Influence of Elevation on Bark Beetle (Coleoptera: Curculionidae, Scolytinae) Community Structure and Flight Periodicity in Ponderosa Pine Forests of Arizona

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ABSTRACT We examined abundance and flight periodicity of five *Ips* and six *Dendroctonus* species (Coleoptera: Curculionidae, Scolytinae) among three different elevation bands in ponderosa pine (*Pinus ponderosa* Douglas ex. Lawson) forests of northcentral Arizona. Bark beetle populations were monitored at 10 sites in each of three elevation bands (low: 1,600–1,736 m; middle: 2,058–2,230 m; high: 2,505–2,651 m) for 3 yr (2004–2006) using pheromone-baited Lindgren funnel traps. Trap contents were collected weekly from March to December. We also studied temperature differences among the elevation bands and what role this may play in beetle flight behavior. Bark beetles, regardless of species, showed no consistent elevational trend in abundance among the three bands. The higher abundances of *Ips lecontei* Swaine, *I. calligraphus ponderosae* Swaine, *Dendroctonus frontalis* Zimmerman, and *D. brevicomis* LeConte at low and middle elevations offset the greater abundance of *I. knausi* Swaine, *D. adjunctus* Blandford, *D. approximatus* Dietz, and *D. valens* LeConte at high elevations. *I. pini* (Say) and *I. latidens* LeConte were found in similar numbers across the three bands. Flight periodicity of several species varied among elevation bands. In general, the flight period shortened as elevation increased; flight initiated later and terminated earlier in the year. The timing, number, and magnitude of peaks in flight activity also varied among the elevation bands. These results suggest that abundance and flight seasonality of several bark beetles are related to elevation and the associated temperature differences. The implications of these results are discussed in relation to bark beetle management and population dynamics.

KEY WORDS *Dendroctonus*, *Ips*, flight seasonality, abundance, *Pinus ponderosa*

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are a significant source of insect-caused pine mortality in the western United States (Furniss and Carolin 1977). Bark beetle–caused tree mortality is frequently related to certain tree and stand conditions (Fettig et al. 2007 and references cited therein). Identifying these patterns of mortality can facilitate the development of management strategies, such as silvicultural treatments (Hedden 1981). Although hazard rating systems that relate forest susceptibility to stand characteristics have been developed for some bark beetle species (Steele et al. 1996, Schmitt and Powell 2005), tree mortality patterns related to physiographic characteristics have not received as much attention. Site quality (Negrón et al. 2000), latitude (Bentz et al. 2001,

Fettig et al. 2004a), and elevation (Hansen 1996, Salinas-Moreno et al. 2004, Fettig et al. 2005) have direct and indirect effects on both hosts and herbivores and can also be important in hazard rating systems. Temperature and precipitation, both environmental factors affected by elevation (Sheppard et al. 2002), can influence tree vigor (Furniss and Carolin 1977, Allen and Breshears 1998, Ayres and Lombardero 2000), limit the geographic distribution of insects (Furniss and Carolin 1977, Ungerer et al. 1999, Ayres and Lombardero 2000, Lombardero et al. 2000, Bale et al. 2002, Williams and Liebhold 2002), and regulate bark beetle phenology and voltinism (Furniss and Carolin 1977, Ungerer et al. 1999, Ayres and Lombardero 2000, Hansen et al. 2001, Bale et al. 2002). Bark beetle species infesting hosts with wide physiographic ranges will be exposed to a broad array of temperature effects.

Differential adaptation to temperature regimens among species may result in unique bark beetle assemblages along elevational gradients. Environmental factors associated with elevation in the Sierra Nevada Mountains of California influenced both the spatial and temporal distribution of four major bark beetle species [*Ips pini* (Say), *I. paraconfusus* Lanier, *Den-*

droctonus brevicomis LeConte, and *D. ponderosae* Hopkins] (Fettig et al. 2005). Two species (*I. para-confusus* and *D. brevicomis*) were inversely related to elevation, whereas the other two species (*I. pini* and *D. ponderosae*) did not display a specific pattern with respect to elevation. In addition, temperature effects associated with elevational gradients have been reported to influence flight initiation and cessation, development time, or number of generations for several bark beetles species, including *Dryocoetes confusus* Swaine in Utah (Hansen 1996) and *D. rufipennis* Kirby in Utah, Colorado, and Alaska (Hansen et al. 2001). Outside of these few studies, there is a paucity of information on spatial/temporal variation of bark beetle communities across elevational gradients of their hosts.

The bark beetle community in Arizona's ponderosa pine (*Pinus ponderosa* Douglas ex. Lawson) forests is complex, comprised of several primary (i.e., capable of attacking, colonizing and killing apparently healthy trees) and secondary (i.e., infesting weakened, dead, or dying trees) bark beetle species. Based on a review of bark beetle taxonomical records, 29 species of bark beetles, including six *Dendroctonus* spp. and 12 *Ips* spp., attack branches, trunks, and roots of ponderosa pine in the southwestern United States (Furniss and Carolin 1977, Wood 1982). Bark beetles recently caused unprecedented levels of ponderosa pine mortality throughout Arizona (USDA 2001–2004). Primary tree-killing species included *I. pini, I. lecontei* Swaine, *D. brevicomis,* and *D. frontalis* Zimmerman; however, their relative importance varied by site and elevation (J.D.M., unpublished data). The community structure and flight periodicity of bark beetles in northcentral Arizona ponderosa pine forests have only been examined at one elevation (2,080 m) near Flagstaff, AZ (Sanchez-Martinez and Wagner 2002, Gaylord et al. 2006). To date, knowledge has been lacking on how this bark beetle community and the flight periodicity of individual species vary across a broader elevational gradient.

The primary objective of this study was to describe species composition, abundance, and flight periodicity of *Dendroctonus* and *Ips* genera occurring in ponderosa pine forests across an elevational gradient in northcentral Arizona. Species composition, abundance, and flight periodicity were determined using Lindgren funnel traps baited with aggregation pheromones. The second objective was to study the role temperature plays in regulating flight behavior of these bark beetle species. Knowledge gained from this project has implications for development of hazard rating systems, timing of silvicultural, semiochemical, and preventative spray treatments, and prediction of bark beetle population dynamics.

Methods and Materials

Site Description. Study sites were located in stands of ponderosa pine on the Coconino, Kaibab, and Tonto National Forests in north central Arizona (Fig. 1). All sites were located in the interior ponderosa

pine cover type of the Society of American Foresters (Eyre 1980). Xerophytic forests at low elevations (1,600–1,736 m) were bordered by pinyon/juniper woodlands and included trees and shrubs such as pinyon pine (*P. edulis* Engelm.), alligator juniper (*Juniperus deppeana* Steud.), Utah juniper (*J. osteosperma* (Torr.) Little), Arizona white oak (*Quercus arizonica* Sarg.), manzanita (*Arcostaphylos pungens* Kunth), and yuccas (*Yucca* spp.) (Moir et al. 1997, USDA 2002a). Middle elevation xerophytic forests (2,058–2,230 m) were dominated by ponderosa pine. Associated understory vegetation ranged from bunchgrasses to one-seed juniper [*J. monosperma* (Engelm.) Starg.] and Gambel oak (*Q. gambelii* Nutt.) (Moir et al. 1997, USDA 2002b). Ponderosa pine stands were intermingled with mixed conifer stands in the high elevation band (2,505–2,651 m), and sites were located in both xerophytic and mesophytic forest zones (Moir et al. 1997). Additional tree species found at high elevation sites included Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco], limber pine (*P. flexilis* James), white fir [*Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr. variety *concolor*], and quaking aspen (*Populus tremuloides* Michx.) (Moir et al. 1997, USDA 2002b, 2002c).

According to the General Ecosystem Survey (Carleton et al. 1991), these sites are mostly located in the High Sun Mild (low elevation) and High Sun Cold (high elevation) climate zones, where mean annual air temperatures range from 4 to 9°C, and mean annual precipitation ranges from 520 to 700 mm (Moir et al. 1997). Precipitation primarily falls in two different times of the year. Summer precipitation occurs from July to September, whereas winter precipitation falls from December through March (Hendricks 1985).

