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Distribution of Adult Cerambycidae and Buprestidae (Coleoptera) in a Subalpine Forest under Shelterwood Management

Kevin M. O'Neill[1], Jessica E. Fultz[2], and Michael A. Ivie[3]
[1]Department of Land Resources and Environmental Sciences
koneill@montana.edu
[2]Department of Animal and Range Sciences
[3]Department of Plant Sciences and Plant Pathology
Montana State University
Bozeman, MT 59717, U.S.A.

Abstract

We examined the distribution of adult Buprestidae and Cerambycidae in the Tenderfoot Creek Experimental Forest in the Little Belt Mountains of central Montana, U.S.A., using pan traps and sweep samples on different species of flowering plants. Using several methods during multi-year (2001–2004), summer-long surveys, we documented the presence of adults of three species of Buprestidae and ten Cerambycidae. Pan traps were placed along transects within meadows, unlogged lodgepole pine forests, and in differentially-logged plots initially logged in 1999–2000 and managed by the U.S. Forest Service. Results from pan trap samples support the conclusion that, compared to unlogged plots and meadows, adult buprestids and cerambycids were more abundant in the shelterwood areas after 2001, perhaps because of the greater abundance of decaying wood in the logged areas. Cerambycids, particularly *Cosmosalia chrysocoma* (Kirby) and *Gnathacmaeops pratensis* (Laicharting), were also commonly collected on flowers, and were most likely to be found on those with white blossoms and readily accessible nectar and pollen.

Beetles of the families Buprestidae and Cerambycidae are common components of forest insect communities and play diverse roles in ecosystem function. Buprestid and cerambycid larvae are most often associated with woody plant tissue of dead or decaying trees; others feed on roots and stems of shrubs and forbs, or mine cones and thick leaves (Linsley 1961; Bright 1987; Bellamy and Nelson 2002; Turnbow and Thomas 2002). In temperate coniferous forests, some species are pests, while others are biological control agents, and many contribute to nutrient cycling (Becker 1942; Nardi *et al.* 2002).

Adult buprestids and cerambycids have varied feeding habits (Bellamy and Nelson 2002; Turnbow and Thomas 2002). Certain buprestids (*e.g.*, *Anthaxia* spp.) and cerambycids (*e.g.*, Lepturinae) are relatively strong fliers that seek out flowers and feed primarily on pollen (Bright 1987; Linsley and Chemsak 1972; 1976; Bellamy and Nelson 2002; Turnbow and Thomas 2002). Adults of others, such as *Melanophila* spp., *Phaenops* spp. (Buprestidae), and *Monochamus* spp. (Cerambycidae: Lamiinae), feed on needles and twigs of healthy trees (Rose 1957; Bright 1987) and are attracted to recently killed or felled trees for oviposition (Peddle *et al.* 2002). Adults of a few buprestids, including some members of the genus *Agrilus*, feed on fungi (Bellamy and Nelson 2002).

During a study of the impact of silvicultural methods on the distribution and abundance of flower-visiting insects in Lewis and Clark National Forest of Montana, we examined the distribution of adult Buprestidae and Cerambycidae among silvicultural treatment areas and across different species of flowering plants. We simultaneously sampled beetles in adjacent unlogged plots and in

nearby meadows. The silvicultural treatments included two forms of shelterwood management (described below) in which selected trees or groups of trees were removed; the remaining standing trees were left to serve as seed sources and as protection for a new cohort of trees. We discuss the data on flower association with respect to several aspects of flower quality, including color and the presentation of pollen by the flower.

Materials and Methods

Study site. We conducted the research, from 2001–2004, in Meagher County, Montana on the Tenderfoot Creek Experimental Forest (TCEF), a 3,650 ha, 1,841–2,422 m elevation forest in the Little Belt Mountains (McCaughey *et al.* 2006). The TCEF, which is part of Lewis and Clark National Forest, is dominated by lodgepole pine (*Pinus contorta* Dougl.), but also contains Engelmann spruce (*Picea engelmannii* Parry), whitebark pine (*Pinus albicaulis* Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), limber pine (*Pinus flexilis* James), ponderosa pine, (*Pinus ponderosa* Dougl.), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco). Mincemoyer and Birdsall (2005) have documented 278 species of herbaceous vascular plants in the TCEF.

