Mountain pine beetle population sampling: inferences from Lindgren pheromone traps and tree emergence cages[1]

Barbara J. Bentz

Abstract: Lindgren pheromone traps baited with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae)) lure were deployed for three consecutive years in lodgepole pine stands in central Idaho. Mountain pine beetle emergence was also monitored each year using cages on infested trees. Distributions of beetles caught in pheromone traps and emergence cages were compared. Each year, mountain pine beetle emergence from infested trees occurred within a 30-d period, although beetles were caught in pheromone traps over a period as long as 130 d. A large proportion of the total number of beetles caught in pheromone traps occurred prior to and following peak emergence from infested trees. Beetles caught in pheromone traps during the main emergence period from infested trees had greater whole-body lipids compared to beetles caught early and late in the flight season. Low lipid content of beetles caught before and after the main emergence period could be the result of a long-distance flight caused by fewer sources of pheromone attraction on the landscape and (or) some proportion of reemerged parents in the sample. Results suggest that pheromone traps disproportionately sample mountain pine beetle populations and that natural pheromone sources may influence the number and timing of beetles caught in synthetically baited traps.

Résumé : Des pièges sexuels Lindgren appâtés avec un leurre du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins (Coleoptera : Curculionidae, Scolytinae)) ont été déployés pendant trois années consécutives dans des peuplements de pin lodgepole dans le centre de l'Idaho. L'émergence du dendroctone du pin ponderosa a également été suivie chaque année à l'aide de cages placées sur des arbres infestés. Les distributions des dendroctones capturés dans les pièges sexuels et dans les cages à émergence ont été comparées. Chaque année, les dendroctones du pin ponderosa ont émergé des arbres infestés à l'intérieur d'une période de 30 j bien que des dendroctones aient été capturés dans les pièges sexuels pendant des périodes allant jusqu'à 130 j. Une forte proportion du nombre total de dendroctones capturés dans les pièges sexuels l'ont été avant et après le pic d'émergence sur les arbres infestés. Les dendroctones capturés dans les pièges sexuels durant la principale période d'émergence sur les arbres infestés étaient globalement plus riches en lipides que les dendroctones capturés au début ou à la fin de la période de vol. Le faible contenu en lipides des dendroctones capturés avant ou après la principale période d'émergence pourrait être le résultat d'une longue distance de vol due à moins de sources d'attraction par les phéromones dans le paysage ou à une certaine proportion de parents qui auraient émergé à nouveau dans l'échantillon. Les résultats indiquent que les pièges sexuels échantillonnent les populations de dendroctone du pin ponderosa de façon disproportionnée et que les sources naturelles de phéromone pourraient influencer le nombre de dendroctones et le moment où ils sont capturés dans les pièges appâtés avec des hormones synthétiques.

[Traduit par la Rédaction]

Introduction

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), is considered the most destructive forest insect in western North America (Furniss and Carolin 1977). Success of mountain pine beetle populations is dependent, in part, on a complex pheromone-mediated tree attack process initiated by newly emerged adults (Borden 1982). To successfully produce brood, a large number of adults must attack at a rate sufficient to overcome host-tree resinous defenses, thereby killing all or part of the host tree (Raffa and Berryman 1983). This is accomplished through a series of synergistic reactions that occur when beetles consume host-tree compounds, resulting in the production of pheromones that direct conspecifics to mass attack a single host tree (Renwick and Vite 1970; Borden 1974; Raffa 2001). The identification and synthesis of compounds that are involved in the mountain pine beetle tree attack process has allowed both research and management to exploit this aspect of bark beetle ecology (Borden 1989). Development of novel traps that can be used in conjunction with bark beetle semiochemicals (Lindgren 1983) provided the capability to monitor directed mountain pine beetle flight.

Currently, pheromone-baited Lindgren funnel traps (Lindgren 1983) (hereafter referred to as pheromone traps) are routinely used by both managers and researchers for a variety of tasks including detection of the presence of a particular species, monitoring adult flight periodicity (Hansen

Received 24 February 2005. Accepted 15 August 2005. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 8 February 2006.

B.J. Bentz. USDA Forest Service, Rocky Mountain Research Station, 860 North 1200 East, Logan, UT 84321, USA (e-mail: bbentz@fs.fed.us).

[1]This article is one of a selection of papers published in the Special Issue on The Ecology of Forest Insect Invasions and Advances in Their Management.

 doi:10.1139/X05-241

1996; Peck et al. 1997; Fettig et al. 2004), and suppression or trap-out of local populations (Ross and Daterman 1997; Bentz and Munson 2000; Laidlaw et al. 2003). Pheromone traps may also be used in conjunction with suppression strategies to time semiochemical deployment with emergence of adults from infested material. While many have attempted to more fully understand bark beetle dispersal in mark–recapture studies using marked beetles and pheromone traps (Salom and McLean 1990; Jactel 1991), the main investigations into understanding how pheromone traps sample bark beetle populations have been aimed at estimating the sampling range of traps (Turchin and Odendaal 1996; Barclay et al. 1998; Franklin and Gregoire 2001; Dodds and Ross 2002). Despite the continued use of pheromone traps, surprisingly little research has focused on the timing of pheromone trap catch as it relates to the timing of bark beetle population emergence on a landscape. Safranyik and Linton (1993) found a moderate correlation between mountain pine beetles caught in passive barrier traps and emergence from infested bolts, although pheromone traps were not included in the study.

Reported here are results from a study that was initially designed to examine variability in timing of mountain pine beetle emergence across a landscape using emergence cages on infested trees and pheromone traps. Unusual patterns in the timing of beetle catch in pheromone traps the first year of the study led to subsequent years of data collection to evaluate the relationship between the timing of mountain pine beetles caught in a pheromone trap and the timing of population emergence from infested trees. Lipid content of beetles was also evaluated as an indicator of the status of adults (e.g., new brood adult or reemerged parent) caught in pheromone traps early and late in the flight season.

Methods

The study was conducted for three consecutive years in the Sawtooth National Recreation Area (SNRA) in central Idaho. The main study area was in the Stanley Basin of the SNRA (~2011 m elevation), a valley that is approximately 32 km × 16 km, with mountain ranges surrounding the eastern, western, and southern edges. Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is the major conifer species in the valley bottom, with increasing numbers of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) as elevation increases on the valley sides. Whitebark pine (*Pinus albicaulis* Engelm.) stands predominate on the surrounding mountain ridges. A mountain pine beetle outbreak began in the SNRA in 2000, resulting in widespread tree mortality. Trees attacked by the mountain pine beetle during the 3 years of the study averaged 178, 155, and 183 trees/ha in 2001, 2002, and 2003, respectively, and lodgepole pine stands averaged 713 trees/ha over the same time period (based on twelve 0.40 ha plots surveyed throughout the study area each year; see Bentz et al. 2005). Air temperature was recorded hourly (Campbell Scientific, Inc., Logan, Utah) at several sites throughout the study area each year.

