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POLLINATORS OF *ASTRAGALUS MONOENSIS* BARNEBY (FABACEAE): NEW HOST RECORDS; POTENTIAL IMPACT OF SHEEP GRAZING

Evan A. Sugden[1]

Abstract.— Important bee species inhabiting the study area are listed, including those observed and collected foraging on *Astragalus monoensis*, a California rare plant. The significance of each species as a potential pollinator is assessed, based on frequency of occurrence in collecting, observed and published host plant records, and morphology. Three pollinator categories are proposed: observed and/or collected on the plant, probable visitors, and possible visitors. New host plant records for these species are listed.

Current sheep grazing practices in the *A. monoensis* habitat endanger pollinators in four ways: (1) destruction of potential nest sites, (2) destruction of existing nests and contents, (3) direct trampling of adult bees, and (4) removal of food resources. Exposure of the major bee species to each of these factors is assessed utilizing experimental data and published information.

Astragalus monoensis Barneby, "Mono Rattleweed" or "Mono Milkvetch," is a perennial legume endemic to the California portion of the Great Basin (Barneby 1964, Munz and Keck 1959). It is listed as endangered by the Federal Government (Ayensu and DeFilipps 1978) and rare and endangered by the California Native Plant Society (Smith et al. 1980). It occurs in the region east of the Mono Craters between 7500 and 8000 feet (2286¼438 m) elevation (Smith et al. 1980, K. Teare, pers. comm., unpubl. data). The number of individual plants in each population varies from several thousand to less than 100.

A detailed description of *A. monoensis* appears in Munz and Keck (1959). It is a papilionaceous bee flower, as characterized by Percival (1965), and produces considerable nectar, as evidenced by the regularity of visits to its flowers by bumble bees. Males of the anthidiine ("carder" or "mason") bees *Anthidium clypeodentatum* and the relatively large *Callanthidium formosum* (Megachilidae) also frequent the flower. Pollen from *A. monoensis* is also collected by these and other species. It is an obligate outcrosser, requiring insect transferal of pollen between flowers of different plants to set seed (Sugden 1984, R. Barneby, pers. comm.). Plant associates are relatively few, dominated by the nectarless *Lupinus duranii* Eastw. (Fabaceae). Also prominent are *Hulsea vestita* Gray and *Chrysothamnus parryi vulcanicus* (Greene) Hall & Clem. (Asteraceae), the primary local nectar sources for early and late parts of the summer, respectively (unpubl. data). Other associates are *Eriophyllum lanatum* var. *monoense* (Rydb.) Jeps. (Asteraceae), *Phacelia frigida* Greene (Hydrophyllaceae), *Calyptridium umbellatum* var. *caudiciferum* (Gray) Jeps. (Portulacaceae), and *Mimulus coccineus* Congd. (Scrophulariaceae). *Eriogonum umbellatum* Torr. (Polygonaceae), a widely insect-utilized nectar source, occurs at several sites.

A majority of the known *A. monoensis* populations occur with the above plant associates in isolated sand flats, the soil of which is composed of coarse gravel and sand of volcanic pumice origin. The flats are typically surrounded by a second-growth forest of *Pinus contorta* Doug. ex Loud. (Lodgepole Pine) and *Pinus jeffreyi* Grev. & Balf. in A. Murr. (Jeffrey Pine). The forest floor is essentially sterile with respect to pollen and nectar. Hence, the wildflower patches of the sand flats exist as resource "islands" for pollinators. Beetle burrows in many trees and logs provide abundant nest cavities that are utilized by solitary bees. *Thomomys talpoides*, the Northern Pocket Gopher, inhabits the sand flats, and its many abandoned burrows are probably utilized by bumble bees as

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nest cavities. *Bombus huntii* queens have been observed entering such burrows, apparently nest-searching (pers. obs.).

The largest populations of *Astragalus monoensis,* which occur on federal land, are subjected annually to the influence of sheep grazing. This usually occurs in midseason, when the plants are in flower and before most seed is set. In the sand flat region, 12,000 sheep in herds of up to 2,000 individuals may be stationed at springs or watering tanks near the known *A. monoensis* populations (C. Chamberlain, pers. inquiry of sheepherders). In the sand flats per se, the ground is often completely denuded of vegetation where the sheep forage. Over the course of several days the grazed area may extend in a continuous swath, 100 m or more in width, to cover an entire flat (pers. obs.). The loose soil of the habitat is subject to extreme disturbance by the spadelike action of sheep hooves, which may uproot or expose the crowns of mature plants and destroy seedlings (pers. obs.). Typical effects of grazing on the habitat are shown in Figure 1.

Although the toxicology of *A. monoensis* is unknown, foliage and flowers of the plant are often grazed (C. Chamberlain, K. Teare, pers. comm.). Sheep merely passing over a site, i.e. not feeding, do less damage than those allowed to forage (C. Chamberlain, pers. comm.).

This paper examines the hypothesis that, in addition to direct disturbance, the plant may suffer reproductive setback due to the negative impact of intensive sheep grazing on its pollinators. These are various bee species, several of which nest in or near the ground where sheep are herded and all of which are part of the sand flat community. Postulated below are four types of impact:

(1) *Destruction of potential nest sites.* Bumblebees often construct their nests in abandoned rodent burrows, including those of *Thomomys* spp. (Thorp et al. 1983). Such burrows are abundant in and near the *A. monoensis* habitat. Sheep collapse the entrances of these burrows and hence remove many potential nest sites from discovery by bumblebee queens in the spring. The frequency of burrow encounter by sheep is indicated by the fact that rodent holes are the major cause of livestock loss (through broken legs) in the region (pers. inquiry of sheepherder). Solitary ground-nesting bee species require specific substrate conditions to establish nests (Linsley 1958). Disturbance of the soil by sheep hooves probably alters the acceptability of many potential nest sites. Pithy stems may be broken and trampled by sheep if near the ground, removing potential cavities for species that utilize stick nests.

