10-8-2009

Relative and seasonal abundance of three bark beetle predators (Coleoptera: Trogositidae, Cleridae) across an elevation gradient in ponderosa pine forests of north central Arizona

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RELATIVE AND SEASONAL ABUNDANCE OF THREE BARK BEETLE PREDATORS (COLEOPTERA: TROGOSITIDAE, CLERIDAE) ACROSS AN ELEVATION GRADIENT IN PONDEROSA PINE FORESTS OF NORTH CENTRAL ARIZONA

Kelly K. Williams[1], Joel D. McMillin[2], and Tom E. DeGomez[1]

ABSTRACT.—We examined abundance and flight periodicity of 3 predators of bark beetles (Coleoptera: Curculionidae, Scolytinae), *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae), *Enoclerus sphegeus* (Fabricius) (Coleoptera: Cleridae), and *E. lecontei* (Wolcott) (Coleoptera: Cleridae), across an elevational gradient of ponderosa pine (*Pinus ponderosa* Lawson) forests in north central Arizona. Predator populations were estimated at 10 sites in each of 3 elevation bands (low: 1600–1736 m; mid: 2058–2230 m; high: 2505–2651 m) for 3 years (2004–2006) using pheromone-baited funnel traps targeting 3 primary bark beetle species. We also investigated how predator abundance and flight seasonality related to those of 5 bark beetle species: *Ips pini* (Say), *I. lecontei* Swaine, *Dendroctonus frontalis* Zimmermann, *D. brevicomis* LeConte, and *D. adjunctus* Blandford. *Temnochila chlorodia* was most abundant in the low- and mid-elevation bands, whereas *E. sphegeus* was most abundant in the high-elevation band. *Enoclerus lecontei* showed no consistent elevational trend in abundance. Within each elevation band, changes in annual abundance of pooled predator species tracked shifts in abundance of pooled bark beetle species. In general, predator flight initiation coincided with or closely followed bark beetle flight initiation in the spring, but predator flight terminated before flight activity ended for most bark beetle species in the fall. In addition, the ratio of prey to predators was lowest in the summer and highest in the fall. This suggests that all bark beetle species examined may be provided temporal escape from their predators in the fall. For all 3 predator species, the pheromone-baited trap targeting *D. brevicomis* was less attractive than the pheromone-baited traps targeting *I. pini* and *I. lecontei*.

Key words: predators, bark beetles, abundance, elevation, flight seasonality, ponderosa pine, Enoclerus lecontei, Enoclerus sphegeus, Temnochila chlorodia, Dendroctonus, Ips.

Bark beetles (Coleoptera: Curculionidae, Scolytinae) cause significant pine mortality in the western United States (Furniss and Carolin 1977). Recently, bark beetles, drought, and forest conditions interacted to cause unprecedented levels of ponderosa pine (*Pinus ponderosa* Lawson) mortality throughout Arizona (USDA Forest Service 2003–2004). The bark beetle community in Arizona's ponderosa pine forests is complex, comprising several primary (i.e., capable of attacking, colonizing, and killing apparently healthy trees) and secondary (i.e., infesting weakened, dead, or dying trees) species. Primary species of concern in Arizona's ponderosa pine forests include *Ips pini* (Say), *I. lecontei* Swaine, *Dendroctonus frontalis* Zimmermann, *D. brevicomis* LeConte, and *D. adjunctus* Blandford (Dahms and Geils 1997, USDA Forest Service 2003–2004, Williams et al. 2008). All 5 species are found throughout the elevational range of ponderosa pine in north

central Arizona; however, their abundance and periods of flight activity vary across elevation (Hayes et al. 2008, Williams et al. 2008).

Natural enemies (predators, parasites, pathogens) can play a role in regulating bark beetle population dynamics (Reeve 1997, Turchin et al. 1999, Gara et al. 1999, Erbilgin et al. 2002, Reeve and Turchin 2002). Coleopteran predators of bark beetles are considered "habitat specialists" because they feed exclusively within trees colonized by bark beetles, but they are also referred to as "feeding generalists" because they prey on several Scolytinae that inhabit the same tree (Erbilgin and Raffa 2001). Three bark beetle predators commonly found in ponderosa pine forests of north central Arizona are *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogositidae), *Enoclerus sphegeus* (Fabricius) (Coleoptera: Cleridae), and *E. lecontei* (Wolcott) (Coleoptera: Cleridae) (Blackman 1931, Ostmark 1966, Sánchez-Martínez and

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Wagner 2002, Gaylord et al. 2006). The larval and adult stages of all 3 predators are known to be predaceous on the larval and adult stages of their bark beetle prey (Blackman 1931, Struble 1942, Miller and Keen 1960, Ostmark 1966, Berryman 1970, Furniss and Carolin 1977). All 3 species are known predators of several primary *Dendroctonus* and *Ips* species in the western U.S. (Blackman 1931, Person 1940, Ostmark 1966, Chansler 1967, Berryman 1970, Stephen and Dahlsten 1976, Massey et al. 1977, Bedard et al. 1980, DeMars and Roettgering 1982, Raffa and Dahlsten 1995, Gara et al. 1999, Aukema et al. 2000a, 2000b, Dahlsten et al. 2003, 2004).

