7-1-2003

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Western North American Naturalist 63(3), ©2003, pp. 333–342

INSECT-MEDIATED POLLINATION IN SLICKSPOT PEPPERGRASS, *LEPIDIUM PAPILLIFERUM* L. (BRASSICACEAE), AND ITS IMPLICATIONS FOR POPULATION VIABILITY

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ABSTRACT.—Field experiments on the pollination biology of slickspot peppergrass, *Lepidium papilliferum* L. (Brassicaceae), a rare species endemic to microsites in sagebrush-steppe habitat in southwestern Idaho, were conducted at 2 sites from May to July 2001. Site KB contained over 10,000 plants, whereas site WG contained less than 150 plants. Insect exclusion experiments revealed that seed production in *L. papilliferum* is dependent on insect-mediated pollination; median percent seed set dropped from 70% to 2% when insects were excluded from flowers. A total of 25 insect families from 5 orders visited *L. papilliferum* flowers: 24 families at KB and 11 families at WG. Only 9 families contained more than trace amounts of pollen on their bodies: Hymenoptera—Anthophoridae, Apidae, Colletidae, Halictidae, Sphecidae, Vespidae; Coleoptera—Cerambycidae, Dermestidae; Diptera—Syrphidae. Insects from these families are likely responsible for pollination of *L. papilliferum*, although some may be of only minor significance due to their infrequent visits to flowers. Two of the 4 most common and pollen-laden insects found at KB, honey bees (*Apis mellifera*) and colletid bees, were absent or rare at WG. Three other pollen-carrying families present at KB, Sphecidae, Vespidae, and Halictidae, were not found at WG. We raise several possible explanations for this disparity in pollinator communities between sites and discuss the importance of pollinator diversity to the long term viability of *L. papilliferum*.

Keywords: Lepidium papilliferum, *slickspot peppergrass, insect-mediated pollination, pollination, pollinator community, Hymenoptera.*

One of the first steps toward developing an effective conservation strategy for an endangered or threatened plant species is to determine how it reproduces. Without such knowledge conservation efforts may overlook conditions critical to mitigating or reversing the species' decline. For example, if insects are the prime means of outcrossing for a rare plant, conservation efforts must consider the viability of the insect pollinators in addition to the habitat requirements of the plant. This is a scenario that may face slickspot peppergrass, *Lepidium papilliferum* L., a threatened mustard endemic to sagebrush-steppe habitats in southwestern Idaho.

Lepidium papilliferum grows sporadically within sagebrush-steppe habitat on microsites known as "slick spots," which are areas characterized by high levels of clay and salt and higher soil water retention than surrounding areas. Slick spots range in size from a square meter to several hundred square meters. Currently, there are 60 known slick spot sites in Idaho that contain *L. papilliferum* populations, only 6 of which are considered high-quality sites by the Idaho Department of Fish and Game (Moseley 1994, Mancuso and Moseley 1998; site quality is based on an index that includes details about the slick spots at a site [e.g., organic debris, competing plant species present, livestock disturbance, etc.] as well as the information about the surrounding habitat [e.g., fire history, off-road vehicle use, livestock disturbance, vegetation, etc.]; see paper for details). An additional 21 sites are known from historical records dating back to 1892, but these sites are now considered extirpated (Mosely 1994). Ongoing threats to the survival of slickspot peppergrass involve general habitat degradation and fragmentation caused by wildfires, livestock grazing, irrigated agriculture, exotic species invasions, urbanization, and off-road vehicle use (Moseley 1994, Mancuso and Moseley 1998). Despite the tenuous and deteriorating situation of *L. papilliferum* populations, and the general importance of the plant as an indicator of sagebrush-steppe habitat quality, little is known about the plant's propagation.

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Lepidium papilliferum begins flowering in early May. The plant reaches 10–40 cm in height and has numerous, multiflowered inflorescences that terminate at the branches. The small flowers are white petaled, and the filaments of its anthers are covered with club-shaped hairs. By late June and early July, flowering ceases and the plant produces large amounts of orbicular, flattened seed about 3 mm in length. It is not clear whether pollination occurs via autogamy (self-pollination), wind pollination, insect-mediated pollination, or some other mechanism (Meyer 1995). The genus *Lepidium* includes a number of species capable of autogamy, although unlike *L. papilliferum*, these species tend to have reduced floral structures (J.L. Bowman, University of California, Davis, personal communication). Attempts at hand pollination of *L. papilliferum* flowers have failed to produce appreciable seed sets (Meyer 1995, Robertson unpublished data), suggesting that autogamy is not the main mode of pollination. The prevalence of insects visiting *L. papilliferum* flowers (Meyer 1995, ICR personal observation) suggests that pollination may be insect-mediated; however, the only experiment designed to establish such a relationship was inconclusive in its findings (Meyer 1995). Moreover, apart from anecdotal observations (Meyer 1995, Quinney 1998), no attempt has been made to identify the variety of insects that visit *L. papilliferum* flowers. If insects are the prime means of outcrossing for slickspot peppergrass, conservation efforts should consider the long-term viability of its pollinators. Therefore, our main objective was to determine whether pollination in *L. papilliferum* is mediated by insects and, if so, to identify which insects are likely responsible for pollination and whether there are differences in pollinator communities between *L. papilliferum* populations.

