Sex Pheromones: Abolition of Specificity in Hybrid Bark Beetles

Abstract. Specificity of sex pheromones maintains breeding isolation among three closely related species of spruce-infesting Ips. Hybrids produced in the laboratory were intermediate in attractiveness and response. Pheromones and pheromone receptor types in the hybrids are probably mixtures of those of the parent species.

The spruce-infesting bark beetles (Scolytidae) Ips amiskwienςis G. Hopping and I. borealis (Eichhoff) are sympatric along the eastern edge of the Canadian Rockies (1). Near Banff, Alberta, these species commonly infest the same host tree, but I have been unable to find them inhabiting the same gallery systems. Ips pilifrons Swaine infests spruce in the southern Rocky Mountains and meets I. amiskwienςis in the vicinity of the Grand Tetons, Wyoming (2).

Although I. amiskwienςis will produce fertile hybrids with I. borealis and I. pilifrons in forced laboratory pairings, putative hybrids are rare in nature. Introgression is presumably averted by specificity of sex pheromones (3). I have found support for this hypothesis in field and laboratory tests of females’ responses to pheromones produced by various pure and hybrid males. The same tests indicate that hybrids produce a mixture of pheromones and inherit pheromone receptor types of both parent species.

For each laboratory test, 36 males (12 each of three kinds) were induced to bore into a freshly cut spruce bolt (4) in a 6 by 6 Latin square design. Each kind of male was represented twice in every row and column. After males were allowed 2 days to excavate nuptial chambers, 72 females of one kind (occasionally less than 72 were available) were released on the infested bolt in a cage made by joining two 1-gallon Sealright (5) food cartons. Four days later the bark was carefully stripped from the log and the number of females in, or constructing egg galleries from, each nuptial chamber was recorded. Nuptial chambers rather than males were considered in the assessment of the relative attractiveness of the kinds tested; occasionally males failed to become established, whereas others abandoned the initial nuptial chamber to construct a second. Correct identification of such males was assured by prior marking of each kind with a different lacquer.

In the first type of field test, small logs, each previously infested with five males of one kind, were placed 5 m apart in a Latin square. Each kind appeared once in every row and column. After 10 days, results were assessed as in laboratory tests. In the second type of field test, logs, each containing 40 males of one kind, were placed in individual greenhouse cages and responding beetles were collected in a tray of water under a window trap (6).

In 56 of 57 laboratory tests, more pure females responded to males of their own species than to males of other species. Based on attraction to males of its own kind as index 100, attraction indices (7) for I. amiskwienςis females to I. pilifrons and I. borealis were 37 and 19, respectively (Table 1). Indices for reciprocal tests were 11 and 15. In field tests, I. amiskwienςis was very slightly, if at all, attracted to other species (Table 2).

Pure females generally responded to hybrid males at a level intermediate to the response to males of the parent species. Attraction indices for I. pilifrons and I. borealis—to the pure species and their F1 and B1 progeny with I. amiskwienςis—are clearly in the same order as their blood relationships. For example, the responses of female I. pilifrons to male pilifrons, B1 (a-p) (8), F1 (a-p), B1 (a-p), and I. amiskwienςis were 100, 35, 27, 13, and 11, respectively (Table 1). Ips amiskwienςis females also responded in order of blood relationship with I. borealis and backcrosses in both laboratory (Table 1) and field tests (Table 2, test 1). However, the ability of I. amiskwienςis to discriminate apparently broke down in laboratory tests involving its F1 hybrid with I. pilifrons. Furthermore, it did not differentiate between the B1 (a-p) and a (a-p) in the laboratory or in the field (Table 2, tests 2 and 3).

Hybrid a-p females were slightly more attractive to males of their own kind than to those of the two parent species (Table 1). Backcross p (a-p) and a (a-p) females were attracted strongly to males of the backcross species, less to males of their own kind, and least to males of the other parental species. F1 a-b were insufficient in number for inclusion in tests. Backcross female b (a-b) responded in the manner just described. However, the a (a-b) females were attracted nearly equally

<table>
<thead>
<tr>
<th>Females</th>
<th>Male pheromone</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
</tr>
<tr>
<td>I. amiskwienςis</td>
<td>100-8</td>
</tr>
<tr>
<td>B1, a (a-p)</td>
<td>189-4</td>
</tr>
<tr>
<td>F1, a-p</td>
<td>78-4</td>
</tr>
<tr>
<td>B1, p (a-p)</td>
<td>30-4</td>
</tr>
<tr>
<td>I. pilifrons</td>
<td>11-8</td>
</tr>
</tbody>
</table>

Table 1. Attraction indices (8) and number of tests (italics) for Ips amiskwienςis (a), I. pilifrons (p), I. borealis (b), and F1 and backcross (B1) hybrids, determined in the laboratory. NT, not tested.