The U.S. Forest Service (USFS) Tenderfoot Research Project encompasses ~ 450 ha portion of the TCEF, and is subdivided into large plots managed using even and group shelterwood methods (Nyland 1996). Details on the logging treatments in the TCEF can be found in McCaughey *et al.* (2006). From Fall 1999 to Summer 2000, eight 6.5–30.8 ha plots were thinned by the USFS to remove much of the mature community of trees in two or more consecutive cuttings, with some of the older trees left standing to serve as seed sources and as protection for seedlings. The distance between adjacent standing trees was less than the heights of the trees. After logging, many cut trees were left on the ground, or were stacked at edges of the plots. The result was even shelterwood stands with a relatively uniform dispersion of standing trees. At the same time, trees in eight 3.7–31.1 ha plots were completely removed in wide swaths, leaving unlogged islands of standing trees 0.2–0.4 ha in area (group shelterwood). The TCEF also includes large unlogged plots, as well as meadows up to ~ 80 ha in extent.

Insect sampling. The research reported here was part of a larger study of the impact of shelterwood management on flower resources and flower-visiting insects in the TCEF (Fultz 2005; O'Neill and Fultz, unpublished). The study involved pan trapping and sweep net sampling, both of which collected large numbers of Buprestidae and Cerambycidae. Pan traps consisted of plastic yellow bowls, 15 cm in diameter and 5 cm deep, which were filled 2.5 cm deep with water and a few drops of unscented dish detergent. Insects were sampled 4–5 times each year, from mid-June to late-August at approximately two-week intervals. For each sample, eight bowls were placed 5 m apart along a linear transect in each plot. In each group shelterwood plot, a transect was set up so that four of the pan traps were within the cleared area and four in unlogged areas. Traps were placed at 1000–1100 h and retrieved between 1400–1500 on the same day. Upon collection, contents of all bowls in a plot were combined and placed in 70% ethanol. Each year, 22 plots were sampled: eight even shelterwood plots, eight group shelterwood plots, three unlogged plots, and three meadows (all within the TCEF); through the course of the study, transects were in the same location within each plot.

We used a 30 cm diameter sweep net to sample flower-visiting insects, taking 50 sweeps in each of 156 samples (Table 1). All samples were taken from 0940–

Table 1. Plant species sampled and the number of 50-sweep samples per species.

Family	Species	Number of samples
Apiaceae	*Heracleum sphondylium* L.	5
	Perideridia gairdneri (H. & A.) Mathias	2
Asteraceae	*Achillea millefolium* L.	9
	Agoseris sp.	1
	Anaphalis margaritacea (L.) Benthe & Hook.	1
	Arnica latifolia Bong.	17
	Aster spp.	3
	Cirsium hookerianum Nutt.	6
	Senecio spp.	11
Boraginaceae	*Mertensia* spp.	9
Brassicaceae	*Thlaspi montanum* L.	5
Campanulaceae	*Campanula rotundifolia* L.	6
Caryophyllaceae	*Cerastium arvense* L.	1
Fabaceae	*Astragalus* spp.	2
Geraniaceae	*Geranium richardsonii* Fisch. & Trautv.	5
	Geranium viscosissimum F. & M.	3
Liliaceae	*Allium schoenoprasum* L.	2
	Camassia quamash (Pursh.) Greene	2
	Zigadenus elegans Pursh.	1
Polygonaceae	*Polygonum bistortoides* Pursh.	5
Primulaceae	*Dodecatheon pulchellum* (Raf.) Merill.	1
Ranunculaceae	*Trollius laxus* Salisb.	5
Rosaceae	*Potentilla* spp.	11
Rubiaceae	*Galium boreale* L.	1
Saxifragaceae	*Saxifraga occidentalis* Wats.	4
Scrophulariaceae	*Pedicularis groenlandica* Retz.	3
Valerianaceae	*Valeriana dioica* L.	7
	Valeriana sitchensis Bong.	8

1810 h under clear to partly cloudy skies. The earliest sampling date in any year was 11 June, the latest 13 August. Twenty sweep samples (''non-flower'' samples) were taken along irregular transects arranged to avoid intersecting plants that were in flower. Another 136 of the samples were each taken on flowering plants of a single species (or genus). The same plant was never sampled twice on any one transect. Certain species on which we observed beetles, such as *Parnassia fimbriata* (Konig.), were not sampled with sweep nets to prevent excessive damage to the plants.