METHODS

Study Site

Field experiments and observations were carried out at 2 sites in southwestern Idaho from early May to mid-July 2001. Site KB (Kuna Butte SW site, Idaho Department of Fish and Game Conservation Data Center (CDC), Element Occurrence No. 018: N43°23′38″, W116°28′45″), which occupies approximately 8 ha and consists of more than 10,000 individual plants, is one of the largest remaining slickspot peppergrass populations. Site WG (Woods Gulch site, CDC Element Occurrence No. 052: N43°45′12″, W116°21′25″), located approximately 50 km from KB, consists of fewer than 150 plants. Two sites were deemed sufficient for this study because our primary goal was to establish the pollination mechanism of *L. papilliferum*.

Pollination Experiment

We conducted an experiment at both sites to determine whether *L. papilliferum* flowers require visitations by insects for pollination and seed production. Within individual slick spots we selected 2 similarly sized plants with unopened (i.e., virgin) flowers in early May ($N = 44$ pairs of plants: 35 at KB, 9 at WG). One plant in each pair was randomly assigned to the control, the other to the treatment. We marked control plants with a small piece of flagging tape and left them undisturbed until it was time for seed collection. Treatment plants were enclosed within cylindrical insect-proof cages (5–15 cm diameter, 10–20 cm height) made from 10-mm hardware cloth covered with fine bridal veil (0.25-mm mesh). The cages were fixed securely to the substrate with pegs to ensure that insects could not enter at the base. Twenty of the 44 cages were opened to insects for a period of up to 3 days during the experiment. These "exposed cages" were used to establish whether pollinated flowers were capable of producing seed while inside the cages. Once a plant ceased active flowering, we determined its percent seed set by counting the number of wilting flower pedicels (i.e., unpollinated flowers) and seed-bearing fruits present on an inflorescence. The date on which seed set was determined for an individual plant was noted.

Insect Inventory

Throughout the study we opportunistically collected insects visiting *L. papilliferum* flowers via sweep net and aspirator and then identified them to family. In late May we placed 10 sticky traps (10 cm × 10-cm cards with Tanglefoot® applied to both sides) overnight among *L. papilliferum* flowers at the KB site to determine whether nocturnal insects were visiting the flowers.

Pollen Loads

Insects landing on *L. papilliferum* flowers were collected individually in clean glass vials and returned to the laboratory to determine whether *L. papilliferum* pollen was present on their bodies. We observed the insects through a stereomicroscope and scored them for pollen load: 0 = no pollen present, 1 = trace amounts (1 to 10 grains) of pollen present, 2 = more than trace amounts of pollen clustered on specific body parts, 3 = more than trace amounts covering much of the insect's body or concentrated on specific pollen-gathering structures such as corbiculae. (Note that although an insect with 11 grains of pollen on its body would have been scored as a 2 or 3 using this system, in reality specimens with more than trace amounts of pollen had orders of magnitude more pollen than those with trace amounts.) We removed a sample of pollen, if present, from up to 10 specimens from each insect family and mounted it in stained glycerin jelly on a microscope slide (Kearns and Inouye 1993). Pollen grains from these insects were compared to those taken directly from *L. papilliferum* flowers to determine whether or not the pollen was the same. Pollen from other plants flowering concurrently at the site was collected and mounted on microscope slides to ensure that they could be distinguished from *L. papilliferum* pollen. Those other species included clasping pepperweed (*Lepidium perfoliatum*), globe mallow (*Sphaeralcea* sp.), penstemon (*Penstemon* sp.), and yarrow (*Achillea millefolium*).

Insect Visitation Rates

From mid-May to mid-June, we monitored 224 *L. papilliferum* plants for 5-minute periods between 0930 and 1500 to determine the frequency with which individuals from specific insect families visited the plants. Upon arriving at a plant, the observer waited at least 1 minute before beginning an observation period to minimize interference with insect activity. The observer maintained a distance of approximately 1 m from the plant during observations. The size of the plant under observation was noted as small, medium, or large (total diameter of flower cluster <5 cm, 5–15 cm, or >15 cm, respectively). The observer recorded which insect families visited the plant's flowers during the observation period. No attempt was made to quantify the activity of individual insects on flowers, although qualitative observations were made.

Statistical Analyses

Nonparametric statistics were used when transformations were unsuccessful in meeting the requirements for parametric analysis. *P*-values are 2-tailed. Power tests on statistically nonsignificant results ($P \geq 0.05$) were conducted using GPower (Buchner et al. 1992). A medium effect size, based on the conventions of Cohen (1988), was used for power tests.

RESULTS

Pollination Experiment

The insect exclusion experiment revealed that *L. papilliferum* flowers are pollinated by insects. Percent seed set (i.e., percent of flowers that produced seeds) was significantly lower when insects were excluded from flowers than in control plants (Fig. 1; paired *t* test, $t_{23} = 10.49$, $P < 0.001$; only control plants paired with insect-excluded plants were included in the test). This reduction in seed set was not due to environmental conditions within the cages; caged plants that were exposed to insect visitations during the experiment produced moderate amounts of seed (Fig. 1). Percent seed set in these exposed cages was lower and more variable than in control plants; however, this result is not surprising given the plants' limited exposure (i.e., 3 days maximum) to insects during the experiment. Caged plants exposed to insect visitations had significantly higher percent seed set on average than caged plants excluded from insect visitations (Mann Whitney U Test, $z = 4.72$, $P < 0.001$). There was no significant difference in percent seed set between control plants at WG and KB (mean $\pm s_{\bar{x}} = 65.0 \pm 0.07$ and $68.5 \pm 0.03\%$, respectively: 2-tailed *t* test, $t_{42} = 0.55$, $P = 0.58$, power = 0.81).

