Seasonality and Lure Preference of Bark Beetles (Curculionidae: Scolytinae) and Associates in a Northern Arizona Ponderosa Pine Forest

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ABSTRACT Ponderosa pine forests in northern Arizona have historically experienced limited bark beetle-caused tree mortality, and little is known about the bark beetle community in these forests. Our objectives were to describe the flight seasonality and lure preference of bark beetles and their associates in these forests. We monitored bark beetle populations for 24 consecutive months in 2002 and 2003 using Lindgren funnel traps with five different pheromone lures. In both years, the majority of bark beetles were trapped between May and October, and the peak captures of coleopteran predator species, *Enoclerus* (F.) (Cleridae) and *Temnochila chlorodia* (Mannerheim), occurred between June and August. Trap catches of *Elacatis* (Coleoptera: Othniidae, now Salpingidae), a suspected predator, peaked early in the spring. For wood borers, trap catches of the Buprestidae family peaked in late May/early June, and catches of the Cerambycidae family peaked in July/August. The lure targeted for *Dendroctonus brevicomis* LeConte attracted the largest percentage of all *Dendroctonus* beetles except for *D. valens* LeConte, which was attracted in highest percentage to the lure targeted for *D. valens*. The lure targeted for *Ips pini* attracted the highest percentage of beetles for all three *Ips* species [*I.pini* (Say), *I. latidens* (LeConte), and *I. lecontei* Swaine] and the two predators, *Enoclerus* and *T. chlorodia*. The lures targeted for *D. valens* and *I. pini* attracted the highest percentage of beetles in the *Elacatis* genus and the Cerambycidae family. Beetles in the Buprestidae family showed no strong preference for any lure type.

KEY WORDS *Dendroctonus*, *Ips*, lure preference, phenology, *Pinus ponderosa*

BARK BEETLES (CURCULIONIDAE: SCOLYTINAE) have caused landscape-level mortality in many conifer forests across North America (e.g., Miller and Keen 1960, Furniss and Carolin 1977, Massey et al. 1977, Thatcher et al. 1980, Schmid and Amman 1992, Holsten et al. 1999) and have been studied extensively in many regions (e.g., Miller and Keen 1960, Stark and Dahlsten 1970, Waters et al. 1985). However, mortality from bark beetles in the ponderosa pine (*Pinus ponderosa* Douglas ex. Lawson) forests on the Colorado Plateau in northern Arizona has been low historically. Previous large-scale outbreaks in this region have been largely confined to the Kaibab Plateau in far northern Arizona (Blackman 1931, Parker and Stevens 1979). Overall, little is known about the bark beetle community in the Southwestern ponderosa pine forests (Sanchez-Martinez and Wagner 2002). In the 100 yr before 2002, no large-scale mortality attributed to bark beetles in the ponderosa pine forests surrounding Flagstaff, AZ, was documented (USDA Forest Ser-

vice Region 3, 1924–1952, Flagstaff Forest Health Protection, 1976–2000, Insect and Disease Condition Reports 2001–2003, Sanchez-Martinez and Wagner 2002).

Between 1995 and 2003, annual precipitation in Arizona was below the long-term mean for all but 1 yr (1998), and 2002 was the driest of these years (National Climate Data Center 2003). Across the state of Arizona, tree mortality attributed to bark beetles increased from 29,000 ha in 2001 to 283,000 ha in 2003 (Insect and Disease Condition Reports 2001–2003). During this same time period on the Coconino National Forest in northern Arizona, ponderosa pine mortality increased from 127 to 29,063 ha, with most of the mortality attributed to *Ips* spp. beetles (Insect and Disease Condition Reports 2001–2003).

Previous bark beetle research in the ponderosa pine forest near Flagstaff has been limited in duration, type of pheromone lures used, and by low beetle population levels. Although the climate in northern Arizona can include extended periods of warm weather at any time of the year, monitoring of bark beetle flights has only occurred between May and September (Sanchez-Martinez and Wagner 2002, Steed 2003). It is well established that several species of bark beetles use mass attack, mediated by unique

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pheromone signals, to kill trees (Wood D. L. 1982). Bark beetle predators and associated wood borers exploit these pheromone signals to locate their prey (Wood D. L. 1982, Miller et al. 1997, Raffa 2001, Allison et al. 2004). However, *I. pini* (Say) is the only species of bark beetle or predator that has been studied for pheromone specificity in northern Arizona (Steed 2003). Knowledge about the flight seasonality and effectiveness of lures for monitoring bark beetle populations and predator populations is needed by resource managers (Raffa 1991, Aukema et al. 2000a, b).

Our objectives were to describe the year-round flight seasonality of the major bark beetles and their associated predators and wood borers in the ponderosa pine forest near Flagstaff, AZ. Additionally we sought to describe the general pattern of lure preference for the bark beetle complex in this region of northern Arizona. We trapped for 2 yr using a range of commercially available pheromone lures.

