FEEDBACK BETWEEN INDIVIDUAL HOST SELECTION BEHAVIOR AND POPULATION DYNAMICS IN AN ERUPTIVE HERBIVORE

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Abstract. We examined the role of population density in host selection behavior of an eruptive insect herbivore, the spruce beetle *Dendroctonus rufipennis*. We conducted field and laboratory experiments on spruce beetles from 29 endemic and eruptive populations in Alaska and Utah, USA, and Yukon, Canada. Beetles from both population phases colonized trees that had been felled to remove host defenses. However, only beetles from eruptive populations colonized defended, healthy trees. A series of laboratory assays using host-based media amended with varying concentrations of phytochemicals identified several factors affecting population-dependent responses to hosts. First, beetles were repelled by high concentrations of the predominant spruce monoterpene, alpha-pinene, but intermediate concentrations elicited entry and gallery construction. Second, heritability assays suggested high genetic variance of host selection behavior within populations, and between-population differences persisted following rearing in a common environment. Third, beetles from eruptive populations were less likely to enter medium amended with phytochemicals and constructed shorter galleries, which disagreed with our prediction and seemingly contradicted the field observations. However, fourth, beetle avoidance of high concentrations of alpha-pinene decreased with the addition of other beetles, and this effect was more pronounced among beetles from eruptive populations than among those from endemic populations. This interaction broadened the host range of eruptive beetles. We propose that such density-dependent behaviors can maintain heterogeneity among population phases and contribute to positive feedback in herbivore population dynamics. A conceptual model suggests how heritable and environmentally induced variation in host selection behavior can affect bimodal equilibria and numerical thresholds in eruptive species.

Key words: Allee effect; bark beetle; bimodal equilibria; Dendroctonus rufipennis; density dependence; eruptive species; heritability; host selection; insect herbivore; monoterpenes; population dynamics; spruce.

INTRODUCTION

Phytophagous insects select host plants in response to a suite of external and internal stimuli, each of which may vary with environmental conditions. External stimuli are often plant derived (Price 1991, Lundberg et al. 1994), and may relate directly to host nutritional suitability or defensive capacity (Zangerl and Rutledge 1996, Chambers et al. 1997). Internal factors include both genetically fixed responses to specific compounds and concentrations (Carriere 1998) and modifications of behavioral sequences arising from experience (Jaenike 1988, Cunningham et al. 1998, Dukas 1998), hunger (Wallin and Raffa 2002*a*), and physiological state (Mayhew 1997). Heritable behaviors presumably reflect variable degrees of reproductive success associated with prior ovipositional or feeding choices.

One factor about which we know very little is the role of herbivore population density in the responses of individual insects to plant chemistry (Bigger and

Fox 1997). Herbivore populations provide both external cues, through the appearance, activities, and metabolites of conspecifics, and internal cues, through density-mediated modifications of herbivore nutrition, development time, and dispersal (Mopper et al. 1995, Mayhew 1997). Integrating environmental variation, insect physiology, and population structure remains an important challenge to our understanding of flexible host selection strategies (Via 1984, Desouhant et al. 1998, Wallin et al. 2002).

Potential feedback between population density and individual host selection behavior has implications for several aspects of plant–insect interaction theory and population dynamics. First, the incidence of such feedback could affect models of feeding breadth, particularly at the level of intraspecific variation (Fox and Morrow 1981, Larsson and Ekbom 1995, Bernays and Minkenberg 1997). Second, the optimal host selection strategy may vary with herbivore density (Bigger and Fox 1997, Hopper 1999). For example, scramble competition could favor acceptance of a broadened host range when resources are limited (Loughrin et al. 1990). Similarly, herbivores that engage in cooperative host procurement or defense might exploit a broader range of host conditions at high densities (Raffa and

PLATE 1. Female spruce beetle excavating an ovipositional gallery. Note eggs along the side of the gallery. Photo by R. Werner, USFS ret.

Berryman 1983, Bigger and Fox 1997). Third, changes in host selection behavior could not only reflect, but also contribute to numerical changes of eruptive species. Both positive and negative feedback on population size could be exerted through the number and nutritional quality of available plants, intraspecific competition, and acquisition of enemy-free space.

We investigated whether responses by individual insects to host phytochemicals change in response to population density, and whether such changes could affect subsequent population dynamics. We selected an eruptive insect species, in which females deposit their entire egg clutch within single plants, and a plant that shows high intraspecific variation in defensive capacity. We compared patterns of host utilization under natural endemic and eruptive conditions, and characterized herbivore responses to a gradient of biologically relevant concentrations of phytochemicals. We also compared responses to host compounds by individuals from eruptive and endemic populations and tested genetic, environmental, and genotype × environment interactions as potential sources of behavioral variation. We predicted that individuals from eruptive populations would be less repelled than individuals from endemic populations by concentrations of phytochemicals present in well-defended plants.

METHODS

Selection of model system

Conifer bark beetles (Scolytidae) feed and develop within subcortical tissues that are well defended by constitutive and induced defenses (Raffa and Berryman 1983, Lewinsohn et al. 1991). Within a few days after beetle entry, local concentrations of monoterpenes and phenolics can rise above the physiological tolerances of adult beetles, their progeny, and symbiotic fungi (Raffa and Smalley 1995, Klepzig et al. 1996). Environmental stress can reduce host defenses, so beetles often prefer defoliated (Waring and Cobb 1992, Wallin

and Raffa 2001), diseased (Klepzig et al. 1995), lightning-struck (Geiszler et al. 1984), or severely drought-injured (Lorio 1993) trees. Populations typically persist at endemic levels for several decades, during which beetles are concentrated within stressed trees. Environmental stress may initially release populations by providing more susceptible substrate, but population growth of eruptive species apparently continues after full utilization of the stressed-tree resource (Berryman 1982). These populations expand into nonstressed trees, less preferred size classes, and less preferred species. Tree mortality can exceed 90% over several million hectares and can affect ecosystem processes such as succession and fire (Amman 1972).

The ability of bark beetles to colonize and kill healthy trees relies on ''mass attacks'' coordinated by aggregation pheromones (Wood 1982). If entering beetles elicit sufficient attack densities, host defenses are exhausted and have little effect on subsequent brood development. However, if the colonizing beetles fail to attract enough conspecifics to surpass a critical threshold, they and their brood are killed by host defenses (Raffa and Berryman 1983). It is not known whether pheromones merely attract beetles to trees, or also mediate their host acceptance criteria. There are important trade-offs affecting the optimal host acceptance decisions of bark beetles. For example, environmentally stressed trees may pose fewer risks, but are also less abundant, nutritionally less suitable, and more available to interspecific competitors than healthy trees (Amman 1972, Wallin and Raffa 2001). Although vigorous trees are more abundant and can support more brood, they pose greater risks to potential colonizers and can only be killed by high densities that increase intraspecific competition, which reduces beetle size, energy reserves, and dispersal capacity (Amman 1972, Kinn et al. 1994).

Adult beetles land on potential hosts in response to olfactory and visual cues (Shepherd 1966, Strom et al.

1999). However, landing shows little specificity with regard to host susceptibility, as beetles land equally on trees that are ultimately colonized or rejected, and even host and nonhost species (Hynum and Berryman 1980, Moeck et al. 1981). Post-landing orientation is influenced by chemical cues, in association with tactile stimuli. For example, monoterpenes incorporated into phloem-based media affect entry and gallery construction by *Ips pini* (Say) in a dose-dependent fashion (Klepzig et al. 1996, Wallin and Raffa 2000).

The spruce beetle, *Dendroctonus rufipennis* (Kirby), exhibits the characteristic eruptive pattern of remaining at low densities for extended periods and intermittently rising to high densities (Werner et al. 1977). Over 2.3 $\times 10^6$ ha of spruce forests in Alaska experienced near total mortality to this native herbivore during 1992–1999, with 30×10^6 trees killed per year at the peak of the eruption (Holsten et al. 1999). In contrast, tree mortality averaged 3.6% of this level from 1955 to 1974 (Werner et al. 2004). *D. rufipennis* females select potential hosts, burrow through the bark, mate, construct single egg galleries within the phloem, and deposit ~6.5 eggs/cm of gallery (Sahota et al. 1987; see Plate 1). Natural enemies appear to have a relatively minor role in the population dynamics of *D. rufipennis*. For example, the ratios of *D. rufipennis* to predators and parasites in colonized trees are much higher than those observed for *Dendroctonus frontalis* Zimmermann (Thatcher et al. 1981, Gara et al. 1995).