Although percent seed set was sharply reduced in the absence of insect visitations, 15 of 24 caged plants produced some seed. Only 4 of these plants had a seed set higher than 10%. Plants in sealed cages flowered 14.4 ± 2.1 days longer on average ($N = 24$, range = 0–34 days) than their paired controls.

Insect Inventory

Twenty-five insect families from 5 orders were observed on and collected from *L. papilliferum*

TABLE 1. Inventory of insects found on *L. papilliferum* flowers at the 2 study sites (+ indicates the presence of insects in that family).

Order	Family	KB site	WG site
Hymenoptera (bees, ants, and wasps)	Anthophoridae	+	
	Apidae	+	
	Colletidae	+	+
	Formicidae	+	+
	Halictidae	+	+
	Sphecidae	+	+
	Tiphiidae	+	
	Vespidae	+	
Diptera (flies)	Anthomyiidae	+	
	Bombyliidae	+	+
	Calliphoridae	+	
	Conopidae	+	
	Milichiidae	+	
	Syrphidae	+	+
	Tachinidae	+	+
Coleoptera (beetles)	Carabidae	+	
	Cerambycidae	+	
	Chrysomelidae	+	+
	Dermestidae	+	+
	Melyridae	+	
Lepidoptera (butterflies)	Gelechiidae	+	+
	Heliodinidae	+	
	Hesperiidae	+	
	Satyridae	+	
Hemiptera (bugs)	Miridae	+	

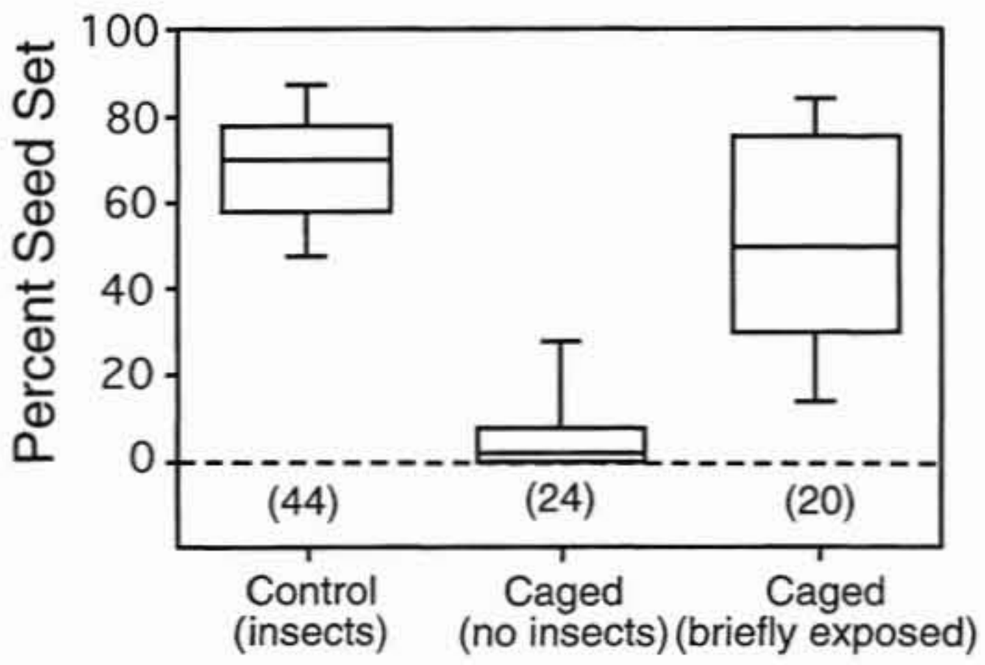

Fig. 1. Box plot chart showing results of the pollination experiment. Top, middle, and bottom horizontal lines of a box show the 75th, 50th, and 25th percentiles, respectively. Vertical lines extend from the 10th to the 90th percentiles. Sample sizes are given in parentheses below the dashed line.

flowers at KB and WG: Hymenoptera (8 families), Diptera (7 families), Coleoptera (5 families), Lepidoptera (4 families), and Hemiptera (1 family; Table 1). Some insect families were represented by as many as 4 species; however, in the following analyses only the family level is considered. The diversity of insects encountered on flowers differed between study sites, with KB having higher insect diversity (24 families, $N = 180$ five-minute observations) than WG (11 families, $N = 44$ five-minute observations). No nocturnal Lepidoptera or other insects were collected from sticky traps.

Pollen Loads

Pollen loads varied greatly across the insect families collected on *L. papilliferum* flowers (Table 2). Mean pollen scores of 2 or higher were found for 6 Hymenoptera (Anthophoridae, Apidae, Colletidae, Halictidae, Sphecidae, Vespidae), 2 Coleoptera (Cerambycidae, Dermestidae), and a Diptera (Syrphidae). The remaining 15 insect families had either trace amounts of pollen on their bodies or lacked pollen completely. In all but 1 family (Diptera: Milichiidae) the pollen collected from insects was confirmed to include *L. papilliferum* pollen, which was easily distinguished from pollen of other species at the site based on size and appearance of pollen grains. In most cases *L. papilliferum* pollen was the overwhelmingly