2001

In May 2001, 10 sites, separated by at least 3.2 km, were located throughout the valley in areas of predominately lodgepole pine. Each site contained at least 10 trees infested with mountain pine beetles. Emergence cages were placed on eight infested trees at each site. Emergence cages consisted of a flexible screen stapled over a 0.60 m × 0.30 m section of the tree bole, centered at 1.37 m height from the ground, one each on the north and south aspect of the bole. A tube attached to the bottom of the screen enclosure collected all adults that emerged from the tree bole within the sample space. A Lindgren funnel trap baited with the mountain pine beetle trap lure (*trans*-Verbenol, myrcen, *exo*-brevicomin, PheroTech, Inc., Delta, British Columbia) was installed on 1 May 2001 at three separate locations throughout the study area. Beetles from emergence cages and pheromone traps were collected daily throughout the flight season (May to September).

2002

Based on results from 2001, the experimental design was altered in 2002. Tree emergence cages, a pheromone trap, and passive traps were installed at each of 10 sites, using 3 of the same sites as in 2001. Sites were distributed across the area of the infestation with particular effort to ensure that sites where early emergence would be more likely (e.g., southern aspects and low elevation) were represented. At each site, two emergence cages per tree were installed (as described previously) on five trees infested with mountain pine beetle. A Lindgren funnel trap baited with a mountain pine beetle lure was installed 100 m from the caged trees in a randomly chosen direction. In a second randomly chosen direction, 100 m distant, four lines of passive traps were installed, with two traps per line. The four passive trap lines were laid out in a square configuration approximately 20 m apart. Each passive trap consisted of two clear Plexiglas panes (29.8 cm × 57 cm), with attached collection buckets, which were vertically suspended on a nylon line (Schmitz 1984). The two traps per line were suspended at heights approximating the middle of the surrounding tree crowns (~15 m) and the middle of the tree boles (~6 m). The passive traps contained no pheromones and were designed to randomly sample nondirected mountain pine beetle flight. Beetles from all traps and emergence cages at each site were collected every other day.

2003

Two sites were monitored in 2003, both of which were repeat sites from 2001 and 2002. At each site, emergence cages were installed on seven trees infested with mountain pine beetle as described previously. A pheromone-baited Lindgren funnel trap was installed in a random direction 100 m from the caged trees at each site, and beetles from all traps and emergence cages were checked weekly.

Trap and cage data analysis

Because of differences in collection intervals and sample sizes, analyses were conducted separately for each year. Emergence cage data from individual trees were summed by site for each collection date. Data from the eight passive traps at each site in 2002 were also summed by site and date. Differences among cumulative distributions of beetles caught in pheromone traps, emergence cages, and passive traps (2002 only) were tested with the nonparametric Kolmogorov–Smirnoff (KS) goodness-of-fit test statistic (Sokal and Rohlf 1969) using R statistical software (R Development Core Team 2005).

The KS procedure tests the equality of two underlying distributions, using the maximum observed difference (D) between the distributions. Quantile–quantile (Q–Q) plots were also developed using R software, to graphically analyze differences between the cumulative distributions (Chambers et al. 1983). A Q–Q plot is a plot of the quantiles of the first data set against the quantiles of the second data set. If the two data sets have distributions within the same family, the points should fall approximately along a 45° reference line. The greater the departure from this reference line, the greater the evidence for the conclusion that the two data sets have different underlying distributions.

Lipid analysis

Lipid analysis of individual beetles was conducted to test the hypothesis that beetles caught in pheromone traps prior to and following the period of emergence from infested trees were reemerged parents rather than new brood adults. In 2002 and 2003, adult mountain pine beetles collected weekly from phermone traps were transported on ice to Logan, Utah. In 2002, live adults were also collected from emergence cages. Adults used for lipid analysis were collected from four traps and 10 emergence cages (five trees) at four sites in 2002 and two traps at two sites in 2003. Adults collected from pheromone traps were sexed (Lyon 1958), and a random sample of up to 30 live males and 30 live females per phermone trap per week were stored at –20 °C. Adults collected from emergence cages in 2002 were also stored at –20 °C, although they were not sexed. Lipid analysis was conducted within 3 months of collection by methods described in Hagen and Atkins (1975). Individual beetles were oven dried for 24 h at 70 °C and weighed. Fats were extracted with petroleum ether for 8 h in a soxhlet apparatus, then beetles were redried for 8 h and reweighed. Lipid content was calculated as the percent dry body mass. Lipid content was estimated for 2299 adults collected in phermone traps and 766 adults from emergence cages in 2002 and 926 adults collected from phermone traps in 2003.

For statistical analysis, adults used in lipid analysis were grouped relative to the time period of emergence from infested trees as follows: emergence group 1: adults caught in pheromone traps prior to the time when emergence from infested trees was observed (<10 July); emergence group 2: adults caught in pheromone traps during the time of emergence from infested trees (10 July – 13 August); and emergence group 3: adults caught in pheromone traps after emergence from infested trees had ended (>13 August). Percent lipid content was transformed with arcsine square root to meet normality assumptions. Differences in transformed percent lipid content among emergence groups, years, and sex were analyzed using mixed-model analysis in SAS (Littell et al. 1996) with site included as a random effect. Differences among the emergence groups by sex were tested with Tukey's honestly significant difference multiple comparison procedure.

Differences in lipid content between adults collected in emergence cages and adults caught in pheromone traps in 2002 were also tested using mixed-model analysis. Only adults caught in pheromone traps during the period of emergence from cages were included in the analysis (e.g., 10 July – 13 August). Trap type (e.g., pheromone trap or emergence cage) was included as a fixed effect in the analysis, and site was included as a random effect.

Results

2001

In 2001, the cumulative proportion of beetles caught in three pheromone traps was significantly different from the cumulative proportion of beetles that emerged from 80 infested trees located at 10 sites throughout the study area (D = 0.401, $P < 0.001$). The large deviation of points from the 45° reference line in the Q–Q plot also demonstrates significant differences in the two distributions. Beetles were caught in pheromone traps significantly earlier than emergence into cages as indicated by the long left tail in the 2001 Q–Q plot (Fig. 1A). Peak catch in pheromone traps occurred on 7 July, 20 d prior to the first peak of beetles emerging into cages, and a third peak in pheromone trap capture occurred following the cessation of emergence from infested trees (Fig. 2A).

