found.
A total of 16 mature *G. retusus* galleries were dissected from D-f logs. There was a significant linear relationship between gallery length and brood production (Fig 4). The regression equation was:

\[
\text{Brood} = -18.9 + 1.0 \text{ Length(cm)} \quad R = 0.84 \quad p \leq 0.05
\]

This indicated that a gallery probably should have a length of at least 19.9 cm in order to be brood productive. The sex ratio of the brood was 1.1:1 (60 females : 54 males). Out of 16 mature galleries dissected in August and early September, ten had noticeable black stain on the gallery surface, and eight had stain restricted to gallery portions which were near entrances and/or in shallow gallery branches. The extent of black stain increased from June to August.

The distribution of gallery length over depth from May 31 to August 9 (Fig 5) indicated that beetles bored the shallow gallery branches first, and gradually tended to shift to boring deep gallery branches. The boring activity reached a peak in June and continued until August 9 when brood had been produced.

Short galleries found in the fall were probably initiated in late summer or fall as *G. retusus* beetles continued flying from the spring to fall. Beetles might overwinter as adults in galleries and start to lay eggs and excavate galleries or re-emerge in the following spring.

Based on gallery dissection, the development from eggs to teneral adults took approximately 40 days or more; the egg stage lasted about 10 days, the larval and pupal stages
Figure 4. Relationship between *G. retusus* brood production and gallery length in D-f logs. UBC Research Forest, Maple Ridge, B.C. 1985.
Figure 5. *G. retusus* gallery length distribution over depth of sapwood in a D-f log at different times. UBC Research Forest, Maple Ridge, B.C. 1985.
30 days or more. But attack and egg laying lasted over several months. This resulted in poorly synchronized brood development. Those eggs found in September probably could not develop to teneral adults before temperatures fell below the threshold for brood development. This resulted in poorly synchronized brood development. Those eggs found in September probably could not develop to teneral adults before temperatures fell below the threshold for brood development. This seems to support earlier speculation that *Gnat hotrichus* may overwinter in all stages (Chamberlin 1939; Doane *et al.* 1936; Prebble and Graham 1957). Asynchronous brood development also occurred within a gallery; both eggs and teneral adults were found in the same gallery in September. However, this was not a common phenomena. The overwhelming majority of galleries examined had synchronized brood development among and within galleries.

One feature of *G. retusus* as well as *G. sulcatus* galleries is that the productive gallery length (the portion of a gallery with brood cradles) only represents a small portion of the total gallery length, and brood cradles are restricted to the section of the gallery near the entrance. In comparison, galleries of *Trypodendron lineatum* do not have an apparent non-brood productive gallery portion (personal observation). Comparing their habitats, *T. lineatum* beetles overwinter in duff. However, *G. retusus* as well as *G. sulcatus* overwinter in host materials and remain in galleries much longer than *T. lineatum* beetles. Therefore, the non-brood productive gallery portion may be an important overwintering habitat and maturation feeding area for brood. The significant positive linear relationship
between *G. retusus* brood production and gallery length supports this hypothesis. To produce one more brood, may require an additional gallery length from the present findings. Similar linear relationships between brood production and gallery length were also found for *G. sulcatus* (Zanuncio 1981).

The gradual shift of boring activities of beetles from shallow to deep portion of sapwood over time may be an adaptation to seasonal environmental changes. Considerable differences in moisture content among different sapwood depths (Chapman and Dyer 1969), as well as seasonal sapwood moisture changes have been reported (Chapman and Dyer 1969; Johnson and Zingg 1969). These changes may cause beetles to develop their galleries into new parts of the sapwood in order to maintain a suitable growing environment for the ambrosia fungi.

3.2 FRASS PRODUCTION AND GALLERY ABANDONMENT

Out of 85 galleries monitored (five of which were *G. sulcatus*) only eight *G. retusus* galleries produced frass continuously up to mid-August, 1985. Yet, trace frass production did not cease until early November, 1985. The frass production pattern from those eight galleries (Fig 5) showed a peak in mid-June. The peak coincided with the time of maximum gallery extension obtained at the UBC Research Forest (Fig 6,7). There were no obvious correlations between frass production or gallery extension and maximum

temperature fluctuations (Fig 6,7).

The number of galleries which ceased frass production increased from June to August, and for most of them, at least one beetle emerged from the gallery before or after the cessation of frass production. All first-emerged beetles in June and July were females, and a small number of males were the first to emerge from galleries through August to October (Fig 8).

Fifteen of the galleries dissected in June 1986 showed that none of the galleries had any cradles for progeny production, and seven of them had a slightly black surface. The length of the galleries ranged from 3.9 cm to 15.2 cm with an average of 8.9±0.9 (S.E.) cm.

Frass colour became noticeably blacker from June on (Fig 9). Two galleries, which were among those that produced frass continuously, had brood which emerged in April and May 1986. The numbers of brood were eight and nine respectively.

Frass collection and gallery dissection from the D-f log sections on the UBC Campus revealed that most galleries were unsuccessful. The reason might be that the wood became too dry for the fungus and/or beetles to grow as time progressed. As the log sections were only about 1.5m long, water loss would be considerable even though the tops were sealed with plastic sheets and the log sections were shaded with a piece of plywood. A second reason might be that the desiccation of the wood halted anaerobic fermentation in the wood and therefore prevented the production of ethanol.
Figure 8. Gallery abandonment by *G. retusus* adults in a D-f log. UBC, Vancouver, B.C. 1985.
Figure 9. *G. retusus* frass colour changes over time in a D-f log. UBC, Vancouver, B.C. 1985.
Ethanol has been identified as a boring stimulant for *Xyleborus furregineus* (Norris and Baker 1969), a possible boring stimulant for *G. sulcatus* (McLean and Borden 1977a), and likely could be a boring stimulant for *G. retusus*. The short gallery lengths found during dissection support this hypothesis.

The lack of significant correlation between weekly frass production and maximum temperature indicates that there is no obvious relationship between frass production and maximum temperature within the range of temperatures recorded. There may be a suitable temperature range for beetle activities. Further increases in temperature may actually inhibit activities of beetles and so inhibit frass production and gallery extension. In this study, maximum temperatures on June 19, 20, and July 3, 8, 9, 10, 11 were well above 30°C which was above the upper limit (26.7°C) for *G. retusus* flight (Rudinsky and Schneider 1969), and would also season the already dry logs further. The two peaks of gallery abandonment by female beetles around June 19, 20, and July 3 support the above explanation. For *Trypodendron lineatum*, it has been stated that after beetles have entered the wood, inadequate moisture undoubtedly influences parent adult abandonment of galleries and survival of the broods (Kinghorn 1956).

As male *G. retusus* are usually at the heads of galleries (Borden and McLean 1979), the fact that females are the first sex to abandon galleries seems logical.
Biologically, females may be more sensitive to host quality than males as females carry eggs and determine progeny production. Abandonment of unsuitable galleries or host materials may lead to higher success rates of brood development as females may eventually find suitable host materials in which to raise their brood. This should be advantageous for the development of *G. retusus* populations. For those galleries from which males emerged in the later summer and fall, females might have died in galleries before emergence of males, since no evidence of the existence of live beetles in those galleries were found after the emergence.