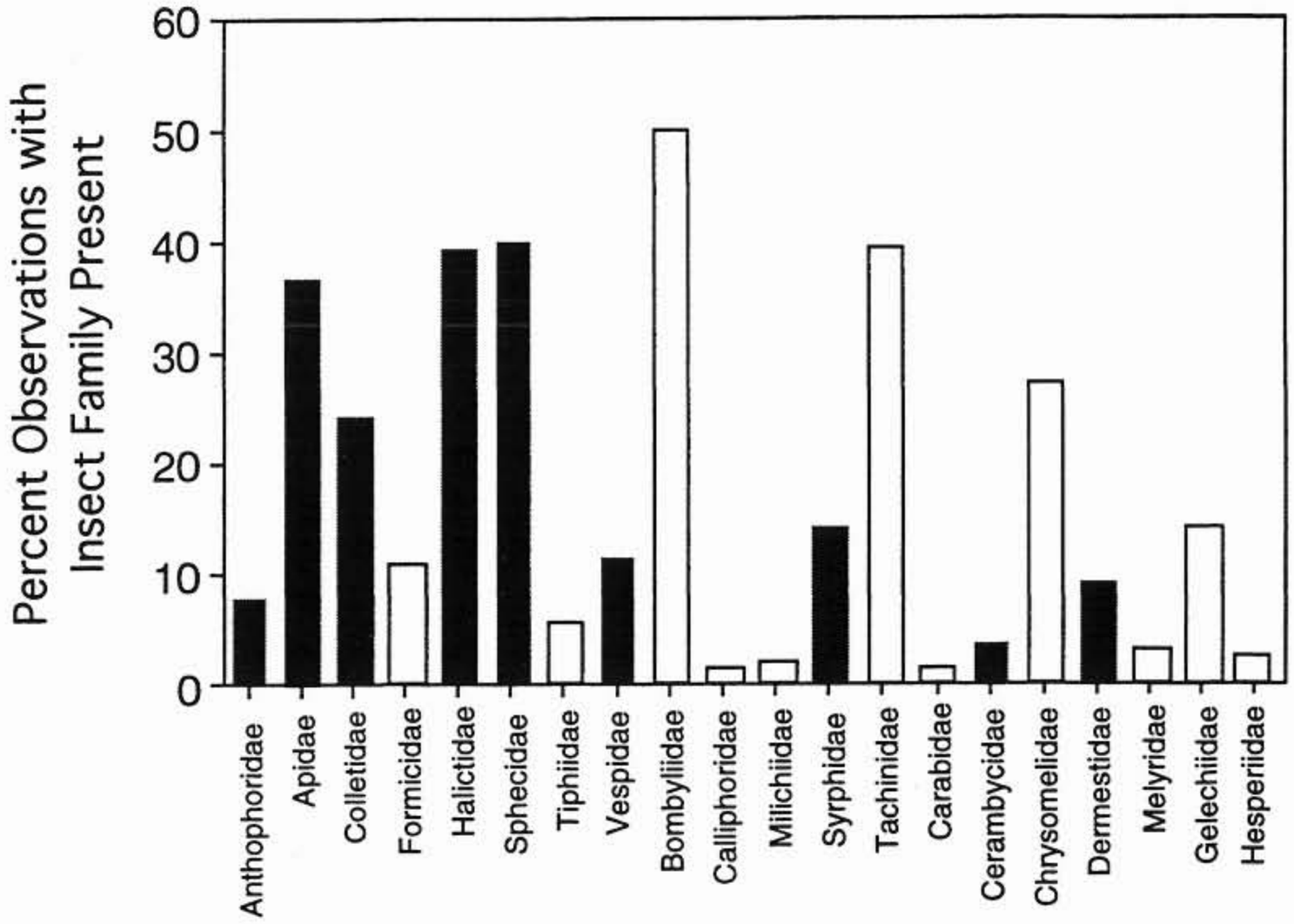

Fig. 2. Insect visitation rates at KB, measured as the percentage of observations during which at least 1 individual from a particular family visited flowers on the plant being observed. Shaded bars represent families with specimens that carried more than trace amounts of pollen on their bodies. Open bars represent families with specimens that had only trace amounts of pollen on their bodies or lacked pollen entirely.

dominant type of pollen in samples taken from the insects we collected.

Insect Visitation Rates

We defined a visitation as an insect contacting at least 1 flower of the plant being observed. Insects climbing on stems but not on flowers were excluded from analysis. Of the 224 five-minute observation periods, 18 were discarded because no insects visited the plants. Figure 2 shows the percentage of observation periods at KB ($N = 170$) during which at least 1 individual from a particular insect family visited the plant under observation.[2] The most common visitors (i.e., >20% visitation rate) included 4 Hymenoptera (Apidae, Colletidae, Halictidae, Sphecidae), 2 Diptera (Bombyliidae, Tachinidae), and a Coleoptera (Chrysomelidae). Of these, only the hymenopterans carried more than trace pollen loads on their bodies (Table 2). Among those insects that did not carry *L. papilliferum* pollen, satyrid and hespiriid butterflies were difficult to observe on flowers because they typically left the area when approached by observers. Thus, their numbers may be underrepresented. There was an overall increase in visitation rate as plant size increased (ANOVA, $F_{2,38} = 16.48$, $P < 0.001$; plant size was included as a categorical variable in the analysis).

At WG halictid bees and dermestid beetles were the only insect families that visited *L. papilliferum* in more than 20% of observations (36% and 47%, respectively). Individuals from both of these families had high pollen loads (Table 2). A comparison of insect visitation rates on small plants at WG and KB (Fig. 3) revealed the following: (1) Anthophoridae, Apidae, and Vespidae were present at KB but not at WG, (2) Colletidae and Sphecidae were less abundant on small plants at WG than at KB (13.5% vs 2.8% and 32.7% vs 11.1%, respectively), and (3) dermestid beetles were absent on small plants at KB but common on small plants at WG. Dermestid beetles at KB were found on medium and large plants, with visitation rates of 10.5% and 16.7%, respectively. However, no comparisons between sites could be made for larger plants because WG contained only small plants.