2002

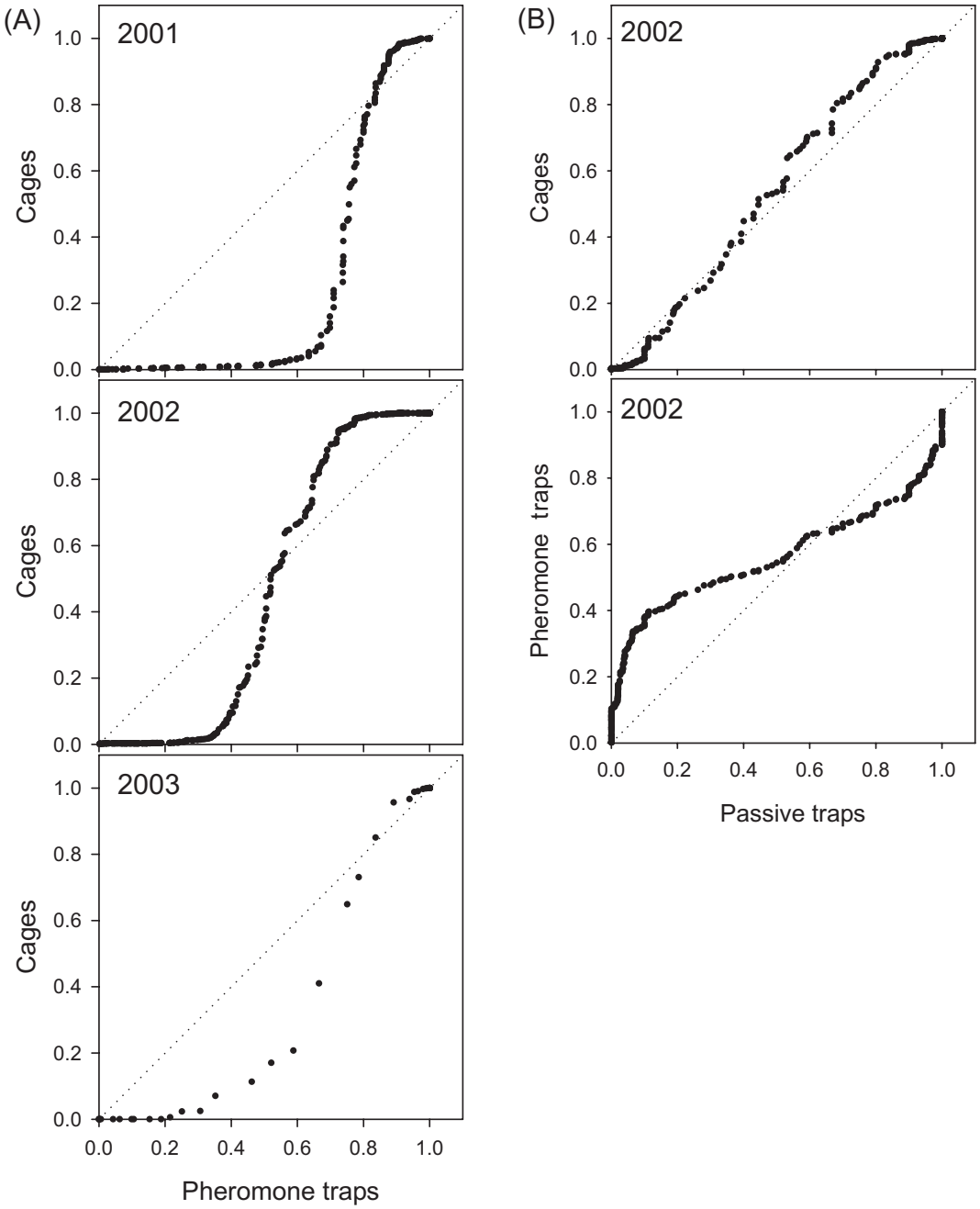
In 2002, each site contained a single pheromone trap, five infested trees with emergence cages, and eight passive traps. The relationship between pheromone trap catch and emergence differed slightly among the sites, and at 8 of the 10 sites the distribution of beetles caught in pheromone traps was significantly different from the distribution of beetles that emerged into cages on infested trees. At these eight sites, the deviance (D) ranged from 0.4412 to 0.3529 with associated significance levels below 0.02, indicating significantly different distributions. At these eight sites, the number of beetles caught in the colocated pheromone trap decreased during the peak of emergence from infested trees, and pheromone trap catch was often greatest both before and after the main emergence period from infested trees at each site (Fig. 3). At only one site, Vienna, where distributions were not significantly different (D = 0.2647, P = 0.1845), did a peak in pheromone trap catch coincide with tree emergence at that site (Fig. 3).

When data for all sites were pooled, the cumulative proportion of beetles caught in pheromone traps was significantly different overall from the distribution of beetles that emerged into cages on infested trees (D = 0.3176, $P < 0.001$) and the distribution of beetles caught in passive traps (D = 0.2707, $P < 0.001$). Large deviation of points from the reference line in Q–Q plots support the KS analysis (Fig. 1A, 1B). As in 2001, beetles were caught in pheromone traps both prior to and following peak emergence from infested trees (Fig. 2B). As indicated by a close alignment of points along the reference line in the Q–Q plot and a lack of significance in the KS test, similar distributions were observed for beetles emerging into cages on infested trees and beetles caught in passive traps (Fig. 1B).

2003

The cumulative proportion of beetles caught in pheromone traps was not significantly different from the distribution in emergence from caged trees in 2003 (D = 0.225, P = 0.134), although the maximum deviation (D) between the distributions was similar to values in 2002 and 2001 and points in the Q–Q plots deviated greatly from the reference line (Fig. 1A).

Fig. 1. Quantile–quantile plots comparing cumulative distributions of mountain pine beetles caught in pheromone traps and emergence cages in (A) 2001, 2002, and 2003 and (B) passive traps and emergence cages and passive traps and pheromone traps in 2002. If the trap and cages share a common distribution, then the plotted points will roughly lie on a 45° reference (e.g., the dotted line).