Study Design. Ten sites were established in each of three elevation bands that covered most of the elevational range of ponderosa pine in Arizona: low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m). Sites within an elevation band were separated by a minimum of 2 km. Trap sites were within 100 m of the edge of ponderosa pine stands and within 50–200 m of forest roads to facilitate collections. Efforts were made to maintain the same trapping locations each year; however, forest management activities and forest road closures required the removal of one low elevation site and one high elevation site and the relocation of one low elevation site and one middle elevation site. Relocation sites were within 9 km of the original sites.

Each trap site contained three 12-unit Lindgren funnel traps (Pherotech International, Delta, British Columbia, Canada) (Lindgren 1983) arranged in an ≈15-m equilateral triangle. Traps were suspended from 3-m aluminum conduit poles with the bottom of traps ≈1 m from the ground. Traps were baited with lures that targeted three species of concern in northcentral Arizona's ponderosa pine forests: *I. pini, I. lecontei,* and *D. brevicomis* (Table 1). Although these lure combinations targeted certain species, they were also expected to capture other *Ips* and *Dendroctonus* species based on a previous study in northern Arizona (Gaylord et al. 2006). Lures were replaced every 7 wk
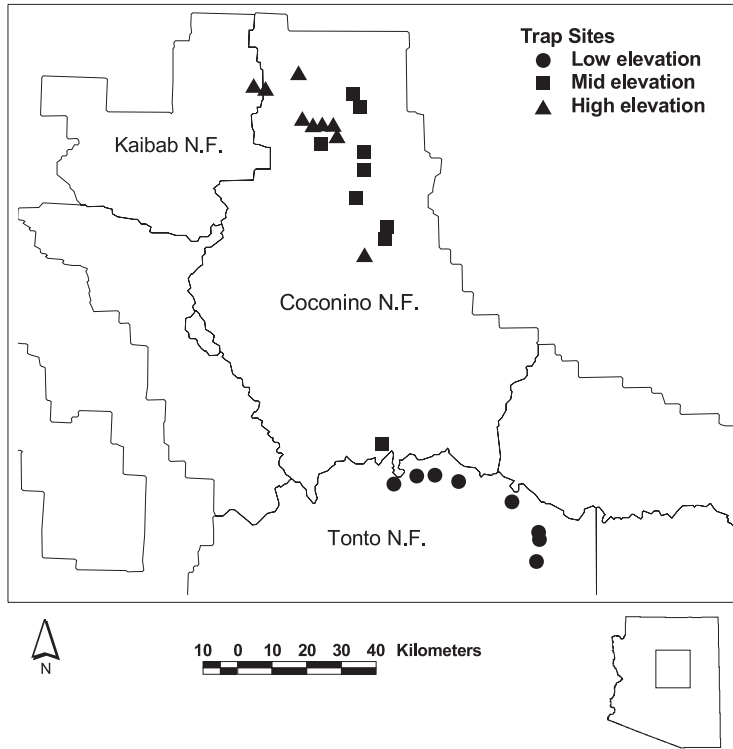
Fig. 1. Map showing the location of low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation trap sites in ponderosa pine forests of northcentral Arizona used in all 3 yr of study, 2004–2006.

to ensure adequate pheromone elution rates. Traps were also rotated on a regular basis to minimize location impacts. A 2.5 by 2.5-cm square of Spectracide Bug Stop pest strip (18.6% Dichlorvos; United Industries, St. Louis, MO) was placed in each collection cup to kill trapped insects and minimize predation.

The length of trapping season varied across elevation and year (Table 2) and was initially based on the results of a recent study near Flagstaff, AZ (Gaylord et al. 2006). Initiation and cessation of trapping at high elevation sites in all years depended on site accessibility caused by spring and fall weather. Based on 2004 data, efforts were made in 2005 and 2006 to extend the length of the trapping seasons for all elevations so that trap catch data would start and end with zero trap

catches, reflecting a true initiation and cessation of flight activity for all species.

Contents of traps were collected approximately once per week. All beetles of the genera *Ips* and *Dendroctonus* were identified and tallied. Bark beetle species were identified using Wood's (1982) taxonomic monograph for bark beetles. Species identifications were confirmed by using existing collections at Northern Arizona University (Flagstaff, AZ) and the Rocky Mountain Research Station (Flagstaff, AZ), by independently comparing samples with collections housed at Texas Agricultural and Mechanical University (conducted by Anthony Cognato, Department of Entomology, Texas Agricultural and Mechanical University, College Station, TX), and by genetic sequencing (conducted by Chris Allender, the Center for Microbial Genetics and Genomics, Northern Arizona University, Flagstaff, AZ). Voucher specimens are

Table 1. Description of semiochemical lures (Pherotech International, Delta, British Columbia, Canada) used in Lindgren funnel traps located in three elevation bands in the Coconino, Kaibab, and Tonto National Forests, Arizona, 2004–2006

Bark beetle species	Semiochemical lure	Chemical purity (%)	Release rate (mg/24 h)
I. pini	Ipsdienol +03/−97	>95	0.2 @ 25°C
	Lanierone	>97	0.009 @ 25°C
I. lecontei	Ipsdienol +50/−50	>95	0.2 @ 25°C
	Ispsenol +50/−50	>96	0.4 @ 25°C
	Cis-verbenol +17/−83	>90	0.6 @ 20°C
D. brevicomis	Frontalin	>99	2.6 @ 23°C
	Exo-brevicomin	>99	1.7 @ 23°C
	Myrcene (×2)	>90	6.5 @ 23°C

Table 2. Dates of sampling bark beetle flight in ponderosa pine forests on the Coconino, Kaibab, and Tonto National Forests, Arizona, 2004–2006

Year	Elevation band		
	Low (1,600–1,736 m)	Middle (2,058–2,230 m)	High (2,505–2,651 m)
2004	12 April to 16 Nov.	13 April to 15 Nov.	28 April to 15 Nov.
2005	8 Mar. to 6 Dec.	23 Mar. to Dec. 8.	25 April to 28 Nov.
2006	7 Mar. to 12 Dec.	9 Mar. to 7 Dec.	27 Mar. to 6 Dec.

maintained at the Rocky Mountain Research Station, United States Forest Service, Flagstaff, AZ.

HOBO data loggers (Onset Computer, Bourne, MA) were installed at diameter breast height (1.37 m) on the north side of a tree nearest to the center of the trap site at six sites in each elevation band. In 2004, data loggers collected temperature data for the duration of the trapping season (Table 2). In 2005, data loggers were reinstalled as traps were deployed in each elevation band, so temperature data collection started much later at high elevation sites than at low elevation sites (Table 2). Data loggers remained in the field throughout the winter of 2005/2006 and continued collecting temperature data through the 2006 trapping season.

Statistical Analysis. For each site and collection period, beetle count was summed across all three traps. Because each lure combination targeted a different species of bark beetle, a wide variety of *Dendroctonus* and *Ips* species were attracted to the site and collected in all three traps. Therefore, the beetle count summed across all three traps represents the total beetle capture for a given site. Although most trap collection periods were 1 wk, collection periods ranged from 4 to 17 d. To standardize data, the total trap catch per site for a collection period was divided by the number of days in that collection period and multiplied by 7 to give a value representing the total trap catch for a week.

The average weekly beetle capture for the trapping season was calculated for each site using data from collection weeks when at least one trap was deployed in each elevation band. Only sites that were installed all 3 yr were included in the analysis. The mean beetle capture for each elevation band was compared for pooled years using a multiple response permutation procedure (MRPP) (Mielke and Berry 2001) for one-factor designs (macros developed by Rudy King, USDA Forest Service, Rocky Mountain Research Station Statistics Unit). MRPP, a nonparametric technique, is similar to analysis of variance (ANOVA) but does not require normal distribution and equal variance of the data (Mielke and Berry 2001). All tests were run with a significance level of $\alpha = 0.05$. Mean weekly trap catch per site ($\pm$SEM) was plotted against time for pooled years to supplement the MRPP analysis. These graphs provided insight into peak bark beetle captures, along with the initiation and cessation of bark beetle flight activity. By pooling years, overall elevational trends of bark beetle abundance and flight periodicity could be observed. Additionally, temporal graphs of individual years were constructed to expose annual fluctuations in the seasonal patterns of trap catches within an elevation band.