(2) *Destruction of existing nests and contents.* Ground nesting bees construct delicate burrows and chambers in the soil. Depending on the species, the brood chambers may be either close to the surface, sometimes within three to four inches (Thorp 1969), or several feet below (Malyshev 1936). Soil disturbance may destroy all or part of such nests, damage existing brood and provisions, and/or displace nest-entrance landmarks, which female bees utilize in orientation to the exact location of their burrows. Many bees construct nests in preexisting cavities above the ground, often in hollow sticks. Such nests may be shattered or disoriented by trampling and exposed to rainfall. Many of the bees concerned here are solitary, nonaggressive species and have no means of nest defense against sheep.

(3) *Removal of food resources.* Sheep grazing greatly reduces the density of many herbaceous plants. Among these are the nectar and pollen sources on which local bee populations subsist. For many species, these resources may be important to the completion of an entire life cycle. (Due to its limited distribution and population size, it is unlikely that *A. monoensis* provides all the annual nutritional requirements for individuals of any single bee species. Its nectar and pollen-yielding plant associates are important in this respect and are heavily impacted by sheep grazing as reported here.)

(4) *Direct trampling.* Male bees of several species are known to "sleep" singly or in aggregations on vegetation close to the nest sites of females (Linsley 1962, Rust et al. 1974) or in shallow, temporary burrows or emergence holes (Linsley 1958). Early in the season, before nests are constructed, female bees may also rest in similar positions. In this situation, particularly during the cool hours of night or morning, when bees are torpid and unable to escape, they may be in danger of being trampled by sheep.

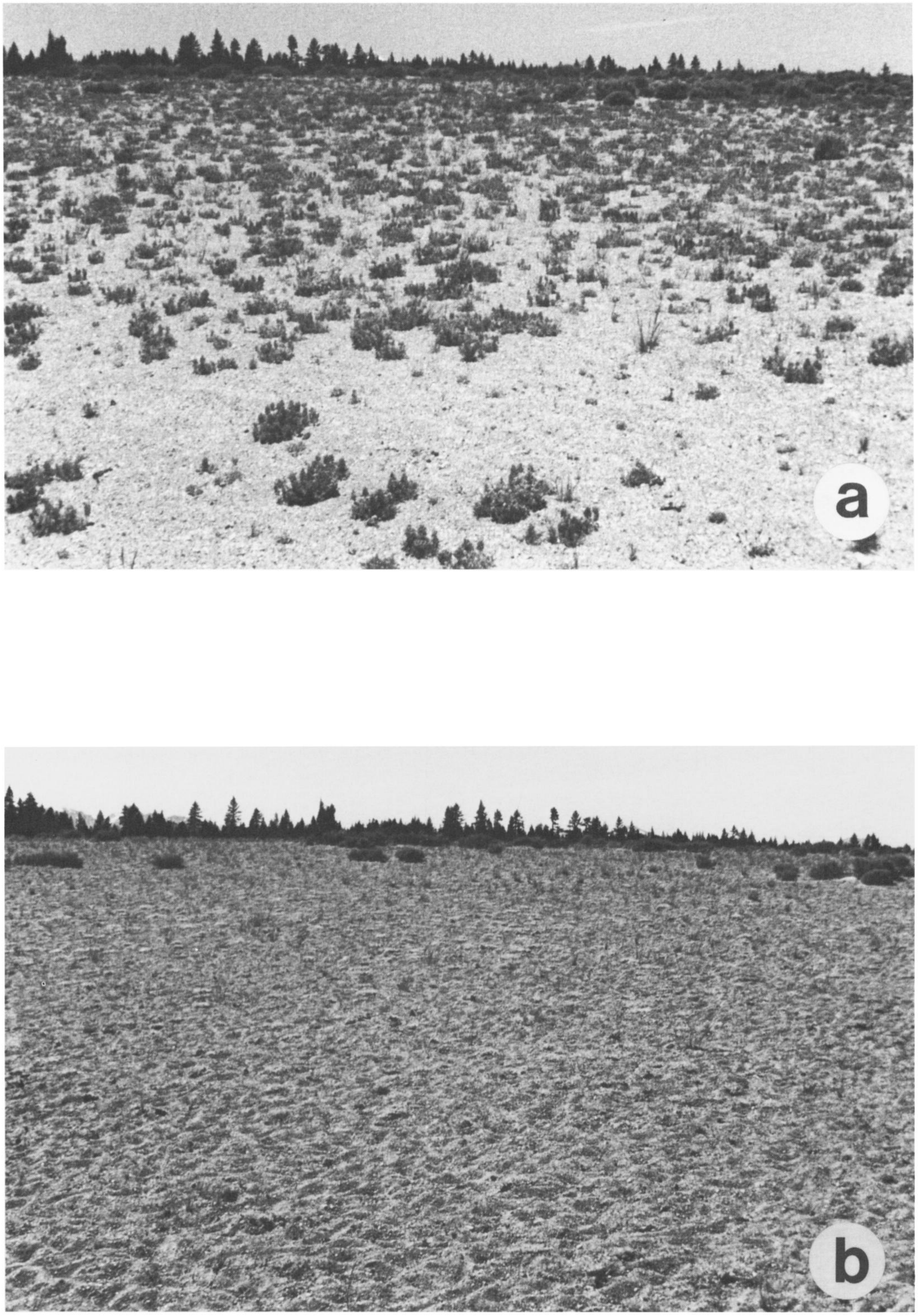

Fig. 1. (a) Typical aspect of *Astragalus monoensis* habitat prior to grazing. Big Sand Flat, June 1980. Plants in foreground are primarily *Lupinus duranii.* (b) Same view following grazing by domestic sheep.