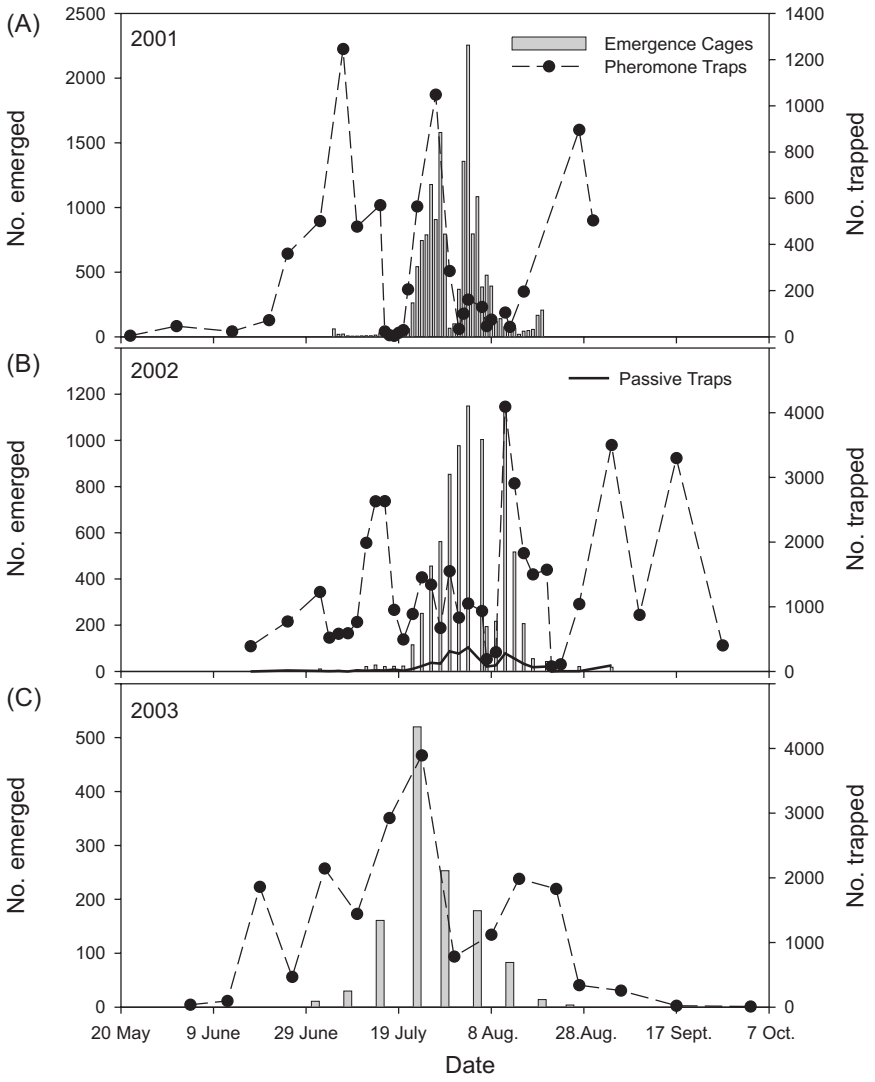
The lack of significance is most likely due to a smaller sample size resulting from weekly rather than daily collections from traps and cages. Similar to results in 2001 and 2002, beetles were caught in pheromone traps prior to the main emergence period from infested and caged trees (Fig. 2C). Unlike results from 2002, pheromone traps in 2003 did not continue to catch a large proportion of beetles into September, following the peak emergence period from infested trees.

Yearly comparisons

To compare distributions among the years, data from all sites each year were summed by week. The timing of pheromone trap catch among the 3 years varied, with multiple peaks throughout a 130-d period (Fig. 4A). Conversely, peak emergence into cages on infested trees occurred within 7 d among the 3 years, was tightly distributed within a 35-d period, and cumulative distributions among the years were not significantly different (Fig. 4B).

Although air temperature varied slightly among the sites, trends among the years at each site were consistent, and temperatures from only one site that was used each year (Vienna) are reported here. Temperature, expressed as cumulative hourly temperature above 15.5 °C, the flight threshold for mountain pine beetle (Reid 1962), was substantially warmer

Fig. 2. Number of mountain pine beetles caught in pheromone traps, emerged into emergence cages on infested trees, and caught in passive traps in (A) 2001 (3 funnel traps and 80 caged trees), (B) 2002 (10 funnel traps, 50 caged trees, and 80 passive traps) and (C) 2003 (2 funnel traps and 14 caged trees) in the Sawtooth National Recreation Area, Idaho.



in July and August 2003 compared to 2001 and 2002 temperatures (Fig. 5).