Hourly temperatures were converted to maximum, minimum, and average weekly temperatures. A one-way ANOVA was performed to test for differences in the mean temperature (maximum, minimum, and average weekly temperature) across the trapping season among the low, middle, and high elevation bands. Only sites with complete data and only weeks when data were collected in all elevation bands were used.

Table 3. *P* values for MRPP testing for differences in beetle species abundance among low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in north-central Arizona

Species	*P* value			
	All bands[a]	L versus M	L versus H	M versus H
I. pini	0.240	—	—	—
I. lecontei	<0.001	0.007	<0.001	0.031
I. calligraphus	<0.001	0.027	<0.001	0.012
I. latidens	0.569	—	—	—
I. knausi	<0.001	0.162	<0.001	<0.001
D. frontalis	<0.001	0.058	<0.001	0.009
D. brevicomis	0.013	0.017	0.217	0.024
D. adjunctus	<0.001	<0.001	<0.001	0.003
D. approximatus	0.002	0.112	0.005	0.007
D. valens	0.002	0.207	0.001	0.019

[a] H$_o$, low, middle, and high elevation means are similar; L, low elevation band; M, middle elevation band; H, high elevation band.

Because significant data loss occurred in 2004, only data from 2005 and 2006 were used in the analysis. Temperature data were collected from all elevation bands from the weeks of 26 April to 29 November 2005 and from the weeks of 7 March to 4 December 2006.

Results

Beetle Abundance. A total of 90,558 bark beetles, comprising five *Ips* species and six *Dendroctonus* species, were collected over three trapping seasons. *Ips* species included *I. pini, I. lecontei, I. calligraphus ponderosae* Swaine, *I. latidens* LeConte, and *I. knausi* Swaine. *Dendroctonus* species included *D. frontalis, D. brevicomis, D. adjunctus* Blandford, *D. approximatus* Dietz, *D. valens* LeConte, and *D. ponderosae*. All species, other than *D. ponderosae*, were found in all three elevation bands. *D. ponderosae* was only captured at six high elevation sites and one middle elevation site. Total Scolytinae abundance was similar across the elevation bands of this study ($P = 0.682$). Separated by genera, *Dendroctonus* abundance was similar among the three bands ($P = 0.926$), whereas *Ips* abundance was different among the elevation bands ($P = 0.050$). *Ips* species as a whole were more abundant at low and middle elevations compared with high elevations.

Ips lecontei and *I. calligraphus ponderosae* abundance differed among the elevation bands (Table 3). Both species were most common at low elevation sites, and abundance decreased with each increase in elevation band. *D. frontalis* was most abundant at low and middle elevation sites, whereas *D. brevicomis* was most common in the middle elevation band (Table 3). *I. knausi, D. approximatus,* and *D. valens* were most abundant at high elevation sites (Table 3). *Dendroctonus adjunctus* was most common at high elevation sites; abundance decreased with each decrease in elevation band (Table 3). *I. pini* and *I. latidens* abundance was similar across elevations (Table 3). *D. ponderosae* (data not shown) abundance was low among all the elevation bands and therefore was not statistically analyzed; however, most beetles (97.9% of 48) were caught at high elevation sites.
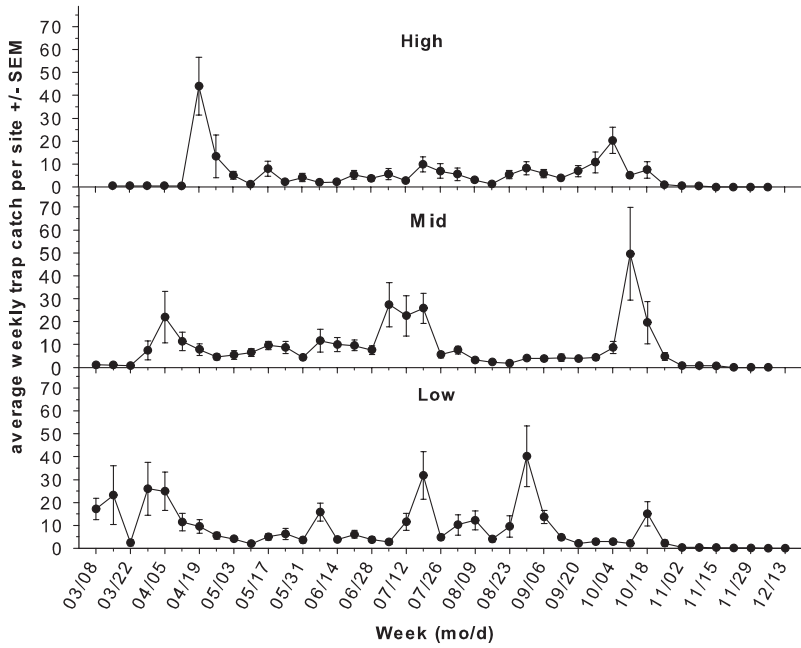
Fig. 2. Seasonal beetle captures of *I. pini* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.

Flight Periodicity. *Ips pini* flight activity in the low elevation band occurred from at least early March through November (Fig. 2). In general, flight was initiated 1–4 wk later and was terminated 1–2 wk earlier with each increase in elevation band. There were distinct peaks in beetle captures in all elevation bands, but the number, timing, and magnitude of those peaks varied across elevation and years (Fig. 3; only data for low elevation sites are plotted). Because of this annual variation, temporal patterns for each year were analyzed individually. *I. pini* trap catches were highest in 2005 in all elevation bands. At low elevation
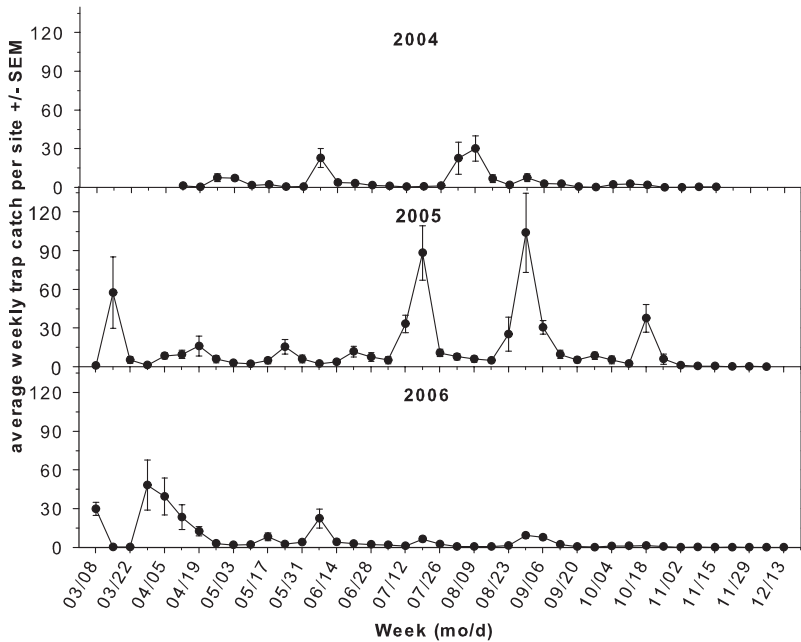

Fig. 3. Annual graphs of seasonal trap catches of *I. pini* in the low elevation band (1,600–1,736 m) in ponderosa pine forests of northcentral Arizona, 2004–2006.
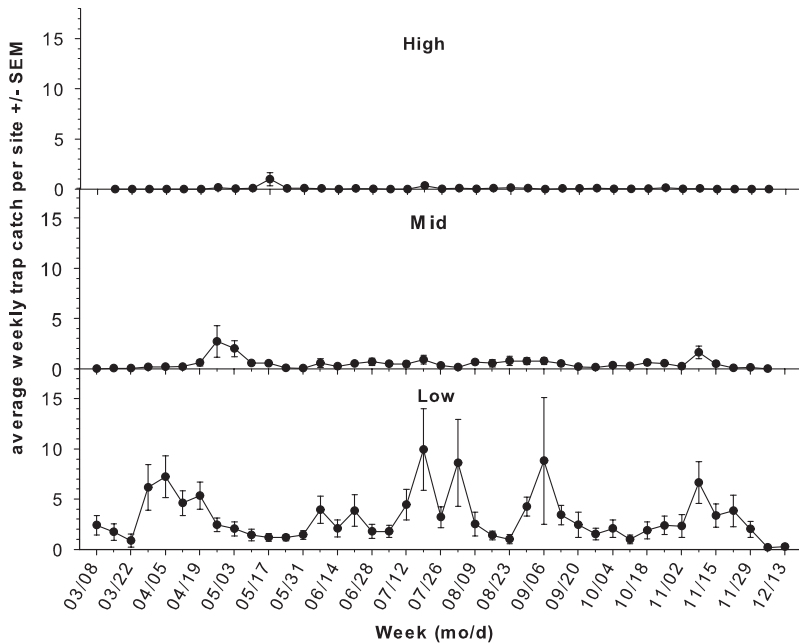
Fig. 4. Seasonal beetle captures of *I. lecontei* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.