Predators exploit bark beetle pheromones as kairomones to locate their prey (Wood 1982) and therefore are attracted to funnel traps baited with semiochemical lures. Pheromone-baited traps have been used to describe and compare the seasonal distributions of bark beetles with those of their predators, including *I. pini* with several predators in California (Dahlsten et al. 2003, 2004) and Wisconsin (Raffa 1991, Aukema et al. 2000a, 2000b, Erbilgin et al. 2002, Aukema et al. 2005); *I. pini* with *T. chlorodia, E. sphegeus,* and *E. lecontei* in Montana (Gara et al. 1999); and *D. brevicomis* with *T. chlorodia* in California (Fettig and Dabney 2006). *Temnochila chlorodia* is attracted to *exo*-brevicomin (Pitman and Vité 1971, Bedard et al. 1980, Byers 1988, Zhou et al. 2001, Hofstetter et al. 2008) and ipsdienol (Seybold et al. 1992, Miller et al. 1997, Dahlsten et al. 2003, 2004). *Enoclerus sphegeus* is attracted to ipsdienol (Miller and Borden 1990, Seybold et al. 1992, Miller et al. 1997, Dahlsten et al. 2004) and a combination of ipsenol and *cis*-verbenol (Miller et al. 1991). *Enoclerus lecontei* is attracted to ipsenol (Wood et al. 1968) and ipsdienol, especially when enhanced with the addition of lanierone in western North America (Seybold et al. 1992, Miller et al. 1997, Dahlsten et al. 2003, 2004, Miller et al. 2005). In a recent study on lure preferences of bark beetles and their predators near Flagstaff, Arizona (Gaylord et al. 2006), *T. chlorodia* and *Enoclerus* species were most attracted to the lure targeted for *I. pini* (ipsdienol +03/–97 and lanierone). Seasonal flight patterns of *T. chlorodia* and *Enoclerus* species were also examined by Gaylord et al. (2006). However, it is unknown how predator abundance and flight seasonality vary across the broader elevational range of ponderosa pine in the Southwest.

The primary objective of this study was to describe the relative and seasonal abundance of 3 bark beetle predators—*T. chlorodia, E. sphegeus,* and *E. lecontei*—across an elevational gradient in north central Arizona's ponderosa pine forests. Abundance and flight periodicity were determined using pheromone-baited funnel traps (Lindgren 1983). In addition, we discuss these results in relation to the abundance and flight seasonality of 5 bark beetle species (*I. pini, I. lecontei, D. frontalis, D. brevicomis,* and *D. adjunctus*) recently investigated by Williams et al. (2008). Secondary objectives of this study included (1) comparing changes in annual abundance of pooled predator species with dynamics of pooled bark beetle species and (2) determining which bark beetle pheromone lure was preferred by each predator.

METHODS

Study Site

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 as described by the Society of American Foresters (Eyre 1980). Xerophytic forests at low elevations (1600–1736 m) were bordered by pinyon-juniper woodlands and included trees and shrubs such as pinyon pine (*Pinus edulis* Engelm.), alligator juniper (*Juniperus deppeana* Steud.), Utah juniper (*J. osteosperma* [Torr.] Little), Arizona white oak (*Quercus arizonica* Sarg.), manzanita (*Arctostaphylos pungens* Kunth), and yuccas (*Yucca* spp.; Moir et al. 1997, USDA Forest Service 2002a). Mid-elevation xerophytic forests (2058–2230 m) were dominated by ponderosa pine. Understory vegetation at mid-elevations ranged from bunch-grasses to one-seed juniper (*J. monosperma* [Engelm.] Starg.) and Gambel oak (*Q. gambelii* Nutt.) (Moir et al. 1997, USDA Forest Service 2002b). In the high-elevation band (2505–2651 m), ponderosa pine stands were intermingled with mixed conifer stands, 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* [Mirb.] Franco), limber pine (*Pinus flexilis* James), white fir (*Abies concolor* [Gord. & Glend.]
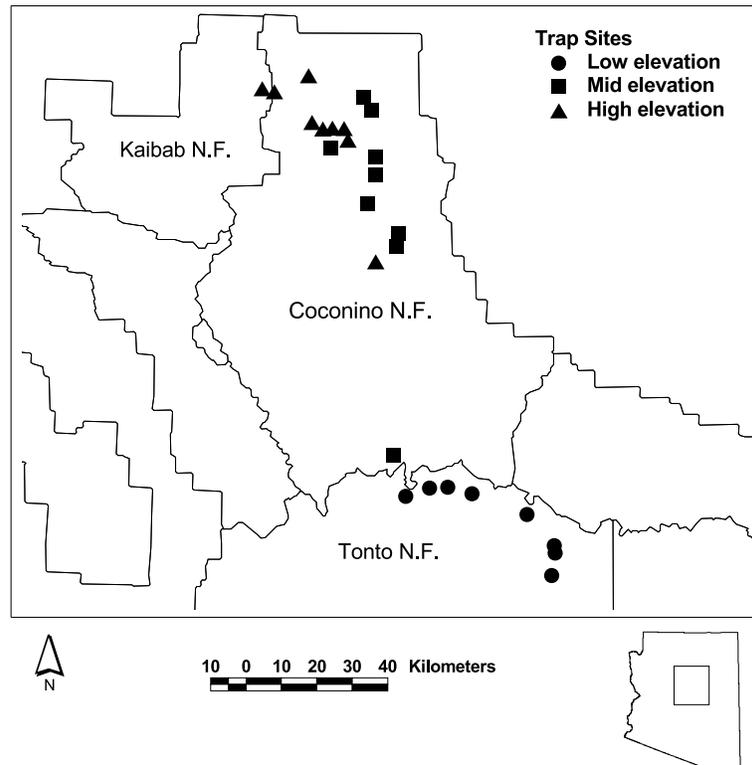
Fig. 1. Map showing the location of low- (1600–1736 m), mid- (2058–2230 m) and high- (2505–2651 m) elevation sites used in all 3 years of study for trapping bark beetles and their predators in ponderosa pine forests of north central Arizona, 2004–2006.