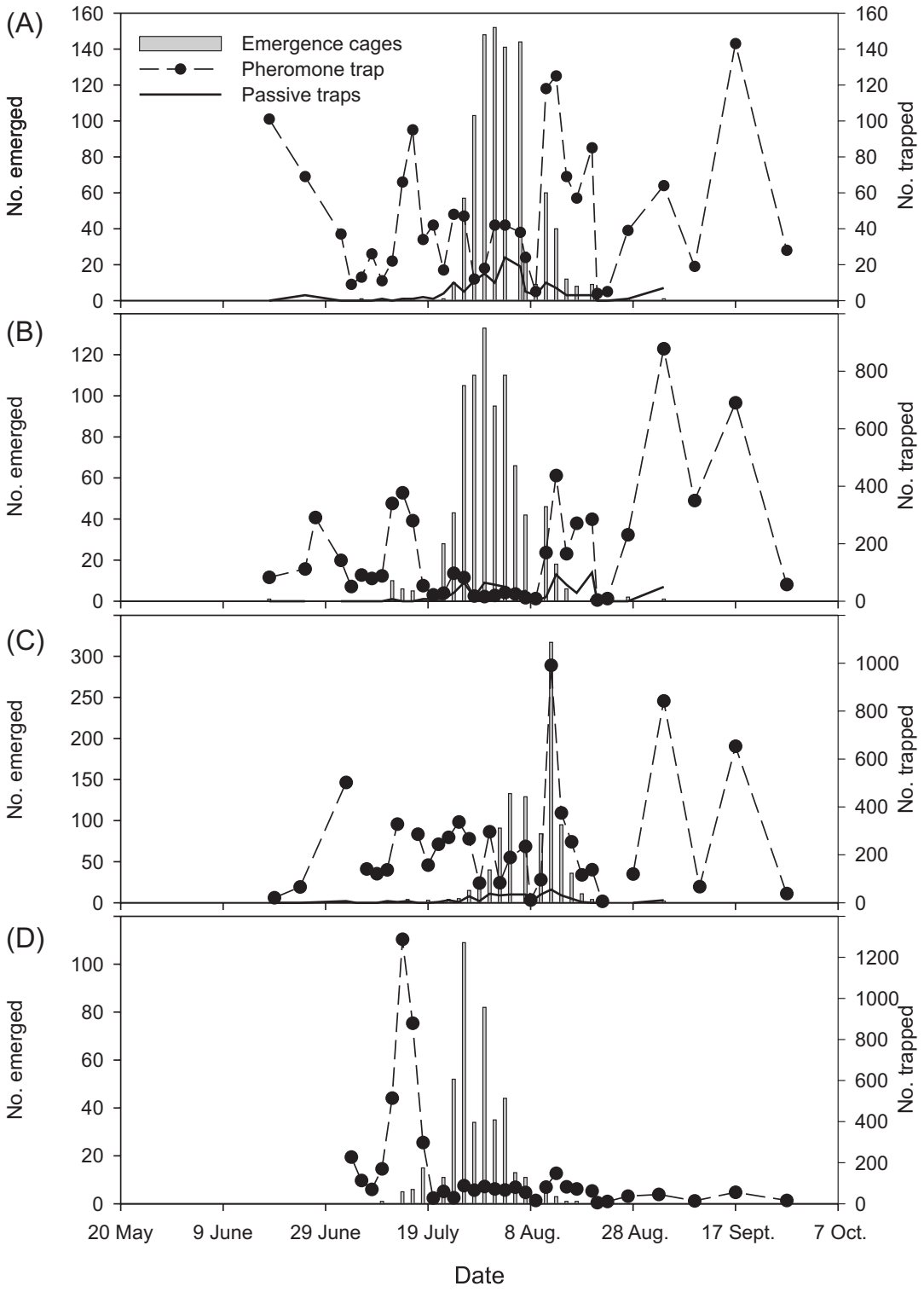
Lipid analysis

Year of collection (2002, 2003) was not significant in explaining differences in lipid content of adult beetles. Female mountain pine beetles caught in pheromone traps contained significantly more whole-body lipids than did males ($F_{[1,3215]}$ = 94.66, $P < 0.001$), and emergence group ($F_{[1,1991]}$ = 53.75, $P < 0.001$) and the emergence group × sex interaction ($F_{[1,3209]}$ = 10.16, $P < 0.001$) were both significant. Female beetles caught in pheromone traps during the main emergence period from infested trees (10 July – 13 August) had significantly more whole-body lipids than did beetles caught in pheromone traps before and after the main emergence period (Table 1, Fig. 6). Male beetles caught in pheromone traps during the main emergence period from infested trees had significantly more lipids than those caught after the main emergence period, but not those caught before the main emergence period (Table 1, Fig. 6). Adult mountain pine beetles collected from cages in 2002 had significantly higher percentage of whole-body lipids (χ = 17.62 ± 6.7, N = 766) than did adults collected in pheromone traps during the same sampling period (χ = 14.8 ± 6.2, N = 1667) ($F_{[1,763]}$ = 49.36, $P < 0.001$).

Discussion

Synchronous emergence and subsequent mass attack is a strategy that allows mountain pine beetle to overwhelm host-tree defenses and thereby successfully colonize new host trees (Raffa and Berryman 1979). For three consecutive years at sites in central Idaho, mountain pine beetle emergence from infested lodgepole pine occurred during a 35-d period each year, with peak emergence among the years synchronized within 7 d. These results confirm those of previous studies conducted in a variety of geographic regions and host types that also demonstrated a highly synchronized mountain pine beetle emergence period within a landscape

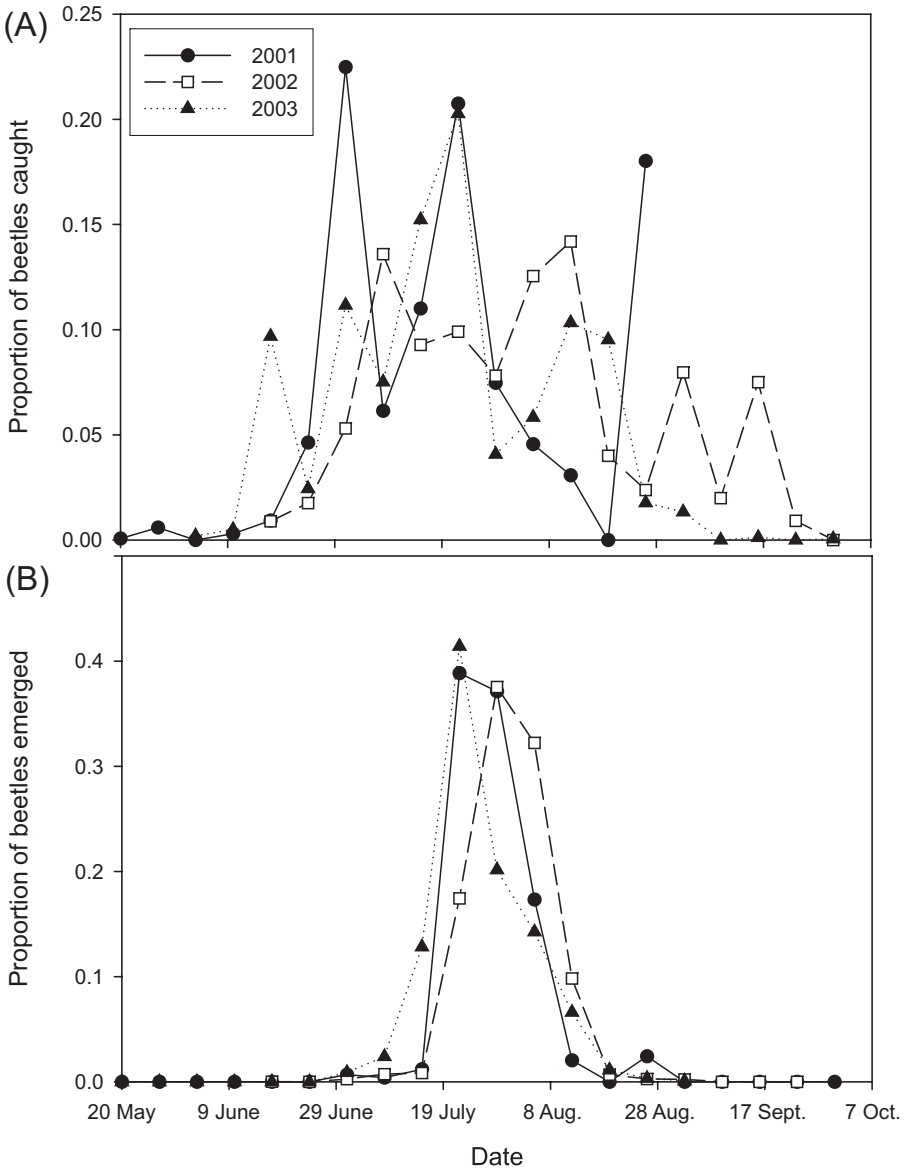
Fig. 3. Number of mountain pine beetle emerging into cages on eight infested trees, the number of beetles caught in a single pheromone trap located 100 m from the infested trees, and number of beetles trapped in eight passive traps at four of 10 sites monitored in the Sawtooth National Recreation Area in 2002: (A) Mogul, (B) No parking, (C) Vienna, and (D) Redfish. Distribution of beetles caught in the pheromone trap and tree emergence cages were significantly different at all sites displayed except Vienna.



