Diversity and pollination value of insects visiting the flowers of a rare buckwheat (*Eriogonum pelinophilum*: Polygonaceae) in disturbed and "natural" areas

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Abstract—We compared flower-visitors of the endangered plant *Eriogonum pelinophilum*, at relatively undisturbed and highly disturbed sites. We found no difference between sites in flower visitation rate or species richness of flower-visitors; species diversity of flower-visitors was higher at disturbed than at undisturbed sites but there was no difference in equitability. We found significant differences in total *E. pelinophilum* pollen carried on the body among 14 abundant bee species; eight abundant wasp species; and 12 abundant fly species. Both bee and wasp species carried significantly more pollen on the ventral compared to dorsal segments of the body; pollen on the body of fly species was more equally distributed across body surfaces. Total pollen carried on flower-visitor bodies was significantly related to visitor length, suggesting that larger visitors were more effective pollinators. Total Pollination Value, a measure combining both visitor abundance and body pollen was greater at the disturbed site than the undisturbed site, further suggesting that pollination in fragments of this rare species is not a major concern. We conclude that the high diversity of insect flower-visitors and the generalized nature of *E. pelinophilum* flowers make a special management programme to conserve pollinators unnecessary. Conservation of this buckwheat is best achieved by simple habitat preservation, together with a program to enlist private citizens to include buckwheat plants in their backyard gardens.

Keywords: pollinators, pollen placement, bees, flies, wasps, degraded remnant population, conservation

Introduction

Foremost among the important causes of plant rarity are habitat loss, modification and fragmentation (Ehrlich 1988; Wilson 1988; McNeeley et al. 1990; Gentry 1996). Such deterioration of habitat can also adversely affect the pollinators (Vinson et al. 1993; Gess & Gess 1993; Westrich 1996) that many rare plants in the western United States depend upon (Tepedino 2000), and thereby further impair their seed production and recruitment. Thus, rare plant declines may be accelerated by a reduction in the number and kinds of animals that visit and pollinate their flowers (Sipes & Tepedino 1995; Kearns et al. 1998).

The effects of pollinator loss are not distributed equally across plant species because not all flowering plants require visitation by pollen vectors to set seed. A recent estimate of the percent of species whose reproduction is aided by pollinators is 85 – 90% (Ollerton et al. 2011), but vulnerability to pollinator loss varies even among pollinator-requiring species. Tepedino (1979), Bond (1994), Kearns et al. (1998) and others have noted that self-incompatible plant species and those that have evolved specialized associations with a few selected pollinator species are more vulnerable to pollinator loss than are self-compatible species and those whose unspecialised flowers are used by many generalised flower visitors. Such unspecialised plant species are forecast to be less prone to the indirect effects of habitat change on their pollinators.

Tests of such hypotheses come mostly from studies of non-threatened plants in fragmented habitats. Rare plants have much in common with plants in habitat fragments (relatively few individuals, reduced habitat area, isolation from other populations) and results of studies of the effects of fragmentation on plant reproductive success should have application to the management of rare plants. Thus far, results have been equivocal. An early review (Aizen et al. 2002), found no support for these hypotheses but an expanded meta-analysis by the same group (Aguilar et al. 2006) found a strong negative effect of fragmentation on plant reproduction; some subsequent studies disagree, e.g., González-Varo et al. (2009). As predicted (Aizen et al. 2002), this effect was found for self-incompatible species but not for self-compatible species. However, counter to expectations, plants with specialised pollination systems were no more vulnerable than those with generalised pollination systems (ibid.).

Such findings make desirable additional information on the pollination biology of rare plant species. A dependency on pollinators for successful reproduction generally means that land managers must plan both for the protection of plant populations and for their pollinators. On the other hand, in a world of limited time and funding, eliminating a need for pollinator management frees up money and effort for other conservation concerns (Schemske et al. 1994). To make such

decisions, conservationists must know a plant's pollination requirements, and the identity and resource requirements of its pollinators.

One rare species that may be less vulnerable to specific pollinator loss is clay-loving wild buckwheat, *Eriogonum pelinophilum* Reveal (Polygonaceae), a narrow endemic listed in 1984 as endangered under the U. S. Endangered Species Act; *E. pelinophilum* occurs in an area of rapid residential and commercial growth in west central Colorado (USA). Although *Eriogonum* is one of the two largest plant genera native to North America (Reveal 2005), the pollination biology of few species is known. All such studies report at least partial self-compatibility (Bowlin et al. 1993, *E. pelinophilum*; Kan 1993, *E. umbellatum* v. *torreyanum;* Duff 1996, *E. argophyllum*; Archibald et al. 2001, Tepedino et al. 2002, *E. ovalifolium* v. *williamsiae;* Neel et al. 2001, *E. ovalifolium* v. *vineum*) and low seed set (see also Kaye et al. 1990, *E. crosbyae*). Buckwheat flowers are visited by many bees, flies, wasps, butterflies and beetles (Kaye et al. 1990; Kan 1993; Archibald et al. 2001; Tepedino et al. 2002; Neel et al. 2001; Neel & Ellstrand 2003) suggesting that few, if any, insects are morphologically excluded from harvesting the small, easily obtained, nectar and/or pollen rewards.

To examine the general vulnerability of *E. pelinophilum* to pollinator loss, we compared a large, relatively undisturbed site with a much smaller, highly disturbed and fragmented site for number and identity of insects visiting the flowers, species richness, and species diversity and equitability of flower visitors. We also evaluated flower-visitors for their potential as pollinators using indirect (Spears 1983) quantitative and qualitative criteria (Herrera 1987, 1989). Our quantitative measures were visitation-rate and frequency on the flowers. Because important pollinators must accumulate pollen on relevant parts of the body (e.g., Lamborn & Ollerton 2000), vector pollen load (Inouye et al. 1994) was used as the qualitative measure. We also asked if there was a connection between total vector pollen load and size of flower-visitor (Kandori 2002). Quantitative and qualitative measures were then combined for abundant species in major taxa to obtain a measure of pollination value. Finally, we relate our findings to efforts to conserve *E. pelinophilum.*

METHODS

The Plant

Eriogonum pelinophilum is a rounded, sometimes spreading (8 – 30 cm diam, 10 – 20 cm hgt), sub-shrub,

endemic to heavy clay soils derived from Mancos Shale in Delta and Montrose counties in west central Colorado USA at an elevation of 1580 – 1935 m. Undisturbed populations dominate local shrub-steppe rangelands; disturbed populations occur in small remnant patches surrounded by farmland. Currently there are fourteen populations (not counting known extirpations or historical populations that have not been visited in 20 years) ranging in size from less than 100 individuals to more than 10,000 (U. S. Department of the Interior 2009).