Lindl. ex Hildebr. var. *concolor*), and quaking aspen (*Populus tremuloides* Michx.) (Moir et al. 1997, USDA Forest Service 2002b, 2002c).

Study Design

Ten sites were established in each of 3 elevation bands: low (1600–1736 m), mid (2058–2230 m), and high (2505–2651 m). Sites within an elevation band were separated by a minimum of 2 km. Sites were within 100 m of the edge of ponderosa pine stands and within 50 to 200 m of forest roads to facilitate collection of traps. 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 mid-elevation site. Relocated sites were within 9 km of the original sites.

Each site contained three 12-unit Lindgren funnel traps (Lindgren 1983, Pherotech

International Inc., Delta, BC, Canada) arranged in an approximately 15-m equilateral triangle. Traps were suspended from 3-m aluminum conduit poles, with the bottoms of traps about 1 m from the ground. Traps were baited with commercially-available lures for *I. pini, I. lecontei,* and *D. brevicomis* (Table 1). These lure combinations were also expected to capture other bark beetle species and their coleopteran predators, based on a previous study in northern Arizona (Gaylord et al. 2006). Lures were replaced every 7 weeks to ensure adequate pheromone elution rates. Traps were also moved within the triangle on a regular basis to minimize location impacts. A 2.5 × 2.5-cm square of Spectracide Bug Stop® pest strip (18.6% Dichlorvos, United Industries Corp., St. Louis, MO) was placed in each collection cup to kill trapped insects and minimize predation by invertebrates.

The length of the trapping season varied across elevation and year (Table 2) and was

TABLE 1. Description of semiochemical lures (Pherotech International Inc., Delta, British Columbia, Canada) used in Lindgren funnel traps located in 3 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^{-1})
Ips pini	Ipsdienol +03/–97	>95	0.2 @ 25 °C
	Lanierone	>97	0.009 @ 25 °C
Ips 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
Dendroctonus brevicomis	Frontalin	>99	2.6 @ 23 °C
	Exo-brevicomin	>99	1.7 @ 23 °C
	Myrcene (X2)	>90	6.5 @ 23 °C

TABLE 2. Dates of sampling bark beetle and associated-predator flight in ponderosa pine forests on the Coconino, Kaibab, and Tonto National Forests, Arizona, at 3 elevations: low (1600–1736 m), mid (2058–2230 m), and high (2505–2651 m), 2004–2006.

	Elevation band		
Year	Low	Mid	High
2004	12 Apr–16 Nov	13 Apr–15 Nov	28 Apr–15 Nov
2005	8 Mar–6 Dec	23 Mar–8 Dec	25 Apr–28 Nov
2006	7 Mar–12 Dec	9 Mar–7 Dec	27 Mar–6 Dec

initially based on the results of a recent study near Flagstaff, Arizona (Gaylord et al. 2006). Initiation and cessation of trapping at high-elevation sites in all years depended on site accessibility due to 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. Bark beetles and predators were identified to species each year except in 2004, when *Enoclerus* beetles were only identified to genus. Voucher specimens are maintained at the Rocky Mountain Research Station, USDA Forest Service, Flagstaff, Arizona.

Statistical Analysis

With the exception of the lure comparison analysis, beetle count was summed across all 3 traps for each site and collection period because all 3 species of predators were caught in each of the different pheromone-baited traps. Although most trap collection periods were 1 week, collection periods ranged from 4 to 17 days. To standardize data, 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 total trap catch for a week (Williams et al. 2008). Average weekly beetle capture for a trapping season was calculated for each site using data from collection weeks when at least one trap was deployed in each elevation band.

Multiple response permutation procedure (MRPP) (Mielke and Berry 2001) for one-factor designs (macros developed by Rudy King, Rocky Mountain Research Station Statistics Unit, USDA Forest Service) was used for multiple comparison of means. MRPP, a nonparametric technique, can be used as an alternative to multivariate analysis of variance (MANOVA). MRPP does not require normal distribution and equal variance of data (Mielke and Berry 2001) because the hypothesis testing only depends on the internal variability of the sample (Sánchez-Martínez and Wagner 2002). The *P* value is calculated using a permutation procedure that involves all possible arrangements of the *N* observations to the different treatments, under the null hypothesis that all permutations have the same probability of occurrence (Zimmerman et al. 2005). All tests were run with a significance level of α = 0.05. MRPP was used to assess elevational trends in predator abundance, relative abundance of predators within each elevation band, and lure preferences of predators. Seasonal and annual changes in prey-predator ratios were also analyzed with MRPP using the prey data presented in the Williams et al. study (2008). When analysis included predators pooled across all species, all 3 years of data were used. When analysis involved individual predator species, 2004 data were omitted because the *Enoclerus* genus was not identified to species.

Graphs that plot the mean weekly trap catch per site against time (pooled years: 2005–2006) for individual predator species were generated

TABLE 3. *P* values for multiple response permutation procedure (MRPP) testing for differences in bark beetle predator abundance among low- (1600–1736 m), mid- (2058–2230 m), and high- (2505–2651 m) elevation bands in north central Arizona. L = low-elevation band, M = mid-elevation band, H = high-elevation band.