Study sites and sources of beetles

We evaluated eruptive and endemic populations within three geographic regions: south-central Alaska (AK) and north-central Utah (UT), USA, and south-central Yukon Territory (YK), Canada (N63W150-N60W156, N42W112-N38W113, and N60W135-N61W137, respectively). Population phase was replicated by collecting beetles from five sites where they were at eruptive densities and four or five sites with populations at endemic densities within each geographic region, for a total of 15 eruptive and 14 endemic populations. All sites had predominantly (>75%) *Picea glauca* (Moench) Voss (AK, YK) or *Picea engelmannii* (Parry and Engelm.) overstory. Eruptive population sites had >50% of the mature spruce colonized by *D. rufipennis* during 1994–1996, beetles continuing to colonize vigorous trees over large regions, and <20% tree mortality at the eruptive edge, based on U.S. Forest Service and Canadian Forest Service data. Endemic sites had <10% tree mortality and the presence of viable populations confirmed by examination of colonized hosts. We selected sites farther apart than the effective dispersal range of *D. rufipennis*, estimated at up to 5 km (Beckwith 1972, Schmidt and Beckwith 1975, Werner and Holsten 1997).

We standardized beetle condition and experience for laboratory assays by collecting overwintering adults from the bases of brood trees, rather than using pher-omone-baited traps, as the latter could risk a biased sample. Preliminary assays demonstrated that *D. rufipennis* females collected in this fashion respond to natural and simulated host tissue (Wallin 2001). We collected adults in May 1997 and 1998, one to two weeks before emergence. We standardized beetle age by examining and marking uncolonized trees during June 1996 and 1997, thus assuring that all test beetles underwent complete development within the previous year. Beetles were placed in 12 × 25-mm vials, provided with duff from around their host tree, placed on ice packs, and shipped by overnight express to the University of Wisconsin–Madison (UW-Madison) under APHIS (Animal and Plant Health Inspection Service) permit number 33559. These beetles were used either for behavioral assays or to establish a colony for subsequent breeding lines.

General laboratory assay used throughout experiments 1–4

We used a common behavioral assay throughout many of the experiments. We observed beetle entrance and gallery construction behaviors in 9-cm petri dishes containing a mixture of denatured spruce phloem, agar, water, and synthetic monoterpenes (Klepzig et al. 1996). In previous experiments with *I. pini*, beetles behaved in this assay as in nature by distinguishing between extracts of stem phloem from trees whose roots were infected with pathogens or healthy, and between constitutive vs. induced reaction tissue (Klepzig et al. 1995, 1996). To avoid potential bias, we obtained phloem from a single location in Wisconsin, USA that was distant from all test populations but within the range of *D. rufipennis*. Phloem was freeze-dried for 72–96 h, ground through a Wiley mill (0.5-mm screen), and autoclaved for 20 min (104.4°C, 33.3 kg pressure) to remove monoterpenes (Wallin and Raffa 2000). We mixed the ground phloem and Bacto-agar (Difco, Detroit, Michigan, USA) in boiling distilled water, poured the medium into a petri dish to a depth of 2.50 mm, and dried it at 22°C in a fume hood for 36 h.

We applied 0.0, 1.5, 5.5, and 30.0 mg monoterpene/g media in pentane to simulate hosts that were, respectively, dead, live healthy, highly vigorous, and induced. Total constitutive monoterpenes of apparently healthy spruce trees in the study sites averaged 1.5 ± 0.8 mg/g (mean ± 1 SE, $N = 60$), as determined by gas chromatography (Wallin and Raffa 2000). We placed a plastic disk over the medium to minimize volatilization, and confirmed the stability of monoterpene concentrations throughout the assay by gas chromatography (Shimadzu GLC 17A, Shimadzu Scientific Instruments, Columbia, Maryland, USA).

Because responses of bark beetles to host compounds can vary during different stages of their orientation sequence and with assay conditions (Raffa 1988, Klepzig et al. 1996, Wallin and Raffa 2000), we evaluated beetles under both no-choice and choice conditions.

Having measures of gallery construction under both no-choice and choice conditions also provided two groups of beetles: a random sample and those that elected to enter the medium. To test gallery construction behavior under no-choice conditions, we drilled a 3.0-mm diameter hole through the arena's side, applied the monoterpene or control, gently inserted a female into the medium, and sealed the hole and lid with a double strip of parafilm. We quantified gallery lengths at 48 h using a map measurer. In choice experiments, we placed the medium in the petri dish's 11-cm diameter lid, leaving a 1-cm open perimeter. We placed a female on the 9-cm plastic disk 1 h after applying monoterpene or control, and observed her for 15 min. During this time, she could stay on the disk, walk around the edge, or enter the medium. We recorded the number of beetles that entered, their time of entry, and gallery lengths at 48 h. We randomly positioned arenas in darkness at 24°C to simulate the subcortical environment.

Experiment 1: Do natural populations colonize trees of different physiological conditions during endemic vs. eruptive phases?

Experiment 1a: Field colonization.—We tested whether *D. rufipennis* colonize trees of different conditions during their endemic vs. eruptive phases. In 1997, we marked six live healthy trees with no visible symptoms of insects or pathogens within each of the 19 endemic and eruptive sites in Alaska and the Yukon. We also felled and left two trees, because felled trees do not retain resistance to bark beetles (Raffa and Berryman 1983). We marked six trees that had pitch tubes (indicating failed colonization attempts during 1996) at each of the five eruptive Alaskan sites. The mean diameter of test trees did not vary among sites or regions (AK, 27.7 ± 0.29 cm, mean ± 1 SE; YK, 22.9 ± 0.28 cm. We recorded the incidence and time of colonization during the spring of 1998. Forest Service cooperators monitored the onset of beetle flight using two 12-unit multiple funnel traps baited with 1-methyl-2-cyclo-1-hexenol, frontalin, and alpha-pinene (PheroTech, Delta, British Columbia, Canada) per site.

A chi-square test was used to analyze relationships among the incidence and time of colonization and tree condition (SAS Institute 1996). We tested for relationships between colonization rates and bole diameter using one-way ANOVA (SAS Institute 1996).

Experiment 1b: Behavior of beetles collected from hosts of varying conditions.—In 1998, we excavated adult progeny from all of the previously healthy and felled trees that were colonized by parental beetles in 1997 (Experiment 1a), and shipped the females to UW–Madison. We assayed 20 female progeny per monoterpene treatment per tree category per site ($N = 2880$) for entrance behavior.

We analyzed entrance behavior using tree condition (live healthy, felled), geographic region (AK, YK), population phase (endemic, eruptive), and alpha-pinene

concentration (0.0, 1.5, 5.5, and 30.0 mg/g) as sources of variation (ANOVA; SAS Institute 1996). Prior to analysis, all assumptions of homogeneity were satisfied based on Levene's test. When significant ($P < 0.05$) treatment effects occurred, mean separations and contrasts were performed using Fisher's Protected LSD (SAS Institute 1996).

Experiment 2: How do conifer phytochemicals affect host acceptance, and do beetles from eruptive and endemic populations respond differently?

Experiment 2a: No-choice gallery construction assay.—We conducted preliminary gallery construction assays with 600 beetles collected during May 1997 from Alaskan endemic and eruptive sites. We tested 20 beetles each at: 0.0, 0.5, 1.5, 5.5, and 30.0 mg/g of racemic alpha-pinene, beta-pinene, and limonene (Aldrich, Milwaukee, Wisconsin), per population category. These compounds together comprise 98.2% of the monoterpene fraction in white spruce phloem (Werner and Illman 1994), and elicit equivalent behavioral responses (Wallin 2001).