Eriogonum pelinophilum blooms from late May to early September. Individual plants produce many small (3 – 5mm) flowers for extended periods (3 – 6 weeks); each plant may produce thousands of protandrous flowers. Flowers contain 6 – 9 stamens, three styles and produce small amounts of nectar at the base of the ovary (see Bowlin et al. 1993 for further details).

Study Sites

We compared flower-visitors at two sites, the relatively undisturbed Wacker's Ranch (UN; EO#018), and the highly disturbed North Mesa site (DI; EO#006) about 5 km away (site EO #s refer to U. S. Department of the Interior (DOI) 2009a). UN, 8 km southeast of Montrose CO is administered by DOI, Bureau of Land Management (BLM); it is approximately 146 hectares of predominantly native shrubs and forbs, elevation about 1875 m. *Eriogonum pelinophilum* was the dominant species in bloom with over 10,000 generally robust, large plants with many flowers. The site was ungrazed for at least three years prior to our study in 1990 (J. Ferguson, BLM, pers. comm.). It was surrounded by mostly private lands of native and improved rangeland, with a predominance of species of *Artemesia* and *Atriplex*. During the study, surrounding areas were moderately to heavily grazed by livestock, mostly cattle.

DI, was just north of Montrose, about 4 hectares in size, at approximately 1735 m elevation. There were approximately 200 *E. pelinophilum* plants in a private pasture/livestock holding area with much bare, heavily compacted ground. Blooming alfalfa fields occurred to the north and south, and a road right-of-way planted to grass, but with many weedy forbs, especially *Melilotus officinalis, Centaurea* sp. and *Convolulus arvensis*, bordered on the west. To the east were several corrals, and a storage area for farm equipment. *E. pelinophilum* plants here were significantly smaller than those at UN (unpublished data), and had little or no new vegetation and few leaves (they had been grazed

TABLE 1. The number of bee, wasp, ant and fly species captured from the flowers of *E. pelinophilum* at the undisturbed (UN), disturbed (DI) and Lawhead Gulch (LG) sites. SH is the number of species shared between UN and DI, $\sum\sum$ is the total number of unique species recorded in the study at UN and DI. LGUN is the number of species shared only between LG and UN, LGDI only between LG and DI, and LGUD at all three sites.

	UN	DI	SH	$\sum\sum$	LG	LGUN	LGDI	LGUD
Bees	18	20	10	28	14	3	2	6
Wasps	22	27	9	40	10	2	1	3
Ants	7	5	4	8	1	0	0	1
Flies	23	18	11	30	17	5	2	7
Totals	70	70	34	106	42	10	5	17

earlier the year by both cattle and sheep; Tepedino and Bowlin, unpublished information). The cattle had been off the site for four weeks when the study started; their return prompted the study's end. Despite having been grazed, plants produced abundant flowers for the entire period (starting a few days later than at the undisturbed site).

We also conducted limited collecting at Lawhead Gulch (LG; EO#001), the type locality for *E. pelinophilum*. LG is north of Montrose, about 5 km NE of Austin, and was about 40 hectares at 1600 m elevation; several thousand plants shared the area with species of *Artemesia* and *Atriplex*. Many *M. officinalis* plants were in bloom in surrounding areas. Parts of LG had been heavily grazed in past years and were being lightly grazed during our collections. Overall, LG was intermediate to UN and DI in disturbance impact; we confined our collections to a lightly disturbed section.

Flower Visitor Diversity

Systematic collections of insects visiting *E. pelinophilum* flowers were begun in 1990 at each site soon after flowering commenced and continued every seven days, except during inclement weather. The sole exception was the last collection date which was two weeks later than the penultimate one. Collection days were: UN – June 12, 19, 26, July 2, 9, 18, Aug 2; DI – June 13, 20, 28, July 3, 10, 19, Aug 3; LG – June 5 (AM), June 11 (PM), June 19, 20 (all day). Collecting ceased when the DI site became unavailable due to the return of cattle; flowering also had declined greatly at both sites. Insect flower-visitors were collected, usually by two collectors (at LG only one collector was active) repeatedly traversing different parts of the sites. Because flower-visitors usually change over a day, we employed four one-hour collecting periods each collection day: 0800 – 0900, 1100 – 1200, 1400 – 1500, and 1700 – 1800 hrs. Rare visitors, not seen on *E. pelinophilum* during systematic collections, were collected during additional short collecting bouts conducted at each site throughout the study. Insects were collected with butterfly nets, and immediately placed in cyanide kill-jars. Later, they were pinned, labeled and stored for identification. Since more time was spent collecting at UN (10 hrs/wk) than at DI (9 hrs/wk), all survey data is presented as insects or species per person-hour per week. Weekly results were compared between sites by taxon using the Wilcoxon Matched-Pairs Signed Ranks Test (Daniel 1990).

To measure diversity (D) and equitability (E) at UN and DI, Simpson's D (Begon et al. 1986), and accompanying E, were used. D is calculated as $[1/\Sigma\ (n_i/N)^2]$, where n = the number of individuals of species i, and N = the total number of individuals. D varies between 1.0 and the total number of species (S) in the collection. Equitability (E) is then D/S. D and E were calculated for each week's collection and compared between sites using the Wilcoxon Matched-Pairs Signed Rank Test.