(Reid 1962; McCambridge 1964; Safranyik and Jahren 1970; Rasmussen 1974).

Pheromone traps are considered important tools for studying bark beetle ecology and have frequently been used to predict flight periodicity (Peck et al. 1997; Fettig et al. 2004). While no published studies have compared the timing of emergence from infested trees and catch in pheromone traps, a high positive correlation is assumed when traps are used

Fig. 4. (A) Proportion of mountain pine beetles caught in pheromone traps and (B) proportion of mountain beetles emerged into cages on infested trees in 2001, 2002, and 2003, summed by week, in the Sawtooth National Recreation Area, Idaho.



for monitoring population emergence (Safranyik and Linton 1993). In the present study, the distribution of beetles emerging from infested trees each year was poorly correlated with the timing of beetles caught in pheromone traps. Beetle emergence was sampled using cages centered at 1.37 m from the ground (e.g., mid-bole) and included approximately 0.4 m^2 of each infested tree. While bark beetle attacks occur above and below the sections sampled, emergence at mid-bole has been found to only vary 5–10 d from the timing observed at other bole locations (Safranyik and Jahren 1970; Coulson et al. 1979; B.J. Bentz, unpublished data). Peaks in pheromone trap catch in 2001, 2002, and 2003 occurred >20 d earlier and up to 30 d after peak emergence into cages on infested trees. Moreover, mountain pine beetle brood production, and subsequent emergence, is greatest at the mid-bole, decreasing above and below this area (Reid 1963; McCambridge 1972). Early and late peaks in pheromone trap catch, therefore, are unlikely a result of beetle emergence from unsampled heights along caged tree boles.

An alternative explanation for the lack of correlation between pheromone trap catch and emergence from infested trees is that the pheromone traps disproportionately sample the flying beetle population throughout the flight season. When few beetles are flying, such as occurs early and late in the season when there is little natural pheromone being produced and few trees are under attack, the pheromone trap will attract a larger proportion of the population than during the peak emergence period, when many trees are under attack and the area is flooded with natural pheromones and kairomones. When neighboring trees are under mass attack, the synthetic pheromone becomes a relatively minor source of chemical cues. Consequently, when many beetles are flying and attacking trees, the number attracted to the pheromone trap is reduced, while disproportionately more are attracted

Fig. 5. Air temperature at the Vienna site in the Sawtooth National Recreation Area, Idaho, in 2001, 2002, and 2003, expressed as cumulative hourly temperature above 15.5 °C.

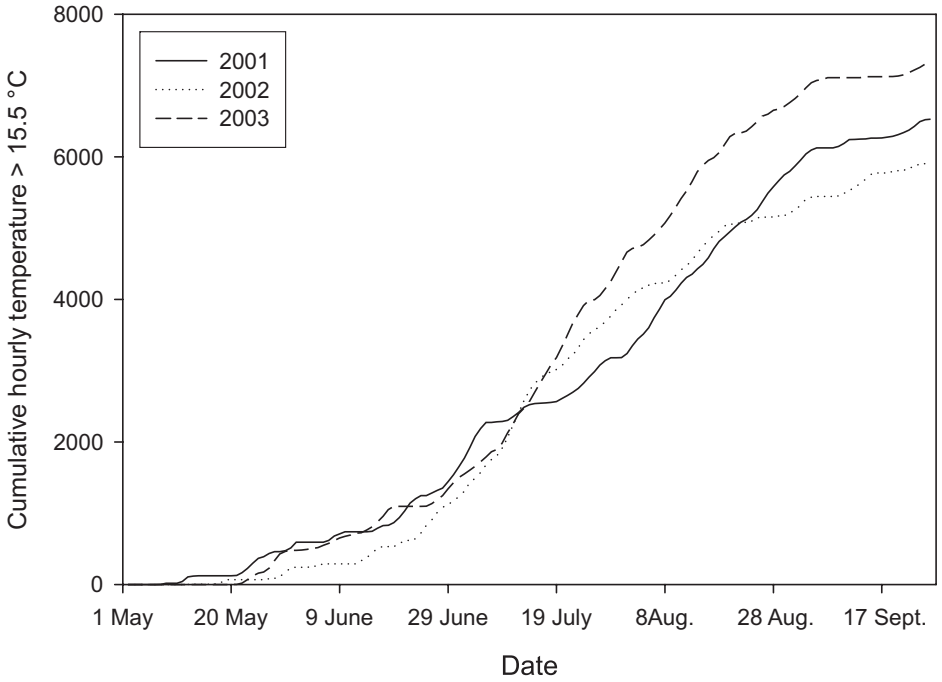


Table 1. Statistical differences of least square means for male and female lipid content among mountain pine beetle emergence groups in 2002 and 2003.

	Female			Male		
Comparison	df	*t*	*P*	df	*t*	*P*
Emergence group 1 × emergence group 2	1469	–8.36	<0.0001	2770	–2.22	0.2307
Emergence group 1 × emergence group 3	2031	0.64	0.9874	3107	–0.57	0.9927
Emergence group 2 × emergence group 3	3154	–9.53	<0.0001	3198	–4.24	0.0003

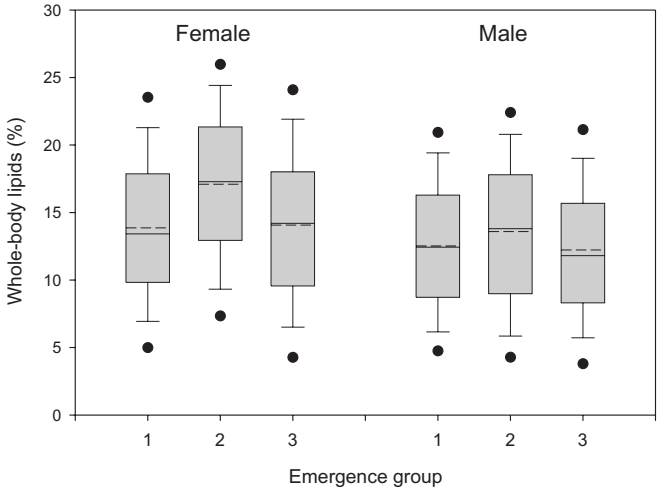
Note: Emergence group 1: adults caught in pheromone traps prior to the time when emergence from infested trees was observed (<10 July); emergence group 2: adults caught in pheromone traps during the time of emergence from infested trees (10 July – 13 August); and emergence group 3: adults caught in pheromone traps after emergence from infested trees had ended (>13 August).

to pheromone traps during periods of low beetle flight, when natural pheromone sources are at low levels. The observed reduction in pheromone trap catch during peak emergence from infested trees within 100 m of a trap in 2002 and large peaks in pheromone trap catch prior to and following emergence into cages both support this explanation. Additionally, the distribution and timing of beetles caught in passive traps, which most accurately reflects nondirected flight activity, was significantly different than pheromone trap catch, but not catch in emergence cages.