Materials and Methods

Site Description

Our study site was located in the core area of the Northern Arizona University Centennial Forest, located ≈10 km west of Flagstaff, AZ (latitude 35°10′ N, longitude 111°45′ E, elevation 2,080 m). Four distinct seasons occur in this area, and it is considered to be in Holdridge's cool temperate steppe/moist forest lifezone class (International Research Institute 2003). Average annual precipitation for Flagstaff is 54 cm (1950–2003), of which >50% falls as winter precipitation and the rest occurs as late-summer rain (National Climate Data Center 2003). The frost-free season averages 115 d.

The first year of our study occurred during an exceptional drought year. In 2002, Flagstaff received only 65% of normal precipitation (National Climate Data Center 2003). The majority of this deficit was caused by lack of winter precipitation (16% of average precipitation in January–April, 53% in May–August, and 128% in September–December). Year 2, 2003, was also dry (84% of normal precipitation); however, the deficit was distributed more evenly throughout the year (95% in January–April, 91% in May–August, and 65% in September–December of normal precipitation).

The overstory at the study site is comprised mainly of ponderosa pine (99%) and Gamble oak (*Quercus gambellii* Nutt.) (1%), and the understory is sparse (10.8% average ground cover) and composed of bunch grasses with low (<5%) forb and shrub cover. There is no evidence of recent logging. Trees at the study site range from seedlings to old-growth. The range of tree size classes and high stand density (average basal area of 36.7 m²/ha) of ponderosa pine suggests an abundance of suitable hosts for several species of beetles (Miller and Keen 1960, Sartwell and Stevens 1975, DeMars and Roettgering 1982, Parker

1991, Schmid and Mata 1992, Kegley et al. 1997, Negrón 1997, Negrón et al. 2000, Negrón and Popp 2004). The aspect is generally east, with an average slope of 13%. Soils at the study site are >80 cm deep (Simonin 2003) and are composed of 65% typic Argiborolls, fine montmorrillonitic, deep gravelly loam, 20% Mollic Eutroboralfs, clayey-skeletal, montmorrillonitic, moderately deep cobbly loam, 10% Mollic Eutroboralfs, fine montmorrillonitic, moderately deep cobbly clay loam, and 5% Typic Argiborolls, clayey-skeletal, montmorillonitic moderately deep cobbly clay loam (Miller et al. 1995).

Study Design

To assess bark beetle flight activity, we used 50 Lindgren funnel traps (Phero Tech, Delta, Canada) (Lindgren 1983) arranged in 10 clusters distributed across ≈417 ha. Each cluster was located 50–430 m from the other clusters and had five eight-unit traps in a pentagon-shaped arrangement with a different lure type for each trap in a cluster. Lures, purchased from Phero Tech, were standard lures targeted for *Dendroctonus ponderosae* Hopkins, *D. brevicomis* LeConte, *D. frontalis* Zimmermann, *D. valens* LeConte, and *Ips pini*. Lure components were: *D. ponderosae* (three-component lure; myrcene, *exo*-brevicomin and *trans*-verbenol), *D. brevicomis* (three-component lure; *exo*-brevicomin, frontalin and myrcene), *D. frontalis* (frontalin), *D. valens* (three-terpene blend of *a*-pinene, *beta* pinene, and 3-carene), and *I. pini* (50/50 blend of ipsdienol and lanierone). Lures were changed using Phero Tech guidelines (≈50 d for *I. pini* lure, 90 d for *D. brevicomis*, *D. valens*, and *D. frontalis* lures, and 120 d for *D. ponderosae* lure at 20°C ambient air temperature) and observation was made of the contents of vials. Therefore, lures were replaced less frequently at cold temperatures and more frequently when temperatures exceeded 20°C. Traps were hung on conduit and placed a minimum of 50 m apart and at least 1 m from the closest tree. The base of each trap was ≈1 m above the ground. Open areas were avoided to minimize dispersal of pheromone plumes. The traps were rotated within each cluster on a regular basis (once every 1 or 2 wk depending on beetle flight activity) to minimize location impacts.

Beetles were collected from traps every 1–2 wk from January 2002 to December 2003 (24 mo). Beetles and their associated predators and wood borers were taken back to the laboratory and sorted to species according to Furniss and Carolin (1977) and Wood S. (1982). Species identifications were confirmed using voucher specimens in the laboratory and from samples shipped to Dr. John Moser, USDA Forest Service, Southern Research Station.

Statistical Analysis

Beetle Flight Seasonality. For each species we summed the total beetles captured across all five lures per cluster (*n* = 10) and divided by number of days in each sample period to obtain a mean number of bee-

tles captured per cluster per day for each sampling period. Trap catches were summed across lures in each cluster by species because of the lack of lure specificity in some species.

Lure Preference by Beetle Species. To test if there was a difference in lure preference for each beetle species, we used only those trapping periods in which we captured 10 or more beetles of a species. For each of these trap periods, we summed the total number of beetles captured for each lure type, divided the sum by the total number of beetles captured across all lure types for the same beetle species and trapping period, and multiplied by 100 to obtain the percentage captured by each lure type. We summed the percentages for each trap period by lure type to obtain a mean and SEM for percentage capture for each lure type. To test for significant differences in lure preference by each beetle species we used a χ^2 analysis. The null hypothesis was no difference in attraction to the different lure types, i.e., 20% of total capture per each of the five lures. Significance was established at $\alpha = 0.05$.