		P value				
Predator species	Year	All bands[a]	L vs. M	L vs. H	M vs. H	Trend
Temnochila chlorodia	2004	0.005	0.031	0.439	0.003	M > L&H
	2005	<0.001	<0.001	0.006	0.522	L > M&H
	2006	<0.001	0.010	<0.001	0.144	L > M&H
Enoclerus sphegeus	2005	<0.001	0.010	<0.001	<0.001	H > M > L
	2006	<0.001	0.001	<0.001	<0.001	H > M > L
Enoclerus lecontei	2005	<0.001	0.006	0.001	0.088	L > M&H
	2006[b]	0.150	—	—	—	—

[a]H_O: Low-, mid- and high-elevation means are similar.
[b]Pairwise comparisons are not shown for *E. lecontei* in 2006 because overall test was not significant.
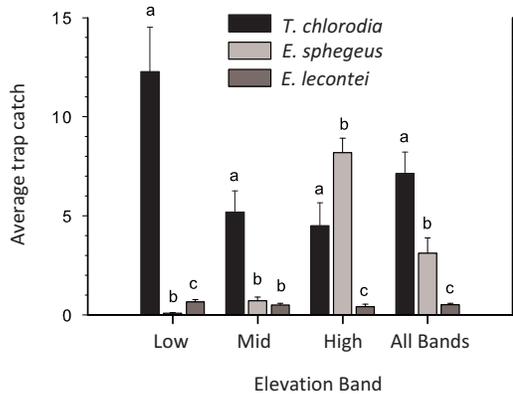

Fig. 2. Relative abundance of 3 bark beetle predators collected in funnel traps in low- (1600–1736 m), mid- (2058–2230 m), and high- (2505–2651 m) elevation bands, and in all elevations bands pooled, in north central Arizona, 2005–2006. Data are presented as mean weekly trap catch per site pooled by years. Error bars represent one standard error. Means followed by the same letter within an elevation band are not significantly different (*P* > 0.05, MRPP).

to supplement the MRPP analysis. These graphs provided insight into peak captures and initiation and cessation of flight activity. Additionally, trap catches of 5 bark beetle species (*I. pini, I. lecontei, D. frontalis, D. brevicomis,* and *D. adjunctus*) examined in Williams et al. (2008) were included in the temporal graphs to facilitate comparisons of seasonal flight patterns between bark beetles and their predators.

RESULTS

Predator Abundance

The 3 predator species examined in this study exhibited different trends in intraspecies abundance among elevations (Table 3). *Temnochila chlorodia* showed a trend of higher abundance at low-elevation (2005 and 2006) or mid-elevation sites (2004; Table 3). *Enoclerus sphegeus* displayed the opposite trend, with abundance being highest in the high-elevation band in both 2005 and 2006 (Table 3). No obvious trend in abundance was found for *E. lecontei;* abundance was highest in the low-elevation band in 2005 but did not vary by elevation in 2006 (Table 3).

Relative interspecies abundance of the 3 predators varied among elevation bands for the 2 trapping seasons (2005 and 2006) in which *Enoclerus* individuals were identified to species (Fig. 2). At low-elevation sites, *T. chlorodia* was the most common predator collected (*P* < 0.001) and represented 94.2% of the 8311 predators collected, followed by *E. lecontei* (5.2%) and *E. sphegeus* (0.5%). At mid-elevation sites, *T. chlorodia* was again the most abundant predator (*P* < 0.001) and represented 78.5% of the 3756 predators captured; *E. sphegeus* (13.0%) and *E. lecontei* (8.5%) were found in lower numbers. At high-elevation sites, *E. sphegeus* was the most abundant predator (*P* < 0.001) and accounted for 62.5% of the 6037 predators captured, followed by *T. chlorodia* (34.4%) and *E. lecontei* (3.0%). Across all elevations, *T. chlorodia* was the most common predator collected (*P* < 0.005), accounting for 71.0% of the 18,104 predators captured, followed by *E. sphegeus* (23.8%) and *E. lecontei* (5.2%).

