Bird-foot Checkerbloom (*Sidalcea pedata*)
Reserve Design Criteria:
Reproductive Potential in a Fragmented Environment

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Project Background

Bird-foot checkerbloom (*Sidalcea pedata*) is a narrow endemic restricted to the Big Bear Valley in the San Bernardino Mountains of San Bernardino County in Southern California. In 1984, it was listed as endangered in response to development pressures across its narrow geographical range (Krantz 1985). *Sidalcea pedata* is endemic to wet montane meadows and some adjacent drier habitats; remaining wet meadow fragments in the Big Bear Valley are estimated to total to 20 acres or less (USDI Fish and Wildlife Service 1998; Stephenson & Calcarone 1999; Butler 2000). Very little checkerbloom habitat is protected, and its habitat is threatened by urban development. Before a reserve or mitigation system can be developed for *Sidalcea pedata*, key biological attributes such as breeding system and pollinator ecology must be identified. The recovery plan (USDI Fish and Wildlife Service 1998) recognized that little is known about the biology of *S. pedata* despite the many surveys that have been done. In order to propose specific actions that will benefit the management and recovery of *S. pedata*, sound biological information on this species is required. Such science-based knowledge is essential for informing those involved in prioritizing habitat protection and in managing protected habitat.

This project investigated two key aspects of checkerbloom biology that are necessary for conservation planning: the breeding system and pollination biology of *S. pedata*. This species has showy rose to lavender flowers and is likely to be an outcrossing species via the services of insect pollinators. Identifying the breeding system is necessary to understand how this species reproduces and how genetic variation arises and is maintained in *S. pedata*. Similarly, understanding which insect floral visitors are effective pollinators of this checkerbloom will aid in management of the meadow habitats that *S. pedata* depends upon. For example, an important question is whether bird-foot checkerbloom requires the services of one or two specialist pollinator species, or whether the services of many generalist pollinator species are needed. If this species depends upon a diversity of generalist pollinator species for continued reproduction, then a diversity of flowering resources within meadow habitats should be maintained, in order to support diverse populations of generalist pollinators.

There are four broad objectives of this project and numerous specific sub-objectives under each of these. All have in common the overall goal of increasing our science-based knowledge of the reproductive processes and pollination requirements of *Sidalcea pedata*, Big Bear Checkerbloom. The four broad objectives are as follows: (1) to determine the breeding system of *S. pedata*; (2) to assess the identity of insect visitors to *S. pedata* flowers; (3) to evaluate the effectiveness of potential pollinators of *S. pedata*; and (4) to review the published scientific literature with regards to *Sidalcea* reproductive ecology and pollination.

(1) Conduct studies to determine the breeding system of *Sidalcea pedata.*

A. *Identify potential study populations for experiments and observations. Selection criteria will include: size of population, size of meadow remnant, nature of the surrounding land use, geographical location. Three to seven populations will be selected.*

Five primary study sites located in the vicinity of Big Bear Lake were chosen based on accessibility, location, and size of meadow habitat (Figure 1). The meadow covers approximately 13 ha at Bluff Lake and about 1 ha at Lot K. The other sites contain much less meadow habitat: each of the remaining three sites cover less than 0.25 ha. The Bluff Lake meadow supported by far the largest checkerbloom population; consequently, most of the manipulative experiments took place at this expansive site. Two other sites, ColdBrook Campground and Presbyterian Conference Center, were visited occasionally, but not much data were taken during the brief visits. An eighth site, reported in Barrows (1990), a Fish and Game reserve at the north end of Baldwin Lake, was visited regularly during the 2004 and 2005 flowering seasons, but we failed to locate any *S. pedata* plants.