Occasionally, because of small sample sizes (<10 beetles captured per species per sample period), we were unable to perform statistical analysis for some years and species. Additionally, for some species, we only obtained data from two or three sample periods; in these instances, *P* values that are close to 0.05 should be interpreted with caution.

Results

Flight Seasonality of *Dendroctonus* Bark Beetles

Dendroctonus brevicomis. We caught a total of 1,651 *D. brevicomis* in 2002 and 2,834 in 2003. Beetles were caught from April to late October or early November (Fig. 1a). The highest trap catches in 2002 were in August and October, but in 2003, the peak was in June.

Dendroctonus frontalis. Initial yearly flights, number of beetles caught, and temporal distribution of peak captures for *D. frontalis* were remarkably similar to *D. brevicomis* in both years. In 2002, we caught a total of 1,274 *D. frontalis* and in 2003, 2,650. In both years, beetles were caught from April through November (Fig. 1b). The highest trap catches in 2002 were in August and October and in 2003 in June.

Dendroctonus adjunctus Blandford. In 2002, we caught a total of 592 beetles and in 2003, 519. Beetles were captured from March through November (Fig. 1c). In both years peak captures occurred in October.

Dendroctonus approximatus. In 2002, we caught only 9 beetles, and in 2003, we caught 75. In 2002, beetles were caught from April through July, and in 2003, from April through October (Fig. 1d). The highest trap catch for 2002 was in July and in 2003 in May.

Dendroctonus valens. We captured a total of 163 *D. valens* in 2002 and 358 in 2003. Beetles were caught from March or April through October. Peak capture in 2002 was in May and was in July in 2003.

Flight Seasonality of *Ips* Bark Beetles

Ips pini. We captured 631 beetles in 2002 and 3,268 in 2003. In 2002, beetles were captured from April through October, and in 2003, the first capture occurred in the first trapping period in January and, other than the months of February, December and the last 3 wk of November, we consistently captured at least one beetle per trapping period (Fig. 2a). In 2002, the highest capture occurred in August and September, and in 2003, the highest capture was in October.

Ips latidens (LeConte). In 2002, we caught a total of 382 *I. latidens*, and in 2003, we caught 587. Beetles were captured from April or May through September (Fig. 2b). Peak capture in 2002 was in April and was in May in 2003.

Ips lecontei Swaine. In 2002, we captured only 6 beetles, and in 2003, we caught 130. In 2002, beetles were not captured until August. In 2003, we caught the first beetle in March and, in both years, the last beetles were caught in October (Fig. 2c). Peak captures in both years were in October.

Flight Seasonality of Predators

Enoclerus Species (Coleoptera: Cleridae). We captured a total of 135 *Enoclerus* in 2002 and 365 in 2003. *Enoclerus* were captured from April through September or October (Fig. 3a). The highest capture of *Enoclerus* was in June for 2002 and July for 2003.

Temnochila chlorodia (Mannerheim) (Coleoptera: Ostomidae). In 2002, we caught 32 *T. chlorodia*, and in 2003, we caught 241. These beetles were captured from May through September (Fig. 3b). The highest capture was in July and August.

Elacatis (Coleoptera: [Othniidae, now Salpingidae]). In 2002, we caught 1,874 beetles, and in 2003, we caught 3,725. In 2002, beetles were captured from March through September, and in 2003, from January through December (Fig. 3c). Highest captures were early in the spring in April or May in both years.

Flight Seasonality of Associates

Cerambycidae. In 2002 we captured 213 wood borers from the family Cerambycidae, and in 2003, we captured 547. In 2002, beetles were captured from June through October, and in 2003, from April through September. Peak weekly capture occurred during July in both years.

Buprestidae. In 2002, we caught 348 wood borers in the family Buprestidae, and in 2003, we caught 156. Beetles were captured from April through September and October (Fig. 4b). Highest captures occurred in May in both years.