Considering only those insect families with pollen loads of 2 or higher (i.e., the insects most likely responsible for pollinating *L. papilliferum*), visitation rates varied over the duration of the

[2]Four insect families (Anthomyiidae, Conopidae, Miridae, Satyridae) that were collected on *L. papilliferum* (see Table 1) were not observed during 5-minute observation periods.

TABLE 2. Mean pollen scores (0 = no pollen present, 1 = trace grains of pollen present, 2 = more than trace amounts of pollen on specific body parts, 3 = more than trace amounts of pollen over much of body or on specific pollen-gathering structures) for insects collected on *L. papilliferum* flowers; nd = no data were collected. Sample sizes (*n*) and the location of pollen found on the insect's body are given for each family. Families with more than trace amounts of pollen on their bodies are in **boldface** type.

Order	Family	*n*	Pollen score	Location of pollen on body
Hymenoptera (bees, ants, and wasps)	**Anthophoridae**	4	2	hairs on notum of thorax
	Apidae	10	3	pollen baskets (corbiculae); body hairs
	Colletidae	10	3	pollen baskets (corbiculae); body hairs
	Formicidae	10	0	
	Halictidae	10	3	pollen baskets (corbiculae); body hairs
	Sphecidae	7	2	primarily on thorax
	Tiphiidae	nd	nd	
	Vespidae	3	2	primarily on thorax
Diptera (flies)	Anthomyiidae	1	1	head, thorax, abdomen
	Bombyliidae	10	1	head
	Calliphoridae	2	1	head
	Conopidae	2	1	head and thorax
	Milichiidae[a]	1	0	
	Syrphidae	6	2	head, thorax, abdomen
	Tachinidae	10	1	mouthparts
Coleoptera (beetles)	Carabidae	3	1	head, thorax, abdomen
	Cerambycidae	10	2	clypeus and trace amounts on thorax
	Chrysomelidae	5	0	
	Dermestidae	10	2	hairs on head and thorax
	Melyridae	6	1	head, thorax, abdomen
Lepidoptera (butterflies)	Gelechiidae	8	1	head and proboscis
	Hesperiidae	4	1	proboscis
	Satyridae	2	0	
Hemiptera (true bugs)	Miridae	1	1	head

[a]Pollen grains on this insect were not from *L. papilliferum* and therefore were not included in pollen scores.

study (Fig. 4). Apidae, Colletidae and Cerambycidae all showed gradual declines in their numbers during the 4 weeks of sampling. By contrast, visitation rates of Halictidae and Sphecidae increased during the study. The remaining 4 families showed no discernable seasonal patterns.

DISCUSSION

The Case for Insect-mediated Pollination

The pollination experiment leaves no doubt that insect-mediated pollination is critical for seed production in *L. papilliferum.* Plants excluded from insect visitations had extremely low seed set and often failed to produce any fruits or seeds. This failure was not a consequence of plants being caged because even caged plants with brief exposure to insects produced moderate to high seed sets. Uncaged plants had consistently high seed sets, as would be expected if the majority of their flowers were visited and pollinated by insects. Plants exposed to insects also had shorter flowering periods than those excluded from insects. From an evolutionary perspective, one would expect pollinated flowers to advance to seed production quickly, whereas unpollinated flowers would be expected to remain open as long as possible to maximize their chances of pollination.

The presence of seeds in some caged plants excluded from insects indicates either that additional pollination mechanisms exist in *L. papilliferum* or that insects found their way undetected into those cages and pollinated flowers. The latter explanation seems more likely given what is known about pollination mechanisms in other *Lepidium* species. Floral morphology in the genus is highly variable (Bowman et al. 1999). According to J.L. Bowman