Because there was very little variation in beetle behavior according to which monoterpene was tested (see *Results*), we limited subsequent, more extensive, and inter-regional tests to alpha-pinene, the predominant monoterpene (96.8%) in spruce phloem. In the full experiments performed in 1998, we conducted gallery construction assays with beetles from all eruptive and endemic sites in AK, YK, and UT to determine if there were differences due to region, sites within each region, and population phase. For each of the 29 sites, we evaluated 20 beetles at each concentration (0.0, 1.5, 5.5, and 30.0 mg/g), totaling 2320 females.

Statistical analyses were performed using ProcGLM ANOVA (SAS Institute 1996). Nonhomogeneous data were log transformed. In the preliminary assay, we tested for effects of monoterpene type, monoterpene concentration, and population phase. After determining that monoterpene type had no, or marginal, effects on beetle behavior (Wallin 2001), we tested for differences in gallery lengths, at varying concentrations of alpha-pinene, constructed by beetles between sites within population phase. Because there were no differences among sites within population phases at each region during 1997 (Wallin 2001), we combined sites within each population phase within each region thereafter. We analyzed gallery length in no-choice assays using three-way ANOVA, in which geographic region, population phase, and concentration of alpha-pinene were potential sources of variation.

Experiment 2b: Population, site, and phytochemical factors affecting entrance behavior.—We tested for potential sources of variation in entrance and subsequent gallery construction behaviors with respect to population phase and geographic region. As in the no-choice assay, we conducted a preliminary assay in 1997 with AK beetles (0.0, 0.5, 1.5, 5.5, and 30.0 mg/g alpha-

pinene; two population phases; $N = 60$) and then a full test in 1998 with beetles from all AK, YK, and UT sites (0.0, 1.5, 5.5, and 30.0 mg/g; $N = 20$). Totals were 600 females in 1997 and 2320 in 1998.

Percentage entrance behavior was analyzed using one-way ANOVA. As in the gallery construction assay, there were no site differences within population phase (Wallin 2001), so sites within each population phase within each geographic region were combined thereafter. Spatial replication was geographic region, and within each geographic region the two treatments were eruptive and endemic population phase. Therefore, final analyses of entrance behavior and total gallery length were conducted using three-way ANOVA, in which geographic region, population phase, and alpha-pinene concentration were potential sources of variation.

Experiment 3: Are differences between endemic and eruptive populations heritable?

Experiment 3a: Performance in laboratory assays of adult progeny of beetles collected from eruptive vs. endemic populations, after rearing in a common environment.—To test whether differences between eruptive and endemic beetles might solely reflect environmental differences in their forest or host tree habitat, we tested the progeny of field-collected beetles following rearing in a common environment. We collected virgin overwintering females and males (F_1) from brood trees in the five eruptive and five endemic populations in Alaska in 1997, and sent them to UW–Madison. Groups of males and females from each site were established on 0.3×0.15 m spruce logs in metal containers (50 cm diameter $\times$ 40 cm tall), vented with 0.3×0.3 m metal screens (1×1 mm). There were five logs per site, and progeny from a site were pooled. Following emergence of the progeny approximately one year later (F_2), we conducted gallery construction assays with 100 females from each population phase for each alpha-pinene concentration and control (0.0, 1.5, 5.5, and 30.0 mg/g; total = 800). These treatments were selected to simulate the range of host conditions previously described. Gallery lengths were analyzed using two-way ANOVA (SAS Institute 1996), where the population phase from which adults were collected and alpha-pinene concentration were potential sources of variation.

Experiment 3b: Daughter–mother heritability indices.—Progeny females emerging from the colonies (F_2) were assayed and then used to establish independent breeding lines. Gallery length in host-based media is approximately normally distributed within a population (Shapiro-Wilks goodness of fit of normality $w = 0.93$, probability $w < 0.08$; JMP, SAS Institute 2001), so we assumed this to be a threshold character inherited in a typical polygenic manner (Falconer and Mackay 1996). Therefore, 10 females from each population phase that constructed the longest galleries at each concentration

were paired singly with virgin males obtained from the general laboratory colony. The 80 pairs were established singly on logs using the previously described methods. We assayed five daughters (F_3) from each of 80 parental pairs under the same conditions and treatments as their mothers. We determined the overall relationship of daughter–mother gallery lengths using heritability indices and regression analysis (Falconer and Mackay 1996). The covariance was computed between the values of the maternal and daughter gallery lengths.

Experiment 4: What environmental factors affect host acceptance, and do they vary with population phase?

Experiment 4a: Association of total lipid content with host acceptance behavior.—Because lipid concentrations have been associated with such density-dependent features as body size and flight of bark beetles (Sahota and Peet 1988, Kinn et al. 1994), we tested whether total lipid content varies between eruptive and endemic populations, and also whether host acceptance behavior varies with lipid content. We collected several hundred overwintering females from the populations in AK, YK, and UT and transported them on dry ice to UW–Madison.

We analyzed total lipid content using the sulfophosphovanillin spectrophotometric method of Kinn et al. (1994). We weighed beetles before and after oven drying at 50–55°C for 24 h, and individually extracted beetles in vials containing H_2SO_4 in a boiling-water bath for 10 min. The mixture was cooled for 10 min, vortexed, filtered, and amended with color agent (vanillin, from Sigma-Aldrich, St. Louis, Missouri, USA). Following a 30-min dark incubation period, 5 mL of solution was analyzed photometrically (530 nm) using a Beckman DU 640 spectrophotometer (Beckman Instruments, Fullerton, California, USA. Quantitative data interpretations were calculated relative to a linear regression equation derived from serial dilutions of purified known amounts of dry cholesterol (Wallin and Raffa 2000). Each standard curve had an $r^2 \geq 0.96$.

In total, 360 beetles were tested, representing 60 beetles of each population phase from each region. Potential relationships of lipid content to geographic region and population phase were analyzed on a per insect basis using two-way ANOVA. Data were log transformed.

Experiment 4b: Association between lipids and entrance behavior.—We conducted an entrance assay as previously described, and compared lipid contents and behavior of 60 beetles each that entered vs. rejected the media. The test media were amended with 5.5 mg alpha-pinene/g because prior experiments indicated that this concentration deterred 50% of the beetles (see *Results*). Control media were treated with pentane solvent only. Beetles that entered the media were immediately removed from the assay arena, and beetles that did not enter within 15 min were scored as rejecting
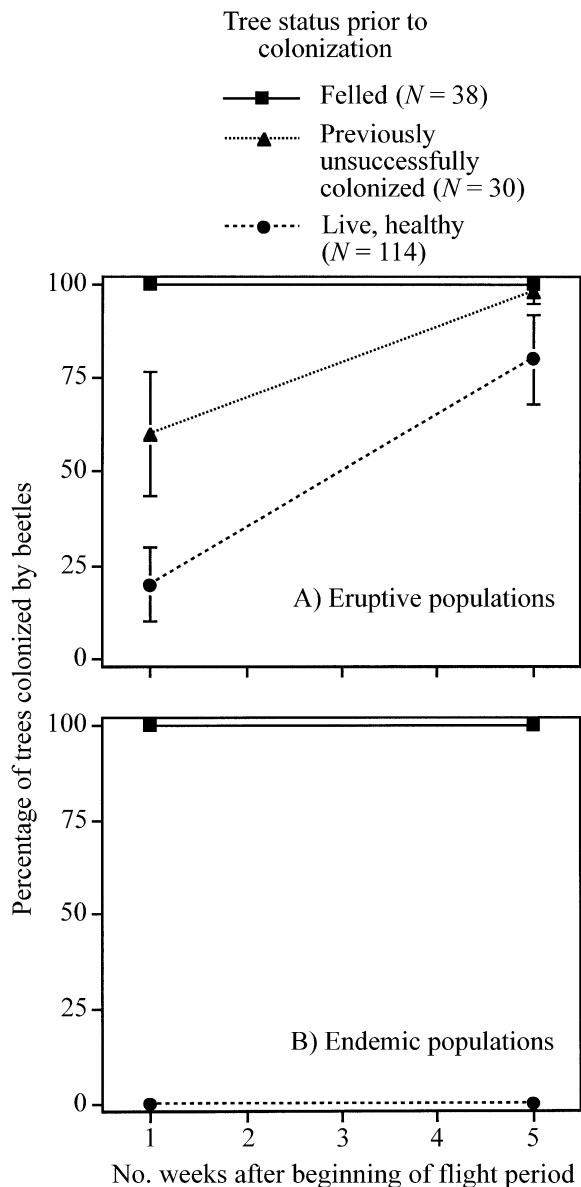
FIG. 1. Experiment 1a: Percentage of felled, previously unsuccessfully colonized, and live healthy trees colonized by spruce beetles during their flight period in (A) eruptive and (B) endemic population phases. There were no previously unsuccessfully colonized trees in endemic stands.

that treatment. Potential relationships between lipid content and entrance behavior were analyzed using one-way ANOVA (SAS Institute 1996).