METHODS

Bee species listed are those which appeared two or more times in occasional collecting during 1979–1982. All specimens were collected with a standard insect net and are currently deposited in the R. M. Bohart Museum, Department of Entomology, University of California, Davis.

For this study, insect "abundance" is defined as the relative number of individuals appearing in occasional collections from the *Astragalus monoensis* habitat.

In recording host plant data from the literature, a conservative approach was maintained. A host record designated only to genus was counted as a species record only if no other species records from that genus were given in the sources consulted. For congeneric listings of more than one species, genus records without species designations were not counted.

Floras and references consulted for plant names and identifications are Munz and Keck (1959), Taylor (1981), and Willis (1973).

Plant distributions were obtained by mapping the study sites into a grid of one square hectare units and sampling randomly near the center of each unit with a one square meter quadrat sampler.

Insect densities were obtained from direct observation of insects on flowers. Two identical walking transects covering 2.2 km and between 36 and 52 minutes in duration were made daily at approximately 11:00 and 14:00 hours. Densities are given as counts per kilometer per hour to make comparisons with a second study site utilized in another project, where transects were of a different length, and as a partial correction factor for variable duration of transects.

Average ambient temperature at 1 m above the ground is expressed as an average of three readings per transect. Previous minimum temperature is the previous night's low ambient temperature at one meter. All readings were taken on a Taylor maximum-minimum mercury thermometer calibrated in salted ice water to 0 C.

RESULTS

Table 1 lists bee species collected in the sand flat region during 1979–1982. These are divided into three groups based on inferred probability of importance as pollinators of *Astragalus monoensis*. Group I consists of those species collected or observed foraging on the plant. For these data and number of individuals collected and/or observed are indicated, with sex and caste, where appropriate, for those collected. Relative abundance is given as the number of discrete collection events (date × locality) resulting in an extant voucher specimen. Group II consists of four species which, although neither collected nor observed foraging on *A. monoensis*, are pollinator candidates by virtue of their locally great abundance, widely polylectic habits, and published or observed host records, including other *Astragalus* spp., *Lupinus duranii*, the dominant flowering plant in the community, and/or other papilionaceous legumes. These bees are robust, moderate to large in size, and morphologically capable of pollinating the *A. monoensis* flower. Group III species have a low or intermediate abundance. Some have been reported to forage on other *Astragalus* spp., and all of them have published papilionaceous legume host records.

Species from Table 1 are listed in Table 2 with host plant information. To these data new information has been added from personal observation (Appendix I). For each bee species the total number of published host plant families, genera, species, and species of *Astragalus* are given. Papilionaceous legume hosts are given as proportions of the total number of host plant genera and species. All bee species appearing in Table 2 whose host specificity is known have been categorized as "polylectic" (many flower hosts), with the exception of *Andrena cleodora* ssp. *cleodora*. It is listed as an "oligolege of ceanothus" (re stricted to a single species or group of closely related species of host plants) (Krombein et al. 1979).

From Table 1, it can be seen that a wide diversity of bees is associated with *A. monoensis*. Observed visitors alone represent 3 families, 5 genera, and at least 7 species. Probable and possible visitors comprise 5 families, 4 genera, and 14 species. The predominance of megachilids in this assemblage, particularly in the genera *Osmia* and *Anthidium*, is a reflection of the general composition of the bee fauna in the dry, high altitude

TABLE 1. Bee associates of *Astragalus monoensis* Barneby. Relative abundance refers to number of collection events in which species appear. w = worker, q = queen, m = male. S = extant specimens, O = field observation, R.A. = relative abundance.

Species	Date	Number, sex, caste	S or O	R.A.
GROUP I—Observed or collected on *Astragalus monoensis*				
APIDAE				
Bombus (*Pyrobombus*) *huntii* Greene	8.VII.'79	7w,2q	S	5
	14.VII.'79	3w	S	
B. (*Bombias*) *nevadensis nevadensis* Cresson	8.VII.'79	4w,1q	S	1
B. (*Pyrobombus*) *vosnesenskii* Radoszkowski	7.VII.'79	1w	S	5
MEGACHILIDAE				
Anthidium (*Anthidium*) *clypeodentatum* Swenk	14.VII.'79	2m,2f	S	1
Anthidium sp.	17.VII.'79	1	0	—
Callanthidium formosum (Cresson)	8.VII.'79	1f,2m	S	6
	14.VII.'79	2f,1m	S	
Osmia (*Monilosmia*) *cara* Cockerell	14.VII.'79	1f	S	1
O. (*Nothosmia*) *grindeliae* Cockerell	7.VII.'79	1f	S	3
	14.VII.'79	1f	0	—
O. spp.	14.VII.'79	1	0	—
	16.VII.'79	4	0	—
	17.VII.'79	4	0	—
GROUP II—Probable visitors				
ANTHOPHORIDAE				
Anthophora (*Anthophora*) *urbana urbana* Cresson			S	10
APIDAE				
Apis mellifera L.			S	10
Bombus (*Separatobombus*) *morrisoni* Cresson			S	9
MEGACHILIDAE				
Hoplitis (*Monumetha*) *albifrons argentifrons* (Cresson)			S	10
GROUP III—Possible visitors				
ANDRENIDAE				
Andrena (*Trachandrena*) *cleodora cleodora* (Viereck)			S	2
A. (*Plastrandrena*) *prunorum prunorum* Cockerell			S	2
COLLETIDAE				
Colletes consors consors Cresson			S	2
MEGACHILIDAE				
Anthidium (*Anthidium*) *banningense* Cockerell			S	4
A. (*A.*) *mormonum* Cresson			S	3
A. (*A.*) *tenuiflorae* Cockerell			S	4
Hoplitis (*Monumetha*) *fulgida platyura* (Cockerell)			S	6
Osmia (*Chenosmia*) *calla* Cockerell			S	3
O. (*Monilosmia*) *densa densa* Cresson			S	3
O. (*Acanthosmia*) *integra* Cresson			S	2