Other Scolytinae species captured in our traps and identified included *Hylurgops* spp., *Hylastes* spp., and *Pityogenes carinulatus.* However, because of very low
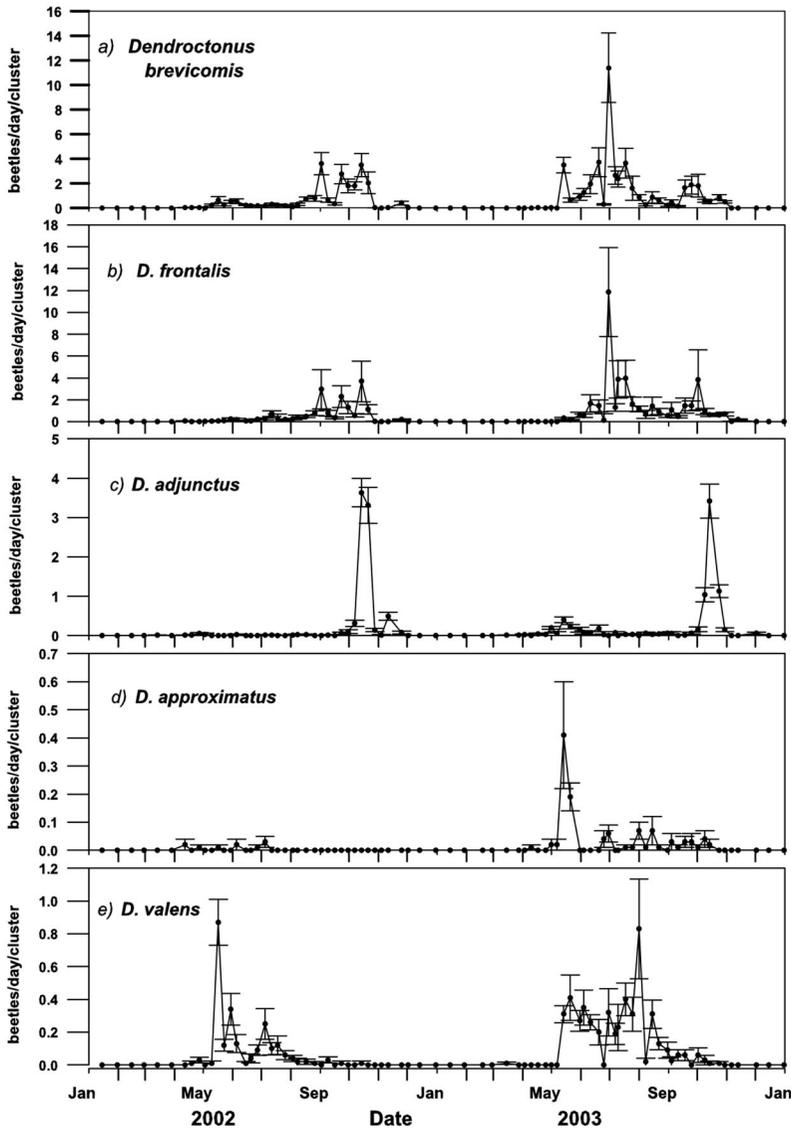
Fig. 1. Mean ± SEM number of (a) *D. brevicomis*, (b) *D. frontalis*, (c) *D. adjunctus*, (d) *D. approximatus*, and (e) *D. valens* caught in baited Lindgren funnel traps using five different lures in 10 clusters (*n* = 10) for each trapping period in 2002 and 2003. Scale of y axis differs among graphs.

numbers, these data were not analyzed. We captured no *D. ponderosae* in our traps.

Lure Preference of *Dendroctonus* by Species

Dendroctonus brevicomis. Captures differed among lures (*P* < 0.0001, *n* = 50, total number of beetles = 4,448). *D. brevicomis* was attracted in the highest percentage to the lure targeted for *D. brevicomis* (Fig. 5a). The other lure types (*D. frontalis*, *D. valens*, *D. ponderosae*, and *I. pini*) attracted only a small percentage of the total *D. brevicomis* caught.

Dendroctonus frontalis. Captures differed among lures (*P* < 0.0001, *n* = 45, total number of beetles = 3,877). *D. frontalis* was attracted in the highest percentage to the lure targeted for *D. brevicomis* (Fig. 5a). Attraction to other lure types was minimal.

Dendroctonus adjunctus. Captures differed among lures (*P* < 0.0001, *n* = 16, total number of beetles = 1,015). The highest percentage of this species was attracted to the lure targeted for *D. brevicomis* (Fig. 5a). However two other lure types, *D. frontalis* and *D. ponderosae*, were also attractive to this species.
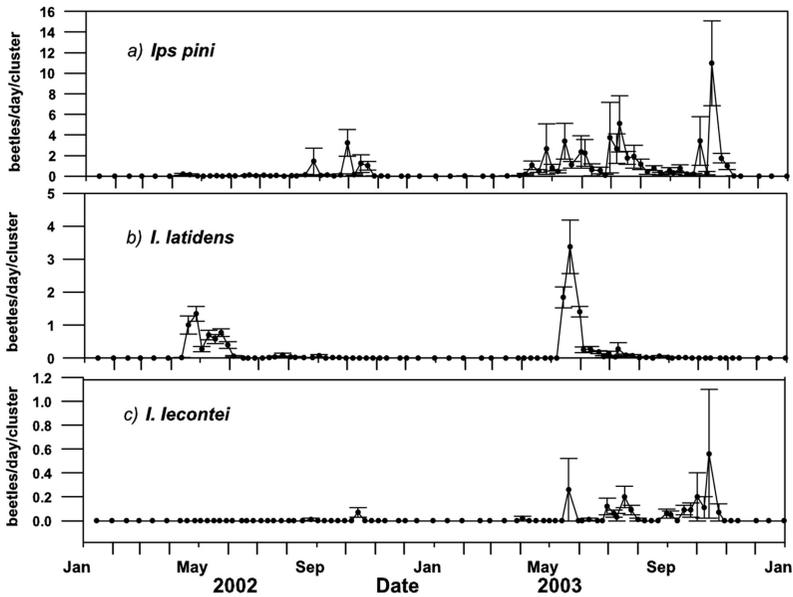
Fig. 2. Mean ± SEM number of (a) *I. pini*, (b) *I. latidens,* and (c) *I. lecontei* caught in baited Lindgren funnel traps using five different lures in 10 clusters (*n* = 10) for each trapping period in 2002 and 2003. Scale of y axis differs among graphs.