sites in 2005, there were four distinct peaks in *I. pini* captures observed in March, July, August, and October. Peaks in trap captures for 2004 and 2006 were smaller in magnitude and less synchronous across sites. In addition, a fall peak in trap catches was not observed. At middle elevation sites in 2005, spring flight activity was followed by large peaks in July and October (data not shown). As in the low elevation band, peaks in flight activity were much smaller and less synchronous across sites in 2004 and 2006. At high elevation sites in 2005, July and September peaks were observed (data not shown). In 2006, traps were deployed a month earlier, and an April peak in trap catches was observed before dropping to much lower numbers the rest of the season. No distinct peaks were observed in 2004.

Ips lecontei flight activity was recorded as early as the first week of March and as late as the first week of December (Fig. 4). With each increase in elevation band, flight activity began at least 1–2 wk later and terminated at least 1–2 wk earlier. Beetle captures were low in the middle and high elevation bands, so seasonal abundance patterns were only analyzed in the low elevation band. Similar to *I. pini*, seasonal abundance was analyzed by year, because there was distinctive annual variation in the temporal patterns of trap catches (Fig. 5; only data for low elevation sites are plotted). However, there was also a high degree of variation among sites each year. For example, peaks observed in the summers of 2004 and 2005 in the low elevation band were driven by high trap catches at only a few sites, and these sites accounted for approximately one half of the total *I. lecontei* captured at low elevations.

Ips calligraphus ponderosae flight activity was observed as early as the first week of March and as late as the end of November (Fig. 6). Flight initiation was delayed 1–3 wk with each increase in elevation band and ended almost 4 wk earlier in the high elevation band than in the low and middle elevation bands. There was annual variation in the temporal pattern of trap catches, so years were analyzed individually (data not shown). In 2004 and 2005, there were three peaks in trap catches in the low elevation band observed in the spring, summer, and fall. In 2006, *I. calligraphus ponderosae* abundance declined sharply, and no peaks were observed. In 2004 and 2006, there were two peaks in captures at middle elevation sites, occurring in May and October (data not shown). In 2005, the highest trap catch occurred in July (data not shown). There was minimal flight activity at high elevation sites (Fig. 6).

Ips latidens captures were low throughout the trapping study, collecting <200 beetles each year in each elevation band (Fig. 7). Flight activity began by mid-April in all elevation bands and peaked by early May. A midsummer increase in flight activity was observed in the low and middle elevation bands. *I. latidens* flight activity ended by late September at all elevations.

Ips knausi trap catches were low, totaling <100 beetles each year in each elevation band (data not shown). *I. knausi* were caught as early as mid-March and as late as mid-November; however, beetles were only captured in the spring and fall. At high elevations, 93.7% of the 158 *I. knausi* captured were caught from September to November. The other 6.7% were captured in April and May.

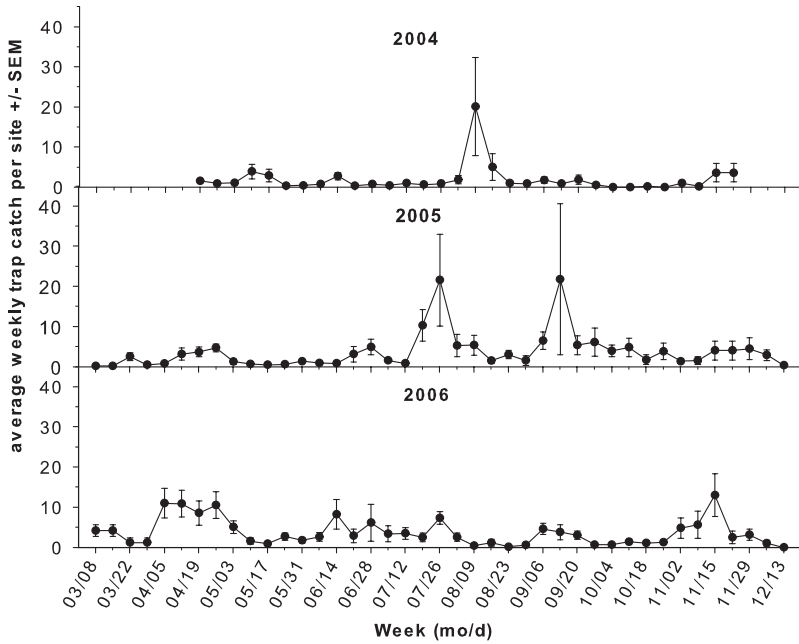*Dendroctonus frontalis* flight activity occurred from early March to late November (Fig. 8). With each

Fig. 5. Annual graphs of seasonal trap catches of *I. lecontei* in the low elevation band (1,600–1,736 m) in ponderosa pine forests of northcentral Arizona, 2004–2006.

increase in elevation band, spring flight activity was delayed by ≈1 mo, whereas flight activity usually terminated within 1 wk of each other. At low elevations, there was low to moderate flight activity through the spring and summer, followed by a large increase in beetle captures from September to November. At middle elevation sites, beetle numbers remained fairly low during the spring, but flight activity increased from July to October. At high elevations, flight activity was low throughout the year.

Dendroctonus brevicomis flight activity occurred from early March to late November (Fig. 9). In gen-
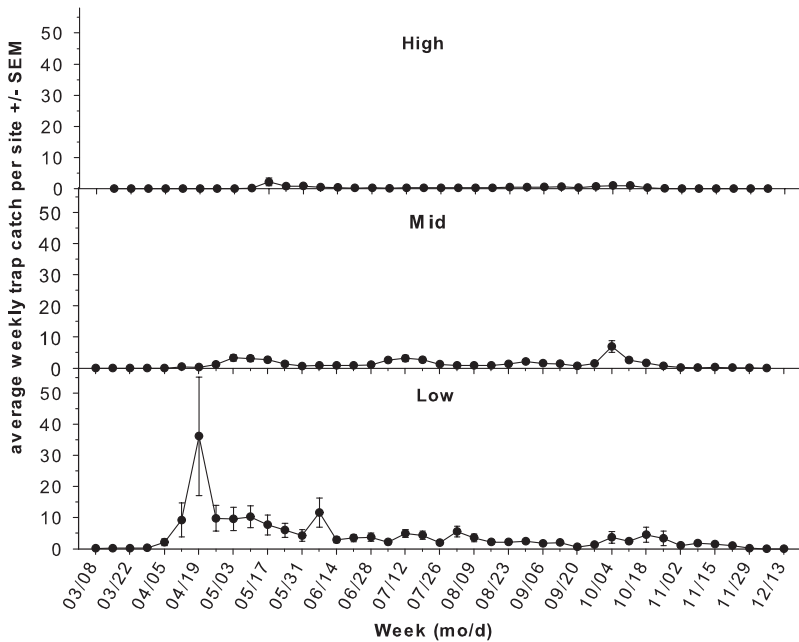