Pollen placement

The amount of pollen on the body of abundant (≥ 5 individuals) hymenopterans (bees, wasps, ants) and dipterans (flies) was scored under a binocular microscope at 160X. For each insect, we confirmed that *Eriogonum* pollen was present
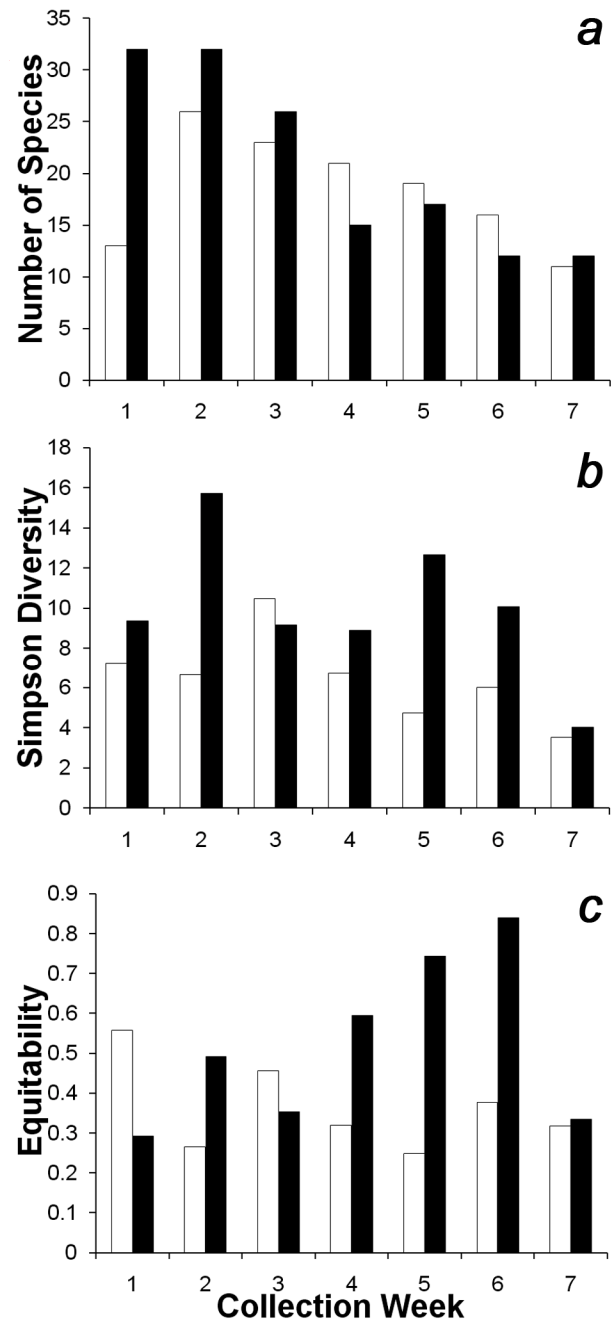

FIG. 1. Three estimates of diversity of insects captured each week from the flowers of *Eriogonum pelinophilum* at undisturbed (open bars) and disturbed (solid bars) sites. Top panel (a) shows total species richness (ants, bees, flies, wasps), mid panel (b) shows species diversity (SD), lower panel (c) shows equitability (EQ).

by its bright yellow hue, size ($\sim 30\mu$) and tricolporate, ellipsoidal shape, and that it comprised the majority of pollen types, although we did not estimate the percentage of buckwheat pollen on any insect. We examined six body parts for pollen (dorsal and ventral head, thorax, abdomen; note that the legs, where most bees collect pollen for transport to the nest, were excluded). When pollen was scored, the length of the insect was measured to the nearest half mm.
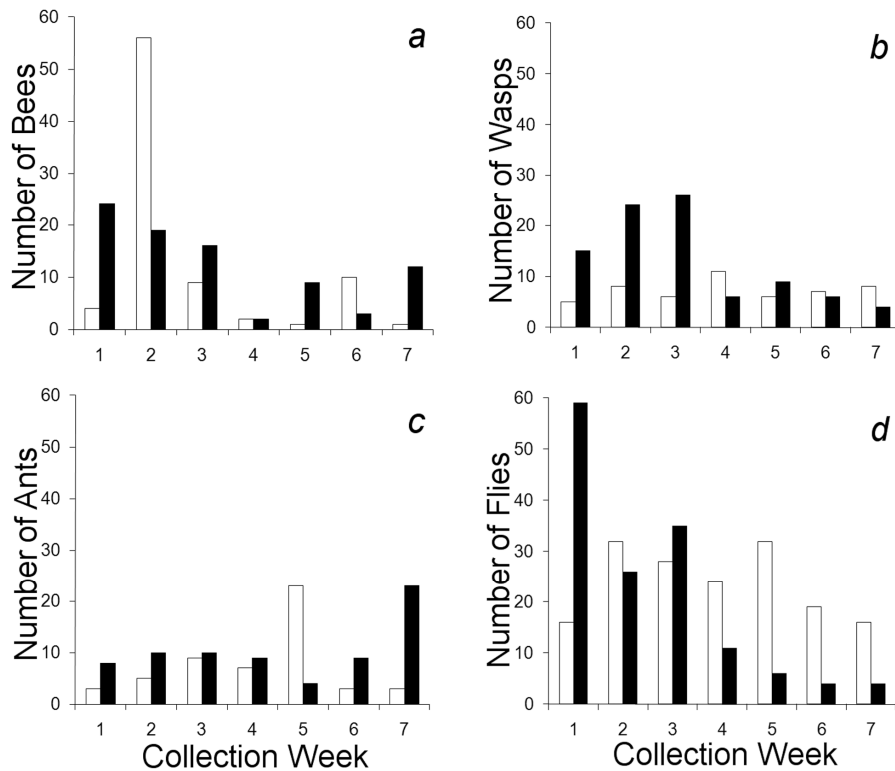
FIG. 2. The total number of a) bee, b) wasp, c) ant and d) fly individuals collected per week from flowers of *Eriogonum pelinophilum* at undisturbed (open bars) and disturbed (solid bars) sites (unadjusted for the 10% lower collecting effort at disturbed).