TABLE 2. Unweighted host plant data for bee associates of *Astragalus monoensis* Barneby. Bee species listed alphabetically by group (see Table 1). Data for *Apis mellifera* omitted. Sources: Krombein et al. (1979), Moldenke and Neff (1974), Thorp et al. (1983), personal observations reported in Appendix I of this paper.

Bee species	No. families	No. genera	No. species	No. *Astragalus* species	Papilionaceous legume hosts as proportion of total: Genera	Species
GROUP I						
Anthidium clypeodentatum	4	6	11	2	.50	.67
Bombus huntii	18	39	39	1	.21	.21
B. nevadensis nevadensis	9	16	16	1	.38	.38
B. vosnesenskii	38	117	142	1	.09	.15
Callanthidium formosum	6	9	9	1	.44	.44
Osmia cara	7	11	18	1	.27	.39
O. grindeliae	3	3	3	1	.33	.33
GROUP II						
Anthophora urbana	3	103	174	1	.10	.11
B. morrisoni	16	35	35	1	.20	.20
Hoplitis albifrons argentifrons	15	29	34	1	.07	.06
GROUP III						
Andrena cleodora cleodora	10	12	15	0	.08	.07
A. prunorum prunorum	32	89	101	0	.03	.03
Anthidium banningense	6	11	16	0	.45	.33
A. mormonum	8	14	26	1	.29	.38
A. tenuiflorae	9	15	19	1	.27	.37
Colletes consors consors	4	5	6	0	.20	.17
Hoplitis fulgida platyura	17	34	49	1	.12	.12
Osmia calla	12	22	33	1	.18	.30
O. densa densa	21	29	43	0	.17	.26
O. integra	3	4	4	1	.50	.50

sand flat region. Three species of *Megachile* and *Dianthidium parvum* ssp. *parvum* occur regularly on the flower heads of *Hulsea vestita* but are not observed to forage on other plants. The latter is considered an oligolege of composites (Krombein et al. 1979).

Group I

It is not surprising that bumblebees visit *Astragalus monoensis*. Although populations fluctuate in the *A. monoensis* habitat, as has been found elsewhere (Bohart and Knowlton 1952), their long-lived colonies, large body size, and caste polyethism make them vigorous foragers and important pollinators of many plant species. *Bombus huntii* and *B. vosnesenskii* were present every year of the study. *Bombus nevadensis* has been collected only once and only on *A. monoensis*. This species is at most an intermittant member of the sand flat fauna, perhaps due to population fluctuation. All three bumblebee species are widely polylectic and readily visit papilionaceous legumes. *Bombus huntii* was the most commonly collected bee on *A. monoensis* and has been regularly observed to forage on *Lupinus duranii*. Its overall abundance is matched by *B. vosnesenskii*.

Close in size to early season bumblebee workers are individuals of *Callanthidium formosum*. This species is relatively common in the study area. It apparently exhibits an affinity for *A. monoensis* and other legume species, based on its minimal host records. Two individuals of *Anthidium clypeodentatum* were collected on *A. monoensis* in 1979. Although its abundance is low, its papilionaceous legume preference is apparently at least as high as that of *C. formosum*, and it has been recorded on at least one other *Astragalus* species. It has not been collected on *L. duranii*.

Osmia is the most speciose bee genus of the sand flats, represented by at least 13 sympatric species (unpubl. data). *Osmia grindeliae* may have some affinity for *A. monoensis*, although its host records are too sparse to be useful as indicators of general papilionaceous legume preference. Its abundance is moderate. *Osmia cara* is rare in the area. Neither of these two species have been collected on *L. duranii.*

Group II

Honeybees, *Apis mellifera,* are present in the sand flats at relatively low density, despite their apparently great abundance in comparison to wild bees of the study area (pers. obs.). It is likely that this relatively resource-depauperate region supports only a few small feral colonies. Honeybees avidly collect pollen from *L. duranii* (pers. obs.). Pollen tentatively identified as that of *A. monoensis* has been observed in pollen trap samples from experimental honeybee hives at Little Sand Flat (unpubl. data). *Bombus morrisoni* is a common bumblebee in the study area. It readily visits *L. duranii* and has been recorded on other *Astragalus* species. Although its general preference for papilionaceous legumes seems somewhat lower than that of other bumblebees, it remains a good candidate for pollination of *A. monoensis.*

Anthophora urbana is a widely occurring species that forages on virtually every major pollen or nectar source plant in the sand flats. It is capable of visiting *A. monoensis* and probably does so, although its papilionaceous legume host record appears moderate because of the large diversity of records.