Fig. 6. Seasonal beetle captures of *I. calligraphus ponderosae* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.
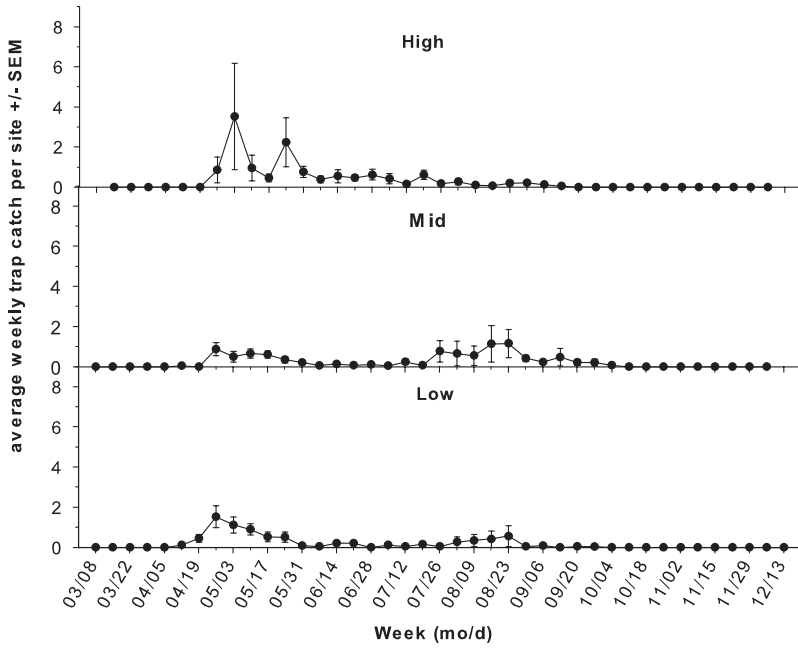
Fig. 7. Seasonal beetle captures of *I. latidens* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.

eral, flight initiation was delayed by 1 mo with each increase in elevation band, whereas flight termination occurred within 1 wk of each other. In the low and middle elevation bands, *D. brevicomis* flight activity was steady throughout the trapping season, with no distinct peaks in beetle captures. In the high elevation

band, increased beetle catches occurred in May and June before falling to lower numbers the rest of the season.

Two distinct flight periods were recorded for *D. adjunctus*, one in the spring and the other in the fall (Fig. 10). The smaller spring flight occurred from late
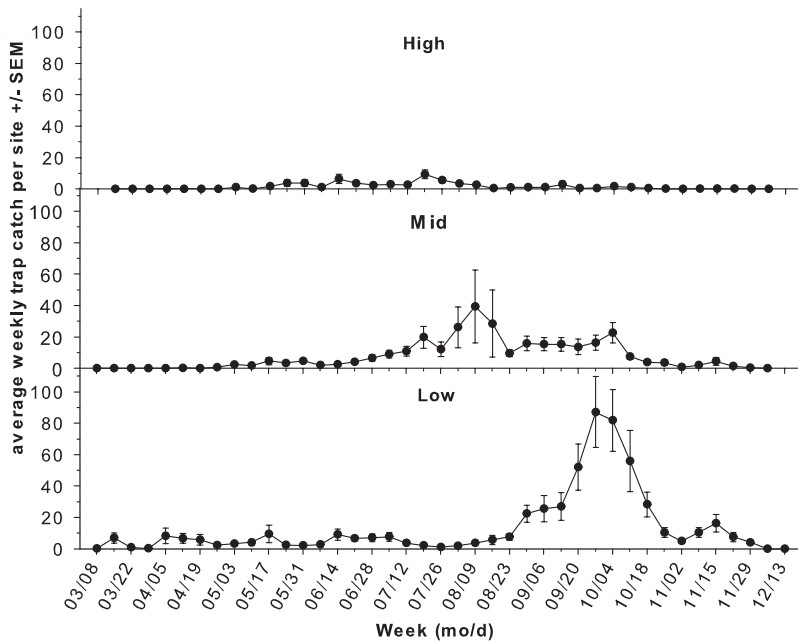

Fig. 8. Seasonal beetle captures of *D. frontalis* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.

Fig. 9.   Seasonal beetle captures of *D. brevicomis* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.
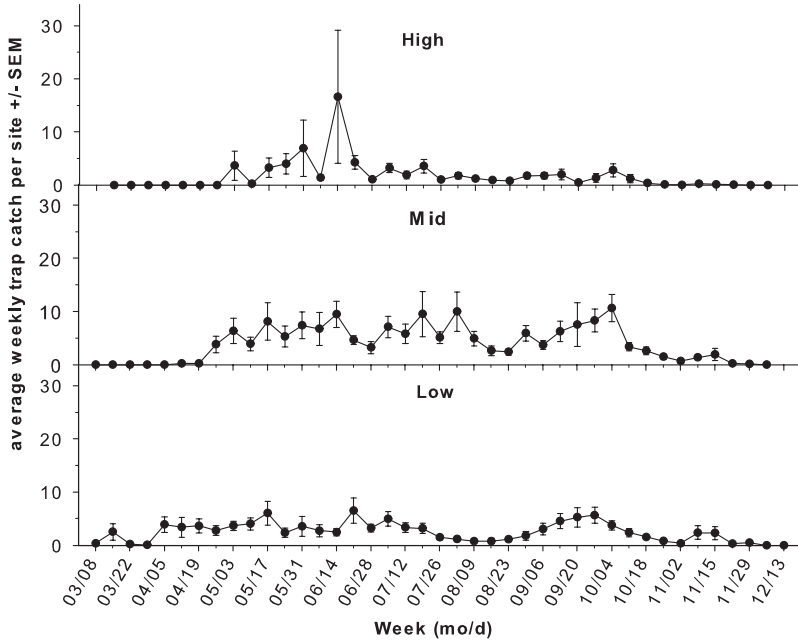
March to early July and the larger fall flight occurred from early September to late November. With each increase in elevation band, the proportion of beetles captured in the spring also increased. At middle elevations, the spring capture accounted for only 13.8% of the 3,371 beetles caught, whereas at high elevations,

the spring flight accounted for 27.6% of the 8,480 beetles captured.

Dendroctonus approximatus flight activity occurred from early March to mid-November (Fig. 11). With each increase in elevation band, beetle flight was initiated 1–2 wk later. Flight activity at high elevation
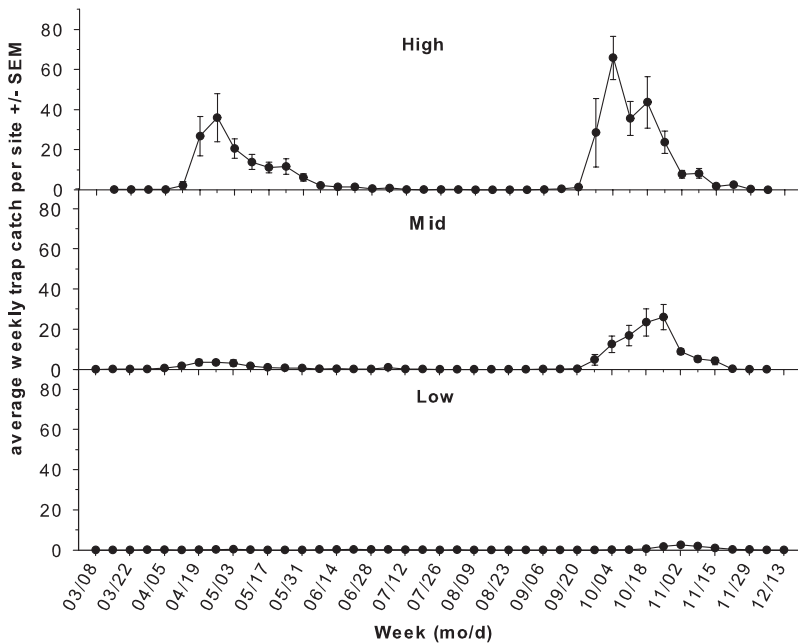

Fig. 10.   Seasonal beetle captures of *D. adjunctus* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.