Experiment 4c: Interaction of beetle density on the substrate surface with population phase.—We varied the number of beetles in the entrance assay arenas to determine if the presence of other beetles alters individual responses to alpha-pinene. Because there was no significant variation due to either geographic region or site within region (see *Results*), we collected beetles from all 10 of the Alaskan sites in 1999 and pooled

sites within eruptive and endemic populations. The number of female beetles placed on the surface of the transparency film was 1, 3, or 5 per assay unit. We used four alpha-pinene concentrations, 0.0, 1.5, 5.5, and 30.0 mg/g. There were 20 assay units per treatment, totaling 480 assay arenas and 1440 beetles. We scored each beetle separately as entering or rejecting the medium within 15 min. Arenas were randomly arranged in environmental chambers as previously described.

Because multiple beetles within an assay arena cannot be considered independent, we treated the arena as the experimental unit. We used the proportion of beetles entering each arena, their average times until entry, and their average gallery lengths for analyses. Population phase, monoterpene concentration, and density within the arena were potential sources of variation among arenas. We compared the proportions of beetles entering the amended medium among population phase, concentration, and beetle densities using three-way ANOVA (SAS Institute 1996). Homogeneity of gallery lengths was tested using Levene's test. Average gallery lengths per assay arena were analyzed using three-way ANOVA (SAS Institute 1996) based on square-root transformation.

RESULTS

Experiment 1: Do natural populations colonize trees of different physiological conditions during endemic vs. eruptive phases?

Experiment 1a: Field colonization.—Regardless of population phase, site, or location, all of the felled trees were colonized by *Dendroctonus rufipennis* (Fig. 1). All were colonized within 10–15 days of the onset of flight. Beetles within endemic populations did not colonize any live, healthy trees, whereas beetles from eruptive populations colonized 78% of them (df = 1, $\chi^2 = 12.3$, $P < 0.05$). However, live, healthy trees were colonized after the supply of felled trees was exhausted (df = 2, $\chi^2 = 16.22$, $P < 0.005$). Only 20% of live, healthy trees were colonized early in the flight season. Beetles in eruptive, but not endemic, populations also colonized trees that had experienced previous unsuccessful colonization attempts. Slightly more than half of these trees were colonized during the early portion of the flight period, and nearly all by the end of the flight period (Fig. 1A). Tree diameter did not vary among population phases (eruptive, 27.2 ± 0.37 cm, mean ± 1 SE; endemic, 28.4 ± 0.46 cm; $F = 0.2$, $P = 0.65$) or among host categories within populations. There was no relationship between bole diameter and colonization attempts ($F = 0.34$, $P = 0.56$).

Experiment 1b: Behavior of beetles collected from hosts of varying conditions.—The entrance of beetles into amended media was related to the status of the host from which they were collected (Fig. 2). Adult progeny of beetles that colonized live trees were significantly more likely to enter media amended with

Status of tree
when colonized by
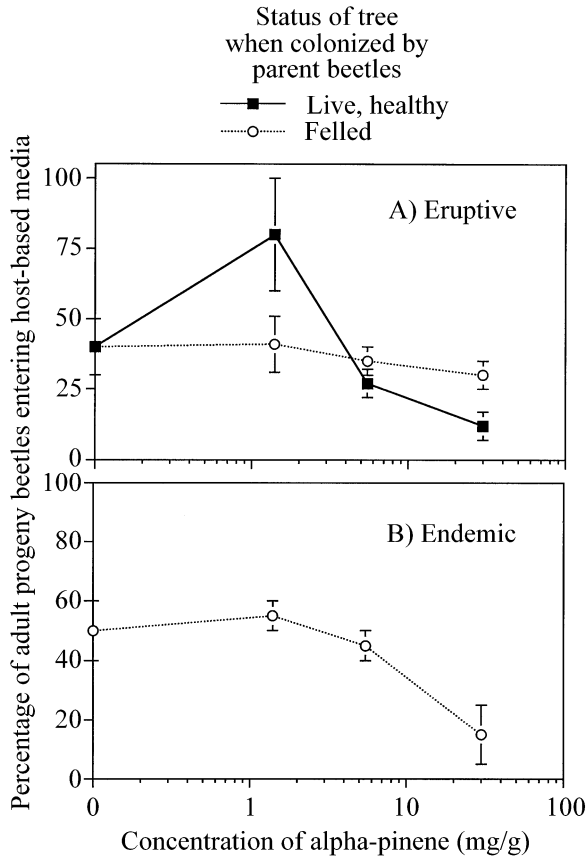parent beetles
—■— Live, healthy
····○···· Felled

FIG. 2. Experiment 1b: Responses to host phytochemistry by adult spruce beetles. Responses by adult progeny vary with the physiological condition of trees selected by, and population phase of, adult parental beetles. Percentage entry into host-based media amended with alpha-pinene (log scale x-axis) is shown for adult beetles emerging from (A) experimentally felled and live, healthy control trees in eruptive populations and (B) felled trees in endemic populations. $N = 20$, totaling 2880 beetles: (two geographic locations × five eruptive sites × two tree categories × four concentrations × 20 replications) + (two geographic locations × ((five endemic sites) − 1) × two trees categories × four concentrations × 20 replications).

alpha-pinene near the concentration present in live, healthy trees (i.e., 1.5 mg/g) than were progeny of beetles that colonized felled trees in the same site (df = 1, 913, $F = 23.4$, $P = 0.002$) (Fig. 2). However, beetles collected from felled trees in endemic sites were ~30% more likely to enter host-based media than were beetles collected from felled trees in eruptive sites. Entry into non-amended media was similar regardless of population phase (df = 1, 913, $F = 0.98$, $P = 0.09$) or host status (df = 1, 913, $F = 1.89$, $P = 0.79$). This was also true of entry into media amended with the highest concentration of alpha-pinene, in which both groups had very low entry rates (df = 1, 913, $F = 1.34$, $P = 0.8$).

Experiment 2: How do conifer phytochemicals affect host acceptance, and do beetles from eruptive and endemic populations respond differently?

Experiment 2a: No-choice gallery construction assay.—In the preliminary (1997) assay, monoterpene concentration significantly influenced gallery construction (df = 4, 571, $F = 1.74$, $P < 0.0001$). For example, gallery lengths in media amended with 30 mg/g were only 5% as long as those constructed in control media. Contrary to our prediction that beetles from eruptive populations would be less deterred by high allelochemical concentrations, beetles from endemic populations constructed longer galleries (df = 1, 458, $F = 4.51$, $P < 0.03$). Likewise, there was a strong population phase × concentration interaction (df = 3, 458, $F = 15.7$, $P < 0.0001$). There were no significant interactions between monoterpene type and population phase (df = 2, 458, $F = 0.6$, $P > 0.23$) or monoterpene type, concentration, and population phase (df = 8, 458, $F = 1.73$, $P > 0.12$).

In the full assay using beetles from all three regions in 1998, concentration and population phase again influenced gallery construction behavior (Table 1). Beetles from endemic populations constructed galleries that averaged 45–50% longer (df = 1, 13, $F = 10.39$, $P = 0.001$) than those constructed by beetles from erup-

TABLE 1. Analyses of variation of entrance behavior and gallery length constructed by *Dendroctonus rufipennis* in no-choice and choice conditions.