For each insect examined, pollen on each of the six body parts was scored as either 0 (no pollen present); 1 (1 – 10 grains), 2 (11 – 25 grains), 3 (26 – 50 grains), 4 (> 50 grains). To determine if pollen distribution varied with location on the body, we compared these pollen ratings for each abundant species (≥ 5 individuals) of bee, wasp, ant, fly using the Friedman nonparametric two-way AOV test (Daniel 1990). The three dorsal and three ventral body segments were then combined and compared for each abundant species using the Wilcoxon Matched-Pairs Signed Rank test. We also compared pollen ratings separately for each of the six body segments among abundant species of bees, wasps and flies using the Kruskal-Wallis test (with experimentwise corrections). Total pollen load among abundant species within each major taxon (bees, wasps, flies) was compared using the Kruskal-Wallis test (with experimentwise corrections). Finally, linear regressions were performed using median body length as the independent variable and total pollen load as the dependent variable. Regressions were performed separately for bees, wasps, flies, and total insects.

Total Pollination Value (TPV)

We combined quantitative and qualitative estimates into a more realistic representation of the "pollination value" (TPV) of *E. pelinophilum* flower visitors. Our objective was to express weekly TPV for each major taxon (bees, wasps, ants, flies) in terms of total TPV calculated for the entire blooming season at each site. For each week we obtained the product of the number of each abundant species captured (uncommon species were ignored) and its total pollen load rating and summed these to obtain a total value for the week. Weekly sums were then added to obtain a total estimate of

TPV for the entire blooming season. Total TPV was then used as the denominator to estimate the pollination due to each major taxon for each week.

Results

Flower Visitor Diversity and Abundance

With its canopy of open, accessible flowers produced over two months, *E. pelinophilum* attracted a wide variety of insects (Appendix I). Although the total number of species captured at UN and DI was identical (70 species, Tab. 1), the sites shared only 32.1% of the combined 106 species. Only five species were abundant (≥ 5 individuals) at both sites (one species each of wasps and ants, three of flies); 14 species at DI and 11 at UN were abundant but present in low numbers or completely absent at the other site.

At LG, 42 species were recorded (Tab. 1, Appendix I) even though collecting was limited to one collector for a few days early in the study. Ten species, all with a single individual, occurred only at LG. Most LG species (76.2%) were shared with at least one other site. A few more species were shared exclusively with UN (10) than with DI (5); 17 species were common to all three sites. Of the nine abundant species at LG (five bees, four flies), seven were also present at both UN and DI (Appendix I).

Weekly species richness comparisons showed that DI had more total species than UN for the first three weeks and the last week (Fig. 1a). Simpson's *D* was greater at DI than at UN for six of the seven weekly comparisons (Fig. 1b) and narrowly missed significance (Z = 1.94, P = 0.052; Wilcoxon matched-pairs Signed Rank Test). DI also had a more even apportionment of individuals into species than UN

Table 2. Mean number of individuals and species (± sd) captured per person hour per week at the flowers of *E. pelinophilum* at disturbed (DI) and undisturbed (UN) sites. Number of weeks sampled = 7 in all cases. P = Probability; Wilcoxon Matched-Pairs Signed Rank Tests.

	Individuals			Species		
	UN	DI	P	UN	DI	P
Bees	1.19 ± 2.0	1.33 ± 0.9	0.53	0.33 ± 0.3	0.53 ± 0.5	0.14
Wasps	0.73 ± 0.2	1.43 ± 1.0	0.27	0.60 ± 0.2	0.81 ± 0.3	0.35
Ants	0.76 ± 0.7	1.17 ± 0.7	0.20	0.24 ± 0.2	0.29 ± 0.1	0.59
Flies	2.39 ± 0.7	2.31 ± 2.3	0.45	0.67 ± 0.4	0.66 ± 0.3	0.67
Total	5.06 ± 2.5	6.31 ± 3.7	0.67	1.81 ± 0.5	2.36 ± 1.0	0.24

TABLE 3. Mean (± sd) of combined pollen ratings (see text) for three dorsal, three ventral and six total body sections for abundant species of bees, wasps, ants and flies (≥ five individuals at UN, DI and LG sites combined). Asterisks in Dorsal or Ventral column indicate significant differences for that species (* = ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001; Wilcoxon Signed Rank test). Different superscripts in Total column indicate significant differences (Kruskal-Wallis and multiple comparison correction tests, P = 0.05) among species of bees, wasps and flies.