Fig. 11. Seasonal beetle captures of *D. approximatus* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.
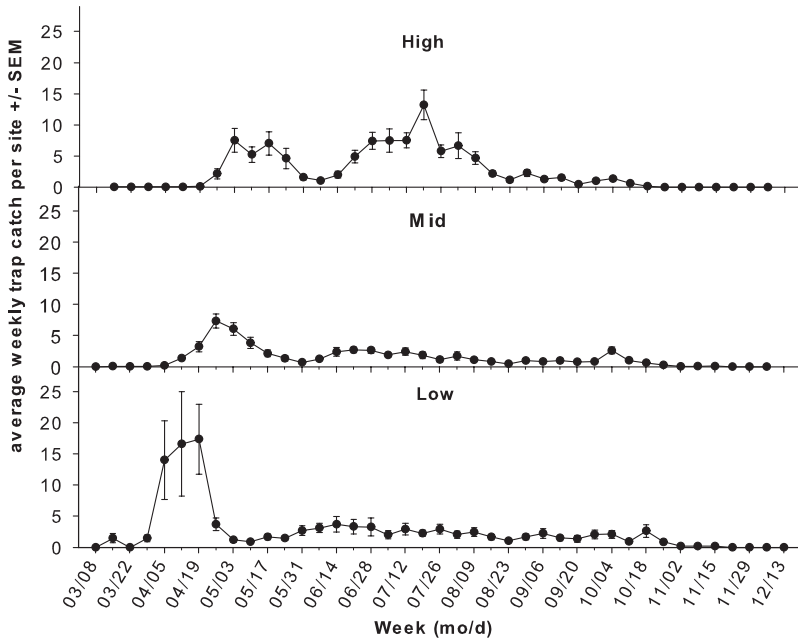
sites terminated ≈3 wk earlier than the low and middle elevation sites. In the low and middle elevation bands, beetle captures peaked in the spring (April/May) before tapering off to lower numbers the rest of the season. At high elevations, there was a May peak in beetle captures, followed by another increase in trap catches in June and July.

Dendroctonus valens flight activity occurred from early April to late October (Fig. 12). Flight initiation and cessation occurred within 1–2 wk of each other
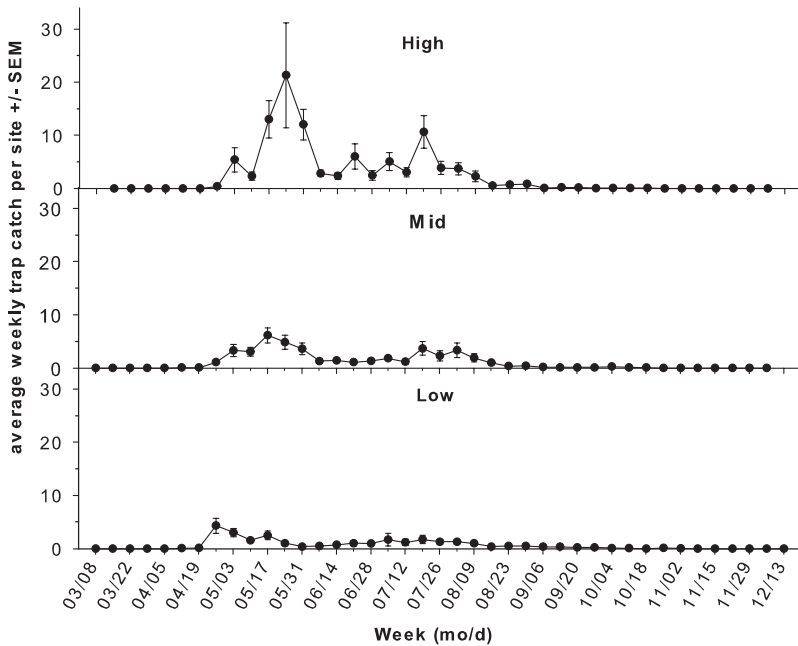

Fig. 12. Seasonal beetle captures of *D. valens* at low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 2004–2006.
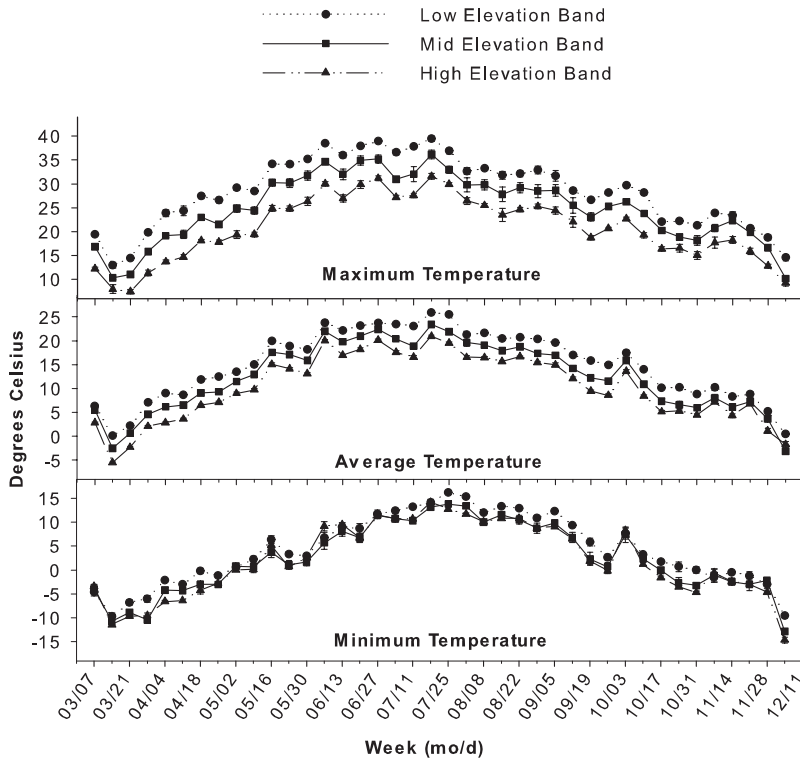
Fig. 13. Weekly maximum, average, and minimum temperatures for low (1,600–1,736 m), middle (2,058–2,230 m), and high (2,505–2,651 m) elevation bands in ponderosa pine forests of northcentral Arizona, 07 March 2006 to 4 December 2006.

across elevation. At all elevations, a spring peak in beetle captures was followed by lower beetle flight activity in the summer. Few beetles were captured in the fall.

Although only 48 *D. ponderosae* were captured in this study, the majority (77.1%) of trap catches occurred from early August to early September (data not shown).

Temperature. Average and maximum weekly temperatures varied among elevation bands ($P < 0.001$ for 2005 and 2006; Fig. 13; only data for 2006 plotted). However, minimum weekly temperatures did not significantly differ across elevation ($P = 0.451$, 2005; $P = 0.132$, 2006; Fig. 13). In 2005 and 2006, the average maximum weekly temperature in the low band was 2.8 and 3.6°C warmer than the middle elevation band, which was 4.5 and 4.4°C warmer than the high elevation band.

Discussion

Beetle Abundance and Seasonality Across Elevation. According to our data, the elevation range within which ponderosa pine grows in northcentral Arizona is suitable habitat for most *Ips* and *Dendroctonus* species. Ten of the 11 species collected were found throughout the entire elevation range of the study (1,600–2,651 m). Total Scolytinae abundance, regardless of species, was similar among elevation bands. *Dendroctonus* abundance showed no strong eleva-

tional trends, whereas *Ips* abundance was greatest in the low and middle elevation bands. *I. lecontei, D. frontalis*, and *D. brevicomis*, all considered primary tree killing species in Arizona, should be more of a concern at elevations between 1,600 and 2,230 m, whereas *D. adjunctus* should be a concern in ponderosa pine above 2,505 m. *I. pini* should be considered an important threat at all elevations.

Elevational trends present in the distribution of certain bark beetle species suggest that elevation should be a factor included in ponderosa pine stand hazard ratings specific to the southwest. However, elevation trends for certain species may vary from region to region. For example, in the Sierra Nevada, *D. brevicomis* abundance was inversely related to elevation (Fettig et al. 2005), whereas, in Arizona, *D. brevicomis* was most abundant in the middle elevation band. Consequently, inclusion of an elevation factor and how it interacts with stand characteristics in stand hazard ratings systems should be specific to individual regions.

Our observations on flight periodicity agree with previous reports for many species in the southwest. However, several aspects of flight seasonality, including length of flight season and timing of peak flight activity, varied across elevation and occasionally among years. Although bark beetle flight activity occurred from March through December at lower elevations, the flight period generally shortened as elevation increased. The shortened flight period was

primarily a result of delayed flight initiation in the spring. Flight initiation occurred at least 2– 4 wk earlier at low and middle elevations compared with high elevation sites for several species. Knowledge of flight activity for several species and how it changes across elevation should improve timing of forest management activities in Arizona.