### 3.3 BROOD EMERGENCE FROM DOUGLAS-FIR AND WESTERN HEMLOCK STUMPS AND *G. RETUSUS* ATTACK AND BROOD PRODUCTION

#### 3.3.1 BROOD EMERGENCE FROM DOUGLAS-FIR AND WESTERN HEMLOCK STUMPS

*G. retusus* brood emergence from D-f stumps began after April 17, and brood were collected from WH stumps immediately after the installation of petri dishes on April 24. The emergence peak occurred between May 15 and May 29, and the emergence ceased on June 19 for D-f stumps and on June 26 for WH stumps (Fig 10). However, there was a gallery in a D-f stump that had 15 brood which emerged in May and June and an additional 3 brood emerged in late July. The emergence peak from D-f stumps came a little earlier than
Figure 10. *G. retusus* brood emergence pattern from D-f and WH stumps (*middle*), and its relationship with temperature (*top*) and the seasonal flight pattern (*bottom*). UBC Research Forest, Maple Ridge, B.C. 1986.
that from WH stumps. Frass production was of considerable quantity for many galleries in both D-f and WH stumps beginning in late April.

The fluctuation of brood emerging over time was positively related to the fluctuation of maximum daily temperatures recorded at the gate of the UBC Research Forest. The flight peak of *G. retusus* recorded with (+)-sulcatol plus ethanol baited Lindgren multiple funnel traps coincided with the brood emergence peak recorded from D-f and WH stumps (Fig 10). However, after the brood emergence ceased, the flight was still at a high level and lasted for quite a long time. Reasons for this continued flight may be the search for suitable hosts and abandonment of unsuitable hosts by beetles, especially females, and the late emergence of brood from host materials. The average sex ratio of emergent *G. retusus* beetles from D-f and WH stumps was 0.9:1 (388 females:429 males) which was not significantly different from 1:1 (p≤0.05). It varied over time in synchronization with the maximum temperature fluctuation, and showed slight increases over time (Fig 11).

Brood emergence of *G. retusus* from D-f and WH stumps lasted about one and half months. This suggests that a considerably large portion of brood feed and develop to mature adults in galleries before emergence in the spring and early summer. Some galleries had frass production in late April, and brood emergence in early June. It appears that the brood may overwinter in stages other than adult and
Figure 11. Relationship between the sex ratio of G. retusus brood ready to emerge and temperature. UBC Research Forest, Maple Ridge, B.C. 1986.
develop into mature adults in the spring and summer. This agrees with the conclusion made earlier (from gallery dissections) that small numbers of beetles may overwinter in stages other than adult, and also agrees with Chamberlin (1939), Doane et al. (1935), and Prebble and Graham (1957).

The synchronization between the sex ratio of brood in galleries ready to emerge and temperature suggests that female emergence is more sensitive to temperature fluctuation than male emergence. Female beetles have greater fluctuations in numbers emerging relative to temperature changes than do males. The slight general increase in sex ratio over time also supports this conclusion as temperature shows a general increase over time in the period. Biologically, this suggests that males may have a wider temperature range and lower threshold than females for emergence, and be better adapted to generally hostile environments than females.

3.3.2 BROOD PRODUCTION AND ATTACK DENSITY

Of 63 Gnat hotrichus galleries covered with petri dishes on D-f stumps, two were G. sulcatus galleries, 41 were G. retusus galleries, and 20 did not have brood emerged. For WH stumps, of 36 galleries covered with petri dishes, one was a G. sulcatus gallery, 22 were G. retusus galleries, and 13 did not have brood emerged. The dissection of six and seven of those unproductive galleries from the four D-f and four WH stumps sampled respectively revealed that those
unproductive galleries were either immature galleries without pupal niches or mature galleries with dead *G. retusus* teneral adults. *G. sulcatus* is bivoltine (Prebble and Graham 1957; Zanuncio 1981). If the stumps were attacked in the spring of 1985 or earlier, the brood would have emerged by the fall of 1985, and empty mature galleries should have been found in gallery dissections. Also, among productive galleries, *G. sulcatus* galleries represented only a very small portion (3%). It is therefore reasonable to presume that *G. sulcatus* galleries would also represent a very small portion of those immature galleries. This implies that both D-f and WH stumps in that area were overwhelmingly colonized by *G. retusus*, and most of those unproductive galleries were *G. retusus* galleries. Based on this conclusion, the *G. retusus* brood distributions for both D-f and WH stumps were obtained (Fig 12) and brood productions were estimated (Table 3).

There were no significant differences in average brood production between D-f and WH stumps. However, significant differences were found among D-f and WH stumps in brood production (Table 4).

The average attack density (±S.E.) on D-f stumps was 3.35±0.18/100 cm² (31.1/ft²) which was significantly higher than the average attack density 1.53±0.27/100 cm² (14.2/ft²) (p≤0.05) on WH stumps. There was also a manifest difference in distribution of gallery density between the two hosts (Fig 13). Significant differences in attack density existed
Figure 12. *G. retusus* brood distributions for D-f and WH stumps. UBC Research Forest, Maple Ridge, B.C. 1986.
Table 3. *G. retusus* gallery success and brood productions in D-f and WH stumps. UBC Research Forest, Maple Ridge, B.C. June 1986.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of Galleries</th>
<th>Success Rate $\pm$S.E. (%)</th>
<th>Average Brood $\pm$S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>D-f</td>
<td>61</td>
<td>67.2±6.0</td>
<td>8.30±1.53</td>
</tr>
<tr>
<td>WH</td>
<td>35</td>
<td>62.9±8.2</td>
<td>7.29±1.84</td>
</tr>
</tbody>
</table>

1. No significant difference between species, t-test $p \leq 0.05$. 
Table 4. *G. retusus* attack density and brood production in D-f and WH stumps. UBC Research Forest, Maple Ridge, B.C. June 1986.

<table>
<thead>
<tr>
<th>Stump No.</th>
<th>D-f(^1)</th>
<th>WH(^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>density(^2)</td>
<td>brood(^3)</td>
</tr>
<tr>
<td>1</td>
<td>2.75 ab(^4)</td>
<td>5.67 ab</td>
</tr>
<tr>
<td>2</td>
<td>2.07 a</td>
<td>4.75 ab</td>
</tr>
<tr>
<td>3</td>
<td>4.96 ab</td>
<td>3.71 a</td>
</tr>
<tr>
<td>4</td>
<td>5.40 b</td>
<td>6.00 ab</td>
</tr>
<tr>
<td>5</td>
<td>3.40 ab</td>
<td>14.83 ab</td>
</tr>
<tr>
<td>6</td>
<td>3.46 ab</td>
<td>9.46 ab</td>
</tr>
<tr>
<td>7</td>
<td>5.05 ab</td>
<td>15.63 b</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>7.25 ab</td>
</tr>
</tbody>
</table>

1. Data transformed to $X' = \log(X+1)$ prior to ANOVA.
2. Density: No. of entrances per 100cm\(^2\).
4. Numbers within a column followed by the same letter not significantly different, Newman-Keul's test, $p \leq 0.05$. 