Flight Seasonality

Flight activity of *T. chlorodia* varied across elevation (Fig. 3). Flight initiated as early as mid-March and terminated as late as mid-November in the low-elevation band; flight
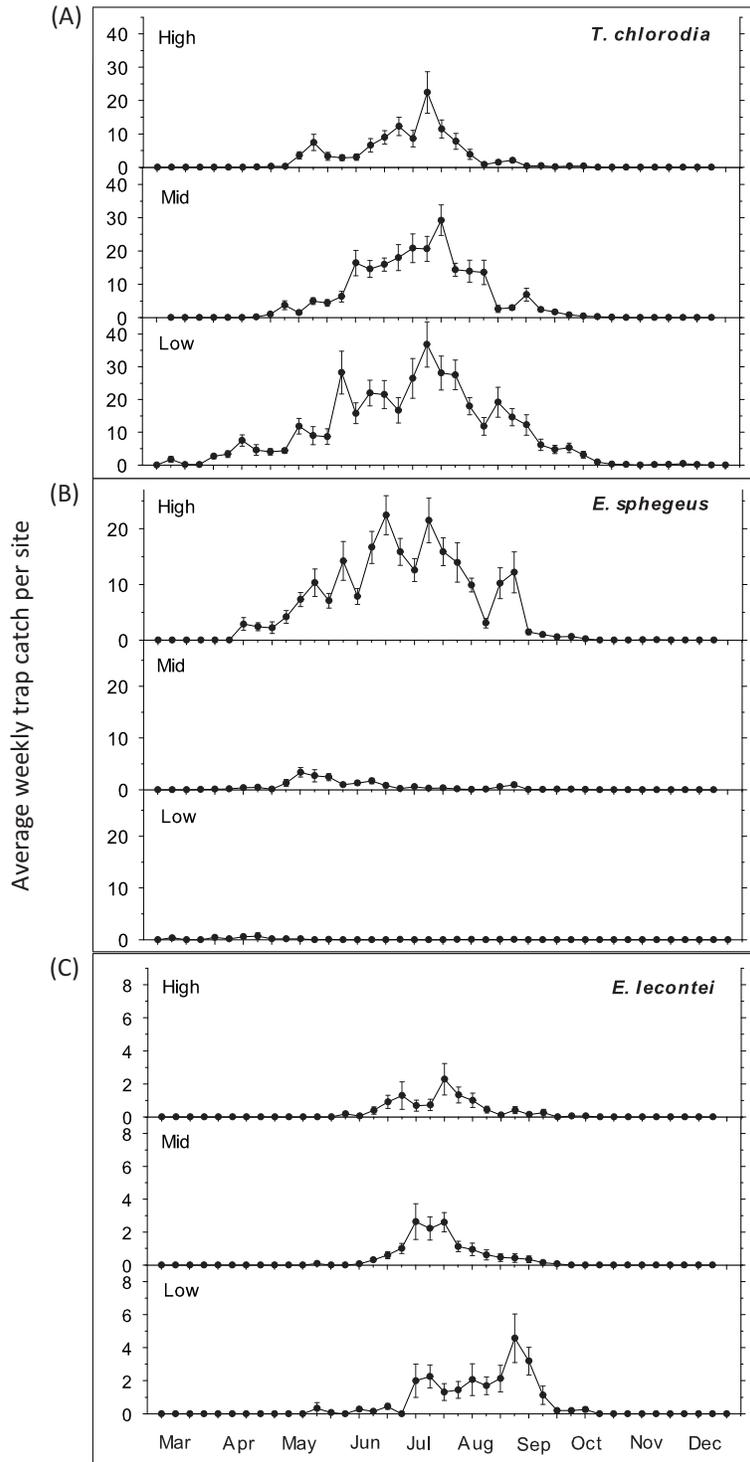
Fig. 3. Seasonal beetle captures of *T. chlorodia, E. sphegeus,* and *E. lecontei* at low- (1600–1736 m), mid- (2058–2230 m) and high- (2505–2651 m) elevation bands in ponderosa pine forests of north central Arizona, 2005–2006. Error bars represent one standard error.
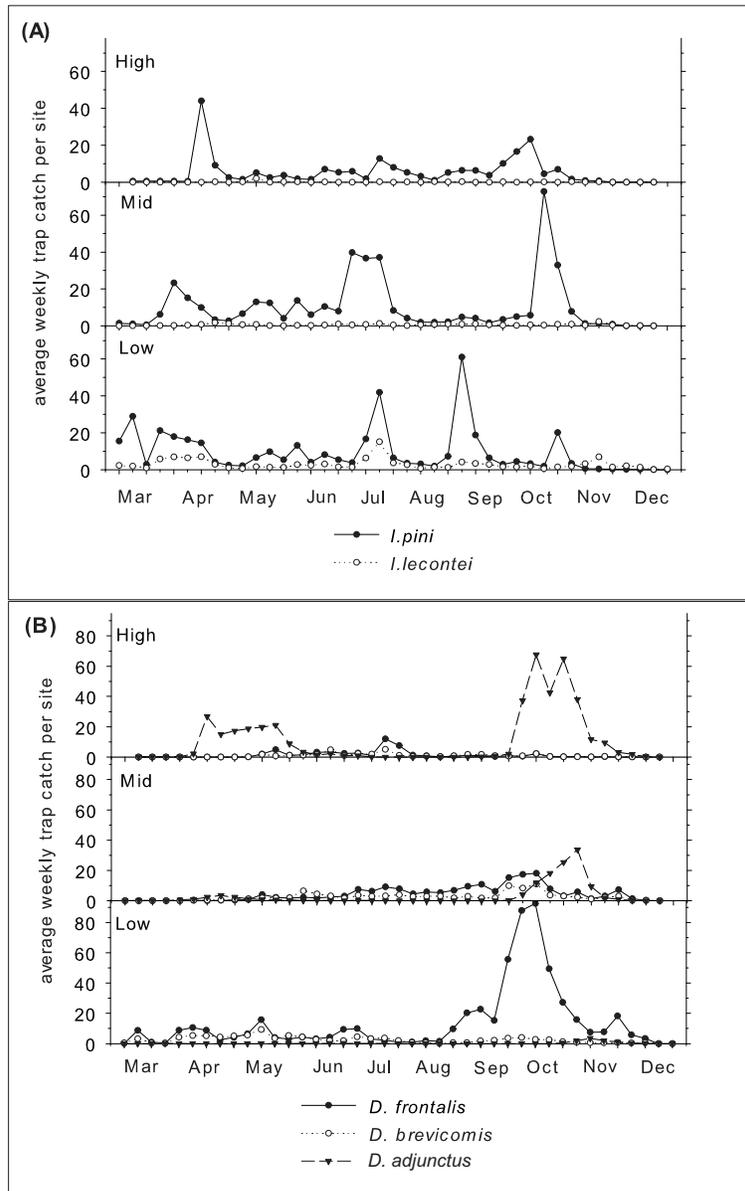
Fig. 4. Seasonal beetle captures of (A) *I. pini* and *I. lecontei* and (B) *D. frontalis, D. brevicomis,* and *D. adjunctus* at low- (1600–1736 m), mid- (2058–2230 m) and high- (2505–2651 m) elevation bands in ponderosa pine forests of north central Arizona, 2004–2006.

initiation was delayed at least one month in the mid- and high-elevation bands. Flight initiation coincided with or shortly followed spring flight initiation of several bark beetle species. At all elevations, *T. chlorodia* trap catches peaked by late July. Flight activity ended at least one month later in the low- and mid-elevation bands than in the high-elevation band.