Ips pini abundance was similar in all elevation bands (Fig. 2). This finding agrees with a recent Sierra Nevada, CA, study that found no significant relationship between trap catch of *I. pini* and elevation (Fettig et al. 2005). *I. pini* flight activity began in March at low and middle elevation sites, whereas spring flight initiated ≈1 mo later in the high elevation band. At middle and high elevations, there were three peaks in beetle captures occurring in April/May, June/July, and September/October, suggesting two generations per year, which agrees with previous reports on *I. pini* flight activity (Livingston 1979, Parker 1991, Kegley et al. 1997, Gaylord et al. 2006). In the low elevation band, there appeared to be four peaks in flight activity (one in the spring, two in the summer, and one in the fall) in 2005 (Fig. 3), suggesting three generations per year. Warmer temperatures (in the low elevation band) favor a longer period of flight activity and faster development time for each generation (Livingston 1979). The temporal pattern in trap catches in 2004 and 2006 at low elevation sites was different than in 2005, when *I. pini* abundance was higher. The 2004 and 2006 patterns were weaker because the timing of peak beetle captures was not as synchronous across sites. This asynchrony may be explained by lower beetle abundance these 2 yr. It has been suggested that when population density is low, there tends to be asynchrony between peaks in emergence and dispersal flights (Gara et al. 1999). Conversely, as populations increase to epidemic numbers, emergence and dispersal become more synchronized.

Ips lecontei was most abundant in the low elevation band (Fig. 4). This finding corresponds with observations that ponderosa pine mortality caused by *I. lecontei* occurs primarily at the lower elevational range of ponderosa pine in Arizona (Parker 1991). *I. lecontei* flight activity at low and middle elevations began in March, which corresponds with recent observations on flight initiation near Flagstaff, AZ (elevation, 2,080 m) (Gaylord et al. 2006). *I. lecontei* has been reported to emerge in April and May in Arizona (Chansler 1964, Ostmark 1966, Massey and Parker 1981), which matches our results for the high elevation band. Our observed dates of flight termination (November–December) are later than observations by Gaylord et al. (2006) but similar to those of Ostmark (1966) in a study on the Prescott National Forest, AZ (elevation, 1,800 m). *I. lecontei* is reported to have three generations a year (Chansler 1964, Ostmark 1966, Furniss and Carolin 1977, Massey and Parker 1981). Because parent adults and their progeny are flying and attacking trees at the same time, determining definite flight periods for each generation can be difficult (Ostmark 1966). Our study did not provide strong insight into the flight periodicity of *I. lecontei*. Peaks observed in

our data were not necessarily reflective of brood emergence across the elevation band, because they were driven by high trap catches at one or two sites occurring at different times of the season (Fig. 5). In addition, the majority of beetle catches were aggregated among a few sites.

To our knowledge, there is no published information on the biology and flight seasonality of *I. calligraphus ponderosae*, the western subspecies of *I. calligraphus* (Germar) (Furniss and Carolin 1977). *I. calligraphus ponderosae* was most abundant at low elevation sites (Fig. 6). Flight initiation at low elevations occurred at least 1.5 mo earlier (March) than flight initiation at middle and high elevations. At low and middle elevation sites, flight activity terminated in November but ended ≈1 mo earlier at high elevation sites. At low elevations there were spring, summer, and fall peaks in beetle captures. There appeared to be the same pattern at middle elevations, but there was much lower flight activity in the middle elevation band, and peaks in captures were not as synchronous across the sites.

Ips latidens was equally abundant across elevation (Fig. 7). *I. latidens* flight activity occurred from April to September in all elevation bands, which matches the flight season observations by Gaylord et al. (2006). There was a distinct peak in beetle flight activity during the spring, which is also consistent with previous reports on flight activity of this species (Miller and Borden 1985, Gaylord et al. 2006). In addition, there was a smaller increase in beetle captures that occurred in midsummer, which was most likely comprised of reemerged adults (Miller and Borden 1985).

Ips knausi was most abundant in the high elevation band and was collected in the spring and fall, primarily during October and November. These findings agree with a previous report on *I. knausi* flight seasonality in the Kaibab National Forest, AZ, north of the Grand Canyon, which also observed an association between *I. knausi* and *D. ponderosae* (Blackman 1931). Although the majority of *I. knausi* and *D. ponderosae* were captured in the high elevation band of this study, *D. ponderosae* trap catches were too low to make observations on an association between the two species. However, seasonal beetle captures of *I. knausi* coincided with the spring and fall flights of *D. adjunctus* (Fig. 10). Additionally, the greatest number of *I. knausi* and *D. adjunctus* were captured at the same high elevation site. This may suggest that this *Ips* species has a close association with *D. adjunctus* in areas where *D. adjunctus* is prevalent and *D. ponderosae* is not.

Dendroctonus frontalis was most abundant in the low and middle elevation bands (1,600–2,230 m; Fig. 8), which overlaps with the preferred elevation range (1,100–2,000 m) found in Mexico (Salinas-Moreno et al. 2004). Flight initiation of *D. frontalis* was related to elevation, as spring flight activity was delayed ≈1 mo with each increase in elevation band. Middle elevation flight activity occurred from April to November, consistent with recent findings on *D. frontalis* near Flagstaff, AZ (Gaylord et al. 2006). Previous research has

suggested that *D. frontalis* has three generations per year near Flagstaff, AZ (Gaylord 2004). The number of generations was difficult to interpret from the seasonal pattern of trap catches for any elevation band in our study. Although there was a large increase in beetle captures that extended multiple months over the summer and fall, there were no distinct peaks (suggesting brood emergence) in flight activity that would suggest multiple generations within a trapping season. This is most likely a reflection of overlapping generations (Wood 1982).

A previous report suggested that *D. brevicomis* was most commonly found in forests with a middle elevation level between 600 and 1,800 m (DeMars and Roettgering 1982). In this study, *D. brevicomis* was most commonly found at an elevation range of 2,058–2,230 m and showed no clear elevational trend. Our results contrast with findings in the Sierra Nevada, CA, study that reported an inverse relationship between *D. brevicomis* and elevation (Fettig et al. 2005). *D. brevicomis* flight initiation was delayed ≈1 mo with each increase in elevation band (Fig. 9). At low elevation sites, flight activity occurred from March to November. These results agree with previous research describing *D. brevicomis* as having three to four generations at lower elevations, with attacks occurring from March to November (Massey 1961, DeMars and Roettgering 1982, Wood 1982). Flight activity at middle elevations occurred from April to November, which corresponds with previous findings by Gaylord et al. (2006) in this elevation band. At higher elevations, *D. brevicomis* is described as having two generations with attacks occurring in early June and late August (DeMars and Roettgering 1982). Although *D. brevicomis* was more active in June and July at high elevation sites, the rest of the summer and fall had greatly reduced beetle captures. There were no distinct peaks in *D. brevicomis* captures, suggestive of overlapping broods or reemerging adults (Miller and Keen 1960, Massey 1961, Stark and Dahlsten 1970, Wood 1982).

Timing of flight activity was similar for *D. frontalis* and *D. brevicomis* (Figs. 8 and 9), with dates of flight initiation and cessation in each elevation band almost identical for both species. Gaylord et al. (2006) reported similar seasonal patterns in *D. brevicomis* and *D. frontalis* captures at a study site near Flagstaff, AZ. This was not evident in the temporal graphs of each species by elevation band. Synchrony between *D. brevicomis* and *D. frontalis* flight activity seems to be more of a site-specific, rather than region-wide, occurrence.

High elevation sites comprised the majority (70.1% of 12,090) of *D. adjunctus* trap catches, followed by middle (27.9%) and low elevation sites (2.0%). This corresponds with a study in Mexico that established *D. adjunctus*, although found at elevations ranging from 1,600 to 3,929 m, was more abundant at a higher elevation interval of 3,100–3,500 m (Salinas-Moreno et al. 2004). The timing of *D. adjunctus* peak flight activity was relatively consistent across elevation (Fig. 10). There were two distinct flight periods, one in each the spring and the fall, with little to no activity in between.

These findings are in agreement with earlier reports on *D. adjunctus* flight activity (Blackman 1931, Chansler 1967, Massey et al. 1977, Wood 1982, Gaylord 2004), suggesting 1–1.5 generations per year. The spring flight, which is mostly comprised of reemerged overwintering adults (Chansler 1967), occurred in April and May. The fall flight occurred primarily in October. The proportion of reemerging adults flying in the spring increased as elevation increased.