Dendroctonus approximatus. Because of a small sample size (total of nine individuals), lure preference was not analyzed in 2002. Captures differed among lures in 2003 (*P* < 0.0001); however, because of small trap catches, there were only two trapping periods that could be analyzed (*n* = 2, total number of beetles = 42). In 2003, the highest percentage of *D. ap-* *proximatus* was attracted to the lure targeted for *D. brevicomis* (Fig. 5a). The *D. ponderosae* lure also attracted ≈30% of the total beetles caught.

Dendroctonus valens. Captures differed among lures (*P* < 0.0001, *n* = 18, total number of beetles = 438). The highest percentage of *D. valens* was attracted to the lure targeted for *D. valens* (Fig. 5a).
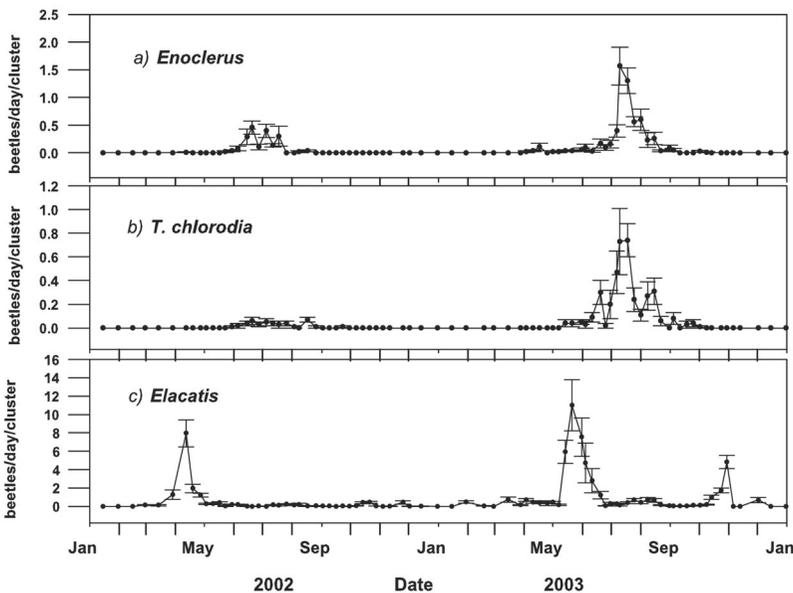

Fig. 3. Mean ± SEM number of (a) *Enoclerus* species, (b) *T. chlorodia,* and (c) *Elacatis* species caught in baited Lindgren traps using five different lures in 10 clusters (*n* = 10) for each trapping period in 2002 and 2003. Scale of y axis differs among graphs.
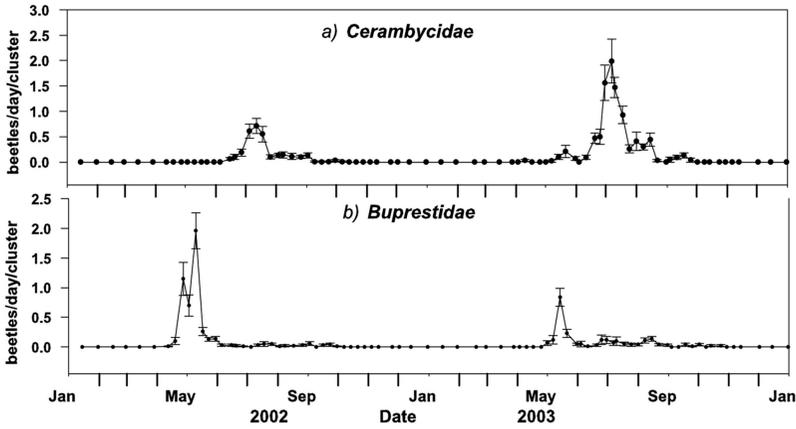
Fig. 4. Mean ± SEM number of (a) Cerambycidae and (b) Buprestidae caught in baited Lindgren traps using five different lures in 10 clusters ($n = 10$) for each trapping period in 2002 and 2003. Scale of y axis differs between graphs.

Lure Preference of *Ips* by Species

Ips pini. Captures differed among lures ($P < 0.0001$, $n = 38$, total number of beetles = 3,812). The majority of *I. pini* were attracted to the lure targeted for *I. pini* (Fig. 5b).

Ips latidens. Captures differed among lures ($P < 0.0001$, $n = 13$, total number of beetles = 900). The majority of this species was attracted to the lure targeted for *I. pini* (Fig. 5b).