While high trap catches of *T. chlorodia* coincided with peak summer flight activity of *I. pini* and *I. lecontei* at low elevations, its abundance was much lower during spring and fall peaks of these 2 bark beetle species (Fig. 4a). Across all elevations, flight activity of *T. chlorodia* overlapped spring and summer flight activity of *D. brevicomis* and *D. frontalis* but

TABLE 4. Mean prey:predator ratios ($s_{\bar{x}}$) for the spring (March–May), summer (June–August), and fall (September–November) trapping periods for low- (1600–1736 m), mid- (2058–2230 m) and high- (2505–2651 m) elevation bands in north central Arizona. Ratios are developed from mean weekly trap catch data per site pooled by years (2004–2006). Prey include *I. pini, I. lecontei, D. frontalis, D. brevicomis,* and *D. adjunctus.* Predators include *T. chlorodia, E. sphegeus,* and *E. lecontei.* Means followed by the same letter within an elevation band are not significantly different ($P > 0.05$, MRPP).

Elevation band	Spring	Summer	Fall
Low	4.66 (0.79) a	1.05 (0.10) b	15.25 (2.88) c
Mid	4.97 (0.786) a	1.73 (0.21) b	62.62 (9.53) c
High	4.86 (0.93) a	0.56 (0.07) b	50.63 (9.12) c

TABLE 5. Mean prey:predator ratios ($s_{\bar{x}}$) during 2004–2006 trapping periods for low- (1600–1736 m), mid- (2058–2230 m), and high- (2505–2651 m) elevation bands in north central Arizona. Ratios are developed from mean weekly trap catch data per site. Prey include *I. pini, I. lecontei, D. frontalis, D. brevicomis,* and *D. adjunctus.* Predators include *T. chlorodia, E. sphegeus,* and *E. lecontei.* Means followed by the same letter within an elevation band are not significantly different ($P > 0.05$, MRPP).

Elevation band	2004	2005	2006
Low	4.37 (5.18) a	2.71 (2.16) a	2.14 (0.90) a
Mid	2.00 (1.16) a	5.26 (2.55) b	5.72 (2.71) b
High	1.82 (1.10) a	2.00 (1.68) a	2.36 (1.30) a
All bands	2.67 (3.11) a	2.35 (2.53) a	3.46 (2.44) a

diminished before bark beetle flight terminated in the fall (Fig. 4b).

Flight activity of *E. sphegeus* varied across elevations, with flight initiation and termination occurring 2–4 weeks earlier for each decrease in elevational band (Fig. 3). At high-elevation sites, flight initiation coincided with spring flight initiation of *D. adjunctus* (Fig. 4b). Trap catches were highest in June and July and corresponded with summer flight activity of *I. pini, D. brevicomis,* and *D. frontalis* (Fig. 4). Trap catches declined before fall peaks in flight activity of *I. pini* and *D. adjunctus* in the high-elevation band. At low- and mid-elevation sites, the highest catches of *E. sphegeus* occurred in April (low-elevation band) and May (mid-elevation band). Trap catches during these months accounted for 78.1% of the 534 beetles caught.

Flight activity of *E. lecontei* did not vary greatly across elevation, with beetles caught mostly from May to October in all elevation bands (Fig. 3). Flight initiated in the spring

after bark beetle flight had already begun (Fig. 4). The majority of flight activity across the elevation bands occurred from early July to early September; trap catches during this period accounted for 88.4% of the 940 total beetles captured. High trap catches in July and August corresponded with peak flights of *I. pini* and *I. lecontei* (low-elevation band only) and overlapped summer flight activity of *D. brevicomis* and *D. frontalis.* Flight activity of *E. lecontei* decreased before peak bark beetle flight activity occurred in the fall.

The ratio of prey (*I. pini, I. lecontei, D. frontalis, D. brevicomis,* and *D. adjunctus*) to predators (*T. chlorodia, E. sphegeus, and E. lecontei*) varied throughout the year (Table 4). The ratio was highest in the fall (Sep.–Nov.) and lowest during the summer months (Jun.–Aug.) in all 3 elevation bands. Overall, predator flight initiation coincided with or shortly followed bark beetle flight initiation in the spring, while predator flight activity tapered off in the fall before bark beetle flight activity ended (Figs. 3, 4). During the fall months, traps captured anywhere from 15 (low-elevation band) to 62 (mid-elevation band) times more prey than predators ($P < 0.001$).

In general, based on the relatively consistent ratio of all bark beetles to all predators, changes in annual abundances of predators and bark beetles followed similar patterns within each elevation band and across all bands pooled (Table 5). Within the low- and high-elevation bands and across all bands pooled, there were no significant differences in this ratio ($P > 0.05$). The ratio for the mid-elevation band was significantly higher in 2005 and 2006 as a result of comparatively fewer predators being trapped than their prey in these 2 years ($P < 0.05$).

Lure Preference

Trap catches of all 3 predators varied among lures (Fig. 5). *Temnochila chlorodia* was most attracted to the *I. pini* and *I. lecontei* lures ($P < 0.001$); trap catches with these 2 lures accounted for 36.9% and 48.1% of the 12,891 *T. chlorodia* collected. *Enoclerus sphegeus* was most attracted to the *I. lecontei* lure, which captured 90.0% of the 4278 *E. sphegeus* ($P < 0.001$). *Enoclerus lecontei* was most attracted to the *I. pini* lure, which captured 74.5% of the 940 beetles collected ($P < 0.001$). All 3 predators were least attracted to the *D. brevicomis*
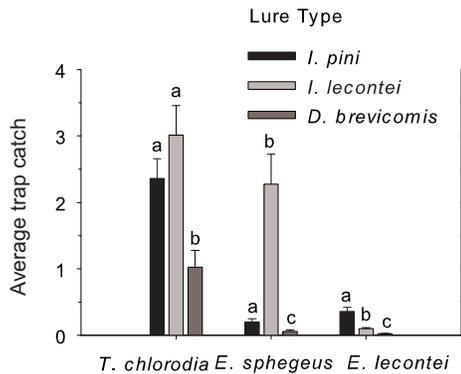
Fig. 5. Lure preferences of 3 bark beetle predators collected in funnel traps baited with a semiochemical lure combination targeting either *I. pini* (ipsdienol +03/–97, lanierone), *I. lecontei* (ispsenol +50/–50, ipsdienol +50/–50, *cis*-verbenol +17/–83), or *D. brevicomis* (frontalin, *exo*-brevicomin, myrcene) in north central Arizona, 2005–2006. Data are presented as mean weekly trap catch per site pooled by years. Error bars represent one standard error. Means followed by same letter within a predator category are not significantly different (P > 0.05, MRPP).

lure, which accounted for <15% of the total trap catches for each predator.