Dendroctonus approximatus was most abundant in the high elevation band (2,505–2,651 m; Fig. 11), which is higher than the favored elevation interval (2,100–2,500 m) in Mexico (Salinas-Moreno et al. 2004). In its northern range, flight activity of this univoltine beetle starts in early June and ends in October (Furniss and Carolin 1977, Wood 1982), whereas flight activity occurs year round in Mexico (Wood 1982). Our results fit somewhere between the two, because the flight period at low elevation occurred from mid-March to mid-November. With each increase in elevation band, flight activity began ≈2 wk later. Aside from a spring increase in beetle captures, there was no consistent pattern in trap catches across elevations or years. This lack of peak flight activity was most likely caused by an extended emergence period lasting through the spring and summer (Blackman 1931, Wood 1982). In the high elevation band, there appeared to be a second increase in beetle captures in June and July, which is consistent with previous knowledge of peak *D. approximatus* flight activity in its northern range (Wood 1982) and peak attack activity in Kaibab National Forest (Blackman 1931).

Dendroctonus valens was most abundant in the high elevation band (2,505–2,651 m; Fig. 12), which is higher than the favored elevation interval (2,100–2,500 m) for this species in Mexico (Salinas-Moreno et al. 2004). The length of flight season for *D. valens* does not seem to be strongly related to elevation, because the flight period occurred from April to October at all elevation bands. This period of flight activity is similar to the reported flight period in its northern range (Wood 1982). *D. valens* has one generation in 2 yr in the coldest parts of its range, but may have two to three generations per year in warmer climates (Smith 1971). Our observations on flight activity are similar to previous findings on flight periodicity of *D. valens* (Blackman 1931, Smith 1971, Fettig et al. 2004b, 2006, Gaylord et al. 2006). Flight activity peaked in May at all elevation bands. After the spring peak, there was an occasional midsummer increase in beetle captures. This could be reflective of the extreme overlapping in generations for this species (Wood 1982). Major flight activity tapered off by August at all elevations.

A small number of *D. ponderosae* were captured in this study. However, it is logical to conclude that *D. ponderosae* prefers higher elevation forests in this region, because most captures occurred above 2,505 m. This corresponds with previous research in Kaibab National Forest, AZ, which reported heaviest infestations occurring above 2,438 m (Blackman 1931). In addition to our results, previous studies also reported limited beetle presence in the ponderosa pine forests

near Flagstaff, AZ (Sanchez-Martinez and Wagner 2002, McHugh et al. 2003, Gaylord et al. 2006). With the exception of the Kaibab Plateau in northern Arizona (Blackman 1931, USDA 2001–2004), its role in the bark beetle community seems to be limited in Arizona ponderosa pine forests. The highest elevation site (2,651 m) comprised 66.0% of the 48 *D. ponderosae* trap catches. This site was located in a mixed conifer tree stand on the San Francisco Peaks. The preferred host for *D. ponderosae* in this part of Arizona seems to be limber pine (USDA 2001–2004; J.D.M., unpublished data). Most *D. ponderosae* were captured from early August to early September, which corresponds with previous reports on *D. ponderosae* flight activity in ponderosa pine forests (Blackman 1931, McCambridge 1964).

In this study, we used lure combinations that targeted three bark beetle species of concern (*I. pini, I. lecontei,* and *D. brevicomis*) in Arizona's ponderosa pine forests. Based on previous research in northern Arizona (Gaylord et al. 2006), it was expected that these three lure combinations would also attract other *Ips* and *Dendroctonus* species. Therefore, these lures were also used to describe the abundance and seasonality of three additional *Ips* and five additional *Dendroctonus* species. However, there are commercially available lure combinations targeting other species in this study that may facilitate a more thorough description of the abundance and flight seasonality of some bark beetle species in this region. While pheromone traps are a widely used tool for monitoring bark beetle abundance and flight seasonality, some bark beetle species experience temporal variation in response to their lures (Teale and Lanier 1991, Aukema et al. 2000, Bentz 2006). This may impact the interpretation (i.e., estimating number of generations and flight seasonality) of pheromone trap results. Further study is needed to verify how the timing of pheromone trap catches relates to beetle phenology and voltinism for the bark beetle species in our region.

Efforts were made to cover the entire flight period, but our study does not account for possible winter flight activity of bark beetles. In a previous study, *I. pini* was the only bark beetle species captured during the winter months near Flagstaff, AZ, and then in only very limited numbers (Gaylord et al. 2006). These results suggest that flight activity of bark beetles during the winter should not be a concern for resource managers (Gaylord 2004). While this conclusion is applicable for bark beetle flight activity in the middle and high elevation bands of this study, the low elevation band may experience more flight activity during mild winters. Zero trap catches were recorded for successive weeks in late fall of 2005 and 2006 for all species except *I. lecontei.* However, temperatures were frequently warm enough in January and February 2006 (several weeks with maximum temperatures above 15°C) for some species, such as *I. pini,* to be flying. Further study is needed to determine the extent of winter flight activity of species at elevations below 1,736 m.

Temperature and Elevation. As expected, maximum weekly temperatures were warmest at low elevation sites, and temperatures cooled as elevation increased (Fig. 13). Specific relationships between temperature and flight data collected in this study and from Gaylord (2004) were analyzed by Gaylord et al. (2007). Based on weekly trap catch data and associated maximum weekly temperatures, temperature thresholds exceeding 15°C were estimated for spring flight initiation for most bark beetle species, with the exception of *D. adjunctus,* which started flying at 14.5°C.

These results provide a physiological explanation for the delay in spring flight initiation for several species as elevation increases. For example, in 2006, temperatures were already >15°C during the first collection week at low and middle elevations, and beetle captures included *I. pini, I. lecontei, I. calligraphus ponderosae, D. frontalis,* and *D. brevicomis.* Threshold temperatures were not reached until mid-April at high elevations, and therefore, flight initiation of the aforementioned beetles did not occur until this time.

Flight cessation also seems to be affected by temperature differences across the elevation gradient. As maximum temperatures fell below threshold levels (15–21°C), bark beetle flight activity tapered off. Temperatures cooled earlier in the year at high elevation sites. For example, in 2005, maximum temperatures declined to threshold levels at least 1 mo earlier in the high elevation band than in the middle and low elevation bands. Accordingly, last captures of *D. frontalis* and *D. brevicomis* occurred ≈1 mo earlier at high elevations. In 2006, maximum temperatures in all elevation bands cooled below threshold levels within 2 wk of each other, and flight cessation of *D. brevicomis* and *D. frontalis* occurred within the same amount of time.

Flight initiation and cessation for some species, such as *D. valens,* did not correspond well with threshold temperatures. For example, in 2006, when several species were flying in March at low elevation sites (presumably as a response to threshold temperatures being exceeded), *D. valens* was not captured until late April, within 1 wk of first trap catches in the middle and high elevation bands. Also, *D. valens* flight terminated before temperature thresholds were met in the fall. These results suggest other environmental cues, or a combination thereof, may influence flight activity of certain species.

Dendroctonus adjunctus and *I. knausi* have distinctly different seasonal patterns than the other beetles collected in this study, flying mostly in the spring and fall. In addition, these two species have a lower temperature threshold for flight initiation and maintain flight longer in the fall than other *Ips* and *Dendroctonus.* Gaylord et al. (2007) suggested the lack of summer flight activity may be explained by a maximum temperature threshold or other environmental cue associated with bark beetle flight.

According to our results, relatively small differences in average maximum weekly temperatures (3–5°C) associated with elevation change influenced the tim-

ing and length of beetle flight activity. These temperature differences could also play a role in the elevational distribution of bark beetle species, because the ability to survive cold winter temperatures may limit the abundance of some bark beetles (Ungerer et al. 1999, Lombardero et al. 2000), such as *I. lecontei* and *D. frontalis*, at higher elevations. This has implications for climate change, where warming temperatures may not only lengthen the period of flight activity and increase the number of generations per year, but also extend the range of abundant lower elevation bark beetles to higher elevations (Bale et al. 2002, Williams and Liebhold 2002), causing greater mortality to Arizona's ponderosa pine forests.

Acknowledgments

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