Taxa			Dorsal	Ventral	Total
Bees	Andrenidae	*Andrena hallii*	5.63 (0.74)	8.13 (1.64)*	13.75 (2.31)[a]
		Perdita calloleuca	0.32 (0.63)	1.52 (1.36)***	1.84 (1.75)[d]
		Perdita wilmattae	0.44 (0.70)	2.28 (2.47)***	2.72 (2.91)[cd]
	Apidae	*Apis mellifera*	6.90 (3.48)	9.00 (2.53)*	15.90 (5.74)[a]
		Bombus huntii	7.20 (1.92)	9.40 (2.41)	16.60 (4.10)[a]
		Ceratina nanula	1.36 (1.43)	4.91 (2.21)*	6.27 (2.97)[abcd]
	Colletidae	*Colletes phaceliae*	3.22 (2.11)	6.00 (2.69)*	9.22 (4.66)[abc]
		Hylaeus episcopalis	3.43 (1.45)	2.43 (1.22)	5.86 (1.79)[abcd]
	Halictidae	*Agapostemon femoratus*	4.63 (2.62)	7.88 (2.42)*	12.50 (4.75)[ab]
		Lasioglossum caducum	0.80 (1.10)	2.00 (2.83)	2.80 (3.90)[bcd]
		Halictus confusus	2.09 (1.70)	6.55 (2.70)**	8.64 (3.98)[abc]
		Halictus ligatus	3.50 (1.22)	8.17 (1.33)*	11.67 (2.16)[ab]
		Halictus tripartitus	1.58 (0.90)	6.75 (2.42)***	8.33 (2.87)[abc]
	Megachilidae	*Ashmeadiella aridula*	4.27 (2.41)	7.00 (3.49)*	11.27 (5.50)[ab]
Wasps	Eumenidae	*Euodynerus annulatus*	5.15 (1.79)	7.75 (2.40)***	12.90 (3.73)[ab]
		Euodynerus exoglyphus.	4.33 (1.21)	7.33 (2.88)*	11.67 (3.88)[abc]
		Stenodynerus apache	2.44 (1.42)	3.89 (2.31)*	6.33 (3.28)[c]
		Stenodynerus sp. 1	3.84 (2.09)	5.16 (2.31)**	9.00 (4.18)[bc]
	Pompilidae	*Anoplius sp.*	4.00 (2.24)	5.71 (2.56)*	9.71 (4.46)[abc]
	Sapygidae	*Sapyga sp.*	5.00 (1.82)	9.29 (2.21)*	14.29 (3.30)[ab]
	Sphecidae	*Cerceris sp.* 1	6.50 (2.83)	8.88 (1.64)*	15.25 (4.06)[a]
		Cerceris sp. 2	4.53 (2.13)	6.00 (2.10)*	10.53 (3.52)[abc]
Ants	Formicidae	*Formica obtusopilosa*	3.00 (2.15)	4.53 (2.49)***	7.54 (4.42)
		Leptothorax tricarinatus	0.11 (0.33)	1.22 (0.83)*	1.33 (1.00)
		Pogonomymex occidentalis	0.88 (0.64)	2.25 (1.28)*	3.13 (1.64)
Flies	Bombyliidae	*Anastoechus sp.*	3.37 (1.67)***	1.05 (0.91)	4.42 (2.17)[b]
		Aphoebantus sp.	0.64 (0.73)	3.86 (2.42)***	4.50 (2.65)[b]
		Chrysanthrax sp. 1	0.33 (0.82)	0.67 (0.82)	0.83 (0.98)[c]
		Phthiria sp.	0.82 (0.74)	0.60 (0.59)	1.42 (0.99)[c]
		Thyridanthrax pallida	6.44 (1.48)	8.15 (1.79)***	14.59 (2.66)[a]
		Villa sp. 1	1.67 (1.37)***	1.00 (0.63)	2.67 (1.75)[bc]
		Villa sp. 2	1.86 (1.28)	3.41 (1.77)	5.27 (2.69)[b]
	Milichiidae	*Leptometopa halteris*	0.69 (0.74)	1.27 (0.53)**	1.96 (1.00)[c]
	Muscidae	*Peleteria sp.*	3.60 (1.37)	6.68 (2.27)***	10.28 (3.40)[ab]
	Syrphidae	*Eupeodes volucris*	3.33 (1.07)	7.08 (2.31)**	10.42 (3.00)[ab]
		Paragus tibialis	2.00 (1.06)*	1.29 (1.00)	3.29 (1.60)[b]
	Stratiomyidae	*Hedriodiscus binotatus*	7.83 (1.60)	10.17 (2.40)	18.00 (3.74)[a]

on five of seven sampling dates (Fig. 1c), but there was no significant difference between them in E ($Z = 1.18$, $P > 0.20$).

UN and DI were similar in the rank order abundance of insect visitors over time (Fig. 2): flies were usually the most abundant taxon, with wasps vying for second position with ants (UN) or bees (DI). Exceptions were the second week at UN, when a large number of *Perdita wilmattae* (Andrenidae) were recorded, and the last two weeks at DI, when ants were most abundant.

Despite the lower collection effort, DI yielded more individuals of bees and wasps than did UN for four of the seven collection weeks and more ants for six of the seven weeks (Fig. 2). UN usually exceeded DI for flies (five of seven weeks). When collection effort was adjusted for person hours per week, the sites did not differ significantly in either the number of individuals or species collected by taxon or in total (Tab. 2).

For our quantitative estimate of pollinator importance, we used the mean number of insects captured on flowers at UN and DI combined (Tab. 2). This estimate gave a ranking of flies > bees > wasps > ants. Because the number of individuals of major taxa was quite variable from week-to-week (Fig. 2), and the important pollinators of buckwheat changed over the course of its extended blooming period, such a ranking, by itself, is suspect. A better estimate of pollinator importance would integrate both visitor abundance and pollen accumulation with flower phenology (see below).

Pollen placement on flower-visitor bodies

Pollen was unequally distributed across the six body parts of most abundant species (Appendices II - IV). Twelve of 14 bee species, seven of eight wasp species, all three ant species and nine of 12 fly species carried significantly more pollen on some body sections than on others (Friedman Tests). Because of the small, open buckwheat flowers with erect stamens and styles, and the scramble-like foraging behaviour of insects across the inflorescence, most abundant flower-visitors carried more pollen ventrally than dorsally (Tab. 3). Thirteen of 14 bee species, and all eight wasp and three ant species carried more buckwheat pollen ventrally than dorsally, and most of these comparisons were significant (Wilcoxon Signed-Rank test). The predominantly ventral distribution of pollen was less pronounced for flies: only eight of 12 fly species accumulated more pollen ventrally, and only five of these comparisons were significant. Conversely, three of four fly species had significantly more dorsal than ventral pollen.

There were also significant differences in total *Eriogonum* pollen grains carried on the body among abundant flower-visiting bee species (Kruskal-Wallis Test, $H = 101.6$, $P < 0.0001$); wasp species ($H = 28.7$, $P = 0.0002$); ant species ($H = 25.9$, $P < 0.0001$) and fly species ($H = 248.5$, $P < 0.0001$) (Tab. 3). The most abundant visitors tended to carry fewer pollen grains than less common visitors. For each major taxon, a Pearson product-moment correlation of number of visitors to the flowers and our pollen accumulation estimate was inverse for each group but was significant only for bees (bee $t_{13} = -2.74$, $P < 0.02$, $r^2 = 0.39$; fly $t_{11} = -0.48$, wasp $t_7 = -0.34$, both $P > 0.50$; no analysis was conducted for ants).

We searched for patterns in pollen placement among bees, wasps and flies by grouping their species and comparing them for pollen placement on each of the six body parts (Tab. 4). There were significant differences among visitors for mean pollen grains on the head ($P < 0.003$), face ($P < 0.03$), and lower abdomen ($P < 0.02$) but not for the upper or lower thorax or upper abdomen (all $P > 0.40$). Surprisingly, wasps accumulated more pollen on four of the six body segments than did the other groups; bees accumulated more on the lower abdomen. Flies had the fewest pollen grains on three of the six body segments. The ant *F. obtusopilosa* was usually intermediate in pollen grains but had many more than flies on the lower thorax and abdomen.