Figure 13. *G. retusus* gallery density distributions on D-f and WH stumps. UBC Research Forest, Maple Ridge, B.C. 1986.
among both D-f and WH stumps (Table 4). No significant
differences in gallery density among different aspects of
either D-f or WH stumps were detected. No significant
correlation between brood production and gallery density
could be detected for the sample of either host species, and
neither were there any significant correlations between
stump diameter and brood production or attack density for
either of the host species.

Within stumps, definite trends of increases in attack
density and brood production from the tops to the bottoms of
D-f stumps were found. For WH stumps, there was also a trend
of increases in attack density from stump tops to the
bottoms (Fig 14). But the brood production in WH stumps had
a very weak negative correlation with distances from stump
tops to gallery entrances. Linear models were also
constructed for above relationships (Fig 14).

The higher attack density of *G. retusus* on D-f stumps
than on WH stumps indicates that D-f stumps are preferred by
*G. retusus* beetles. This may be due to a possible higher
production rate of the host attractant ethanol in D-f
stumps. D-f stumps have much thicker bark than WH stumps and
therefore may have better anaerobic fermentation conditions
in the bark and sapwood than do WH stumps. This will
probably enhance production of ethanol and induce mass
attack by *G. retusus* beetles. But the difference in ethanol
production level between the two hosts may not cause a
significant difference in boring activity in sapwood even
Fig 14. Relationship between *G. retusus* attack density, brood production and positions on D-f and WH stumps. UBC Research Forest, Maple Ridge, B.C. 1986.

H: distance from the top of a stump to the gallery entrance or attack density sampling unit on the stump.
though ethanol is a possible boring stimulant of *G. retusus*.

The suitabilities of D-f and WH stumps seem to be the same for *G. retusus* brood development since there are no significant differences in average gallery success rates and average brood production between the two hosts. The lack of correlation between stump diameter and attack density or brood production implies that the range of tree diameters in this study is not sufficient to cause differences in attack density and brood production. The lack of significant differences in attack density among different aspects of D-f stumps implies that differences among different aspects are not big enough for beetles to discriminate by aspect once they are oriented to stumps.

The lack of significant correlation between attack density and brood production for D-f or WH stumps may be due to large variances within stumps in attack density and brood production since trends of attack density and brood production in relation to positions on stumps have been demonstrated. The same trends of increases in attack density and brood production from tops to bottoms within D-f stumps seems to indicate a positive relationship between attack density and brood production.

The trends of increases in attack density and brood production for D-f and in attack density for WH with decreasing distances from stump tops to bottoms reflect increases in host quality for *G. retusus*. After logging, water and volatile oils will evaporate from the top of
stumps much faster than from other parts of stumps. But water may be replenished through absorption by the roots. This will result in a moisture gradient from the tops to the bottoms of stumps in the sapwood. Moisture condition in the sapwood is a very important factor influencing attacks and brood production of ambrosia beetles (Kinghorn 1956; McLean and Borden 1977a). In the top of a stump, as wood is considerably dehydrated, anaerobic fermentation will be reduced. This will result in a decreased production of ethanol, the primary host attractant and possible tunnelling stimulant for *G. retusus*.

On the other hand, dehydration will also render the wood difficult to bore in and unsuitable for growth of ambrosia fungi. Other micro-organisms will certainly colonize sapwood through cut sections and may also make the wood in their vicinity unsuitable to grow ambrosia fungi. All this may result in low attack densities and low brood production near the top of a stump. In addition, volatile oils extracted from wood has been found to retard or deter attacks of conifer logs by *Trypodendron lineatum* (Nijholt 1973; Werner and Graham 1957). For *G. retusus*, emission of volatile oils from cut sections of stumps may also be a cause of low attack densities near the tops of stumps. However, the brood production trend in WH stumps does not fit the above hypothesis. Brood production had a very weak negative correlation with distance from the top of a WH stump. This may well be an artifact caused by the small
sample size.

3.4 GALLERY DISTRIBUTION AND STRUCTURE

3.4.1 GALLERY DISTRIBUTIONS IN A DOUGLAS-FIR LOG, DOUGLAS-FIR STUMPS, AND WESTERN HEMLOCK STUMPS

Gallery distributions in all three host categories had a peak frequency at depths of 11-20mm in sapwood. Beyond this peak, frequencies decreased steadily with increasing sapwood depth (Fig 15). The distributions of gallery depths were dependent on sapwood depths. Except for a small portion of gallery holes in heavily attacked D-f stumps distributed in heartwood, most gallery holes in the D-f log and stumps did not penetrate deeper than the sapwood (Fig 15). The distribution in the D-f log was the same as those reported for *Gnathorichus* species or *G. sulcatus* (McLean 1985; Prebble and Graham 1957). For D-f and WH stumps, gallery distributions over depth of sapwood were similar to those constructed for *Gnathorichus* species or *G. retusus* in D-f and WH logs except for much deeper penetrations were found in the stumps (McLean 1985; Prebble and Graham 1957).

Comparing percentage depth distributions of galleries between the D-f log and D-f stumps (Fig 16), there were no gallery holes in the first 10% of sapwood depth and only a very small portion in the second 10% of sapwood depth for the D-f log and decreases in frequency after 40% of sapwood depth. This may due to the small sapwood depth in the D-f
Fig 15. C. Residual gallery distributions over depth of sapwood.

Depth in Sapwood (mm)

0

Percentage frequency

Middle Bolton, UBC Research Forest, Maple Ridge, B.C., 1986.

Figure 16. _G. retusus_ gallery distributions over percentage depth of sapwood in a D-f log and D-f stumps. 
*bottom:* UBC Research Forest, Maple Ridge, B.C. 1986.
log compared with D-f stumps and the lack of success of most
G. retusus galleries in the D-f log. The D-f log had an
average sapwood depth of 34.2±0.9(S.E.)mm. However, D-f
stumps had an average sapwood depth of 65.4±8.8(S.E.)mm. The
first 10% of sapwood depth in the D-f log ranged only from 0
to 4 mm, and the second 10%, 4 to 7 mm. G. retusus gallery
dissections revealed that most galleries were immature
galleries which had only one short shallow gallery branch
and little extension of deep gallery branches. This could
result in a decrease of frequency of gallery holes in the
depth portion of the sapwood.

The sapwood of D-f stumps was used more evenly by G.
retusus beetles except for low frequencies of gallery holes
in the first 10% and the last 10% of sapwood depth. The
first 10% sapwood depth took a depth range of 0 to 7 mm, in
which range the absolute depth distribution also showed a
low frequency of gallery holes. The even distribution
pattern of G. retusus galleries and presence of gallery
holes in heartwood in D-f stumps seem to reflect
intra-species space competition in the sapwood. The
competition resulted in full usage of the majority of the
sapwood. The high gallery density and inter-gallery
crossings discussed later appear to support this
explanation.
3.4.2 GALLERY STRUCTURE

A mature *G. retusus* gallery, which is similar to a *G. sulcatus* gallery in structure (McLean 1975a; Zanuncio 1981), usually has at least one shallow and one deep gallery branch which very often extend in opposite directions in the less dense spring wood of annual growth rings. More main branches can often be observed and they may have several short sub-branches (Fig 17). The complexity of gallery structure seems to be related to brood production. Galleries which have a large brood production often have complicated gallery structure.