Sources of variation	df	Gallery length†		Beetles entering‡		Gallery length‡	
		F	P	F	P	F	P
Geographic region (GR)	2	0.40	0.500	0.7	0.37	1.5	0.090
Population phase (PP)	1	6.35	0.020	4.9	0.02	14.0	0.001
Concentration (CONC)	3	7.85	0.001	3.5	0.05	12.5	0.001
GR × PP	2	2.25	0.140	0.6	0.34	1.8	0.120
GR × CONC	6	2.20	0.160	2.2	0.16	0.6	0.290
PP × CONC	3	23.00	0.001	2.3	0.21	5.8	0.059
GR × PP × CONC	6	2.50	0.100	2.5	0.10	2.6	0.580

Notes: There were 20 replicates per monoterpene concentration tested at each population phase and geographic location. Sites are pooled within population phase at each geographic region.
　† No-choice conditions.
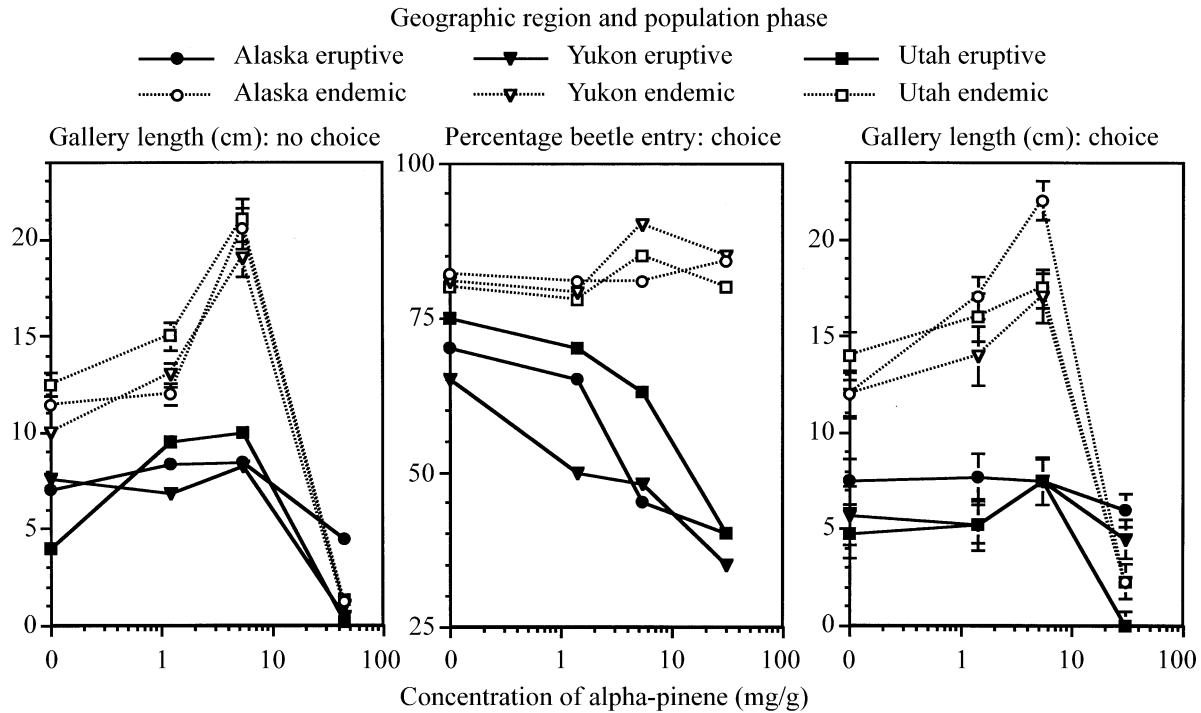　‡ Choice conditions.

FIG. 3. Experiment 2: Effect of population phase and geographic region on host selection by adult spruce beetles at varying concentrations of alpha-pinene (log scale). (Left) Experiment 2a: gallery construction under no-choice conditions. (Center) Experiment 2b: host entry under behavioral choice conditions. (Right) Experiment 2b: gallery construction under choice conditions. Error bars indicate ±1 SE of the mean and are present for all gallery lengths but may not be visible. For each population phase from each geographic region, $N = 20$ per concentration of alpha-pinene. There are five eruptive sites each in Alaska, Utah, and Yukon; there are five endemic sites each in Alaska and Utah, and four in Yukon.

tive populations (Fig. 3). There was no difference in gallery length due to geographic origin or to any interaction other than population phase × concentration (Table 1). There were no interactions among monoterpene concentration, population phase, and year (df = 3, 1369, $F = 1.2$, $P = 0.1$). In the Alaska populations tested in both 1997 and 1998, variation between population phases (df = 1, 78, $F = 303.4$, $P = 0.001$) was greater than variation within population phase across time (df = 1, 1369, $F = 6.35$, $P = 0.02$). The geographic region from which beetles were collected did not affect gallery construction (Table 1), and sites within population phase did not vary (df = 26, 1369, $F = 0.55$, $P = 0.15$). Therefore, we pooled sites within each population phase at each geographic region for subsequent analyses.

Experiment 2b: Population, site, and phytochemical factors affecting entrance behavior.—In the preliminary (1997) assay, concentration significantly influenced entrance (df = 4, 591, $F = 1.6$, $P < 0.001$). Likewise, beetles from endemic populations were more likely than eruptive beetles to enter media amended with alpha-pinene (df = 1, 591, $F = 2.4$, $P < 0.01$). There were no interactions between concentration and population phase (df = 4, 591, $F = 0.54$, $P > 0.25$).

In the full (1998) bioassay, beetle entry again was strongly influenced by alpha-pinene concentration (Ta-

ble 1). As with gallery construction, geographic region had no effect, and beetles from endemic populations were more likely to enter amended media. Host entry was 79% among endemic beetles vs. 62% among eruptive beetles at the concentration simulating live trees (Fig. 3). There were no interaction effects (Table 1).

After beetles entered the media under choice conditions, population phase continued to influence their gallery construction behavior (Table 1). Beetles from endemic populations constructed galleries 41% longer than beetles from eruptive populations, across all concentrations (Fig. 3B). This difference did not occur in control media or media amended with the highest concentration of alpha-pinene. There was no difference due to geographic origin or to any interaction other than population phase × concentration (Table 1).

Experiment 3: Are differences between endemic and eruptive populations heritable?