Body Size and Pollen Load

The variability in pollen accumulation among abundant species of flower-visitors can be partially explained by their size. The relationship of average length to pollen carried on the body was positive and highly significant for all abundant species ($t_{1.35} = 5.96$, $P < 0.0001$, $r^2 = 0.50$, Fig. 3). (Removing two outlier species, the flies *Villa* sp. 2, *Chrysanthrax* sp. 1, both present in relatively low numbers (N = 6), increased r^2 to 0.72.)

Not all groups of taxa contributed equally to the size-pollen accumulation association (Fig. 3). The relationship was significant for bees ($t_{13} = 6.62$, $P < 0.0001$, $r^2 = 0.79$) and flies ($t_{11} = 2.96$, $P < 0.02$, $r^2 = 0.44$), but not for wasps ($t_7 = 0.85$, $P > 0.40$); ants, with only three species were not analysed. (An identical analysis using only ventral pollen accumulation yielded similar results). However, wasps generally carried more pollen per unit length than did other taxa. Bees and flies accumulated pollen on their bodies at the same rate, but for a given size, bees carried more pollen than

	Bees (14)	Wasps (8)	Flies (12)	Ants (1)
Head	1.28 (0.89)[ab]	2.40 (0.53)[a]	0.82 (0.72)[b]	1.7
Face	1.90 (0.84)[ab]	2.73 (0.71)[a]	1.28 (1.30)[b]	1.26
Upper Thorax	1.01 (0.79)	1.12 (0.45)	1.14 (0.98)	0.67
Lower Thorax	1.97 (1.06)	2.28 (0.59)	1.71 (1.29)	2.11
Upper Abdomen	0.95 (0.74)	0.96 (0.43)	0.77 (0.76)	0.63
Lower Abdomen	1.99 (1.11)[a]	1.74 (0.75)[ab]	0.78 (0.96)[b]	1.16
Total	9.10 (4.80)	11.27 (3.03)	6.47 (5.57)	

TABLE 4. Mean ($\pm$ sd) rating for pollen scores for bee, wasp and fly species for the six body parts surveyed. Pollen rating follows that in text: scale 0 (no pollen) to 4 (> 50 grains). Numbers in parentheses adjacent to taxa denote number of species in each group. Different superscripts within a row denote significant differences between taxa ($P = 0.05$; Kruskal-Wallis tests, multiple comparison correction tests). Ant species *Formica obtusopilosa* shown only for comparison.
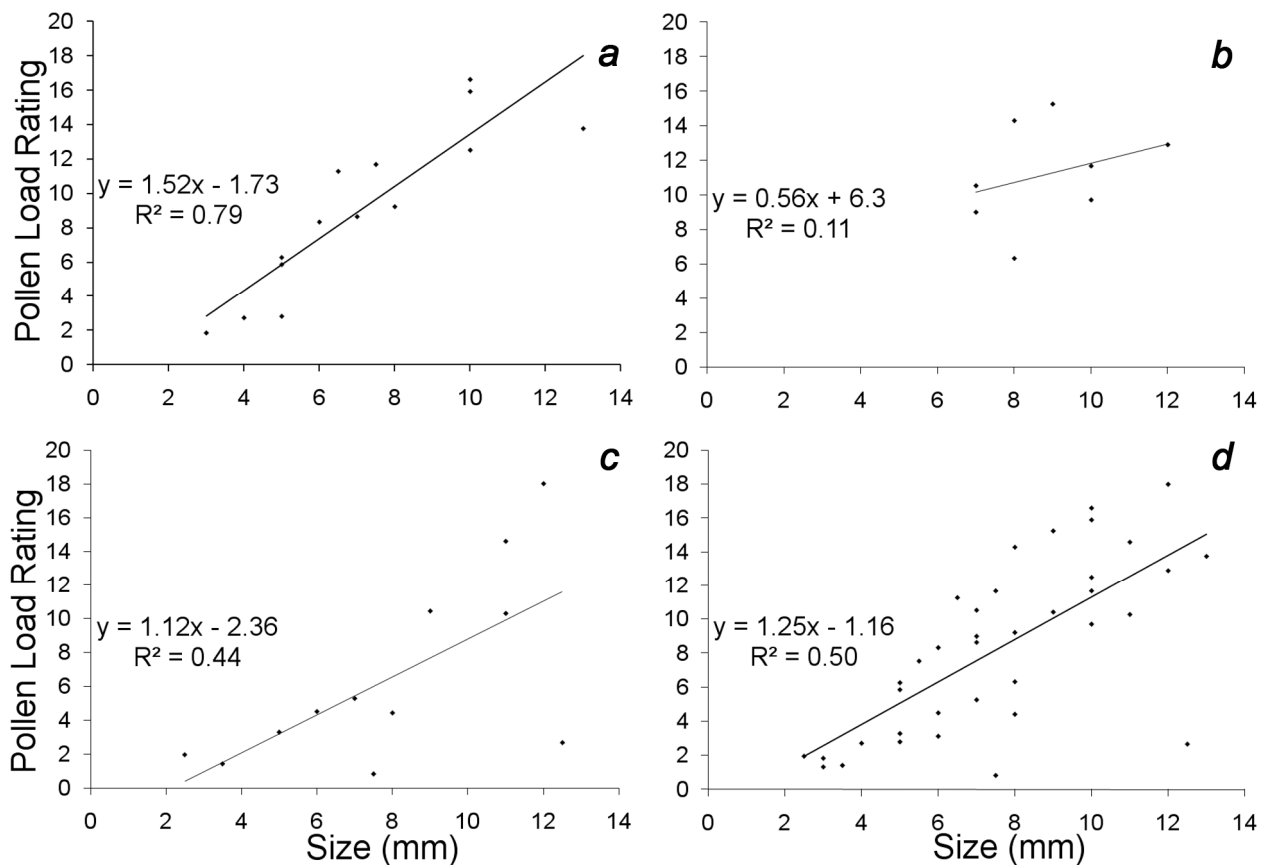
FIG.3. Median size of abundant insect species vs. rating for amount of pollen carried, by taxonomic group (a) bees, (b) wasps, (c) flies (d) total flower visitors.

did flies. A comparison of the regression lines for bees and flies was insignificant for slope ($F_{1,22} = 0.57$, $P > 0.40$) but significant for elevation of the intercept ($F_{1,23} = 7.54$, $P = 0.01$). The common ant, *F. obtusopilosa*, also carried more pollen than did flies.