Ips lecontei. In 2002, we caught few of these beetles (total of six) and therefore we limited our analysis to 2003. Captures differed among lures in 2003 ($P < 0.0001$, $n = 5$, total number of beetles = 84). In 2003, the highest percentage of this species was
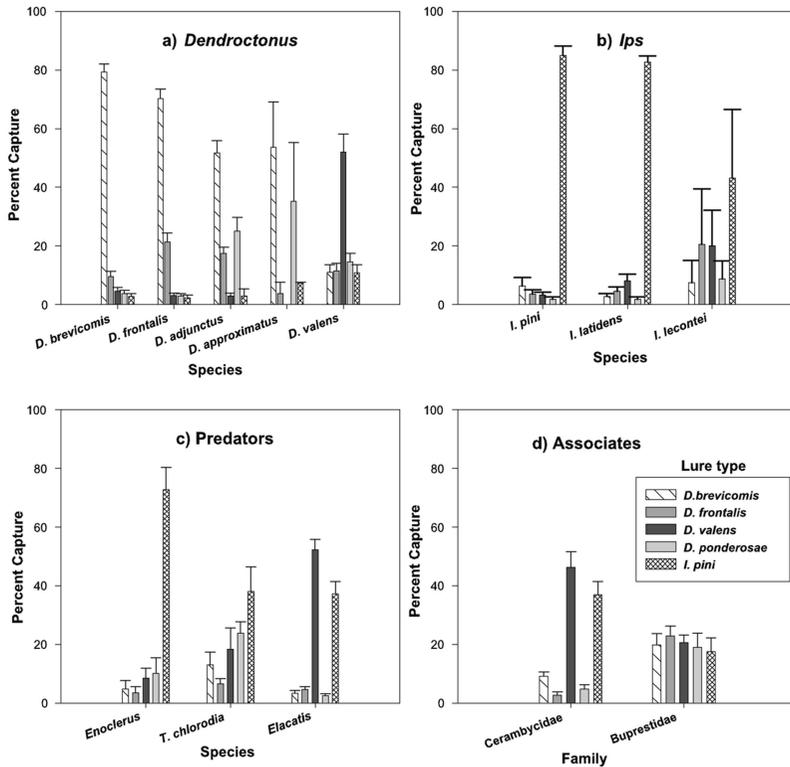

Fig. 5. Mean ± SEM percent capture by lure type of (a) *Dendroctonus*, (b) *Ips*, (c) predators, and (d) associates caught in baited Lindgren funnel traps using five different lure types for 24 consecutive months in 2002–2003. Only those sample periods in which ≥10 individuals of the respective species were trapped were used in the analysis.

attracted to the *I. pini* lure (Fig. 5b), but the *D. frontalis* and *D. valens* lures also captured ≈20% each.

Lure Preference by Predators

Enoclerus **species.** Captures differed among lures ($P < 0.0001$, $n = 13$, total number of beetles = 416). The highest percentage of this predator was attracted to the lure targeted for *I. pini* (Fig. 5c).

Temnochila chlorodia. Captures differed among lures ($P < 0.0001$, $n = 5$, total number of beetles = 244). The highest percentage of this species was attracted to the lure for *I. pini* (Fig. 5c), but, the *D. ponderosae* and *D. valens* lures also captured ≈20% each.

Elacatis. Captures differed among lures ($P < 0.0001$, $n = 46$, total number of beetles = 5518). The majority of *Elacatis* beetles were attracted to the lure for *D. valens* and *I. pini.* (Fig. 5c).

Lure Preference by Associate

Cerambycidae. Captures differed among lures ($P < 0.0001$, $n = 16$, total number of beetles = 657). The highest percentage of the wood borers in the family Cerambycidae was attracted to the lure targeted for *D. valens* and *I. pini* (Fig. 5d).

Buprestidae. Captures did not differ significantly among lures ($P = 0.0857$, $n = 8$, total number of beetles = 384).

Discussion

Flight Seasonality of Bark Beetles, Predators, and Associates

For the *Dendroctonus* species, our results were generally consistent with previously published reports of seasonality and number of peaks in capture corresponding to different generations (Massey et al. 1977, Wood, S. 1982). However, our results show *Dendroctonus* beetle activity extending later in the fall than previously thought. In addition, our results for *D. brevicomis* show a noted lack of definitive peak capture periods that also has been previously noted in northern Arizona (Sanchez-Martinez 2001) and other regions (Stark and Dahlsten 1970, Wood, S. 1982) and may indicate overlap of generations or reemergence of adults (Miller and Keen 1960). With the exception of a late August peak capture for *D. frontalis* in 2002, seasonal trapping patterns for *D. brevicomis* and *D. frontalis* were almost identical in both years.