Experiment 3a: Performance in laboratory assays of adult progeny of beetles collected from eruptive vs. endemic populations, after rearing in a common environment.—The differences that we observed in amended diet assays between beetles collected from eruptive vs. endemic populations persisted when beetles were reared in a common environment (Fig. 4). Progeny of beetles collected from endemic populations
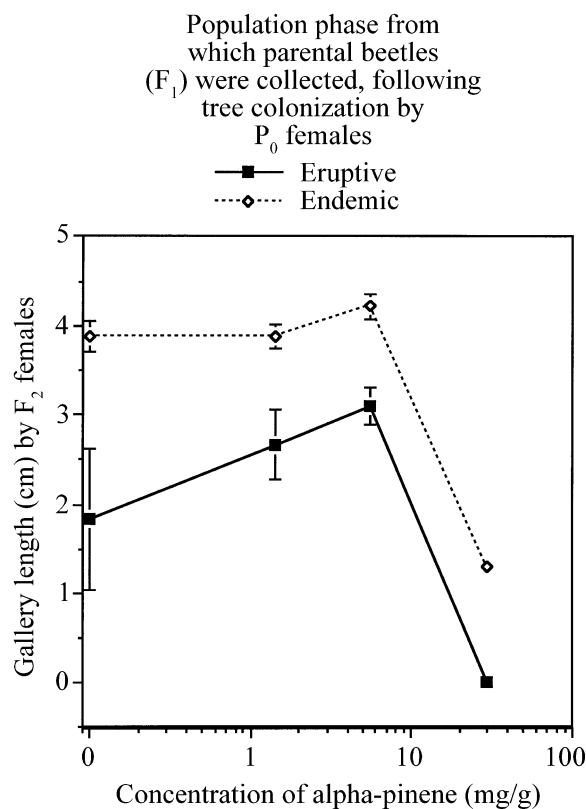
FIG. 4. Experiment 3a: Differences in host selection behavior associated with population phase persist following rearing in a common environment. After initial tree colonization by P_0 females under natural conditions, adult brood females (F_1) collected from eruptive and endemic sites were reared in logs. Adult brood females emerging from logs (F_2) were assayed for gallery construction behavior in media amended with alpha-pinene (log scale).
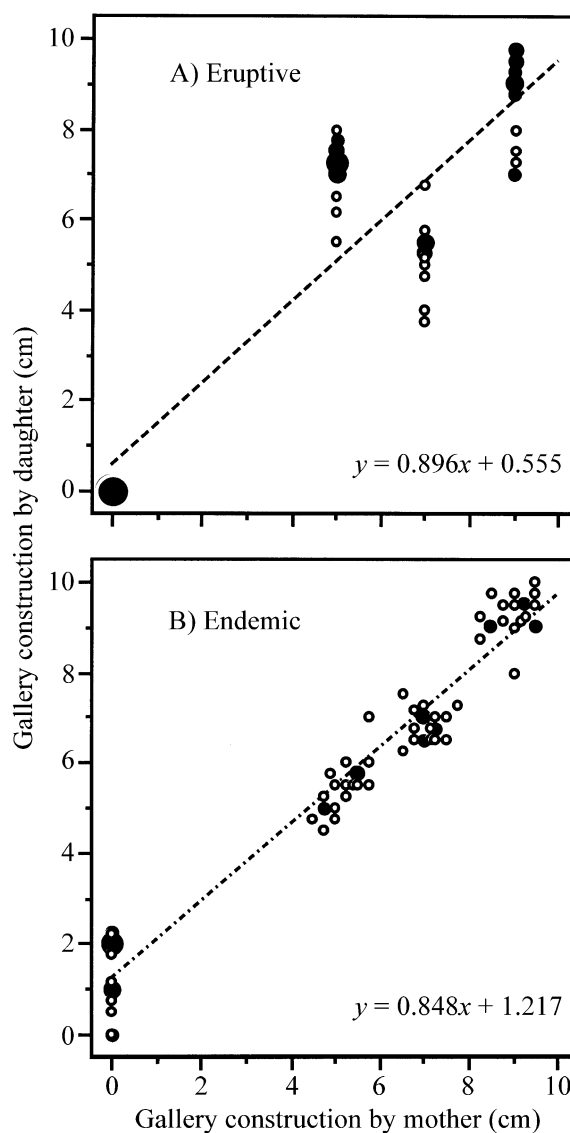

FIG. 5. Experiment 3b: Heritability of gallery construction behavior by spruce beetles. Independent breeding lines were established in logs using females and males (F_1) collected as preemergent brood adults in the field. Emergent virgin females (F_2) were assayed (mothers) and then established singly on logs with single virgin F_2 males. Gallery lengths constructed by their daughters (F_3) in the same assay are regressed against maternal gallery lengths: (A) grand-dams collected from the eruptive phase (only available within 1-cm categories); (B) grand-dams from the endemic population phase. Solid circles indicate multiple data points, with the number of points indicated by relative circle size.

constructed longer galleries than those from eruptive populations (df = 1, 1369, F = 12.4, P = 0.001). These beetles were the granddaughters of the females that originally selected hosts in the field. This indicates significant genetic variance for gallery construction behavior within the population.

Experiment 3b: Daughter–mother heritability indices.—Maternal beetles constructed galleries ranging from 0 to 9.5 cm in host-based media. Those that did not construct galleries in this medium were probably expressing behavioral responses rather than an inability to tunnel, as almost all of them constructed galleries in dead logs when they were provided, and produced daughters for subsequent testing. There was a significant positive correlation between gallery lengths constructed by mothers and daughters in phloem-based media. Heritability (h^2) was 0.35 for beetles collected from eruptive population phases (Fig. 5A) and 0.64 for beetles collected from endemic populations (Fig. 5B). Among mothers that would not construct galleries in this medium, 55% of their daughters showed similar

behavior. Conversely, no daughters of tunneling mothers failed to construct galleries.

Experiment 4: What environmental factors affect host acceptance, and do they vary with population phase?

Experiment 4a: Association of total lipid content with host acceptance behavior.—Beetles from endemic
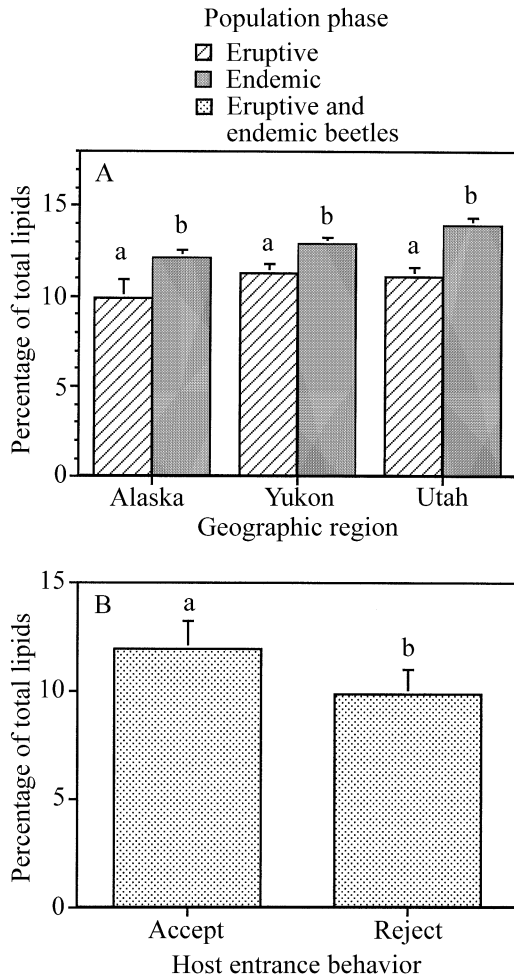
FIG. 6. (A) Experiment 4a: Effect of population phase and geographic region on the total lipid content of univoltine adult spruce beetles; $N = 60$ beetles per population phase per geographic region. (B) Experiment 4b: Relationship between total lipid content of beetles and entrance behavior. The total lipid content of beetles that entered ($N = 60$) or did not enter ($N = 60$) host-based media amended with 5.5 mg alpha-pinene/g is given. Error bars indicate one standard error of the mean. Bars with the same letter are not significantly different at $P < 0.05$.

populations had 34% higher total lipid content than beetles from eruptive populations (df = 1, 348, F = 9.56, P = 0.006) (Fig. 6A). There were no significant effects due to geographic region (df = 2, 348, F = 0.193, P = 0.6622) or to the interaction of geographic region and population phase (df = 2, 348, F = 0.398, P = 0.5298).

Experiment 4b: Association between lipids and entrance behavior.—Regardless of the population phase from which a beetle was collected, its likelihood of entering media amended with alpha-pinene was related to its total lipid content (Fig. 6B). Beetles that entered amended media within 15 min had 22% more total lipids than those that rejected the media (n = 60, df = 1, F = 5.3, P = 0.05).

Experiment 4c: Interaction of beetle density on the substrate surface with population phase.—The density of beetles within the assay arena affected their entrance and gallery construction behaviors (Table 2). However, the effects of within-arena density differed between spruce beetles from eruptive vs. endemic populations, as indicated by significant within-arena density × population phase interactions in both the proportions entering and their average gallery lengths. This effect is illustrated for entry in Fig. 7, which normalizes for innate differences in solitary beetle behavior associated with population phase. The ratio of communally tested to singly tested eruptive beetles entering the medium varied with alpha-pinene concentration (Fig. 7A). Entry by eruptive beetles into media amended with high concentrations was much higher when three beetles were present than when only one beetle was present. This effect increased further when five beetles were present in the arena. At the highest concentration (30 mg/g), entry was nearly four times as high when five eruptive beetles, rather than one, were in the arena. In contrast, the presence of additional beetles had little or no influence on host entry among endemic beetles (Fig. 7B). The ratio of communally tested to singly tested endemic beetles entering the medium was always near 1.

Gallery lengths were influenced by the density of beetles in the arena, but again there was a significant

TABLE 2. Sources of variation in host entrance behavior and subsequent gallery construction at varying densities of *D. rufipennis* on the surface of the assay arena.