Hoplitis albifrons ssp. *argentifrons* is the most common species associated with *Hulsea vestita.* Its foraging habits are so flexible that it frequently visits plants from two widely disparate taxa on a single foraging flight, e.g., *L. duranii* and *Mimulus coccineus* or *Hulsea vestita* and *Chrysothamnus parryi* var. *vulcanicus* (pers. obs.). An intense survey would probably show that *H. albifrons* visits and pollinates *A. monoensis.*

Group III

Bees in this group are variable in their pollination potential for *A. monoensis.* The smaller species, *Anthidium mormonum, A. tenuiflorae, Osmia calla,* and *Hoplitis fulgida* ssp. *platyura* have each been recorded on *Astragalus*; *A. tenuiflorae* and *O. calla* have been collected on *L. duranii.* The three remaining megachilids are relatively large, robust species that would be expected to be good pollinators of papilionaceous legumes. Only *O. integra* has not been recorded on *L. duranii. Andrena prunorum* ssp. *prunorum* and *A. cleodora* ssp. *cleodora* are the least likely pollinator candidates, but they have both been recorded on papilionaceous legumes. It appears possible that these species contribute to pollination of *A. monoensis.*

Table 3 lists Group I, II, and III bee species with known or probable nest type and respective susceptibility to the three types of grazing-associated damage described above. Ground-nesting bumblebees are particularly vulnerable in this regard. *Bombus nevadensis* may be less vulnerable, because it is known to nest in aboveground cavities on occasion. *Anthophora urbana, Colletes consors consors,* and *Andrena* spp. represent species whose nests are in jeopardy. The anthidiines, including *Anthidium* spp. and *Callanthidium formosum,* are apparently flexible in their nest location. They may be exposed to nest or nest site damage, depending on their local nest-building habits. Many cavity nesters, principally *Osmia* spp., are presumably exempt from this hazard because their nests are mostly in beetle holes in logs or standing trees (pers. obs.). Possible exceptions are species in the *Acanthosmioides* subgenus, many of which nest in open, sandy sites in ground burrows. Burrows of *Acanthosmioides* species were not found at the study sites but likely occur there. An existing population of *O.* (*A.*) *integra* at Panum Crater, several kilometers west of the nearest known *A. monoensis* population, nests at the base of *Lupinus duranii* plants (pers. obs.). This species is also found in ground nests associated with sparse vegetation on sand dunes in northwestern California (D. Gordon, pers. comm.). Nests of *O.* (*A.*) *nigrobarbata* also occur at the base of plants (Rozen and Favreau 1967). Grazing hazards are significant for these ground-nesting bees and others that may nest in hollow or pithy stems of herbaceous plants, which includes many of the species from Table 3.

Small solitary bees are limited in their flight range (Kapyla 1978) and are therefore more dependent on local floral resources. Since a large proportion of nectar and pollen plants may be decimated by sheep grazing in the *A. monoensis* habitat, solitary bees dependent on such resources may be subject to

TABLE 3. Nesting habits and type of exposure to intensive sheep grazing for bee associates of *Astragalus monoensis* Barneby. Nest type of a congenor may be listed where information on an *A. monoensis* associate is unavailable or supplementary. N = potential nest substrate disturbance, C = damage to nests and contents, R = depletion of trophic resources, T = direct trampling, ( ) = questionable.

Species	Exposure	Nest
GROUP I		
Bombus huntii	N C (R)(T)	Abandoned rat nest in building (Medler 1959); underground, surface, and aboveground domiciles (Hobbs 1967, Richards 1978); abandoned rodent burrows (pers. obs.).
B. nevadensis	N C (R)(T)	Aboveground domicile (Richards 1978); surface and aboveground hives (Hobbs 1965, Hobbs et al. 1962); rafters of building (pers. obs.).
B. vosnesenskii	N C (R)(T)	Abandoned rodent burrows (Thomomys spp.) (Thorp et al. 1983).
Anthidium clypeodentatum	(N)(C) R (T)	*A. maculosum*: wooden trap nests (Horning 1971); probably beetle burrows in trees or other insect ground burrows in study area.
Callanthidium formosum	(N)(C) R (T)	Wooden trap nests (Parker and Bohart 1966); *C. illustre*: floral scape of *Yucca* sp. and oak stumps (Krombein et al. 1979).
Osmia cara	R (T)	Driftwood (Graenicher 1935); probably beetle burrows in study area.
O. grindeliae	R (T)	*O. pumila*: wooden trap nests (Krombein 1967, Medler 1967).
GROUP II		
Apis mellifera	R	Aboveground cavities, hollow trees or logs (Seely and Morse 1976).
B. morrisoni	N C (R)(T)	Abandoned rodent burrows?
Anthophora urbana	N C R (T)	Horizontal and vertical soil banks (Mayer and Johansen 1976).
Hoplitis albifrons	R (T)	*Hoplitis* spp.: elderberry stems (Clement and Rust 1976); probably beetle burrows in study area.
GROUP III		
Andrena cleodora	N C R (T)	Ground burrows (Krombein et al. 1979).
A. prunorum	N C R (T)	Ground burrows (Krombein et al. 1979).
Colletes consors	N C R (T)	*C. stepheni*: ground burrows (Hurd and Powell 1958).
Anthidium banningense	(N)(C) R (T)	Paper and wooden trap nests (Jaycox 1967); ground burrows (Krombein et al. 1979).
A. mormonum	(N)(C) R (T)	Beetle burrows, oak stumps, ground burrows (Hicks 1929).
A. tenuiflorae	(N)(C) R (T)	Rock crevices (Krombein et al. 1979).
Hoplitis fulgida	R (T)	Elderberry stems (Clement and Rust 1976); probably beetle burrows in study area.
O. calla	R (T)	*O. atriventris* and *O. clarescens*: wooden trap nests (Fye 1965; Krombein et al. 1979).
O. densa	(N)(C)(R)(T)	unknown.
O. integra	N C R (T)	Ground burrows (pers. obs.); *O. longula*: under stones (Parker 1975); *O. nigrifrons*: trap nests (Rust et al. 1974); *O. nigrobarbata*: ground burrows (Rozen and Favreau 1967).