Although ponderosa pine is one of the primary host species of the bark beetle *D. ponderosae* (Wood, S. 1982, Amman et al. 1985) and widespread mortality of this tree species has occurred from this beetle in North America (Amman et al. 1985, Schmid and Amman 1992), we did not catch a single *D. ponderosae* beetle in our traps despite our use of a lure specifically targeted for *D. ponderosae*. Low numbers of *D. ponderosae* are consistent with previous studies in our region

that captured only three individuals of this species in 2 yr of trapping (Sanchez-Martinez and Wagner 2002), and a report of no *D. ponderosae* in wildfire burned sites in the Flagstaff vicinity (McHugh et al. 2003). The absence of *D. ponderosae* captures in our study may be caused by the limited geographic distribution of the trapping sites and/or geographic variation in lure preference. However, this species does not seem to be common in ponderosa pine forests south of the Grand Canyon in Arizona (USDA Forest Service Region 3, 1924–1952, Insect and Disease Condition Reports 2001–2003).

Our results for the *Ips* species are also generally consistent with previous reports for our region and others (Livingston 1979, Miller and Borden 1985, Kegley et al. 1997, Steed 2003). However, relatively high captures of *I. pini* occurred continuously between late April and the middle of June in 2003. Our results suggest that the large number of beetles trapped during this period in 2003 was primarily caused by a large catch occurring in one cluster, with a different cluster driving the large peak in each trapping period. Therefore, this extended emergence period/peak may have been associated with different microclimates and thus, different emergence times of overwintering beetles, although further research is needed to support this hypothesis. In contrast, later peaks (July and October) reflected a more uniform capture of beetles among all the traps.

Our trap catches for *I. lecontei* suggest three flight peaks (May, July, and October). Previous research conducted south of Flagstaff at a slightly lower elevation near Prescott, AZ, indicated this species has three complete generations per year (Ostmark 1966). The peaks in our data are not clearly defined, perhaps because of the small numbers trapped. A description of the life cycle of *I. lecontei* (Ostmark 1966) indicates that the first spring flight, consisting of overwintering adults, produces two broods. Flight times of the second brood from the parent adults and the first brood from the new spring generation are not clearly defined and may overlap. Considering this overlap, and because of the relatively small numbers of this beetle trapped in our study and the limited geographic area of our study, we suggest further study is needed to determine actual number of generations per year for this insect.

The two major predators, *Enoclerus* species and *T. chlorodia*, appeared to have one flight peak per year with peaks in June/July. Because we did not identify *Enoclerus* to species, interpretation of the number of generations from our data are unclear for this genus. However, previous reports on *E. sphegus* Fabricius (one of the species of *Enoclerus* present in northern Arizona), as well as *T. chlorodia*, indicate one generation per year for these predator species (Furniss and Carolin 1977). In 2002, overall numbers were very low, and peak capture of these two predators did not coincide with peak beetle flight of any bark beetle species. However, in 2003, peak captures of both predators corresponded with the second flight of *I. pini* and mid-season peak flights of *D. brevicomis* and *D. fron-*

talis. In California, *E. lecontei* (Wolcott), has a closely synchronized life cycle with its major prey (*D. brevicomis*) (Furniss and Carolin 1977). Additionally, consistent with an increase in bark beetle trap collections, there was an overall increase in trap catches of predators from 2002 to 2003 (Moser et al. 1971, Reeve 1997).

Little is known about *Elacatis* species in any region. However, it was captured in large numbers in our traps early in the spring. *Elacatis* species have also been observed in association with galleries of *D. adjunctus* (Cibrian-Tovar 1987). We suspect it may be a predator of bark beetles. However, further research is needed to confirm this association.

Lure Specificity by Beetle Species

Our research was not designed to test the best aggregation lure for each species per se. Nor, because of the lack of knowledge regarding lure effectiveness, should our results be used to infer that any species of bark beetles was at higher population levels relative to other species based on trap catch results. Rather, our research was designed to determine which of the commercially available lures captured the highest percentage of each bark beetle species and their associates at our study site. Because the lure for *D. frontalis* had, to our knowledge, never been used in northern Arizona, and there is evidence of geographic variation in pheromone preference for *D. frontalis* (Berisford and Payne 1988, Berisford et al. 1990) and therefore the preferred pheromone/terpene combination used in the southeastern United States may not be the most effective lure for the northern Arizona population, we used the *D. frontalis* lure without the terpene component commonly used in the southeastern United States.

In addition to having virtually identical seasonal flight patterns, *D. frontalis* and *D. brevicomis* had very similar lure preference with both species showing a preference for the lure targeted for *D. brevicomis*, which contained *exo*-brevicomin, frontalin, and myrcene. Previous research conducted on *D. frontalis* in Texas has shown that one component of the *D. brevicomis* lure, *exo*-brevicomin, significantly reduced landing rates of *D. frontalis* (Payne et al. 1977). In addition, the lure for *D. brevicomis* contained an associated terpene (myrcene), while the lure for *D. frontalis* contained only the aggregation pheromone frontalin with no associated terpene; therefore, the number of *D. frontalis* captured in our traps could be a very small percentage of the total population and may not be reflective of actual peak flight periods or lure preference. We suggest continued research to assess *D. frontalis* lure preference, which includes several different terpenes and pheromone components to determine the optimal lure.