Brood production of *G. retusus* appears to be confined to the portion of the gallery closest to the main radial gallery (Fig 17). The depth distributions of brood cradles (Fig 18) demonstrated that both pupal and larval niches had a concentration from 10 to 20 mm depth of sapwood in D-f and from 20-30mm depth in WH stumps. Both shallow and deep branches have considerable distal lengths without any egg or larval niches. The total length of non-brood productive portions in a mature gallery is several times that of the brood productive portions.

A striking difference in gallery structure was that *G. retusus* galleries in D-f stumps had considerable elongation of pupal niches and inter-gallery crossings especially in heavily attacked ones (Fig 19,20). The elongation of pupal niches was never observed in D-f logs but was quite common in D-f stumps and occasionally occurred in WH stumps.
Figure 17. A model of a *G. retusus* gallery in D-f logs. E: egg niche; L: larval niche; P: pupal niche. Scale=1:1.
Figure 18. Distributions of *G. retusus* gallery length, larval niche, and pupal niche over sapwood depth and distributions of larval niche and pupal niche density per unit gallery length over sapwood depth in D-f and WH stumps. UBC Research Forest, Maple Ridge, B.C. 1986.
Figure 19. *G. retusus* gallery structure in D-f stumps: elongation of pupal niches into maturation feeding tunnels and inter-gallery crossings. UBC Research Forest, Maple Ridge, B.C. 1986.
Figure 20. *G. retusus* gallery structure in D-f stumps: elongation of pupal niches into maturation feeding tunnels and inter-gallery crossings. UBC Research Forest, Maple Ridge, B.C. 1986.
Pupal niches in D-f stumps could be elongated up to three centimeters, and inter-gallery crossings occurred through conjunctions of pupal niches or elongated pupal niches of two or more galleries. In WH stumps, elongated pupal niches were much shorter (Fig 21) than those in D-f stumps.

The inter-gallery crossings are a consequence of the high attack density of D-f stumps as well as elongation of pupal niches. The elongated pupal niches may function as maturation feeding tunnels to cope with overcrowding and shortage of feeding areas in main tunnels resulting from space competition and successful large brood production. Since gallery density was very high in some host materials, the extension of main gallery branches could be limited considerably. As no conjunctions of two galleries in main branches were found, adults seem to avoid gallery crossings by detouring or stopping gallery extension. Acoustic communication has been demonstrated in bark beetles (Rudinsky et al. 1978a, 1978b), and it may also exist in ambrosia beetles and enable them to detect boring activities in their vicinity.

In a earlier part of this thesis, a significant positive correlation between gallery length and brood production was demonstrated, and the vital function of non-brood productive gallery portions as feeding areas has been suggested. In the present case, competition for space could result in reduction of non-brood productive gallery
Figure 21. *G. retusus* gallery structure in WH stumps: slight elongation of pupal niches. UBC Research Forest, Maple Ridge, B.C. 1986.
portions, crowdedness of brood, and shortage of feeding areas in galleries. In addition, inter-gallery brood movement was possible since gallery crossings were quite common. This could result in inaccurate estimation of gallery brood production and in overcrowding in some galleries. It is also possible that a beetle might die in a gallery, and this could result in the rest of brood being isolated temporarily in some parts of the gallery. The excavation of maturation feeding tunnels at the heads of pupal niches by terneral adults probably can not only secure their own food supply but also lessen the crowdedness and shortage of feeding space in main branches.

3.5 DIURNAL FLIGHT OF G. RETUSUS AND SEASONAL FLIGHT OF G. RETUSUS AND G. SULCATUS

3.5.1 DIURNAL FLIGHT OF G. RETUSUS

G. retusus had crepuscular flight habits and showed a bimodal flight pattern. The first flight, in the morning, occurred about 0700h and reached a peak between 0800 and 0900h which was very small and constituted only 3.3% to 10% of the total catch in a day. In the morning of a clear day during the experiment, light intensity increased from about 70 Watts/m² at 0700h to about 120 Watts/m² at 0800h, temperature increased from around 14°C at 0700h to 17 or 19°C at 0800h, and relative humidity decreased from 87% at 0700h to 58% at 0800h. The dusk flight was much greater than
the morning flight and constituted more than 90% of the total catch during a day. It occurred between 1800h and 2100h or 2130h (Figs 22-25). From 1800h, the number of beetles flying increased rapidly over time and reached a peak between 2000h and 2030h, and then terminated quickly. During this mass flight period, light intensity decreased dramatically from 120 Watts/m² to about 12 Watts/m², temperature decreased from about 24.7°C to 14.5°C, and relative humidity increased from 40% to 83% at 2100h. The lowest temperature at or above which beetles flew was 14°C.

Between the two flight peaks, light intensity on a clear day increased from a low level in the morning up to 199 Watts/m² at noon and then decreased gradually. Temperature also increased from a low level in the morning to a peak at about 1500h, which varied from 24.1°C to 30.5°C, and relative humidity decreased from a high level in the morning to the lowest level at about 1700h, which varied from 40% to 28% on different days, and then it increased dramatically as light intensity decreased. During this period, very few beetles were caught.

At 0700h, light intensity was almost identical to that at 1900h to 1930h when mass flight started. But temperatures up to 0700h were lower than temperatures during the dusk flights. Although temperature increased to reach a suitable range for beetle flight as the day progressed, light intensity also increased to above the upper limit for mass flight. This may well be an important reason why morning
Figure 22. Record of temperature, relative humidity, light intensity, and *G. retusus* flight on May 27, 1986. UBC Research Forest, Maple Ridge, B.C.
Figure 23. Record of temperature, relative humidity, light intensity, and *G. retusus* flight on May 28, 1986. UBC Research Forest, Maple Ridge, B.C.
Figure 24. Record of temperature, relative humidity, light intensity, and G. retusus flight on May 29, 1986. UBC Research Forest, Maple Ridge, B.C.
Figure 25. Record of temperature, relative humidity, light intensity, and G. retusus flight on May 30, 1986. UBC Research Forest, Maple Ridge, B.C.
flight peaks of *G. retusus* were much smaller than dusk flights.

On May 27, light intensity and temperature reached only 80 Watts/m$^2$ and 17°C respectively at 1300h as a result of heavy fog in the morning (Fig 20). Although this light intensity and temperature combination was not identical to that under which mass flights occurred, it was in a similar range. However, few beetles were caught before 1300h on this date. The major difference between this date and other three dates was in relative humidity which decreased from 100% in the morning to 80% at 1300h on May 27. For the other three days, it was sunny all day, light intensity and temperature were high, and relative humidity was very low before the initiation of the evening mass flight. The peak on May 27 was the smallest among the four dusk flight peaks recorded. It appears that warm days with low relative humidity are required for the beetles to fly in the evening.