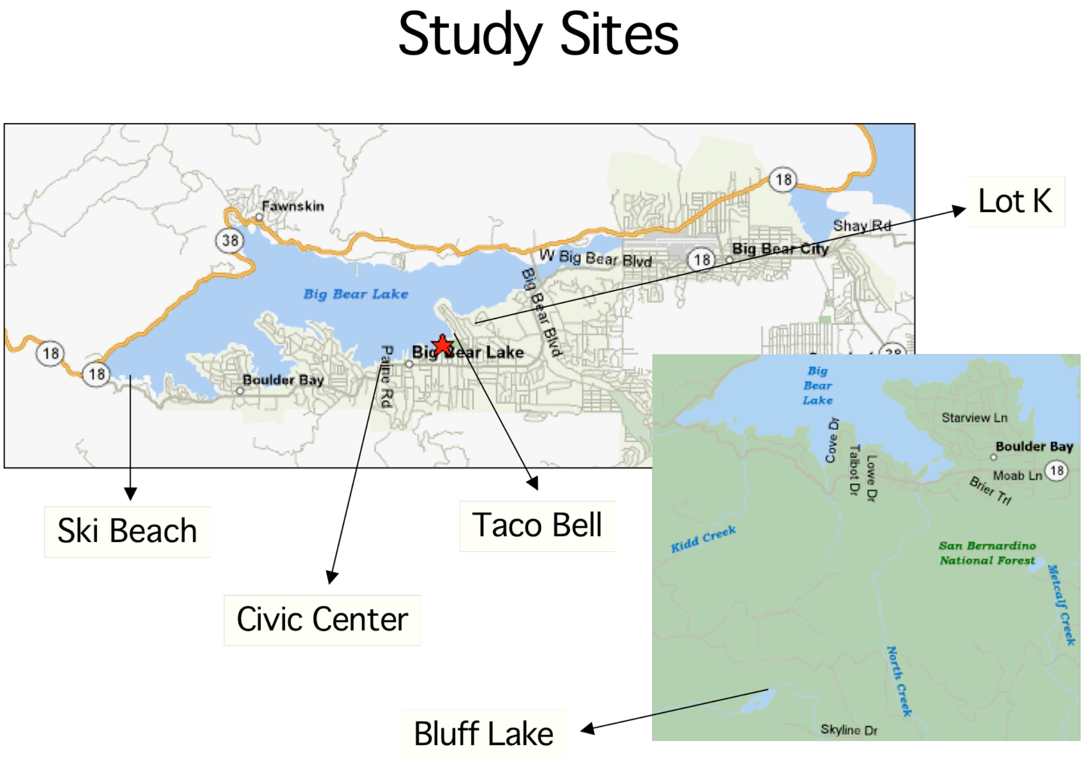

Figure 1. The five main sites where *Sidalcea pedata* populations were studied from 2002-2005.

Surveys of all five sites in 2002 revealed the presence of *Sidalcea pedata* female and hermaphrodite individuals at all five sites. In other words, bird-foot checkerbloom is indeed a gynodioecious species. Subsequent surveys of other sites such as the Presbyterian Conference Center and an empty lot at Park and Oriole were consistent with our five primary study sites. The most obvious difference between the sex morphs is that female individuals bear flowers that are typically almost half the size of flowers borne on hermaphrodite individuals (Figure 2). Female flowers have sterile anthers that appear whitish and flattened, while hermaphrodite flowers have fully functional pollen-producing anthers that are colored white and pink, and are rounded rather than flat (Figure 3).

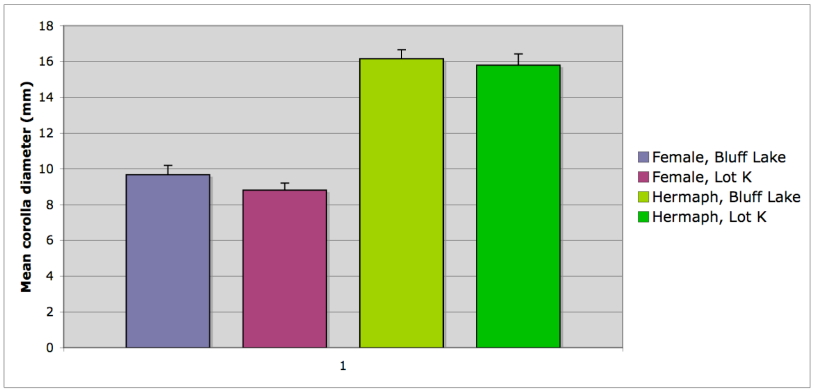

Figure 2. Comparison of the mean corolla diameter of female and hermaphrodite flowers from Bluff Lake and Lot K sites.

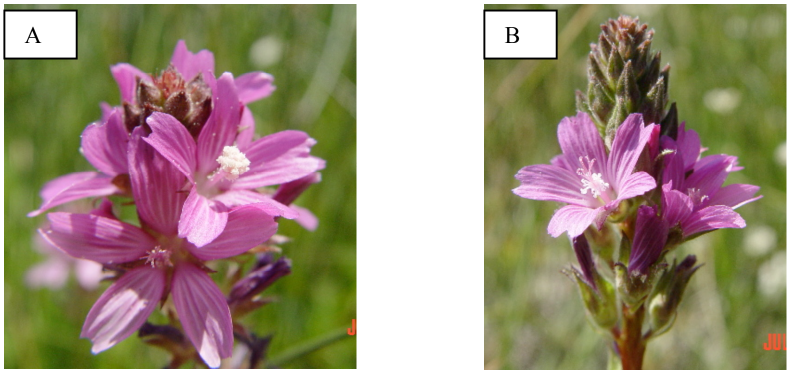

Figure 3. A. Hermaphrodite flowers of *S. pedata*. B. Female flowers of *S. pedata*.