Sources of variation	df	Proportion of beetles entering		Mean gallery length	
		F	P	F	P
Density (DEN)	2	8.34	0.003	8.89	0.002
Concentration (CONC)	3	5.8	0.01	5.7	0.01
Population phase (PP)	1	4.51	0.02	5.5	0.01
DEN × CONC	6	6	0.05	6.25	0.05
DEN × PP	2	5.29	0.04	5.69	0.03
CONC × PP	3	6.31	0.01	5.67	0.008
DEN × CONC × PP	6	1.06	0.09	1.02	0.12

Notes: N = 20 assay arenas per concentration of alpha-pinene for each beetle density within each population phase. Analyses were computed on the proportion of beetles within an arena that entered simulated host medium, and their mean gallery lengths, on a per-arena basis.
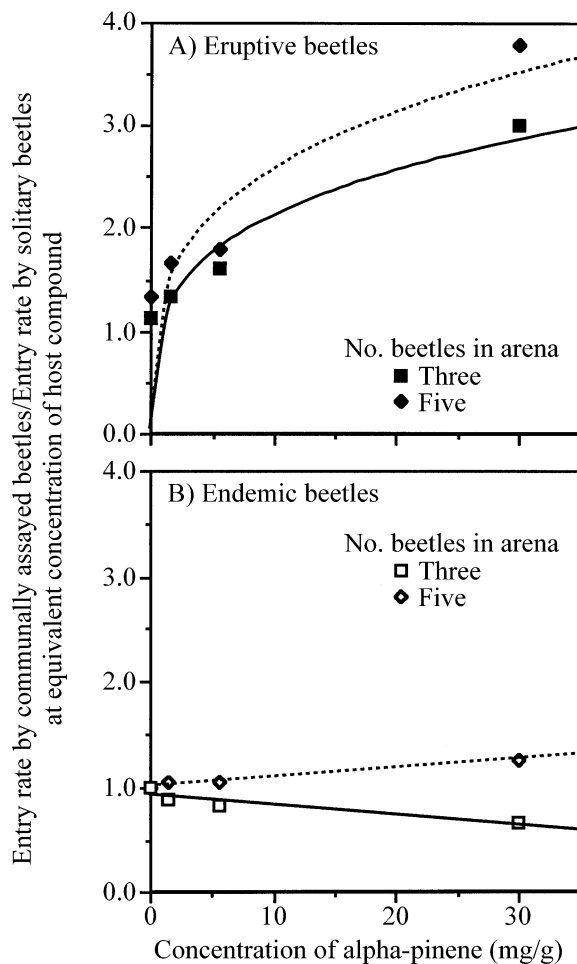
FIG. 7.   Experiment 4c: Effect of population phase on the interaction between the number of spruce beetles on substrate surface and concentration of alpha-pinene in the substrate. Data are normalized for comparative purposes, so that the value of entry by three or five beetles is relative to that of one beetle. For each concentration of alpha-pinene, the ratio of communally assayed beetles that entered to singly assayed beetles that entered is shown: (A) beetles from eruptive populations; (B) beetles from endemic populations. The curve was fit using Cricket Graph III (Computer Associates International, Malvern, Pennsylvania, USA).

local density × population phase interaction (Table 2). Among eruptive beetles, gallery length per female increased for all four alpha-pinene treatments when the local density increased from one to three beetles (the ratio of gallery lengths by three communally assayed to single beetles ranged from 1.2 to 2.3; mean = 1.7). At the highest density (five beetles), however, gallery lengths were always lower than at three beetles, suggesting a competitive effect. In contrast, gallery lengths of endemic beetles remained relatively constant when densities in amended media rose from one to three (the ratio of gallery lengths by three communally assayed to single beetles ranged from 0.6 to 1.25, mean = 1.3). Overall, the sources of variation were the same for

entry and gallery construction (Table 2). Mean time prior to entry into host-based media averaged 9.25 ± 0.5 minutes, and was not affected by density among either endemic or eruptive beetles (df = 2, F = 0.88, P = 0.6).

DISCUSSION

Colonization patterns in the field substantiate that host acceptance behavior of eruptive bark beetles changes with their population phase. During endemic phases, beetles restrict their host range to nondefended trees, but during population eruptions, they accept healthy trees as putative hosts (Fig. 1). These results are consistent with observations by forest protection specialists that beetles are "more aggressive" during outbreaks (Keen 1938, Evenden et al. 1943, Safranyik et al. 1975). However, the preference for felled over standing trees under all conditions suggests that an expansion, rather than alteration, of host acceptance behavior occurs during population eruptions. An alternative interpretation is that the felled trees "captured" all beetles in the endemic plots, and hence none were available to enter healthy trees. This seems unlikely, as it would require us to fell the precise number of trees to obtain 100% colonization, yet deplete local populations in each of 9 endemic sites in two widely separated regions. The possibility that some environmental difference between endemic and eruptive sites generated these distinct colonization patterns also seems unlikely because there were no differences in host size, monoterpene concentrations, stand density, or stand composition. A third alternative is that the patterns in Fig. 1 do not represent differences in host selection, but rather differences in the proportion of colonization attempts that were successful. However, we observed no failed attacks in endemic stands, either when we initially established plots or after the flight season, despite extensive efforts to locate such trees. Moreover, a behavior by which many individuals in endemic populations die during failed colonization attempts seems counteradaptive and unlikely to be maintained (Alcock 1981).

Laboratory assays indicate that post-landing decisions are important components of the spruce beetle's overall host selection process, and that monoterpene concentrations are important signals mediating entrance and gallery construction behaviors. Different responses to host chemicals by females whose mothers selected live vs. dead trees, particularly the greater likelihood of progeny from live trees entering media with concentrations simulating a healthy spruce (Fig. 2A), suggest that host acceptance has a genetic and/or maternal component. The role of a genetic component is supported by the maintenance of behavioral differences after rearing in a common environment (Fig. 4), daughter–mother correlations in assays following full-sib mating (Fig. 5), and directional selection experiments with full-sib breeding lines in *Ips pini* (Wallin et al.

2002). Thus, increased tree mortality at high population densities appears to reflect qualitative changes in individual beetle behavior in addition to increased beetle numbers.

Overall, population phase was a stronger predictor of response to host allelochemicals than the geographic region, or sites within a region, from which beetles originated. It is unlikely that this resulted from some environmental difference between endemic and eruptive stands, because of the replication within and across broad geographic regions, the similarities among test trees, and the strong genetic component to this behavior. In contrast to *Dendroctonus rufipennis*, the non-eruptive bark beetle *Ips tridens* Mannerheim showed no variation in host entry and gallery construction behaviors among populations collected from these same Alaskan sites (Wallin 2001). This suggests that site-specific factors are less important than inherent interspecific differences in how individuals respond to increased population densities.

Intraspecific competition associated with high brood densities reduces lipid contents of adult progeny (Atkins 1966, Sahota et al. 1987), which probably explains the lower mean values of eruptive beetles (Fig. 6A). Beetles with low lipid content are less likely to enter, and construct smaller galleries in, both non-amended and amended media (Fig. 6B). This suggests that without behavioral shifts, beetles would fail to fully exploit their resource during eruptions.

The expanded range of host physiological conditions accepted by spruce beetles from eruptive populations is largely due to altered interactions among conspecifics on the plant surface. Whereas responses of endemic beetles to host phytochemicals are largely independent, beetles from eruptive populations are less repelled when others are present (Fig. 7). The basis for this communication is unknown, but probably includes factors other than, or in addition to, aggregation pheromones (Wallin and Raffa 2002*b*).

Raffa (1988) proposed that increasing population densities impose progressively less selection on beetles to ''discriminate'' hosts based on defensive capacity. Two lines of evidence suggest the need to modify this model. First, beetles colonized felled and stressed trees before live, healthy trees in both eruptive and endemic phases. If beetles from eruptive populations were less discriminating, they would colonize all tree classes at equivalent times and rates. Second, heritability of host entry behavior was high, as predicted by Raffa (1988), but contrary to his prediction, solitary beetles from eruptive populations were not less deterred by allelochemical concentrations characteristic of healthy trees. Rather, discrimination by beetles from eruptive populations is more easily modified by the presence of other beetles on the plant surface. Several factors may underlie these population-dependent responses. First, beetles from different population phases may experience different selective pressures. Individuals in an en-

demic population risk being killed by host defenses, whereas those in eruptive populations risk being outcompeted by conspecifics. Thus the ''cooperative'' outcome at the whole-tree level may reflect scramble competition at a more local scale. Second, flight duration is related to lipid stores (Kinn et al. 1994), so individuals that develop in crowded environments may have less capacity to search for an optimal host. This could concentrate individuals on nearby trees, and improve their likelihood of eliciting aggregation on trees that might otherwise inhibit communication (Raffa 2001).