<table>
<thead>
<tr>
<th>Tgt</th>
<th>Total taken (No.)</th>
<th>p</th>
<th>p (a-p)</th>
<th>a-p</th>
<th>a (a-p)</th>
<th>a</th>
<th>a (a-b)</th>
<th>b (a-b)</th>
<th>b</th>
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<tbody>
<tr>
<td>1</td>
<td>71</td>
<td>10</td>
<td>15</td>
<td>66</td>
<td>NT</td>
<td>100</td>
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<td>21</td>
<td>9</td>
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<td>16</td>
<td>69</td>
<td>NT</td>
<td>66</td>
<td>100</td>
<td>62</td>
<td>0</td>
<td>NT</td>
</tr>
</tbody>
</table>

Table 2. Attraction indices (8) of female Ips amiskwienςis to various pure and hybrid males determined in the field. Tests 1 and 2, females taken from nuptial chambers of males; test 3, females captured in traps. NT, not tested.
to males of the same kind and to I. amiskwiensis.

From these tests it is clear that specificity of sex pheromones tends to prevent natural hybridization between I. amiskwiensis and I. borealis or I. pilirons. Comparisons of laboratory and field tests with I. amiskwiensis suggest that specificity is greatest under field conditions and that greater discrimination is exercised in entering nuptial chambers (log tests) than in flying to the attractant (trap tests). However, natural hybrids which might occur could readily breed among themselves, or assimilate with either parent species.

Pheromones and pheromone receptors of hybrids theoretically could be new, the same as those of the parent species (either singly or in combination), or a combination of new and parent types. Receptors of pheromones in some insects have been shown to be quite specific; even isomers of the same compound often fail to produce responses similar to the degree of heterosis. If the olfactory response is a lents response to males it would also be predicted (11). Lack of discrimination by I. amiskwiensis between pheromones produced by male p (a-p) and a (a-p) and the partial breakdown in response specificity of this species in the presence of the F2 a-p pheromone may be associated phenomena—the cause of which could come to light when the chemistry of the component pheromones is known.

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References and Notes
2. Based on recent collections by the author.
3. The male Ips selects the host tree, initiates the attack, and constructs a nuptial chamber in the phloem-cambium region. In so doing it discharges a pheromone which attracts both sexes, stimulates mass attack on the host selected, and induces females to enter the nuptial chambers and mate [R. F. Anderson, J. Econ. Entomol. 41, 596 (1948); D. L. Wood and J. P. Vité, Contrib. Boyce Thompson Inst. 21, 79 (1961)]. Cross attractiveness of sex pheromones has been demonstrated for several closely related allopatric bark beetles [J. P. Vité, R. I. Gara, H. D. von Scheller, ibid. 22, 461 (1964); D. L. Wood and G. N. Lanier, unpublished data]. However, sympatric species are generally not cross attractive [R. C. Wilkinson, Fla. Entomol. 47, 57 (1964); J. P. Vité, Naturwissenschaften 52, 267 (1965)].
4. Picea engelmannii, 40 cm long and 10 to 20 cm in diameter.
5. Crown Zellerbach Ltd.
7. Attraction index of b to a, for example, is calculated as follows: b per a nuptial chamber divided by a per a nuptial chamber times 100.
8. I. amiskwiensis, a; I. pilirons, p; I. borealis, b; the progeny resulting from a cross (B) of I. amiskwiensis-I. pilirons hybrids to I. pilirons are designated p (a-p).
11. The simplest genetic situation possible is single locus for pheromone and pheromone receptor type. Thus, the genotype for receptors of the F2 amiskwiensis-pilirons would be ap and those of the backcross to pilirons would be 1/2 ap and 1/2 pp. The response of backcross females with the ap genotype is expected to be similar to that of the F2. Those with the pp genotype should respond in a manner similar to I. pilirons. If the response levels of the two genotypes predicted by the attraction indices in Table 1 are summed, it is clear that the I. pilirons pheromone will provide the greatest aggregate attraction to backcross females. If more than one locus is responsible for determining receptor type, this preference of the B, to the backcross species should be accentuated. These approximations could be further complicated if more than one compound differs in the respective pheromones. The sex pheromone of Ips confusus (LeConte) consists of three compounds, only one of which has been isolated by R. M. Silverstein, J. O. Rodin, D. L. Wood, Science 154, 509 (1966); D. L. Wood, R. W. Stark, R. M. Silverstein, J. O. Rodin, Nature 215, 206 (1967). Ips latidens (LeConte), a primitive species in my judgment, was attacked by a combination of two of these compounds, but response was inhibited by addition of the third compound [D. L. Wood et al., cited above].

3 February 1970; revised 14 May 1970

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