Natural pheromone sources will be at low levels when few beetles are flying and attacking new host trees. Genetic variability and weather may result in ovipositional and developmental timing differences (Bentz et al. 1991), causing a small proportion of the population to develop faster or slower and thereby emerge earlier or later than the majority of the brood. Additionally, some proportion of beetles caught in pheromone traps prior to and following the main emergence period may not be brood adults at all, but reemerged parents. In years with moderate temperatures, adult mountain pine beetles that have laid a complement of eggs may overwinter and reemerge the following spring to make a second egg gallery (Amman and Bartos 1991). Following the main flight in the summer, adults may also reemerge to attack an additional tree. In both cases, lower lipid content would be expected, as a large proportion of the fat reserve would have been expended during initial egg laying. Reemerged spruce beetles, *Dendroctonus rufipennis* (Kby.), collected in the spring were found to have significantly fewer lipids than new brood adults collected at the same time (Hansen and Bentz 2003), and over-wintered southern pine beetle, *Dendroctonus frontalis*, and *Ips typographus* adults sampled in the spring were also characterized by a reduced fat content (Hedden and Billings 1970; Botterweg 1982). In the present study, adult mountain pine beetles collected from pheromone traps early (prior to the period of emergence from infested trees) and late (following peak emergence) had fewer lipids than adults collected during peak emergence from infested trees. These results suggest that at least a portion of the mountain pine beetles caught in pheromone traps early and late in the season may be reemerged adults.

Alternatively, low lipid content of beetles caught before and after the main emergence period could be a result of a long-distance flight caused by fewer sources of pheromone attraction on the landscape. Lipids have been shown to be

Fig. 6. Percent whole-body lipid content of male and female mountain pine beetles caught in pheromone traps in 2002 and 2003, by emergence group. Emergence group 1: adults caught in pheromone traps prior to the time when emergence from infested trees was observed (<10 July); emergence group 2: adults caught in pheromone traps during the time of emergence from infested trees (10 July – 13 August); and emergence group 3: adults caught in pheromone traps after emergence from infested trees had ended (>13 August).



consumed for long flights in *Dendroctonus pseudotsugae* (Thompson and Bennett 1971) and are associated with flight potential in many other bark beetle species (Hagen and Atkins 1975; Slansky and Haack 1986; Jactel 1993). In the current study, lipid content of mountain pine beetles prior to flight (e.g., from emergence cages) was significantly greater than that of beetles after a period of flight (e.g., from pheromone traps). Both males and females trapped during the main emergence period had the highest whole-body lipid content, suggesting that they flew a shorter distance and (or) were new brood adults.

In 2002, but not 2003, a large proportion of beetles were caught in pheromone traps in September more than 30 d after the main emergence period from infested trees. Annual variation in trap catch could be a result of a complex variety of factors including topography, stand density, wind direction and strength, temperature, population size, and host-tree patterns (Salom and McLean 1991; Schmid et al. 1992). Because the same sites were sampled in 2002 and 2003, site factors will undoubtedly remain the same and in this case not be a strong causal factor. Conversely, temperature, which has a direct impact on beetle development and flight, could be a strong influencing factor. Cumulative temperature above the mountain pine beetle flight threshold was much greater later in the flight season in 2003 than 2002, which is counterintuitive to an extended flight period in 2002 and not 2003. Although we have no data to quantify numbers of trees attacked surrounding each study site, population size may also be an influencing factor in the timing of trap catch. Several recent studies have found a correlation between number of bark beetles caught in pheromone traps and number of trees attacked in the surrounding forest (Faccoli and Stergule 2004; E.M Hansen and B.J. Bentz, unpublished data). Studies designed to investigate the effect of population size on the timing of pheromone trap catch are needed.

Pheromone traps are widely used for monitoring bark beetle populations and may be influenced by a variety of factors. Results from the present study suggest that data from pheromone-baited Lindgren traps are not always a reliable estimate of mountain pine beetle flight periodicity and that natural pheromone sources may influence the timing and number of beetles caught in synthetically baited traps. In this study, peaks in pheromone trap catch did not always coincide with peak emergence from nearby infested trees or trees within the contiguous landscape. When knowledge of the timing of adult emergence is not important, pheromone traps remain a valid tool for mountain pine beetle population management.

Acknowledgments

This study was made possible by substantial effort from a number of people including Amy Adams, Jason Barker, Leslie Brown, Amanda Cangelosi, Rebecca Gerhart, Estella Gilbert, Matt Hansen, Justin Heavilin, Jeff Leek, Jim Powell, Lynn Rasmussen, Jackie Redmer, Greta Schen, and Jim Vandygriff. Kimberly Wallin assisted with lipid analysis in 2002. Discussions with Jesse Logan and Jim Powell influenced the experimental design and final data interpretation. Matt Hansen and three anonymous reviewers provided helpful comments on the manuscript. This research was funded in part by a grant from the National Science Foundation (Award No. 0077663).

References

Amman, G.D., and Bartos, D. 1991. Mountain pine beetle offspring characteristics associated with females producing first and second broods, male presence, and egg gallery length. Environ. Entomol. **20**(6): 1562–1567.

Barclay, H.J., Safranyik, L., and Linton, D. 1998. Trapping mountain pine beetle *Dendroctonus ponderosae* (Coleoptera: Scolytidae) using pheromone-baited traps: effects of trapping distance. J. Entomol. Soc. B.C. **95**: 25–31.

Bentz, B.J., and Munson, A.S. 2000. Spruce beetle population suppression in northern Utah. W. J. Appl. For. **15**(3): 122–128.

Bentz, B.J., Logan, J.A., and Amman, G.D. 1991. Temperature dependent development of the mountain pine beetle (Coleoptera: Scolytidae), and simulation of its phenology. Can. Entomol. **123**: 1083–1094.

Bentz, B.J., Kegley, S., Gibson, K., and Their, R. 2005. A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle attacks. J. Econ. Entomol. **98**(5): 1614–1621.

Borden, J.H. 1974. Aggregation pheromones in the Scolytidae. *In* Pheromones. *Edited by* M.C. Birch. North-Holland Publishing Co., Amsterdam. pp. 135–160.

Borden, J.H. 1982. Aggregation pheromones. *In* Bark beetles in North American conifers. *Edited by* J.B. Mitton and K.B. Sturgeon. University of Texas Press, Austin, Tex. pp. 74–139.