Statistical methods. For both buprestids and cerambycids, we first conducted one-way analyses of variance of pan trap counts with silvicultural treatment as the factor, combining counts for all dates and all years within each of the 22 plots. Pairwise comparisons were conducted using Student-Neuman-Keuls tests, with differences considered significant at $P < 0.05$. We next analyzed the pan trap counts for each beetle family using repeated-measures analyses of variance with silvicultural method as the between-treatment factor and year as the within-treatment factor; all counts were combined across sampling dates for each year, and were square-root transformed prior to analysis. Because the TCEF is subdivided between two drainages (Sun Creek and Spring Park), with half of each type of shelterwood plot within each drainage, we blocked sites by drainage in the analyses; two of the three unlogged areas were in the Spring Park drainage,

Table 2. Analysis of total (4-year) pan-trap counts of Buprestidae and Cerambycidae in four treatment areas at TCEF. Means followed by different letters significantly different at $P < 0.05$ (Student-Newman-Keuls Test).

Treatment	*n*	Buprestidae	Cerambycidae
Shelterwood (even)	8	$43.1^{A} \pm 9.8$	$31.8^{A} \pm 2.3$
Shelterwood (grouped)	8	$15.3^{B} \pm 3.6$	$16.9^{B} \pm 3.4$
Meadows	3	$11.7^{B} \pm 9.7$	$3.7^{C} \pm 0.9$
Unlogged	3	$3.7^{B} \pm 2.3$	$0.7^{C} \pm 0.7$
One-way ANOVA comparisons among treatment (combined four-year counts)		$F_{3, 18} = 4.68$ ($P = 0.01$)	$F_{3, 18} = 29.20$ ($P < 0.001$)
Repeated measures ANOVA treatment effects		$F_{3, 18} = 7.49$ ($P = 0.002$)	$F_{3, 18} = 29.18$ ($P < 0.001$)
Repeated measures ANOVA treatment × year interactions		$F_{9, 54} = 2.05$ ($P = 0.05$)	$F_{9, 54} = 3.15$ ($P = 0.004$)

whereas two of the three meadows were within the Sun Creek drainage. The distributions of the two most abundant cerambycid species among flowers of different color were analyzed using Mann-Whitney or Kruskal-Wallis tests depending on the number of flower colors involved. Correlations between species counts on flowers and pan traps were analyzed using a Spearmann's Rank Correlation tests.

Results

Buprestid and cerambycid fauna in the TCEF. The 515 buprestids collected using both methods included 510 *Anthaxia inornata* Randall, 4 *Agrilus politus* Say, and 1 *Phaenops drummondi* (Kirby); all but one of the *A. inornata* and all four *A. politus* were found in pan trap samples, so only two buprestids were found on flowers. In contrast, 63.5% of 1099 cerambycids came from sweep samples. Ten cerambycids were represented: *Acmaeops proteus* (Kirby), *Cosmosalia chrysocoma* (Kirby), *Gnathacmaeops pratensis* (Laicharting), *Judolia montivagans* Casey, *Monochamus scutellatus* Say, *Pachyta lamed liturata* Kirby, *Pygoleptura nigrella* (Say), *Stenocorus obtusus* (LeConte), *Trachysida aspera* (LeConte), and *Xestoleptura tibialis* (LeConte). All but *M. scutellatus* (Lamiinae) are members of the subfamily Lepturinae.

Distribution among the treatment areas: pan trap data. In combined counts for the four years, buprestid and cerambycids were most abundant in samples from the shelterwood areas (Table 2). In 2001, trap catches of buprestids were similar in the four treatments, but they diverged during the next two years, before converging in 2004 (Table 2, Fig. 1). During both 2002 and 2003, buprestid catches (primarily *A. inornata*) were highest in even shelterwood treatments and intermediate in group shelterwood treatments. Cerambycid catches also diverged in 2002; differences among treatments declined thereafter, but counts were still highest in the even shelterwood areas by 2004 (Table 2, Fig. 1). These differences were primarily due to *G. pratensis*, which made up 94.3% of the samples; the remaining cerambycids in pan traps were *M. scutellatus* (4.2%), *S. obtusus* (1.5%), *P. lamed* (1.2%), and *A. proteus* (0.2%).