Comparing dusk flight peaks of *G. retusus* in the four days, the flight rhythm was probably entrained by light intensity since all dusk flight peaks occurred at a constant light intensity but various temperatures and relative humidities. A light intensity of 120 Watts/m$^2$ seems to be an upper limit for beetles to initiate dusk mass flight, and 12 Watts/m$^2$ a low threshold. In the four days, the temperature profile showed steady increases. But there was no detectable advance or delay of the dusk flight. A temperature of 14°C seems to be a low threshold for beetle flight. The
temperature range during dusk flights was from 17°C to 25°C which was wider than the 18.8 to 22.2°C range reported by Rudinsky and Schneider (1969). The upper light intensity limit for beetle flight established in this study was much lower than 2000 ft-c (215 Watts/m²) reported by Rudinsky and Schneider (1969).

Ecologically, the dusk flight rhythm could be advantageous to this species. Light intensity decreases dramatically from late afternoon to evening so that beetles may be able to easier differentiate changes in light intensity. Also, as a result of higher temperature and higher light intensity during the day prior to a dusk flight, synthesis of aggregation pheromone inside the bodies of beetles may be enhanced, as is anaerobic fermentation inside host materials. It could be that the accelerated anaerobic fermentation during warm hours which usually lasts from late morning to late afternoon would result in a high concentration of host kairomone (ethanol) during the dusk flight period. Also, beetles may become dehydrated during the hot daytime hours and be better able to fly long distances at dusk. Mass flight at dusk may also minimize losses of beetles to predators by reducing exposure time, visibility, and synchronization with preying periods of predators. Various predators including birds have been reported to exert influences on bark beetle populations at adult stages (Moeck and Safranyik 1984).
3.5.2 SEASONAL FLIGHT OF *G. retusus* AND *G. sulcatus*

The first emergent *G. retusus* and *G. sulcatus* beetles caught in traps occurred between April 17 and April 24 when the maximum temperature recorded at the gate of the UBC Research Forest reached only 13.5°C. From then on, numbers of both *G. retusus* and *G. sulcatus* beetles captured in traps increased over time. The flight peaks of both species occurred between May 22 and May 29 when the weekly mean maximum temperature reached 22.6°C and the highest daily maximum temperature reached 25°C. Catches of *G. retusus* remained high until mid-July and decreased gradually from then on. However, catches of *G. sulcatus* dropped more dramatically after this peak but included a second small peak on July 24, and then decreased steadily but more slowly than *G. retusus* catches. The seasonal flights ceased in early October when weekly mean maximum temperatures dropped below 15°C (Fig 26).

The fluctuation of both *G. retusus* and *G. sulcatus* beetle captures coincided with the fluctuation of maximum temperatures. Changes in sex ratios of both species also coincided with the maximum temperature fluctuation (Fig 26). In the diurnal flight experiment with *G. retusus*, it has been concluded that low relative humidity and high daytime temperatures are very important for the dusk flight. This also appears to be a major cause of fluctuations of beetle catches in the seasonal flight patterns. High temperatures usually correspond to clear sunny days with low relative
Fig 26. Temperature record (top), seasonal light patterns of G. Reinus, sex ratio (f:m) of G. sulcatus (middle), and seasonal sex ratio fluctuations (bottom).

UBC Research Forest, Maple Ridge, B.C., 1986.
humidities, and these conditions will enhance dusk flights.

The coincidence of the sex ratio fluctuation with the temperature fluctuation confirms the same relationship in brood emergence, and supports the conclusion that males are better adapted to environmental extremes than females. As the male is the pioneer sex, this enable males more time to explore host materials. Another factor which may also contribute to high sex ratios in seasonal flight on warm days is the abandonment of galleries by female beetles, since peak abandonment by *G. retusus* females on the D-f log was recorded on days with high temperatures.

The seasonal flight pattern of *G. retusus* observed herein agrees with those reported by Lindgren and Borden (1983), McLean and Borden (1977b), and Shore and McLean (1985), and confirms the observation from gallery dissection work with D-f logs that *G. retusus* is primarily univoltine.

*G. sulcatus* had an evident second flight peak during mid-July. But it was far smaller than those reported by Lindgren and Borden (1983), McLean and Borden (1975b), and Shore and McLean (1985). Comparing experimental sites, all other surveys were conducted in dryland sorts and sawmills where fresh logs were replenished continuously over time. In the present study in the forest, most host materials were left in 1984 except for a small logging operation in May 1986. Most of these host materials left in 1984 whether attacked or not probably became unsuitable for ambrosia beetles to attack in the spring 1986. Therefore, emergent *G.*
sulcatus beetles in spring would probably not be able to find adequate suitable host materials to maintain its population in that area. This seems also to be a reason for long lasting flight of G. retusus. In addition, G. sulcatus would face a strong competition from G. retusus since G. retusus was the dominant ambrosia beetle species in that area. For population suppression of Gnathotrichus species with pheromone-based mass trapping systems, traps should be set out before a weekly mean maximum temperature of 15°C is reached in the spring.

3.6 EFFECTS OF SEMIOCHEMICALS ON THE BEHAVIOUR OF G. RETUSUS AND G. SULCATUS

3.6.1 EFFECTS OF SEMIOCHEMICAL BAIT COMBINATIONS

Both G. retusus and G. sulcatus of both sexes responded significantly to ethanol and their aggregation pheromones, (+)-sulcatol and (±)-sulcatol respectively (Table 5-8). Significant synergistic effects of ethanol with (+)-sulcatol for G. retusus of both sexes existed (Table 5,6). But no significant synergistic effects of ethanol with (±)-sulcatol were verified for G. sulcatus of either sex since there was no a significant interaction between ethanol and (±)-sulcatol (Table 8).

Neither G. retusus nor G. sulcatus of either sex responded significantly to a-pinene baited traps. No synergistic effects of a-pinene with sulcatol or ethanol
Table 5. ANOVA of *G. retusus* 8X8 Latin Square experiment.  
UBC Research Forest, Maple Ridge, B.C. 1986.

<table>
<thead>
<tr>
<th>Source</th>
<th>D.F.</th>
<th>Male¹</th>
<th>Female¹</th>
<th>Sex ratio (f:m)</th>
<th>EMS²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Time</td>
<td>7</td>
<td>0.04681</td>
<td>7.53**</td>
<td>0.02548</td>
<td>4.21**</td>
</tr>
<tr>
<td>Position</td>
<td>7</td>
<td>0.00486</td>
<td>0.78</td>
<td>0.01025</td>
<td>1.69</td>
</tr>
<tr>
<td>Sulcatol</td>
<td>1</td>
<td>0.64173</td>
<td>103.21**</td>
<td>1.51098</td>
<td>249.36**</td>
</tr>
<tr>
<td>α-Pinene</td>
<td>1</td>
<td>0.00001</td>
<td>0.002</td>
<td>0.00536</td>
<td>0.88</td>
</tr>
<tr>
<td>S+P</td>
<td>1</td>
<td>0.00125</td>
<td>0.20</td>
<td>0.00483</td>
<td>0.79</td>
</tr>
<tr>
<td>Ethanol</td>
<td>1</td>
<td>0.66836</td>
<td>107.49**</td>
<td>0.39529</td>
<td>65.24**</td>
</tr>
<tr>
<td>S+E</td>
<td>1</td>
<td>0.07810</td>
<td>12.56**</td>
<td>0.07496</td>
<td>12.37**</td>
</tr>
<tr>
<td>P+E</td>
<td>1</td>
<td>0.00852</td>
<td>1.37</td>
<td>0.02337</td>
<td>2.38</td>
</tr>
<tr>
<td>S+P+E</td>
<td>1</td>
<td>0.00304</td>
<td>0.49</td>
<td>0.00196</td>
<td>0.32</td>
</tr>
<tr>
<td>Error</td>
<td>42</td>
<td>0.00622</td>
<td>7.53**</td>
<td>0.00606</td>
<td>7.53**</td>
</tr>
</tbody>
</table>

1. Data transformed to $X' = \log(\log(X+1)+1)$ prior to ANOVA.
2. Expected mean square.
*  Significance level $p \leq 0.05$.
** Significance level $p \leq 0.01$. 