artificial resource depletion, which could constrain or curtail their brood-rearing activities. Catastrophic lowering of nectar availability may stress individual adult bees and induce or increase competition for this resource. Partial pollen depletion might negatively influence brood development. In support of these assertions, data have been collected on temporary changes in foraging bee density on *Hulsea vestita* and *Lupinus*

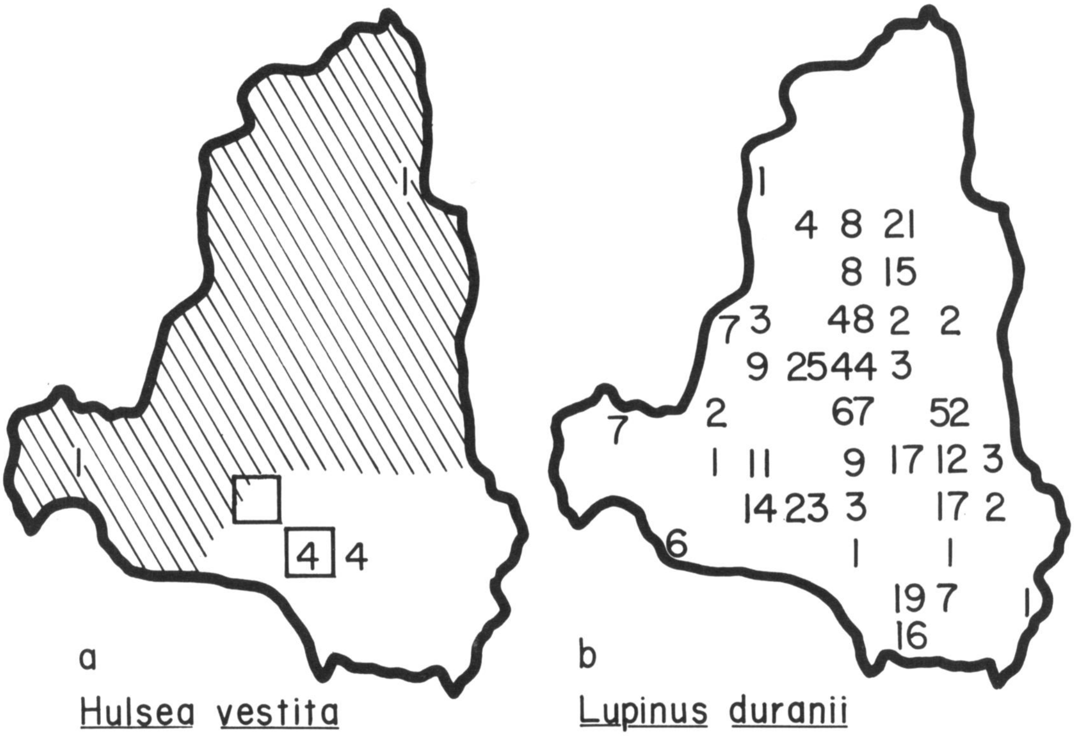

Fig. 2. Distributions of (a) *Hulsea vestita* and (b) *Lupinus duranii* as mapped in June and July 1980. Both species are perennial. Figure 2a shows the location of the two, one square hectare study plots utilized for insect density transects and the approximate area that was grazed 2 August 1982 (hatched).

duranii in response to grazing of adjacent areas.

In 1982 the density of flower-foraging insects was recorded on two study plots at Little Sand Flat before and after sheep were introduced to the area. The distributions of the dominant plant species at the study site appear in Figure 2. On the afternoon of 2 August, approximately 75% of the flat was grazed by a herd of 2000 sheep (Fig. 2a). Essentially all the aboveground vegetation was removed in the grazed area (cf Fig. 1).

Results for the most often observed bee/plant combinations are shown in Figure 3. Note that densities of bees increase dramatically after sheep grazing. Transects from before and after grazing were compared utilizing the Mann-Whitney two sample rank test. Differences were not significant for native bees on *Hulsea vestita* ($p = 0.1071$), although this analysis does not take into account the progressive decline in bee densities prior to grazing. This was probably due to a drop in ambient temperature (Fig. 3) and a decline in nectar availability, accentuated by a severe freeze on the evening of 1 August. Extrapolation from this trend would predict a density close to zero 3 August. Densities for honeybees on *Lupinus duranii* differed significantly between pre- and postgrazing transects ($p = 0.0413$), displaying an increase of several fold 3 August, despite relatively low ambient temperature. Note that the relative proportion of *L. duranii* removed by grazing was greater than that of *H. vestita* (Fig. 2a,b).