Quantitative and qualitative criteria: Total Pollination Value

Several intriguing findings emerged from our estimates of TPV (Fig. 4): 1) TPV was over 30% greater at DI than at UN (2083 – DI; 1587.5 – UN); 2) most pollinations at both sites were likely accomplished during the first three weeks of the flowering season when many more pollinators with high pollen accumulation ratings were present; 3) in general, all major taxa participated in the seasonal decline; 4) variability among major taxa in pollination value also declined with time; 5) summing pollination values for each major taxon across the seven weeks gave, for UN: bees – 30.8; wasps – 17.6; ants – 17.2; flies – 34.6; for DI: bees – 18.5; wasps – 27.9; ants – 20.3; flies – 33.1. Thus, bees were likely to be much more important pollinators at UN than at DI while wasps displayed the reverse pattern. Overall, neither ants nor flies differed much between sites.

DISCUSSION

In the United States, plants comprise 54.9% of the 1361 species listed under the Endangered Species Act, yet in 2009, the latest year for which statistics are available, the federal government spent only 3.7% of its total species budget on rare plant conservation (U. S. Fish & Wildlife Service 2009). As expenditures on animals are likely to remain disproportionately high for the foreseeable future, funding for rare plant management and research must be allocated effectively. Thus, it is important to help managers of listed plants such as clay-loving wild buckwheat to prioritise their list of concerns. If pollinator-limitation of reproduction were important, direct management intervention to encourage pollinator populations, such as nest site designation and preparation, might be warranted, particularly at highly disturbed sites such as DI.

Earlier studies provisionally suggested that management of pollinators to enable *E. pelinophilum* reproduction was unnecessary. Using pollen supplementation at the flower level (Knight et al. 2006) in a protocol with a strong bias towards finding pollinator limitation, Bowlin et al. (1993) found only occasional pollinator limitation of seed production at UN. But are pollinators more likely to be uncommon in disturbed areas? Our results suggest not. We addressed this question at

DI by comparing several indirect measures of pollinator effectiveness; each suggested that reproduction at DI was not being limited by inadequate pollination to a greater extent than at UN.

First, as with other species with small, open flowers and readily accessible rewards (e.g., Ramirez 2003; Fenster et al. 2004; Olesen et al. 2007; Zych 2007), buckwheat flowers at both sites were visited by a large assortment of non-specialized insects. We found no difference between UN and DI in species richness, diversity or equitability of flower-visitors (Tab. 2; Fig. 1; App. I), suggesting that plants at the two sites were equally attractive, and that there was a comparable diversity of visitors to attract. Such measures are useful for describing the range of insect visitors and, thereby, the potential for pollinator species redundancy or insurance at a site (e.g., Winfree and Kremen 2009). They therefore suggest that *E. pelinophilum* plants at DI were as resistant to pollinator limitation as were plants at UN.
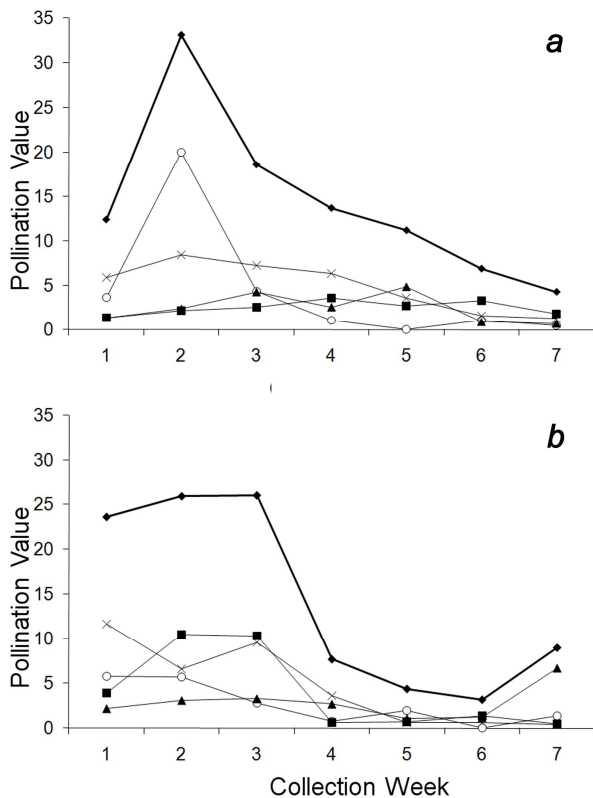

FIG. 4. Total Pollination Value (♦; see text for details), a measure combining abundance on the flowers with pollen accumulation on the body of bees (O), wasps (■), ants (▲) and flies (X) by collection week at UN (a) and DI (b).

Second, we found no significant differences between DI and UN in overall pollinator-visitation rates or in frequency on the flowers (Tab. 3, Fig. 2, App. II - IV). Thus, if Vazquez et al. (2005; see also Morris 2003; Sahli & Conner 2006), are correct in their provisional conclusion that visit-frequency is more valuable as an indicator of pollinator effectiveness than total vector pollen load or pollen deposition, then our sites were indistinguishable. However, unlike Vazquez et al. (2005), who based their conclusion on visitation rates that varied much more widely than did pollen

deposition, we found that abundant visitors in all major taxa varied greatly in vector pollen load (Tab. 3), and that commonness on the flowers and vector pollen load were inversely related for all comparisons. (We used pollen load because, like Zych (2007) with *Heracleum*, we found pollen deposition studies with *E. pelinophilum* infeasible. Usage of pollen load assumes it is positively related to pollen deposition, a reasonable assumption given the similar heights of dehiscing anthers and receptive stigmas of *E. pelinophilum*.) Some examples: common bees such as *Perdita calloleuca*, *P. wilmattae* and *Hylaeus episcopalis* and the flies *Phthiria* sp., *Villa* sp. 1, and *Leptometopa halteris*, carried little pollen (App. II - IV) and, as a result, were likely to be inferior pollinators. Conversely, visitors overladen with pollen, such as the bees *Andrena hallii* and *Bombus huntii*, the wasps *Sapyga* sp. and *Cerceris* sp. 1, and the fly *Hedriodiscus binotatus*, were uncommon and, therefore, unreliable pollinators.