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Table 6. Analysis of factorial effects in *G. retusus* 8X8 Latin Square experiment. UBC Research Forest, Maple Ridge, B.C. 1986.

<table>
<thead>
<tr>
<th>Factor²</th>
<th>Mean catch¹</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td></td>
</tr>
<tr>
<td>Ethanol-0</td>
<td>11.2 a³</td>
<td>28.2 a</td>
<td></td>
</tr>
<tr>
<td>Ethanol-1</td>
<td>77.6 b</td>
<td>158.8 b</td>
<td></td>
</tr>
<tr>
<td>Sucatol-0</td>
<td>12.2 a</td>
<td>10.4 a</td>
<td></td>
</tr>
<tr>
<td>Sucatol-1</td>
<td>76.6 b</td>
<td>186.6 b</td>
<td></td>
</tr>
<tr>
<td>E-0 + S-0</td>
<td>0.4 a</td>
<td>0.4 a</td>
<td></td>
</tr>
<tr>
<td>E-1 + S-0</td>
<td>23.9 b</td>
<td>20.3 b</td>
<td></td>
</tr>
<tr>
<td>E-0 + S-1</td>
<td>22.0 b</td>
<td>75.9 c</td>
<td></td>
</tr>
<tr>
<td>E-1 + S-1</td>
<td>131.2 c</td>
<td>297.3 d</td>
<td></td>
</tr>
</tbody>
</table>

1. Data transformed to X' = log(log(X+1)+1) prior to ANOVA.
2. 0 indicates absence of the treatment factor. 1 indicates presence of the treatment factor.
3. Numbers within a column followed by the same letter not significantly different, Newman-Keuls test, p≤0.05.
Table 7. ANOVA of *G. sulcatus* 8X8 Latin Square experiment.

<table>
<thead>
<tr>
<th>Source</th>
<th>D.F.</th>
<th>Male(^1)</th>
<th></th>
<th>Female(^1)</th>
<th></th>
<th>Sex ratio (f:m)</th>
<th></th>
<th>EMS(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>7</td>
<td>0.452</td>
<td>3.76**</td>
<td>0.480</td>
<td>4.19**</td>
<td>0.601</td>
<td>0.58</td>
<td>(\sigma^2 + 64\sigma^2_{\text{time}})</td>
</tr>
<tr>
<td>Position</td>
<td>7</td>
<td>0.137</td>
<td>1.14</td>
<td>0.223</td>
<td>1.94</td>
<td>0.511</td>
<td>0.49</td>
<td>(\sigma^2 + 64\sigma^2_{\text{posit}})</td>
</tr>
<tr>
<td>Sulcatol</td>
<td>1</td>
<td>8.166</td>
<td>67.84**</td>
<td>15.077</td>
<td>131.60**</td>
<td>40.877</td>
<td>39.22**</td>
<td>(\sigma^2 + 256\sigma^2_{S})</td>
</tr>
<tr>
<td>(\alpha)-Pinene</td>
<td>1</td>
<td>0.263</td>
<td>2.18</td>
<td>0.466</td>
<td>4.06</td>
<td>0.004</td>
<td>0.00</td>
<td>(\sigma^2 + 256\sigma^2_{P})</td>
</tr>
<tr>
<td>S+P</td>
<td>1</td>
<td>0.078</td>
<td>0.65</td>
<td>0.001</td>
<td>0.01</td>
<td>0.511</td>
<td>0.49</td>
<td>(\sigma^2 + 128\sigma^2_{SP})</td>
</tr>
<tr>
<td>Ethanol</td>
<td>1</td>
<td>5.643</td>
<td>46.88**</td>
<td>4.616</td>
<td>40.29**</td>
<td>2.569</td>
<td>2.46</td>
<td>(\sigma^2 + 256\sigma^2_{E})</td>
</tr>
<tr>
<td>S+E</td>
<td>1</td>
<td>0.040</td>
<td>0.33</td>
<td>0.009</td>
<td>0.08</td>
<td>2.328</td>
<td>2.23</td>
<td>(\sigma^2 + 128\sigma^2_{SE})</td>
</tr>
<tr>
<td>P+E</td>
<td>1</td>
<td>0.000</td>
<td>0.00</td>
<td>0.008</td>
<td>0.07</td>
<td>0.015</td>
<td>0.01</td>
<td>(\sigma^2 + 128\sigma^2_{PE})</td>
</tr>
<tr>
<td>S+P+E</td>
<td>1</td>
<td>0.046</td>
<td>0.38</td>
<td>0.099</td>
<td>0.86</td>
<td>0.804</td>
<td>0.77</td>
<td>(\sigma^2 + 64\sigma^2_{SPE})</td>
</tr>
<tr>
<td>Error</td>
<td>42</td>
<td>0.120</td>
<td></td>
<td>0.115</td>
<td></td>
<td>1.042</td>
<td></td>
<td>(\sigma^2)</td>
</tr>
</tbody>
</table>

1. Data transformed to \(X' = \log(X+1)\) prior to ANOVA.
2. Expected mean square.
*  Significance level \(p \leq 0.05\).
**  Significance level \(p \leq 0.01\).

<table>
<thead>
<tr>
<th>Factor²</th>
<th>Mean catch¹</th>
<th>Sex ratio (f:m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>α-Pinene-0</td>
<td>8.6 a²</td>
<td>15.0 a</td>
</tr>
<tr>
<td>α-Pinene-1</td>
<td>13.0 a</td>
<td>19.8 a</td>
</tr>
<tr>
<td>Ethanol-0</td>
<td>4.6 a</td>
<td>10.3 a</td>
</tr>
<tr>
<td>Ethanol-1</td>
<td>17.1 b</td>
<td>25.5 b</td>
</tr>
<tr>
<td>Sulcatol-0</td>
<td>3.0 a</td>
<td>2.5 a</td>
</tr>
<tr>
<td>Sulcatol-1</td>
<td>18.7 b</td>
<td>32.3 b</td>
</tr>
</tbody>
</table>

1. Data transformed to $X' = \log(X+1)$ prior to ANOVA.

2. 0 indicates absence of the treatment factor.
   1 indicates presence of the treatment factor.

3. Numbers within a column followed by the same letter not significantly different, t-test, $p \leq 0.05$. 
were found for either *G. retusus* or *G. sulcatus* (Table 5-8).

The sex ratios of both *G. sulcatus* and *G. retusus* for any treatments with either (+)-sulcatol or (-)-sulcatol present were significantly higher than those for treatments including only host odors (α≤0.05). All treatments containing only host odors had sex ratios smaller than one, and all treatments containing aggregation pheromones had sex ratios larger than one (range 1.79 to 10.6).