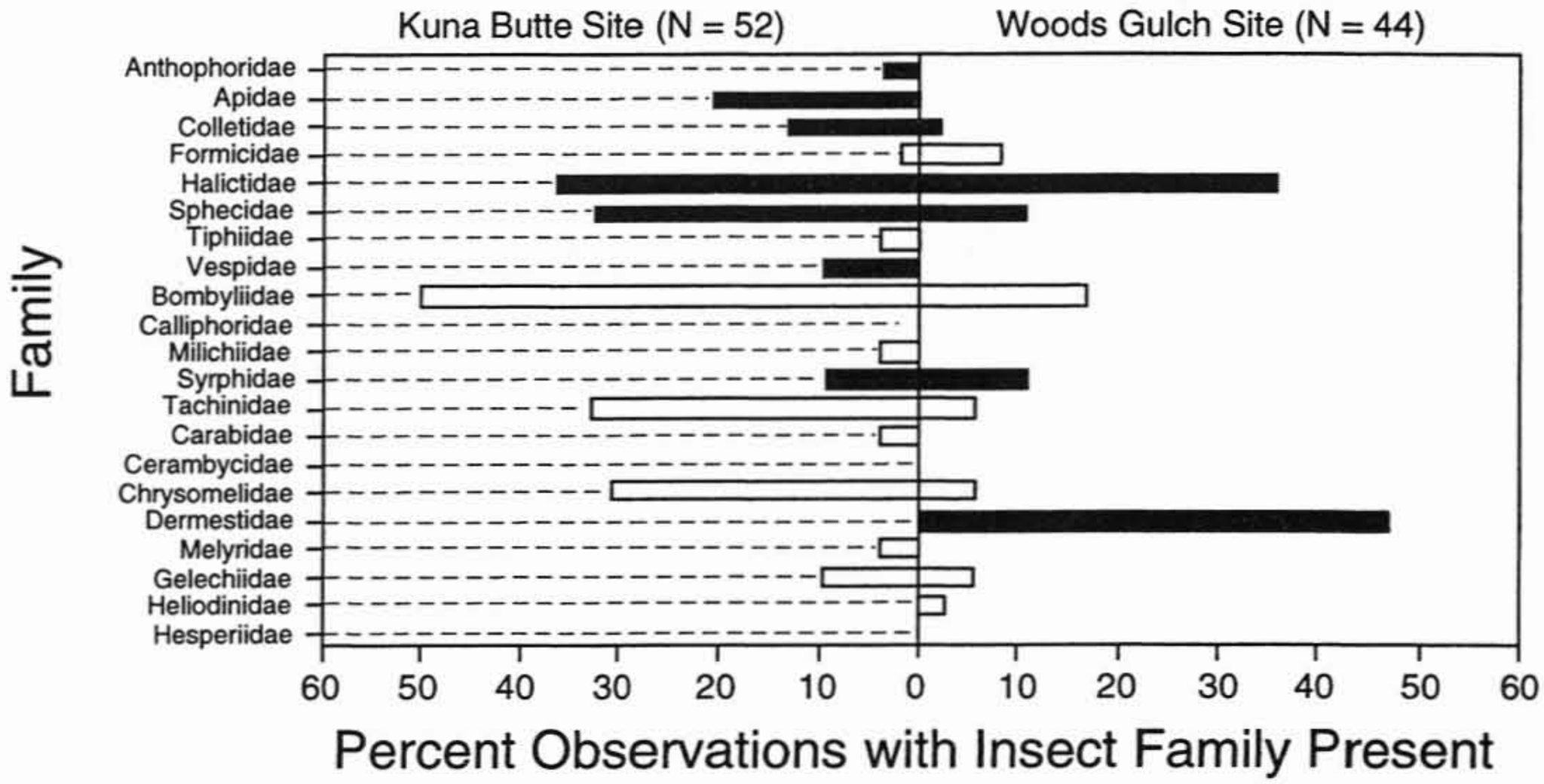

Fig. 3. Comparison of insect visitation rates on small plants at KB and WG. Shaded bars represent families with specimens that carried more than trace amounts of pollen. Open bars represent families with specimens that carried only trace amounts of pollen on their bodies or lacked pollen entirely.

(personal communication), *Lepidium* species with showy flowers, such as *L. papilliferum*, are generally self-incompatible, whereas species with reduced flower structures are autogamous. Nevertheless, Meyer (1995) presented data suggesting that *L. papilliferum* is at least capable of autogamy if not reliant on it for pollination; however, in those experiments it is possible that insects found their way into cages at the base and thus were responsible for pollination. In the present study seed set in caged plants was generally very low or nonexistent, suggesting that if autogamy occurs in *L. papilliferum*, it does not play a major role in reproduction. To resolve these discrepancies, genetic analysis or controlled laboratory experiments will likely be needed to establish definitively whether or not the species is self-compatible.

The possibility of wind-mediated pollination seems remote for *L. papilliferum* given that individual plants are often isolated from other individuals (Meyer 1995). Moreover, the structures of *L. papilliferum* flowers and pollen grains are not consistent with those of anemophilous species, which generally produce copious amounts of smooth-surfaced pollen and have an exposed stigma and long stamens with exposed anthers (Proctor et al. 1996). *Lepidium papilliferum* reproductive structures are relatively protected within the flower's corolla, and pollen production in this species could not be described as copious. Thus, wind pollination seems an unlikely explanation for seed set in the caged plants in our study.

Which Insects Matter for Pollination?

All 25 insect families that visited *L. papilliferum* flowers are known to have representatives that are anthophilous (flower-visiting; Proctor et al. 1996). However, flower visitation alone does not equate with pollination (Larson et al. 2001). For effective cross pollination to occur, pollen must be transferred from the anther of a single individual to the stigma of another individual. Insects from only 9 of 25 families collected from *L. papilliferum* flowers contained more than trace amounts of pollen on their bodies. Although demonstration of pollen transfer will require additional experiments, we consider families that had individuals with pollen loads of 2 or 3 to be the most likely pollinators of *L. papilliferum*.

Bees (superfamily Apoidea) are generally considered the most significant insect pollinators (Proctor et al. 1996). Thus, it is not surprising that all bee families collected from *L. papilliferum* flowers (Anthophoridae, Apidae, Colletidae, and Halictidae) contained individuals with high pollen loads. Many of these bees