DISCUSSION

All 3 predators, *T. chlorodia, E. sphegeus,* and *E. lecontei,* were collected across the entire elevation range (1600–2651 m) of this study; however, like their bark beetle prey (Williams et al. 2008), predators varied with elevation in both abundance and flight activity. In general, flight initiation of predators closely followed flight initiation of bark beetles in the spring. However, predator flight terminated much earlier than bark beetle flight, contributing to high prey-predator capture ratios in the fall. Seasonal differences in flight activity between prey and predators were also observed with *I. pini* and predators in Wisconsin (Raffa 1991, Aukema et al. 2000a, 2000b) and California (Dahlsten et al. 2003, 2004). Seasonal differences in flight activity suggest that certain bark beetle species may be afforded some temporal escape from predators in the fall.

Temnochila chlorodia, the most abundant predator collected in this study, was most commonly found below 2230 m, which corresponds with the elevational distribution of its major prey: *I. pini, I. lecontei,* and *D. brevicomis* (Williams et al. 2008). The high number

of *T. chlorodia* captured in the low-elevation band may also be influenced by pinyon ips *I. confusus* (LeConte) serving as an additional food source at lower elevations. High trap catches of *T. chlorodia* were observed in pheromone-baited traps targeting *I. confusus* in pinyon-juniper woodlands (elevation 1270–1441 m) in north central Arizona (DeGomez unpublished data); however, *E. lecontei* was caught more frequently than *T. chlorodia* in similarly baited traps in southern Arizona (Cane et al. 1990). Hofstetter et al. (2008) also reported *T. chlorodia* to be the most abundant bark beetle predator collected in a recent study examining lure preferences of *D. brevicomis* and *D. frontalis* and associated insects at mid-elevations in north central Arizona. The observation that *T. chlorodia* flight initiation usually followed flight initiation of its bark beetle prey by 1–3 weeks also corresponds with findings by Gaylord et al. (2006) near Flagstaff, Arizona. This pattern is likely a reflection of the higher temperature threshold required for flight initiation of *T. chlorodia* than for flight initiation of most of its bark beetle prey (Gaylord et al. 2008). Peak flight activity during June and July matches previous reports on flight seasonality of *T. chlorodia* (Stephen and Dahlsten 1976, Gara et al. 1999, Dahlsten et al. 2003, Fettig and Dabney 2006, Gaylord et al. 2006). A coincidence of high trap catches of *T. chlorodia* and peak flight activity of *D. brevicomis, I. pini,* and *I. lecontei* corresponds with observations made by Gaylord et al. (2006). Additionally, *T. chlorodia* has exhibited close synchrony with the arrival of *I. pini* to *I. pini*–infested logs (Raffa and Dahlsten 1995) and with the mass arrival of *D. brevicomis* to ponderosa pine trees (Stephen and Dahlsten 1976).

Enoclerus sphegeus was most commonly collected at higher elevations, where bark beetle prey such as *D. adjunctus* (Blackman 1931, Chansler 1967, Massey et al. 1977), *D. ponderosae* (Boving and Champlain 1920, Blackman 1931, Amman 1970, Furniss and Carolin 1977), and *D. pseudotsugae* (Kline and Rudinsky 1964, Cowan and Nagel 1965, Furniss and Carolin 1977) are also commonly found (Blackman 1931, USDA Forest Service 2003–2004, Williams et al. 2008). Abundance of this predator decreased with decreasing elevation. Our observations on seasonal flight activity of *E. sphegeus* are consistent with

previous reports in Arizona (Blackman 1931, Ostmark 1966), New Mexico (Chansler 1967), and Montana (Gara et al. 1999). Flight initiation coincided with the minor spring flight of *D. adjunctus,* and peak trap catches overlapped summer flight activity of *I. pini* and *D. brevicomis.* The high abundance of *E. sphegeus* captured from June to August in the high-elevation band corresponds with peak flight activity of *D. pseudotsugae* (Furniss and Carolin 1977, Wood 1982, Schmitz and Gibson 1996), indicating this bark beetle may serve as an additional food source during the summer months. Flight activity of *E. sphegeus* diminished before the major flight of *D. adjunctus* occurred in October, suggesting that *D. adjunctus* may be afforded some temporal escape from one of its primary predators during the fall.

Enoclerus lecontei* is recognized as a major predator of bark beetles, specifically of *D. brevicomis* (Person 1940, Berryman 1970, Stephen and Dahlsten 1976), but it was collected in relatively low numbers in our study. Low *E. lecontei* trap catches were also reported by Fettig and Dabney (2006) in a study of predators collected in *D. brevicomis*-pheromone-baited traps in northern California. The observation that *E. lecontei* peak flight activity occurred in July and August is consistent with other reports in Arizona (Ostmark 1966) and California (Stephen and Dahlsten 1976) but contrasts with reports of spring peaks in California and Montana (Person 1940, Berryman 1970, Gara et al. 1999). A coincidence of high trap catches of *E. lecontei* and summer flight activity of *I. pini* and *D. brevicomis* corresponds with previous reports that this predator exhibited close synchrony with the arrival of *I. pini* to *I. pini*–infested logs (Raffa and Dahlsten 1995) and with the mass arrival of *D. brevicomis* to ponderosa pine trees (Stephen and Dahlsten 1976).