This experiment represents the first time that *G. retusus* of both sexes have been found to respond significantly to ethanol alone, although ethanol had been demonstrated to be a primary host kairomone for ambrosia beetles for quite a long time. The results for α-pinene effects agree with Borden *et al.* (1980b), and indicate that α-pinene does not play a significant role in either *G. retusus* or *G. sulcatus* orientation.

Ethanol is a major product of anaerobic fermentation in dead or dying wood tissue (Graham 1968; Moeck 1970). However, α-pinene is a major naturally-occurring terpene component in both live and dead tree tissue (Fengel and Wegner 1984; Kurth 1952). Apparently, ethanol is more characteristic of the dead or dying trees which ambrosia beetles attack than α-pinene, and is therefore a better host indicator. If ambrosia beetles used α-pinene as a major host kairomone, they would be attracted to live trees which certainly were not suitable hosts for them. Based on the above discussion, and the results of field experiments, it
can be concluded that α-pinene is neither a major host attractant nor a synergist of aggregation pheromones for the two *Gnathotrichus* species. It would thus seem unnecessary to include an α-pinene bait in mass trapping systems for *Gnathotrichus* species.

The significant differences in sex ratio between host odor treatments and treatments containing aggregation pheromones imply that females of both species are more responsive to aggregation pheromones than are males, and males of both species are more responsive to ethanol than are females. This appears logical since males are the pioneer sex which initiates attacks and females are the responding sex.

### 3.6.2 EFFECTS OF (±)-SULCATOL RELEASE RATES

(±)-sulcatol at a 1.5mg/day release rate in combination with ethanol (100mg/day) and α-pinene (20-30mg/day) caught the largest numbers of both male and female *G. sulcatus* beetles. Catches of male beetles decreased steadily and more dramatically than female catches as the (±)-sulcatol release rate increased beyond 1.5mg/day (Fig 27). But catches of males and females for all treatments with (±)-sulcatol were not significantly different. However, the sex ratio showed significant increases with (±)sulcatol release rates (Table 9).

The lack of significant difference in sex ratio between the combination of ethanol with α-pinene and the ternary
Figure 27. Relationship between (±)-sulcatol release rate and *G. sulcatus* trap catch. UBC Research Forest, Maple Ridge, B.C. 1986.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>(±)-sulcatol release rate (mg/day)</th>
<th>Mean catch</th>
<th>Sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>P+E</td>
<td>0.0</td>
<td>3.0 a³</td>
<td>1.2 a</td>
</tr>
<tr>
<td>P+E+S1</td>
<td>0.5</td>
<td>162.8 b</td>
<td>267.0 b</td>
</tr>
<tr>
<td>P+E+S2</td>
<td>1.5</td>
<td>211.8 b</td>
<td>411.6 b</td>
</tr>
<tr>
<td>P+E+S3</td>
<td>5.0</td>
<td>154.4 b</td>
<td>356.4 b</td>
</tr>
<tr>
<td>P+E+S4</td>
<td>10.0</td>
<td>112.2 b</td>
<td>376.6 b</td>
</tr>
</tbody>
</table>

1. Data transformed to $X' = \log(X+1)$ prior to ANOVA.
2. P+E = $\alpha$-pinene + ethanol; release rates: $\alpha$-pinene 20-30mg/day, ethanol 100mg/day.
3. Numbers within a column followed by the same letter not significantly different, Newman-Keuls test, $p \leq 0.05$. 
mixture with (±)-sulcatol at a release rate of 0.5mg/day was apparently due to low catches in the ethanol and α-pinene baited trap which resulted in the absence of sex ratios in three of the five Latin Square replicates, and a large variance. Although there were no significant differences in trap catches of both males and females, the significant differences in sex ratio among different (±)-sulcatol release rates demonstrated effects of the aggregation pheromone on behaviour of both males and females. High release rates of (±)-sulcatol seems to inhibit responses by male beetles.

With respect to G. sulcatus population management and survey using aggregation pheromone based systems, these results suggest that the 1.5mg/day release rates of (±)-sulcatol may be used since it would be more economical and apparently an optimal release rate for both sexes of G. sulcatus.

3.6.3 ALLELOCHEMIC ACTIVITY OF AGGREGATION PHEROMONES BETWEEN G. RETUSUS AND G. SULCATUS

Relatively large numbers of G. retusus beetles of both sexes were caught in the two seasonal flight monitoring traps baited with ethanol and (±)-sulcatol. In these traps, G. retusus beetles made up 10.7% of the total catch, but the proportion of G. retusus varied over time. The fluctuation of numbers of G. retusus beetles in the ethanol and (±)-sulcatol baited traps was similar to the G. retusus
catches in the ethanol and (+)-sulcatol baited traps (Fig 28). During the peak flight of both species, *G. retusus* beetles in the (±)-sulcatol made up 14.3% of the total catch, and then decreased as the flight peaks passed.

As the traps were baited with both ethanol and (±)-sulcatol, and ethanol has been demonstrated to be a primary host attractant of *G. retusus*, it is not reliable to claim a cross attraction of *G. retusus* to (±)-sulcatol because the (±)-sulcatol effects can not be distinguished from ethanol effects. But, at least, it can be concluded that *G. retusus* can tolerate (-)-sulcatol to a certain extent. As hosts colonized by *G. sulcatus* will have the primary host kairomone ethanol emitted by hosts and (±)-sulcatol excreted by the beetles, this material could be attacked by *G. retusus* beetles based on results reported here. But it has been reported that *G. retusus* was never found to attack logs infested by *G. sulcatus* (Borden *et al.* 1979) although slight cross attraction of (±)-sulcatol to *G. retusus* was later reported (Borden *et al.* 1981a).

A small number of *G. sulcatus* was caught in the ethanol and (+)-sulcatol baited traps. But due to the same reason stated above, the data were not adequate to reach the conclusion reported by Borden *et al.* (1981a) that (+)-sulcatol has slight cross attraction to *G. sulcatus*. 
Figure 28. Comparison between *G. retusus* catches in (±)-sulcatol and ethanol baited traps (top) and *G. retusus* catches in (+)-sulcatol and ethanol baited traps (bottom). UBC Research Forest, Maple Ridge, B.C. 1986.

**Legend**

- *G. retusus*
- *G. r. %*
4. SUMMARY

This research was conducted in 1985 and 1986 at the UBC Research Forest and at UBC. The scope of the research covered the biology of *G. retusus* and behavioural responses of *G. retusus* and *G. sulcatus* to semiochemicals. The main results are summarized as follows:

1. *G. retusus* brood development from egg to adult in D-f logs in the spring and summer takes 40 days or more. This species is primarily univoltine, but a small portion of the population may take more than one year to complete the life cycle. It overwinters mainly as an adult, but other life stages may also be found.

2. Boring activities shifted gradually from shallow sapwood in the spring to deep sapwood in late summer. Neither frass production nor gallery extension had a consistent relationship with maximum temperature, and both showed a similar pattern.