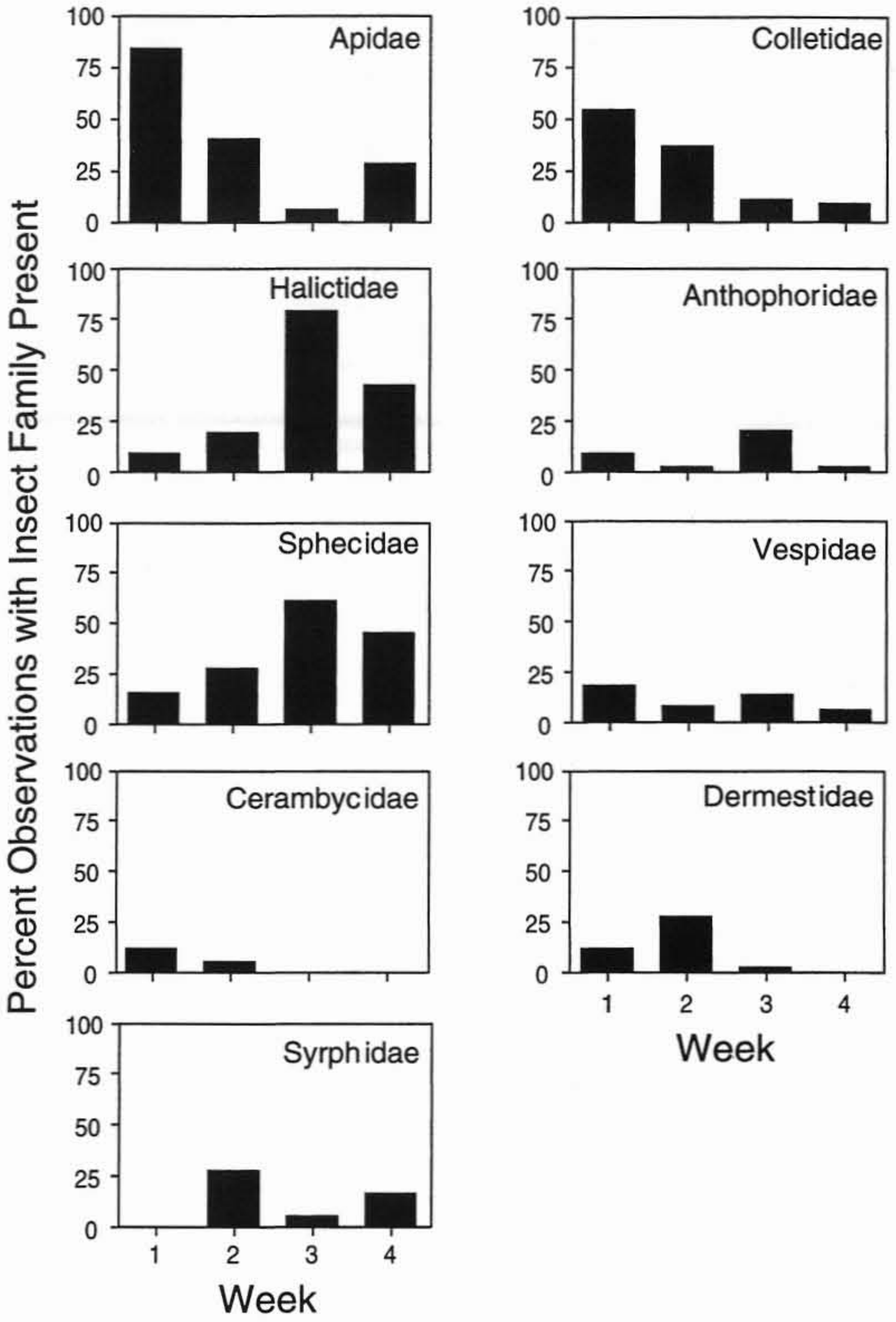

Fig. 4. Weekly changes in visitation rates at KB for the 9 insect families found to carry more than trace amounts of pollen.

had corbiculae (pollen baskets) as well as dense pubescence on their bodies, both of which facilitate pollen collection and transfer. When present at a site, honey bees (Apidae: *Apis mellifera*), colletids, and halictids foraged widely over the flowers of individual plants, making numerous stops at individual flowers before moving on. Their pollen baskets were often heavily loaded with *L. papilliferum* pollen, indicating that the reproductive structures of the flowers were being contacted.

Two families of wasps collected from *L. papilliferum* flowers carried more than trace amounts of pollen: Sphecidae and Vespidae. According to Proctor et al. (1996), sphecids are often anthophilous, yet as pollinators they are likely to be important only occasionally. Although sphecids were common in terms of their visitation rate (approximately 40% of plants were visited by at least 1 sphecid during an observation period), their visits were typically brief and restricted to only a few flowers on a

plant. Vespids had moderate amounts of pollen on their thorax but were not very common visitors to *L. papilliferum*. Thus, their contribution to pollination was likely minimal.

Flies are generally viewed as ranking second only to bees in terms of importance as pollinators (Larson et al. 2001). However, of the 7 dipteran families collected from *L. papilliferum* flowers, only syrphids carried more than trace amounts of pollen. Syrphids are known to be important pollinators (Larson et al. 2001), although their prevalence on *L. papilliferum* was relatively low and thus their contribution to pollination may have been small. However, it is worth noting that syrphids were quick to leave slick spots when approached by observers, thus raising the possibility that we have underestimated their visitation rates and importance as pollinators.

Of 5 beetle families found on *L. papilliferum* flowers, only cerambycids and dermestids carried more than trace amounts of pollen. Cerambycids, which were common at the onset of the flowering period but disappeared later, contained moderate amounts of pollen on their clypeus. During feeding, the beetle's clypeus likely comes in direct contact with the flower's sexual organs, which would facilitate pollination. Thus, cerambycids may be important pollinators, at least early in the flowering season. Dermestid beetles may also be important for pollination. These beetles are small (<3 mm in length), moderately pubescent, and often found directly on a flower's sexual organs. Distributions of these beetles were often contagious, with 5 to 10 beetles per plant not uncommon. Although small size and low mobility may limit the effectiveness of individual dermestids as pollinators of *L. papilliferum*, the cumulative effect of these beetles on flowers may result in substantial pollen transfer.