There are no documented predators of *D. frontalis* west of Texas. *Temnochila virescens* (Fabricius) and *Thanasimus dubius* (Fabricius) are known associated predators of *D. frontalis* in eastern Texas (Moser et al. 1971) but were not collected in this study. Our observation that high trap catches of *T. chlorodia* and *E. sphegeus* coincided with spring and summer flight activity of *D. frontalis* corresponds with previous findings (Gaylord et al. 2006) near Flagstaff, Arizona. While these results suggest potential predator-prey associations,

further investigation is needed to confirm these relationships.

Our results suggest that resource partitioning is occurring on an elevational scale. While all 3 predators share common food sources, their elevational distribution differs. *Temnochila chlorodia* was most abundant in low- and mid-elevation bands, where *I. pini, I. lecontei,* and *D. brevicomis* are common. *Enoclerus sphegeus* was most profuse at high elevations, where *I. pini, D. adjunctus,* and *D. pseudotsugae* are common. *Enoclerus lecontei* was found across all elevations in low numbers. Although we are not aware of resource partitioning taking place across elevation gradients for other prey-predator systems, resource partitioning of prey (*I. pini*) among *E. sphegeus, E. lecontei,* and *T. chlorodia* has been found to occur temporally (Gara et al. 1999). The authors reported that the densest flight of each predator coincided with a different peak in *I. pini* flight in southeastern Montana. Resource partitioning among predators on a temporal scale was not observed in our study; predator flight activity, including the highest trap catches of the season, typically overlapped. Partitioning of prey by predators may be mediated by their differential response to bark beetle pheromones (Raffa et al. 2007).

This study was not explicitly designed to test for lure preference of predators, and results should be interpreted with caution; however, our results suggest the *D. brevicomis* lure was least attractive to all 3 predators. A lack of response by *E. sphegeus* and *E. lecontei* to the *D. brevicomis* lure has been reported in previous research (Zhou et al. 2001, Fettig and Dabney 2006, Gaylord et al. 2006, Hofstetter et al. 2008). In contrast, *exo*-brevicomin, a component of the *D. brevicomis* lure and other *Dendroctonus* species lures, is known to be highly attractive to *T. chlorodia* (Pitman and Vité 1971, Bedard et al. 1980, Byers 1988, Zhou et al. 2001, Hofstetter et al. 2008). Nevertheless, our results correspond with a recent study near Flagstaff, Arizona, which also found *T. chlorodia* to be more attracted to the *I. pini* lure than the *D. brevicomis* lure (Gaylord et al. 2006). This may suggest that *T. chlorodia* exhibits geographic differences in its attraction to semiochemicals. Preference by *E. sphegeus* for the *I. lecontei* lure corresponds with its reported attraction to a combination of ipsenol and *cis*-verbenol (Miller et al. 1991). Similarly,

preference by *E. lecontei* for the *I. pini* lure is consistent with its reported attraction in western North America to a combination of ipsdienol and lanierone (Seybold et al. 1992, Miller et al. 1997, Dahlsten et al. 2003, 2004, Miller et al. 2005). It is interesting to note that *E. sphegeus*, which is most abundant at high elevations in our study, is most attracted to the *I. lecontei* lure; however, *I. lecontei* is most commonly found at low- to mid-elevations. In contrast, *E. lecontei*, which has no consistent trend in abundance with respect to elevation, shows preference for the *I. pini* lure. *Ips pini* was previously found to exhibit no trend in abundance by elevation (Williams et al. 2008). Similarly, *T. chlorodia* is most abundant at low elevations and shows preference for the *I. lecontei* lure, coinciding with where *I. lecontei* is most prevalent. Thus, *E. sphegeus* seems to be an anomaly in Arizona; it is attracted to a semiochemical lure produced by a prey species that is relatively uncommon in the habitat where *E. sphegeus* is most abundant.

Our results have implications for semiochemical management of bark beetles. Late-season pheromone trapping would be least detrimental to the natural enemy complex; fewer predators would be trapped and, therefore, they could have a greater impact on bark beetle populations. Our results also provide insight into how flight seasonality of predators relates to the flight seasonality of several bark beetle species. Prey-predator ratios have been used for predicting bark beetle population trends and forecasting infestations (Billings 1988). Additional research to evaluate the impact of each predator, or their combined effects, on population dynamics of bark beetle species is a necessary step toward developing similar predictive models in this region. Based on the relatively consistent ratio of all prey to all predators, combined abundance of the 3 predators examined in our study seemed to track abundance of the bark beetle complex. The exception was for the mid-elevation band, where comparatively fewer predators were trapped in 2005 and 2006 than their prey, resulting in significantly higher ratios for these 2 years.

To our knowledge, this is the first study examining abundance of bark beetle predators and their flight seasonality across an elevational gradient using pheromone-baited traps. While pheromone traps are a widely used tool for monitoring bark beetle abundance and flight seasonality, several studies have demonstrated disparate responses among bark beetles and their predators to semiochemical lures (Raffa and Klepzig 1989, Herms et al. 1991, Raffa 1991, Seybold et al. 1992, Aukema et al. 2000a, 2000b, Dahlsten et al. 2003, 2004). These differences can influence the interpretation of pheromone-trap results such as estimations of relative abundance, flight seasonality, and prey-predator ratios. Further investigation is needed to determine whether bark beetles and their predators exhibit chemical, seasonal, or geographic differences in their attraction to synthetic pheromones in this region.

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