3. Gallery abandonment occurred mainly in June and July and was commenced by females. This implies a high sensitivity of females to host quality. The abandonment seems to be induced directly and/or indirectly by high temperatures.

4. Frass colour changed from white in June to completely black in August. This reflected stain development in galleries. Stain generally is restricted in shallow branches and gallery portions near entrances.

5. *G. retusus* brood production in D-f logs had a
significant linear relationship with gallery length. This implies a vital function of the large proportion of non-brood productive parts of galleries.

6. Structure of *G. retusus* galleries is similar to that of *G. sulcatus* galleries. Brood niches were restricted to gallery portions near entrances. A mature gallery system usually had at least one shallow and one deep branch or several branches distributed at different depths. Pupal niches had a concentration in 10-20mm depth of sapwood in D-f stumps and in 20-30mm depth in WH stumps. Many *G. retusus* galleries in D-f stumps showed unique structure: pupal niches were elongated which may function as maturation feeding tunnels, and inter-gallery crossings were quite common. Slight elongation of pupal niches was also found in WH stumps.

7. D-f stumps were significantly more heavily attacked by *G. retusus* than WH stumps. There were no significant differences in gallery success rate and brood production between the two host species. Significant differences were found in attack density and brood production among D-f and WH stumps. Within D-f stumps, increases in attack density and brood production were noted from tops to the root collar zone. Within WH stumps, only attack densities showed a similar gradient.

8. *G. retusus* was the dominant ambrosia beetle species in the F-3 area of the UBC Research Forest colonizing D-f and WH stumps. Brood emergence from D-f and WH stumps
started in late April when maximum daily temperatures reached about 13.5°C, reached a peak in late May when weekly mean maximum temperature reached 22.2°C, and ceased in early June. But a few brood might emerge as late as the end of July. The number of brood emerged and the sex ratio of brood in galleries ready to emerge were positively related to maximum temperatures.

9. *G. retusus* showed a bimodal diurnal flight rhythm: a very small morning flight and a larger dusk flight. Flight seems to be triggered mainly by light intensity and occurred within a light intensity range of 12 Watts/m² to 120 Watts/m². Temperature and relative humidity also influenced the diurnal flight. Temperatures above 14°C were essential for beetles to fly. Temperatures from 17 to 25°C were a suitable range for the dusk flight. High temperature and low relative humidity during the day also appeared to enhance the dusk flight.

10. Seasonal flights of both *G. retusus* and *G. sulcatus* started in late April when maximum daily temperatures only reached 13.5°C, reached peaks in late May which coincided with the brood emergence peak, and ceased in October when weekly mean maximum temperatures dropped below 15°C. *G. retusus* showed only one flight peak, and *G. sulcatus* showed a small second flight peak in late July. The flights and sex ratios of both species were positively related with maximum temperatures.
11. *G. retusus* and *G. sulcatus* of both sexes responded significantly to ethanol. Significant synergistic effects of ethanol with (+)-sulcatol in catching *G. retusus* of both sexes were verified. No synergistic effects of ethanol with (±)-sulcatol were found. Alpha-pinene did not have significant effects as either a primary host attractant or a synergist of aggregation pheromones.

12. Sex ratios of both *G. retusus* and *G. sulcatus* shifted from less than one for treatment with only host odors to above one for treatments including aggregation pheromones. For *G. sulcatus*, the sex ratio increased with increases of (±)-sulcatol release rate.

13. Both *G. retusus* and *G. sulcatus* occurred in each other's aggregation pheromone plus ethanol baited traps, and the conclusion of mutual tolerance of *G. retusus* and *G. sulcatus* to each other's aggregation pheromones was reached.
REFERENCES


pheromone in the scolytid beetle *Gnathotrichus sulcatus*. J. Insect Physiol. 20:1895-1900.


Prebble, M.L. and K. Graham. 1957. Studies of attack by
ambrosia beetles in softwood logs on Vancouver Island, British Columbia. For. Sci. 3:90-112.


Appendix 1. ANOVA of *G. retusus* attack density on D-f stumps and their aspects. UBC Research Forest, Maple Ridge, B.C. 1986.

<table>
<thead>
<tr>
<th>Source</th>
<th>D.F.</th>
<th>Mean Square</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stump</td>
<td>6</td>
<td>0.2579</td>
<td>4.23**</td>
</tr>
<tr>
<td>Aspect</td>
<td>3</td>
<td>0.1746</td>
<td>2.86*</td>
</tr>
<tr>
<td>SA</td>
<td>18</td>
<td>0.0949</td>
<td>1.56</td>
</tr>
<tr>
<td>Error</td>
<td>110</td>
<td>0.0609</td>
<td></td>
</tr>
</tbody>
</table>

1. Data transformed to X' = Log(X+1) prior to ANOVA.
2. No significant differences were detected among different aspects, Newman-Keul's test, p ≤ 0.05.
* *. Significance level p ≤ 0.05.
**. Significance level p ≤ 0.01.
Appendix 2. ANOVA of *G. retusus* attack density on WH stumps and their aspects. UBC Research Forest, Maple Ridge, B.C. 1986.

<table>
<thead>
<tr>
<th>Source</th>
<th>D.F.</th>
<th>Mean Square</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stump</td>
<td>3</td>
<td>0.9529</td>
<td>10.76**</td>
</tr>
<tr>
<td>Aspect</td>
<td>3</td>
<td>0.1183</td>
<td>1.34</td>
</tr>
<tr>
<td>SA</td>
<td>8</td>
<td>0.0702</td>
<td>0.79</td>
</tr>
<tr>
<td>Error</td>
<td>41</td>
<td>0.0886</td>
<td></td>
</tr>
</tbody>
</table>

1. Data transformed to $X' = \log(X+1)$ prior to ANOVA.
2. Significance level $p \leq 0.01$. 
Appendix 3. Layout and data of *G. retusus* 8x8 Latin Square experiment.
UBC Research Forest, Maple Ridge, B.C. 1986.

<table>
<thead>
<tr>
<th>Date</th>
<th>1 treatment M²</th>
<th>2 treatment M³</th>
<th>Trap Location</th>
<th>3 treatment M</th>
<th>4 treatment M</th>
<th>5 treatment M</th>
<th>6 treatment M</th>
<th>7 treatment M</th>
<th>8 treatment M</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 8</td>
<td>C</td>
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<td>P</td>
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<td>S</td>
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<td>S+P+E</td>
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<td>E</td>
<td>S+P+E</td>
<td>S+P</td>
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<td>C</td>
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1. C=control, S= (+)-sulcatol, P=α-pinene, E=ethanol.
2. M=male catch.
3. F=female catch.
Appendix 4. Layout and data of *G. sulcatus* 8X8 Latin Square experiment.

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<th>1 treatment*</th>
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1. C=control, S=(±)-sulcatol, P=α-pinene, E=ethanol.
2. M=male catch.
3. F=female catch.
Appendix 5. Layout and data of (±)-sulcatol release rate 5×5 Latin Square experiment. UBC Research Forest, Maple Ridge, B.C. August 1985.

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<th>3 treat M F</th>
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1. treat=treatment: P=α-pinene; E=ethanol; S=(±)-sulcatol; 1-4=release rate levels;
2. M=male catch.
3. F=female catch.