The fact that adults were more likely to be captured away from dense stands of trees was further confirmed by examining trap catches from group shelterwood areas, where pan traps were evenly divided between logged and unlogged areas. Here, most buprestids (75.2%, n = 117) and cerambycids (97.0%, n = 134) were

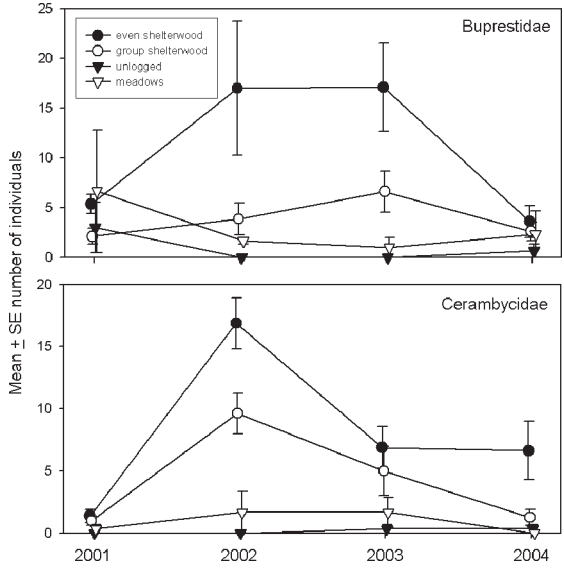

Fig. 1. Mean number of Buprestidae (top) and Cerambycidae (bottom) in samples from different treatments for each of the four years (samples on different dates for each year combined).

collected in the open areas (Chi-square goodness-of-fit; Buprestidae, $\chi^2 = 29.8$, $P < 0.001$; Cerambycidae, $\chi^2 = 118.5$, $P < 0.001$). Thus, the number of cerambycids collected per trap in the logged portions of the grouped shelterwood plots probably approached that in the even shelterwood areas.

Distribution of cerambycids on flowers. Among those collected in sweep samples on vegetation, adult cerambycids were clearly aggregated on flowering plants. Just a single individual, of *G. pratensis*, was taken in the 20 non-flower sweep samples (mean ± SE = 0.05 ± 0.5 / sample), whereas 5.1 ± 1.0 (range: 0–93) were taken in 136 samples on flowers (Mann-Whitney Test, $P < 0.001$); 49% of the sweep samples on flowers picked up at least one cerambycid. *Gnathacmaeops pratensis* comprised 87.1% of cerambycids from flowers, and was the only species collected both in pan traps and on flowers. Five other species also occurred on flowers, but never in pan traps: *C. chrysocoma* (78 individuals collected on flowers), *J. montivagans* (6), *P. nigrella* (2), *T. aspera* (1), and *X. tibialis* (1). We found no correlation between pan trap and sweep net counts for the 10 species of Cerambycidae (Spearmann rank order correlation, $r_S = -0.30$, $P = 0.38$). Both *G. pratensis* and *C. chrysocoma* tended to be found on white flowers (Table 3, Fig. 2), as did 9 of 10 individuals of other species.

Among sweep samples in which we found at least one individual of either *G. pratensis* or *C. chrysocoma*, there was a significant correlation between the counts of the two species ($r_S = 0.77$, $P < 0.001$) (Fig. 2), so they have similar distributions on flowers. Of the 10 highest counts of *G. pratensis*, four were on *C. hookerianum* (including the three highest counts: 47, 48, and 78), three on *G. richardsonii*, and one each on *Achillea millefolium, Valeriana dioica*, and *Heracleum sphondylium*. Sweeps on *C. hookerianum* (n = 4) and *H. sphondylium* (n = 3) accounted for seven of the ten highest counts for *Cosmosalia chysocoma*,

Table 3. Numbers of *Cosmosalia chrysocoma* and *Gnathacmaeops pratensis* collected on flowers of different color.

		Cosmosalia chrysocoma		*Gnathacmaeops pratensis*	
Flower color	Number samples	Number collected	Mean ± SE	Number collected	Mean ± SE
White	68	77	1.1 ± 0.3	530	7.8 ± 1.7 A
Yellow	40	1	0.03 ± 0.03	68	1.7 ± 0.4 AB
Violet	17	0	-	12	0.7 ± 0.6 B
Blue	8	0	-	0	-
Pink	3	0	-	0	-
Chi-square[1]		$\chi^2 = 73.2$ $P < 0.001$		$\chi^2 = 338.5$ $P < 0.001$	
Mean comparison[2]			$P = 0.02$		$P < 0.001$