Current taxonomy separating *D. brevicomis* and *D. frontalis* for northern Arizona is based on fairly distinct morphological traits; however, our research and others (Sanchez-Martinez and Wagner 2002) have noted the behavioral similarity of these two

species in northern Arizona, and therefore, we feel that genetic analysis may be necessary to truly determine if these are two distinct species and/or their genetic relationship to other, geographically distant populations. While there has been genetic research on *D. brevicomis* and *D. frontalis* in Arizona (Namkoong et al. 1979, Bentz and Stock 1986), neither of these studies included populations from the Flagstaff vicinity, and only one directly compared the two species. When genetic comparisons were made between populations of *D. brevicomis* and *D. frontalis* from southeastern Arizona, *D. brevicomis* was distinct from *D. frontalis* (Namkoong et al. 1979). Moreover, *D. frontalis* from Arizona was quite different from *D. frontalis* in the southeastern United States (Namkoong et al. 1979). These results suggest that further research is needed on *D. frontalis* to understand its biology and ecology in northern Arizona. Clearly, caution should be used in transferring knowledge about this beetle species directly from one geographic region to another.

In our study *D. adjunctus* was attracted in highest proportion to the lure targeted for *D. brevicomis.* These results agree with previously published results (Hughes et al. 1976), which found frontalin and *exo*-brevicomin (both components of the *D. brevicomis* lure) to be attractive to *D. adjunctus* in field tests. This earlier experiment also showed that male *D. adjunctus* were more responsive to frontalin, and females were more responsive to *exo*-brevicomin. Although the beetles were not sorted by sex in our study, sex differences might explain the attraction of *D. adjunctus* to the lure targeted for *D. frontalis* (composed of frontalin) and *D. ponderosae* (contains *exo*-brevicomin) and the lack of strong affinity for one lure type.

Dendroctonus approximatus also showed a preference for the lure targeted for *D. brevicomis*, although it was attracted to the other lure types as well. Because of the low numbers of *D. approximatus* analyzed and the limited geographic area of our study, we suggest further research is still needed on lure preferences for this species.

All three *Ips* species (*I. pini, I. latidens,* and *I. lecontei*) analyzed had a stronger attraction to the *Ips* lure than any of the *Dendroctonus* lures. *I. lecontei* showed less of a preference for the *I. pini* lure than the other *Ips* species. However, because of the relatively small sample size for this beetle, caution should be used interpreting our results, and further research is warranted to determine the best lure for monitoring this species.

Of the two wood borer families we monitored, the Cerambycidae and Buprestidae, the cerambycids appeared to be more selective of lure type, showing a strong affinity for the lures for *D. valens* and *I. pini*. The buprestids were evenly distributed over all the lure types used. There could be numerous explanations for the differences in lure specificity we observed between the two families. One explanation could be the lack of species identification in our study. Species of buprestids and cerambycids may differ in attraction among lures. Alternatively, there could be competi-

tive advantages for the cerambycids to find already dead trees. This explanation would explain their high rates of attraction to the *D. valens* lure, which is composed of only terpenes. The buprestids, however, might need to exploit resources (such as the phloem) of trees recently killed; therefore, they would need to arrive with, or shortly after, the bark beetles, which would require a higher attraction to pheromones.

Implications

Our data on pheromone-mediated trap catches are the most thorough description to date of the flight periodicity and lure preference of bark beetles and their associates in the ponderosa pine forest in northern Arizona and provide a strong and needed foundation for future research. Our results suggest that flights of most bark beetle species and their associates begin in April and are heaviest between May and the end of October at our study site near Flagstaff, AZ. Most importantly, our results show that beetle flights in both years extended well into October, whereas most previous monitoring efforts in northern Arizona often stopped in August. This finding has important implications for seasonal planning of thinning projects and slash disposal to minimize bark beetle impacts. Additionally, although some beetles were caught outside the May–October period, the small numbers suggest that mass attack between November and April is unlikely at our study site (elevation 2,080 m). Knowledge of lure preference and seasonality of bark beetles and the major predators may minimize impacts on the predator populations (Aukema et al. 2000a, b) when deploying traps.

We recognize that trap catches and lure preference can be impacted by multiple factors, including physiological and or seasonal/yearly changes in beetles, temporal shifts in specificity to different enantiomeric ratios (Teale and Lanier 1991, Aukema et al. 2000a, Steed 2003), re-emergence of adult beetles (Miller and Keen 1960, Veysey et al. 2003), increased overall attraction and decreasing isomeric specificity under cooler weather conditions (Raffa 1991, Teale and Lanier 1991), conditions of host trees, wind speed, and associated stand structure or density (Dent 1991, Turchin and Odendaal 1996, Thistle et al. 2004). To determine the best aggregation pheromone for each bark beetle species, predator, and wood borer associate, a more complete study design that includes different enantiomeric compositions of lure components (e.g., Steed 2003) and/or combinations of different release rates and associated terpenes (e.g., Miller and Borden 2000, 2003) and multiple locations is necessary.

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