Borden, J.H. 1989. Semiochemicals and bark beetle populations: Exploitation of natural phenomena by pest management strategists. Holarct. Ecol. **12**: 501–510.

Botterweg, P.F. 1982. Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. Z. Angew. Entomol. **94**: 466–489.

Chambers, J., Cleveland, W., Kleiner, B., and Tukey, P. 1983. Graphical methods for data analysis. Wadsworth, Belmont, Calif.

Coulson, R.N., Fargo, W.S., Pulley, P.E., Poe, D.N., Foltz, J.L., and Bunting, A.M. 1979. Spatial and temporal patterns of emergence for within-tree populations of *Dendroctonus frontalis* (Coleoptera: Scolytidae). Can. Entomol. **111**: 273–287.

Dodds, K.J., and Ross, D.W. 2002. Sampling range and range of attraction of *Dendroctonus pseudotsugae* pheromone-baited traps. Can. Entomol. **134**: 343–355.

Faccoli, M., and Stergule, F. 2004. *Ips typographus* (L.) pheromone trapping in south Alps: spring catches determine damage thresholds. J. Appl. Entomol. **128**(4): 307–311.

Fettig, C.J., Shea, P.J., and Borys, R.R. 2004. Diurnal flight pattern of *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in northern California. J. Entomol. Sci. **39**(3): 453–456.

Franklin, A.J., and Gregoire, J.C. 2001. Dose-dependent response and preliminary observations on attraction range of *Ips typographus* to pheromones at low release rates. J. Chem. Ecol. **27**(12): 2425–2436.

Furniss, R.L., and Carolin, V.M. 1977. Western forest insects. USDA For. Serv. Misc. Publ. 1339.

Hagen, B.W., and Atkins, M.D. 1975. Between generation variability in the fat content of and behavior of *Ips paraconfusus* Lanier. J. Appl. Entomol. **79**: 169–72.

Hansen, E.M. 1996. Western balsam bark beetle, *Dryocoetes confuses* Swaine, flight periodicity in northern Utah. Great Basin Nat. **56**: 348–359.

Hansen, E.M., and Bentz, B.J. 2003. Comparison of reproductive capacity among univoltine semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). Can. Entomol. **135**: 1–16.

Hedden, R.L., and Billings, R.F. 1970. Seasonal variation in fat content and size of the southern pine beetle in east Texas. Ann. Entomol. Soc. Am. **70**: 876–880.

Jactel, H. 1991. Dispersal and flight behavior of *Ips sexdentatus* (Coleoptera: Scolytidae) in pine forest. Ann. Sci. For. **48**: 417–428.

Jactel, H. 1993. Individual variability of the flight potential of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) in relation to day of emergence, sex, size, and lipid content. Can. Entomol. **125**: 919–930.

Laidlaw, W.G., Prenzel, B.G., Reid, M.L., Fabris, S., and Wieser, H. 2003. Comparison of the efficacy of pheromone-baited traps, pheromone-baited trees, and felled trees for the control of *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). Environ. Entomol. **32**(3): 477–483.

Lindgren, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). Can. Entomol. **115**: 299–302.

Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. SAS system for mixed models. SAS Institute Inc., Cary, N.C.

Lyon, R.L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. Can. Entomol. **90**: 582–584.

McCambridge, W.F. 1964. Emergence period of Black Hills beetles from ponderosa pine in the Central Rocky Mountains. USDA For. Serv. Res. Note RM-32.

McCambridge, W.F. 1972. Treatment height for mountain pine beetles in front range ponderosa pine. USDA For. Serv. Res. Note RM-218.

Peck, R.W., Eqihua-Martinez, A., and Ross, D.W. 1997. Seasonal flight patterns of bark and ambrosia beetles (Coleoptera: Scolytidae) in northeastern Oregon. Pan-Pac. Entomol. **73**(4): 204–212.

R Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from http://www.R-project.org [accessed 11 August 2005]. ISBN 3-900051-07-0.

Raffa, K.F. 2001. Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communications systems. Chemoecology, **11**(2): 49–65.

Raffa, K.F, and Berryman, A.A. 1979. Flight responses and host selection by bark beetles. *In* Dispersal of forest insects: evaluation, theory and management implications. *Edited by* A.A. Berryman and L. Safranyik. Washington State University, Pullman, Wash. pp. 213–233.

Raffa, K.F., and Berryman, A.A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Can. Entomol. **114**: 797–810.

Rasmussen, L.A. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. USDA For. Serv. Res. Note INT-180.

Reid, R.W. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae*, in the east Kootenay region of British Columbia. I. Life cycle, brood development, and flight periods. Can. Entomol. **94**: 531–538.

Reid, R.W. 1963. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. Can. Entomol. **95**: 225–238.

Renwick, J.A.A., and Vite, J.P. 1970. Systems of chemical communication in *Dendroctonus.* Contrib. Boyce Thompson Inst. **24**: 282–292.

Ross, D.W., and Daterman, G.E. 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. For. Sci. **43**: 65–70.

Safranyik, L., and Jahren, R. 1970. Emergence patterns of the mountain pine beetle from lodgepole pine. Can. Dep. Fish. For. Bi-mon. Res. Notes, **26**(2): 11, 19.

Safranyik, L., and Linton, D.A. 1993. Relationships between catches in flight and emergence traps of the mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Col.: Scolytidae). J. Entomol. Soc. B.C. **90**: 53–61.

Salom, S.M., and McLean, J.A. 1990. Dispersal of *Trypodendron lineatum* within a valley setting. Can. Entomol. **122**: 43–58.

Schmid, J.M., Mata, S.A., and Allen, D.C. 1992. Potential influences of horizontal and vertical air movement in ponderosa pine stands on mountain pine beetle dispersal. USDA For. Serv. Res. Note RM-516.

Schmitz, R.F. 1984. A passive aerial barrier trap suitable for sampling flying bark beetles. USDA For. Serv. Res. Note INT-348.

Slansky, F., and Haack, R.A. 1986. Age-specific flight behavior in relation to body weight and lipid content of *Ips calligraphus* reared in slash pine bolts with thick and thin inner bark (phloem). Entomol. Exp. Appl. **40**: 197–207.

Sokal, R.R., and Rohlf, F.J. 1969. Biometry. W.H. Freeman and Co., San Francisco.

Thompson, S.N., and Bennett, R.B. 1971. Oxidation of fat during flight of male Douglas fir beetles, *Dendroctonus pseudotsugae.* J. Insect Physiol. **17**: 1555–1563.

Turchin, P., and Odendaal, F.J. 1996. Measuring the effective sampling area of a pheromone trap for monitoring population density of southern pine beetle (Coleoptera: Scolytidae). Environ. Entomol. **25**(3): 582–588.