[1] Chi-square goodness-of-fit, expected values calculated based on proportion of samples on flowers of each color (d.f. = 4).
[2] Mann-Whitney test for *C. chrysocoma* and Kruskal-Wallis test for *G. pratensisis* (non-zero values only). Differences with Dunn's Test ($P < 0.05$).

the remaining being on *A. millefolium, G. richarsonii, and Polygonum bistortoides.* Of the ten individuals from species other than *G. pratensis* or *C. chrysocoma*, eight were found either on *Geranium richardsonii* (3 *J. montivagans*, 1 *P. nigrella*) or *Heracleum sphondylium* (2 *J. montivagans*, 1 *P. nigrella*, 1 *X. tibialis*). One *J. montivagans* was also found on *Arnica latifolia*; the lone *T. aspera* collected came from *Cirsum hookerianum*.

Besides the 13 plant species listed to the left of the non-flower sample on Fig. 2, *G. pratensis* was also collected in three other samples: 17 in one sample on *Zigadenus*

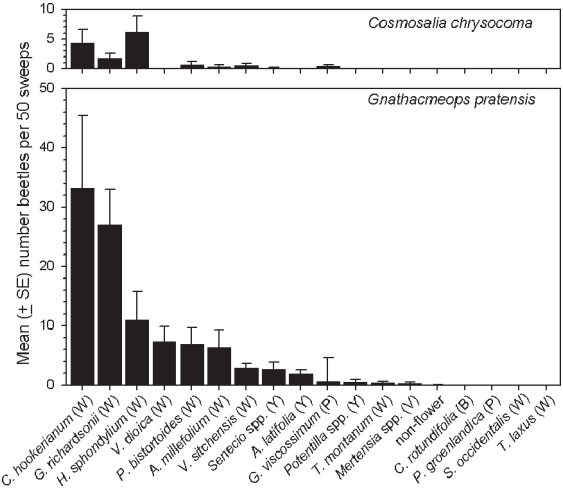

Fig. 2. Mean numbers of individuals of two species of Cerambycidae collected on different species of flowers on which at least 3 sweep samples were collected. Letters in parentheses following plant names indicate flower color (B = blue; P = pink; V = violet; W = white; Y = yellow).

elegans, four in one sample on *Anaphalis margaritacea*, and four in a *Perideridia gairdneri* sample. Besides the four plant species listed on Fig. 2 on which neither *G. pratensis* nor *C. chrysocoma* were ever found, samples (1–2 each) on *Agoseris* sp., *Allium schoenoprasum*, *Astragalus* sp., *Camassia quamash*, *Cerastium arvense*, *Dodecatheon pulchellum*, and *Galium boreale* also never picked up cerambycids.

Discussion

Using several methods during multi-year, summer-long surveys, we documented the presence of adults of three species of Buprestidae and ten species of Cerambycidae in a subalpine lodgepole pine habitat in Lewis and Clark National Forest in Montana. We do not know what proportion of the actual buprestid/cerambycid assemblage was detected using our methods, or whether the proportions of different species reflected their actual relative densities. In boreal forests, wood-boring beetles are more commonly sampled using flight intercept traps or traps designed to present obvious vertical visual profiles that mimic standing wood (*e.g.*, Lindgren 1983; Chénier and Philogéne 1989; de Groot and Nott 2001; McIntosh *et al.* 2001). But studies comparing pan traps with other types of traps do little in helping interpret our trap catches because those studies used larger, chemically-baited pans traps that were either green (de Groot and Nott 2001) or blue (McIntosh *et al.* 2001) rather than yellow. No Lepturinae are listed among the six cerambycids most commonly collected by McIntosh *et al.* (2001). This is consistent with our observations that lepturines are attracted to yellow pan-traps and are most commonly observed on white or yellow flowers. For Cerambycidae other than *Gnathacmaeops pratensis*, pan traps of the type we used proved a poor surrogate for estimating the abundance of beetles likely to be visiting flowers. Thus, the level of assessment of the buprestid/cerambycid assemblage that we obtained required the use of both pan traps and sweep samples.