Species occurrences on *L. duranii* also changed markedly (Table 4). Prior to grazing, no more than 3 bee species per day were observed (average 1.4), compared to 6 species 3 August. In addition, 5 of the 6 species observed 3 August had not been observed during the previous 5 days, and, of the 3 species observed prior to grazing, only *Apis mellifera* was recorded 3 August. Species occurrences on *Hulsea vestita* remained unchanged from pre- to postgrazing transects, with the exception of the appearance of a previously unrecorded *Osmia* sp. and the conspicuous absence of *Apis mellifera* 3 August. Pre- and postgrazing densities of less frequently occur-

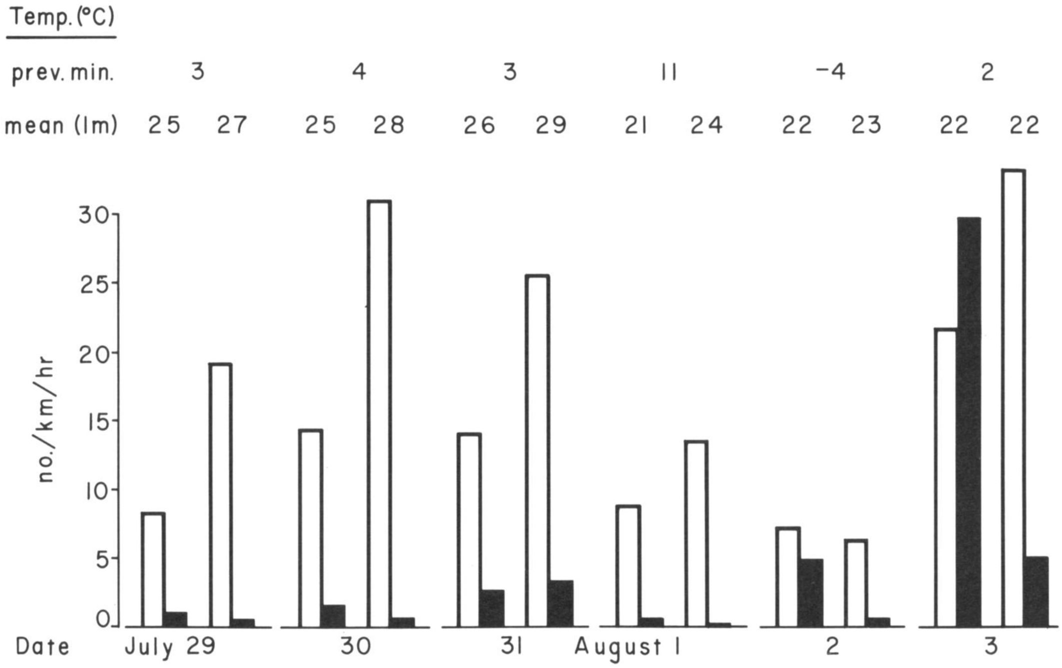

Fig. 3. Insect densities on flowers before and after nearby sheep grazing. Open bars: native bees on *Hulsea vestita*. Shaded bars: Honeybees on *Lupinus duranii*. Each pair of bars represents one of two daily transects taken at 1030 and 1300 hrs. Appearing above are average ambient temperature at one meter for each transect and the previous night's low temperature. Native bees in decreasing order of abundance: *Hoplitis albifrons, Osmia montana, Megachile* spp., *Anthidium* spp., *Anthophora urbana, Xeromelecta californica, Hoplitis fulgida, Osmia* spp., *Bombus morrisoni*, Misc.

ring insect/plant combinations were recorded and tested as above for those cases where data permitted analysis. None were significantly different between treatments.

The remainder of the flat was grazed on the evening of 3 August, and insect densities dropped effectively to zero on the following day.

Apis mellifera and *Bombus* spp. may forage many kilometers from the colony (Gary 1979, Heinrich 1979, respectively) and therefore might be less affected by the outcome of local flower grazing as mentioned above. If, however, grazing is extensive, bumblebees and honeybees nesting in this area may be forced to fly longer distances to forage, incurring a greater energy cost through local foraging. If such costs are significant, colony survival may be reduced. Potential effects of resource depletion may be intensified by natural spatiotemporal variation in floral resources, as demonstrated for similar habitats (Tepedino and Stanton 1980).

The danger of direct trampling is the least known and therefore most speculative of the three hazard types. Sleeping behavior is known for many bee and wasp species in which adults gather, often in large aggregations, on vegetation or in shallow ground shelters (Linsley 1958, Evans and Linsley 1960). Bumblebee queens are active and nestless in the early season, April through June, after emerging from winter hibernation. They often spend the evenings in temporary shelters near the ground and thus exposed to physical crushing by passing sheep. Males are produced in the late summer. Currently, sheep are herded in the sand flat region between these times, i.e., late June through August. Trampling hazard may be variably important for different bumblebee species depending on yearly weather patterns, timing of the colony cycle, and arrival of sheep in the area. Most solitary species have begun nesting by the time sheep grazing commences. For these, trampling exposure may interfere with nest orientation by females due to the disruption of local landmarks. Sleeping aggregations of males might also be disrupted.

TABLE 4. Bee species on *Lupinus duranii* at Little Sand Flat before and after nearby sheep grazing.

	Pregrazing					Post grazing
	July			August		
Species	29	30	31	1	2	3
Anthophora urbana						X
Apis mellifera	X	X	X	X	X	X
Bombus huntii						X
B. morrisoni	X					
B. vosnesenskii						X
Callanthidium formosum						X
Osmia montana			X			
unidentified species						X

CONCLUSION

In this study, field observations and literature survey have contributed to an analysis of the most important pollination relationships of *Astragalus monoensis*, a rare, bee-pollinated plant. Pollinators of maximum importance are bees that forage from its flowers and other species that would be expected to do so based on local abundance, host plant records, morphology, and behavior.