A conceptual diagram showing multiple interactions of environmental and genetic factors on host selection behavior and population dynamics is shown in Fig. 8. Each of these relationships has been validated in our system. Host habitat structure, weather, predation, and competition set initial population densities. As with many herbivores, increasing population density decreases the remaining pool of suitable hosts (Jaenike and Holt 1991, Hunter et al. 1997), which generates negative feedback and reduces density (a-b-a). Likewise, high populations generate high within-tree brood densities, which reduce lipid content and lower fecundity, causing populations to decline (a-c-d-e-a). High brood density conditions yield beetles that are less responsive to host cues, which could further lead to population decline (a-c-d-g-a). However, three sources of positive feedback oppose these processes. First, as populations increase, beetle density on the plant surface increases, which broadens the range of hosts that beetles enter (a-f-g-a). Second, these responses to conspecifics become more pronounced at high population densities (a-h-g-a). Third, responses of individual beetles do not remain static when stressed trees are unavailable, because the repeated rejection of unsuitable hosts induces a broader range of acceptable phytochemical concentrations (Wallin and Raffa 2002*a*). Under most conditions, the negative feedback processes in Fig. 8 predominate, keeping populations stable about an equilibrium (Berryman 1982). However, an increase in population size due to sudden availability of stressed trees or altered climate could change the relative strengths of negative and positive processes, and thereby generate nonequilibrium behavior. Additional factors, such as the generally higher nutritional quality of vigorous than stressed trees (Amman 1972, 1984, Haack et al. 1987), reduced interspecific competition in healthy trees (Sahota et al. 1987, Reeve et al. 1998), and inability of predators to track rapidly growing populations (Turchin et al. 1991), could contribute to this transition.

Our understanding of host feeding breadth has evolved considerably over recent decades. Early models emphasized the number of plant species that a particular herbivore species consumes. Subsequent models emphasized phytochemical classes that an herbivore might encounter, rather than species designations per se (Freeland and Janzen 1974, Ehrlich and Murphy
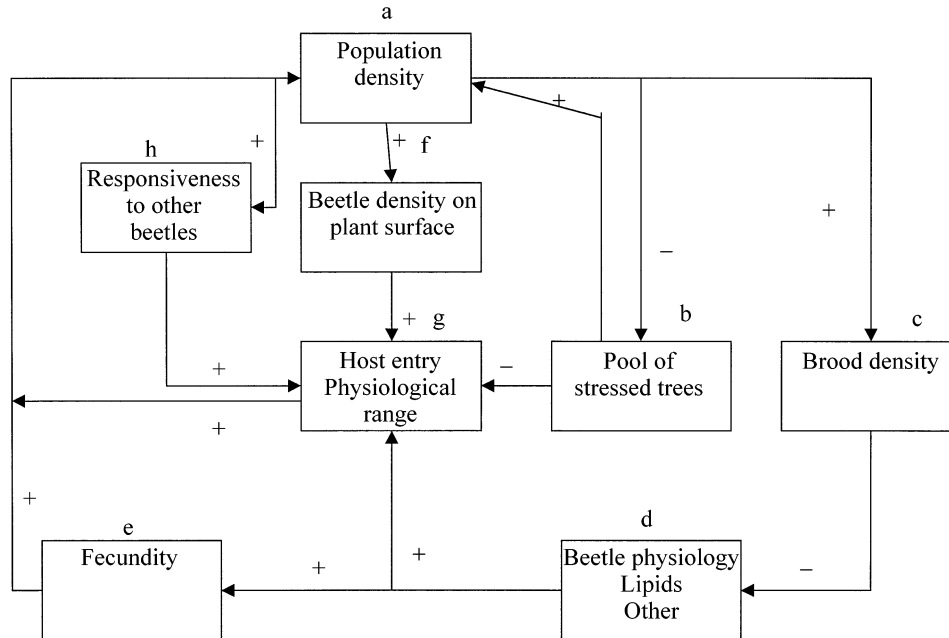
Fig. 8. Proposed feedback between population density and multiple effects of environmental and genetic factors affecting host selection behavior. ''Plus'' symbols (+) indicate a direct relationship; that is, an increase in one parameter within a box causes an increase in the second parameter within the next box. ''Minus'' symbols (−) indicate that an increase in one parameter causes a decrease in the second parameter, i.e., an inverse relationship. When evaluating interactions across multiple parameters, either a series of (+) or an even number of (−) relationships generates a positive feedback loop, whereas odd numbers of (−) relationships alone or coupled with (+) relationships generate a negative feedback. Interaction sequences (lowercase letters) are described in the *Discussion*.

1988). More recent models have refined this perspective by incorporating variation within herbivore (Rossiter 1996, Bernays and Minkenberg 1997) and plant (Carriere and Roitberg 1994) populations and phenotypic plasticity (Jaenike 1988, Bernays 1999, Agrawal 2001). Our results suggest that population phase is an additional component affecting host feeding breadth, and that intraspecific interactions can play an important role in individual host selection decisions. Moreover, expanding host breadth can exert positive feedback on population processes, which can lead to further exploitation of the host population.

We currently have limited understanding of how density- and frequency-dependent genotypes are maintained during unfavorable conditions (Carius et al. 2001, Lemire and Lessard 2001). Our results suggest that interactions between genetically based host selection behaviors (Fig. 5) and environmental inducers, such as cues associated with herbivore density on the plant surface (Fig. 7), may allow maintenance of eruptive genotypes during lengthy endemic periods. In this system, partial reproductive isolation may occur at the level of whole trees, based on resistance capacity (Fig. 2), and also at the level of sites simultaneously experiencing different phases (Figs. 1 and 3). Isolation could be facilitated by pheromone-based assortative mating, which has been demonstrated in *I. pini* (Teale et al. 1994). The ability of eruptive beetles to colonize

dead trees is likely to prevent their extinction during endemic phases. Similarly, the availability of a few stressed trees, plus the opportunity to arrive at trees being colonized by eruptive beetles (but at a reproductive cost; Raffa 2001) is likely to prevent extinction of endemic beetles during eruptions. In the case of these and perhaps other herbivores, interactions between heritable behaviors and environmental inducers may partially explain observed expansions onto less preferred species at high population densities (Bigger and Fox 1997). Such density-induced expansion could contribute to speciation (Kelley and Farrell 1998), although we lack data to support this hypothesis.

Most native herbivores do not show eruptive behavior. Rather, they remain about apparent equilibrium densities, the absolute values of which vary dramatically with environmental conditions, but departure from which exerts negative feedback (Barbosa and Schultz 1987). Several authors have proposed multi-equilibria models, including Allee effects, to describe how eruptive species may show distinct relationships between replacement rate vs. density along different zones of a population gradient (Southwood and Comins 1976, Berryman 1978, Larsson et al. 2000). Although factors favoring temporary release to high populations have been identified for many species, underlying mechanisms behind continual positive feedback are not well understood. Our results suggest that feedback be-

tween host feeding breadth and population phase can be an important factor affecting the net impact of positive vs. negative processes. For example, the initial release of spruce beetle populations probably was favored by warm temperatures that increased the proportion of beetles developing in one, rather than two, years (Werner and Holsten 1985, USDA Forest Service 1998). However, even after temperatures returned to near normal, the eruptive phase persisted and there was no apparent relationship between beetle replacement rates and temperature (USDA Forest Service 1998, NOAA 2003; E. Holsten, *personal communication*). In this system; the major effect of population phase on host breadth appears to be mediated through counteraction of host resistance, but in others it might affect the relative importance of lateral processes such as inter- and intraspecific competition (Wellington 1957, Denno et al. 1990, 2000) and top-down effects such as group defense (Costa and Ross 1994) and enemy-free space (Rossiter 1987, Stamp and Bowers 1988, Bernays 1999).

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