Twenty of the 30 flower records we report at the plant genus level are not among those listed by Linsley and Chemsak (1972, 1976) for lepturine Cerambycidae. This is not surprising, because lepturines are likely to be opportunists willing to visit any flower that presents accessible pollen in sufficient abundance. The only recent study of Cerambycidae in Montana forests that serves as a general comparison for the TCEF study is a 5-year survey in Glacier National Park (GNP), ~250 km to the northwest of our sites (Ivie *et al.* 1998). The GNP sites were lower in elevation (1,061–1,257 m) and represented a greater diversity of habitats, some of which had burned the year before the study began; they were also sampled using a greater variety of methods (*i.e.*, flight intercept traps, Lindgren funnels, pitfall traps, and hand collecting). The GNP list includes 38 species of Cerambycidae, including all ten that we collected at TCEF. In GNP, the most common species were *G. pratensis, Spondylis upiformis* Mannerheim (Spondylidinae), *Megasemum asperum* LeConte (Aseminae), and *Rhagium inquisitor* (Lepturnae), only one of which was represented in TCEF samples.

Our results from pan trap samples support the conclusion that, compared to unlogged plots and meadows, adult buprestids and cerambycids were more abundant in the shelterwood areas, perhaps because of the greater abundance of decaying wood and flowers. Thus, *A. inornata*, *G. pratensis*, and *M. scutellatus* apparently spent a significant portion of their adult lives in these areas, while seeking flowers or oviposition sites, or while in transit between stands. But there are several difficulties in interpreting the relatively low trap catches in the unlogged areas and meadows. Relative to logged areas, pan traps may have been less visible to beetles under the tree canopy in unlogged plots. Conversely, low

trap catches in the meadows, which had the highest flower diversity and abundance (Fultz 2005), may have resulted from pan traps being less attractive against the background of natural flowers. However, pan trap catches in shelterwood areas increased from 2001 to 2002 and 2003, during which time flower resources also greatly increased, particularly due to large blooms of *Arnica latifolia* and *Valeriana dioica*. Thus, the lower trap catches of beetles in the meadows may reflect real distributional differences among treatments.

According to Proctor *et al.* (1996), Cerambycidae in Europe tend to be found on flowers with "exposed to moderately deep-seated nectar" (and, presumably, easily accessible pollen). According to Crowson (1981), beetle-pollinated flowers are typically 1) white (or rarely red, purple, or yellow; and hardly ever blue), 2) either individually large, or massed into heads, and 3) open, actinomorphic flowers, rather than tubular or labiate ones. Such was generally the case for the 10 species most commonly visited by cerambycids are our site (Fig. 2). Seven of the ten are white, two are yellow, and one is purple. Each species presents either large individual flowers (*e.g.*, *Arnica latifolia, Geranium* spp.) or clusters of small, closely-spaced flowers (including those of the Asteraceae such as *C. hookerianum*). Most have anthers with pollen easily accessible to beetles of the sizes we collected. Among plants on which we found cerambycids, only *Mertensia* have flowers that are tubular and deep relative to the size of the beetles' heads and mouthparts; and *Mertensia* ranked13th on the list of flowers on which we collected *G. pratensis*, and it was apparently not frequented by *C. chrysocoma.* Other flowers with either deeply hidden pollen (*e.g., Pedicularis groenlandica*) or with inverted flowers (*e.g.*, *Campanula rotundifolia, Dodecatheon pulchellum*) not easily accessed by relatively large beetles with limited abilities to hover appeared to be unattractive to cerambycids. Many of the lepturines in this study have large eyes, antennae, and mouthparts, characteristics listed by Crowson (1981) as common features of flower-frequenters. Bense (1995) points out the additional importance of flowers as mating sites for cerambycids. The large, upright surfaces of individual flowers or clusters of flowers characteristic of the most-visited species in our study likely provide excellent platforms for mate-finding; we commonly observed copulating pairs of *G. pratensis* on flowers.

Beetles are considered "mess-and-soil" pollinators that move from flower to flower consuming nectar, pollen, flower parts, or special food bodies (Faegri 1979; Crowson 1981; Kevan and Baker 1983). Because beetles are less active on flowers than are many flies, butterflies, and bees, they are thought to be less effective pollinators (Kevan and Baker 1983), but this might not always be the case. In montane forests of Oregon, *Cosmosalia chrysocoma* was common visitor at flowers of *Xerophyllum tenax* (Melanthiaceae) (Vance *et al.* 2004). All 25 *C. chrysocoma* collected carried *X. tenax* pollen, and nearly two-thirds carried pollen solely of that species. Although individuals often stayed on the same inflorescence for over an hour, they also flew from flower to flower so may have potential as cross-pollinators. In addition, the mean number of pollen grains found on individual cerambycids at our sites were within the range of values we observed on many of the smaller bee species on the TCEF (Fultz 2005).

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