Results of other studies also raise doubts that commonness on the flowers is always indicative of pollinator effectiveness: some common visitors actually lower plant reproduction by removing large amounts of pollen from flowers but depositing little (Thomson and Thomson 1992; Franzen and Larsson 2009; Hargreaves et al. 2009). More disquieting is the common disassociation between visitation rate and pollination, especially for simple flowers. Zych (2007), for example, working with a common umbellifer, found that 2-21% of all visits accounted for 70% of pollinations. Herrera (1989, 1990) reported similar findings for *Lavendula*, as did Kandori (2002) for *Geranium*. Thus, we doubt that some measure of flower-visitation rates alone is a sufficient estimate of pollinator effectiveness, at least for plants with simple pollen removal and deposition systems like buckwheats.

More realistic was our measure TPV, which like similar measures (e.g., Zych 2007) combined frequency on the flowers with pollen load. TPV was no greater at UN than at DI. Indeed, TPV estimated that pollination value was actually one-third greater at DI than at UN (Fig. 4). Thus, like our results using diversity measures and estimates of abundance and flower-visitation, TPV clearly indicated that disturbance had no negative effect on pollination.

It is not clear why TPV was higher at DI than at UN (Fig. 4). The most obvious difference between sites was a shift from bees as most common flower-visitors at UN to wasps at DI. However, such a change is not usually associated with an increase in pollination potential: wasps are usually thought to be inferior to bees as pollinators, primarily because their less hairy bodies accumulate less pollen (obviously not true here), and because they forage only for nectar and therefore visit fewer flowers than do bees which visit flowers for both nectar and pollen. Thus, it is unlikely that changes in species composition *per se* were responsible for differences in TPV (see also Kandori 2002). More suggestive was an increase in visitor size at DI compared to UN, and a significant relation between visitor size and pollen load (Fig. 3). Kandori (2002) also reported that larger visitors were more effective pollinators of *Geranium*. In addition to carrying more pollen grains, larger species have other potential

advantages as pollinators: because they must visit more flowers to satisfy their greater nectar and pollen demands, they are likely to visit and pollinate more flowers per foraging bout and over their lifetimes.

Conservation

Although we uncovered no evidence that reproduction by *E. pelinophilum* was likely to be pollinator-limited, pollinator welfare cannot be removed from the priority list of management objectives, though it may be lowered. Others have also downplayed the importance of pollinators and the need for pollinator management for species in disturbed or fragmented areas. Donaldson et al. (2002) and Yates & Ladd (2005) found that species with generalised pollination systems had no problems reproducing in fragments and that pollinators were not a major concern. Aizen & Feinsinger (2003) thought that concerns other than pollination (e.g., recruitment, soil compaction, grazing, trampling) merited more attention, at least over the short term. Likewise, if seed production of *E. pelinophilum* was more limited at DI than at UN, it was more likely due to grazing or general habitat deterioration than to pollinators.

With their numerous niches and life histories, the diverse and unpredictable group of insects that visit and pollinate *E. pelinophilum* flowers limits and simplifies management options for pollinators. Management of particular pollinator species or groups of species is both futile and unnecessary because it is doubtful that there is a predictable suite of buckwheat pollinators. Insect flower-visitors commonly change from site-to-site and from year-to-year as has been shown in many other autecological and community studies (e.g., Tepedino & Stanton 1981; Herrera 1989, 2005; Aizen & Feinsinger 2003; Alarcon et al. 2008; Olesen et al. 2008; Petanidou et al. 2008) and this is especially expected with species like *E. pelinophilum* whose flowers are so readily exploitable. Indeed, evidence of such spatial variation in pollinator composition, and buckwheat's relative independence from the composition of the pollinator fauna, was present here (Tabs. 1,2; Figs. 1, 2). Even though our sites were only about 5 km apart, only five insect species were abundant at both disturbed and undisturbed sites; in general, frequency of particular species varied appreciably between sites. It is highly unlikely that any of these between site differences had, or is likely to have, any substantive effect on reproductive success of this rare plant.

To encourage such insect diversity, one can only strive for 1) general habitat preservation of as many separate areas as is possible, and 2) enrichment of areas adjacent to, and surrounding, buckwheat population fragments. The former policy is a truism; evidence of the importance of the latter is suggested by the likely contribution to insect abundance and diversity on buckwheat flowers by adjacent weed and alfalfa/lucerne fields. Such alternates to extirpated native plant species likely supported numerous generalist native flower-visitors which also included buckwheat in their foraging ambit. Others also have suggested that adjacent vegetation can help augment flower-visitors to plants within fragments (Steffan-Dewenter et al. 2002; Ricketts et al. 2008; Winfree et al. 2009).

Buckwheat reproductive biology enables another approach: institutional efforts to encourage small private plantings within both typical Mancos shale badlands habitat, and perhaps other edaphic substrates as well. For example, backyards of concerned, conservation-minded private citizens are being touted for preservation of biodiversity (Goddard et al. 2009) and as areas that improve connectivity between patches of endemic species. Such connectivity increases gene flow and dispersal among patches, and between patches and larger source areas (Rudd et al. 2002; Parker et al. 2008; Davies et al. 2009). One envisions a programme to distribute one-or two-year old plants that have been propagated as part of a community conservation project. Such efforts should be encouraged in areas like west central Colorado, where rapid residential development is impinging upon rare endemic plants like clay-loving wild buckwheat.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Bee, wasp, ant and fly species captured on *E. pelinophilum* flowers at three Colorado sites.
Appendix II. Mean scores of *E. pelinophilum* pollen carried on six body parts of 14 bee species.
Appendix III. Mean scores of *E. pelinophilum* pollen carried on six body parts of eight wasp and three ant species.
Appendix IV. Mean scores of *E. pelinophilum* pollen carried on six body parts of 12 fly species.

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