Pollinator Communities

One of the most striking differences in pollinator communities (i.e., the species composition of pollinator insects at an *L. papilliferum* population) between KB and WG was the absence or rarity of several pollinators at the smaller site: honey bees (absent), anthophorid bees (absent), vespid wasps (absent), cerambycid beetles (absent), colletid bees (rare), and sphecid wasps (rare). Reasons for the absence or rarity of these families at WG are unknown. It is possible that local population fluctuations limited or precluded these insects from the site in 2001 and that their numbers could rebound in subsequent years. Alternatively, the habitat around WG may not be suitable to support populations of these insects. Another possibility is that the insects were present in the vicinity of WG but were not attracted to *L. papilliferum* flowers. Anthophilous insects often exhibit constancy or labile preference (i.e., a preference that may change over time) for a particular flower species (Free 1963, Waser 1986, Proctor et al. 1996), focusing on species that provide the highest energy return for foraging investment (Ribbands 1949, Proctor et al. 1996). The small size of the *L. papilliferum* population at WG, along with the small size and dispersed nature of individual plants, may have made *L. papilliferum* flowers unattractive to many pollinators. If true, the long-term viability of small *L. papilliferum* populations may be vulnerable to competition with surrounding flower species. However, it remains to be determined whether pollinator communities are generally more diverse at larger *L. papilliferum* populations, and whether *L. papilliferum* competes with other flowers for pollinators.

Although WG had a less diverse pollinator community than KB, seed production (i.e., percent seed set) did not differ significantly between sites. From this standpoint the size of the pollinator community seems unimportant to *L. papilliferum* population viability. However, the lack of a diverse pollinator community could be detrimental to *L. papilliferum* populations in years when specific pollinators are rare or absent due to natural or human-induced fluctuations in population size. Many insect populations fluctuate in response to factors such as extreme climate, competition, parasitism, predation, and altered habitat. A diverse pollinator community may be more robust than a small pollinator community in its ability to compensate for perturbations that cause the temporary or permanent decline of a particular insect species.

Conservation Implications

In July 2002, *L. papilliferum* was proposed for listing as an endangered species by the U.S. Fish and Wildlife Service. The species is also listed as a Global Priority 2 species (Idaho Native Plant Society 1999). Now that it is clear *L. papilliferum* relies on insects for pollination, it is important to determine with certainty

which insects contribute most to pollen transfer. Studies also are needed to investigate the potential causes of variation in pollinator communities between sites by looking for correlations between specific site variables (e.g., population size, vegetation profiles, proximity to agriculture and commercial apiaries, competing flower species, geographic location) and diversity of pollinator communities. Differences in pollinator communities between sites may provide insight into why some *L. papilliferum* populations are in decline while others seem to flourish, as well as offer potential management solutions to improve the plant's prospects for survival. Effective conservation efforts for *L. papilliferum* must include the long-term success of its pollinating insects.

ACKNOWLEDGMENTS

Funding was provided by a Challenge Cost Share Grant to ICR sponsored by the Bureau of Land Management (BLM) and Boise State University. Ann DeBolt (BLM) provided expertise on *L. papilliferum* biology and identified the study locations. Comments from Ann DeBolt, Peter Koetsier, Wilma Robertson, and Roger Rosentreter were helpful in improving the manuscript.

LITERATURE CITED

BUCHNER, A., F. FAUL, AND E. ERDFELDER. 1992. GPOWER: a priori-, posthoc- and compromise power analyses for the Macintosh (computer program). Bonn University, Germany.

BOWMAN, J.L., H. BRÜGGEMANN, J.-Y. LEE, AND K. MUMMENHOFF. 1999. Evolutionary changes in floral structure within *Lepidium* L. (Brassicaceae). International Journal of Plant Science 160:917–929.

COHEN, J. 1988. Statistical power analysis for the behavioural sciences. 2nd edition. Erlbaum Press, Mahwah, NJ. 474 pp.

FREE, J.B. 1963. The flower constancy of honey bees. Journal of Animal Ecology 32:119–131.

IDAHO NATIVE PLANT SOCIETY. 1999. Results of the 15th annual Idaho Rare Plant Conference. Unpublished documents on file at Idaho Department of Fish and Game, Conservation Data Center.

KEARNS, C.A., AND D.W. INOUYE. 1993. Techniques for pollination biologists. University Press of Colorado. Boulder, CO. 583 pp.

LARSON, B.M.H., P.G. KEVAN, AND D.W. INOUYE. 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. Canadian Entomologist 133:439–465.

MANCUSO, M., AND R.K. MOSELEY. 1998. An ecological integrity index to assess and monitor *Lepidium papilliferum* (slickspot peppergrass) habitat in southwestern Idaho. Unpublished report on file at State of Idaho Military Division, Boise.

MEYER, S.E. 1995. Autecology and population biology of *Lepidium papilliferum.* Unpublished report on file at State of Idaho Military Division, Boise.

MOSELEY, R.K. 1994. Report on the conservation status of *Lepidium papilliferum*. Idaho Department of Fish and Game, Conservation Data Center.

PROCTOR, M., P. YEO, AND A. LACK. 1996. The natural history of pollination. Timber Press, Portland, OR. 479 pp.

QUINNEY, D. 1998. LEPA (*Lepidium papilliferum*). Idaho Army National Guard Report, Boise. 25 pp.

RIBBANDS, C.R. 1949. The foraging method of individual honeybees. Journal of Animal Ecology 18:47–66.

WASER, N.M. 1986. Flower constancy: definition, cause, and measurement. American Naturalist 127:593–603.

Received 10 December 2001
Accepted 22 June 2002