The evidence presented herein supports the hypothesis that pollinating bees, including those found in association with *Astragalus monoensis*, may be adversely affected by the regular movement of large numbers of domestic sheep through the sand flats. An investigation on the local nesting biology of these bees would require a specialized and intensive effort. However, the existing literature suggests that the nests of many of these species are made within the range of substrate disturbance by passing sheep. The data presented here demonstrate that bees respond to localized resource depletion by sheep grazing. The resultant long-term effects on the population size and structure of *A. monoensis* remain to be investigated. If pollination becomes limiting for the plant, seed set may decline.

Other factors are obviously important to the system as it is perturbed. For example, a certain degree of soil disturbance, as would be caused by movement of sheep through the habitat, may create favorable conditions for seed germination, such as increased scarification, which has been shown to be important to many desert plant species (B. Kay, pers. comm.). *Astragalus monoensis* usually occurs in low density compared to its most abundant insect-visited plant associates. For this reason, it could be under competition for insect pollination. Heavy grazing might alter such a relationship by increasing the pollinator/flower ratio in favor of *A. monoensis* if its flowers were relatively less grazed and if bee populations did not proportionately decline.

Further research into the floral ecology, autecology, and population genetics of *Astragalus monoensis* is necessary for the establishment of criteria necessary for its protection, as suggested for other endangered plant species (Järvinen 1982). The importance of such research is emphasized by a recent increase in grazing allotments for the Mono Basin and adjacent areas (BLM 1982).

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APPENDIX I. New host records for bees associated with *Astragalus monoensis* Barneby. Location for all records: Mono Craters region, Mono County, California. *Astragalus monoensis* records included in text, Table 1. f = female, q = queen, m = male. Host plant abbreviations: C.p.v. = *Chrysothamnus parryi vulcanicus* (Greene) Hall & Clem. (Asteraceae), H.v. = *Hulsea vestita* Gray (Asteraceae), L.d. = *Lupinus duranii* Eastw. (Fabaceae), P.f. = *Phacelia frigida* Greene (Hydrophyllaceae), E.u. = *Eriogonum umbellatum* Torr. (Polygonaceae), C.u. = *Calyptridium umbellatum* (Torr.) Greene (Portulacaceae), M.c. = *Mimulus coccineus* Congd. (Scrophulariaceae).

Species	Host plant	Date	Number, sex, or caste
ANDRENIDAE			
Andrena (*Trachandrena*) *cleodora cleodora* Viereck	E.u.	28.VI.'81	2f
	E.u.	1.VII.'81	4f
A. (*Plastrandrena*) *prunorum prunorum* Cockerell	E.u.	28.VI.'81	2f
ANTHOPHORIDAE			
Anthophora urbana urbana Cresson	H.v.	26.VI.'79	1f
	L.d.	7.VII.'79	1f
	C.p.v.	8.VIII.'79	1f
APIDAE			
Bombus (*Pyrobombus*) *huntii* Greene	H.v.	8.VII.'79	1w
	P.f.	24.VII.'79	2w,1q
	C.p.v.	8.VIII.'79	1w
	L.d.	21.VIII.'81	1w
B. (*Separatobombus*) *morrisoni* Cresson	P.f.	13.VII.'79	3w,1q
	P.f.	14.VII.'79	3w,1q
	P.f.	24.VII.'79	1w
	P.f.	8.VIII.'79	2w
	L.d.	24.VII.'79	4w
	L.d.	8.VIII.'79	1w
	L.d.	21.VIII.'81	4w
	C.p.v.	8.VIII.'79	3w
	C.p.v.	21.VIII.'81	1w
B. (*Pyrobombus*) *vosnesenskii* Radoszkowski	P.f.	14.VII.'79	1w
	P.f.	24.VII.'79	1w
	L.d.	8.VIII.'79	1w
	C.p.v.	21.VIII.'81	1w
COLLETIDAE			
Colletes consors consors Cresson	P.f.	13.VII.'79	3f
	P.f.	14.VII.'79	3f
MEGACHILIDAE			
Anthidium (*Anthidium*) *banningense* Cockerell	P.f.	14.VII.'79	1f
	L.d.	4.VII.'80	1m
A. (*A.*) *mormonum* Cresson	P.f.	4.VII.'80	1f
A. (*A.*) *tenuiflorae* Cockerell	H.v.	8.VII.'79	1f
	H.v.	14.VII.'79	1f
	L.d.	14.VII.'79	1f

Appendix I continued.

Species	Host plant	Date	Number, sex, or caste
Callanthidium formosum (Cresson)	L.d.	24.VII.'79	1f
	C.p.v.	21.VIII.'81	1m
Hoplitis (*Monumetha*) *albifrons argentifrons* (Cresson)	M.c.	15.VII.'80	1f
Osmia (*Chenosmia*) *calla* Cockerell	L.d.	8.VI.'79	5f
O. (*Monilosmia*) *densa densa* Cresson	P.f.	24.VII.'79	1f
	L.d.	13.VII.'79	1f
O. (*Nothosmia*) *grindeliae* Cockerell	M.c.	9.VI.'80	1f
O. (*Acanthosmia*) *integra* Cresson	M.c.	9.VI.'80	1f