B. Review pertinent literature on the breeding system and reproductive ecology of other Sidalcea species.

See section 4.

C. Assess floral behavior and development of reproductive structures in two or three populations. Periods of pollen release, stigma receptivity and individual floral longevity will be assessed by direct observations of individual flowers.

Observations of individual flowers (n=41) in 2002 at the Ski Beach and Bluff Lake sites indicated that floral longevity differs between the two sex morphs of *S. pedata,* with hermaphrodite flowers open longer than female flowers. Hermaphrodite flowers are protandrous and appear to be in the staminate phase for about two days, followed by the pistillate phase for a day or less. Female flowers were open for one to two days, but when they first opened the stigma lobes were adhered together (unreceptive) as opposed to being spread and receptive to pollen. Subsequent observations of female flowers and female phase flowers at Bluff Lake in 2003 revealed that most stigmas were receptive to pollen (stigma lobes spread apart) for a period of 4-6 hours before the flower started to close.

Observations of many closed or closing hermaphrodite flowers from Bluff Lake (n=114) revealed that there is marked variation in the development of the pistil/stigma in hermaphrodite flowers. Closed-up flowers that were sampled from transects on two dates (27 June 2002 and 5 July 2002) exhibited degrees of development from no visible pistils/stigmas to fully developed and mature pistils/stigmas.

D. Evaluate the range of pollen loads found on open-pollinated Sidalcea pedata flowers during, or just after, the period of stigma receptivity. Stigmas will be examined in the field, and if necessary, excised, and taken into the lab for further examination under a dissecting scope. Pollen loads will be examined in 20-25 plants, one flower per plant, in one or two populations. This data will be used to develop appropriate pollen loads for the hand-pollination treatments of the experiment described below.

Methods

At Bluff Lake, on 27 May 2002, my assistants and I sampled female flowers (n=21) along two 24 m linear transects oriented north-south in the meadow. One transect was near the berm, while the other was near the lower road. In the lab, we counted the number of *S. pedata* pollen grains on the open stigmas and also noted the presence of conspecific pollen grains. On 27 June 2002, at the same site, we sampled flowers from two 40 m transects located in the middle of the meadow. In the lab, we counted the total number of pollen grains, including *S. pedata* pollen, on the stigmas of female and hermaphrodite flowers. From a pollen reference collection we assembled, we were able to identify many of the conspecific pollen grains. The pollen of *S. pedata* is easy to identify under a dissecting scope due to the large size of each pollen grain, its spherical shape, and its characteristic surface sculpturing.

Results

The mean number of *S. pedata* pollen grains adhering to the stigmatal surfaces of a female flower was about 13. The number of pollen grains observed varied from 0 – 30 grains on the first date. *Achillea* pollen, as well as the pollen from a purple-flowering composite was commonly observed on *S. pedata* stigmas. On the second sampling date, the sex morphs had similar stigmatal pollen loads (all species): the mean number of pollen grains per flower was 42 pollen grains for females (n=32) and 41 pollen grains for hermaphrodites (n=33). Total number of pollen grains varied from 2-120 for female flowers, and 0-160 for hermaphrodite flowers. Pollen from *Achillea*, *Lupinus*, and a purple-flowering composite was commonly observed on *S. pedata* stigmas.

E. Conduct a field experiment to determine whether Sidalcea pedata is capable of self-pollination. In two to four populations, twenty-five plants will be chosen and five flowers on each plant will be subject to experimental treatments. The five treatments are as follows (one flower/treatment/plant): (i) bagged control, (ii) unbagged control, (iii) bagged and hand-pollinated with self pollen, (iv) bagged and hand-pollinated with outcross pollen. (v) bagged and emasculated. The response variables fruit set and seed set will be analyzed for the selected experimental flowers. Fine mesh netting will be used to bag individual flowers.

Methods

The originally proposed experiment was redesigned in light of the discovery that *S. pedata* is gynodioecious. At Bluff Lake in 2003, 80 experimental plants, 40 of each morph, were exposed to a bagged, hand-pollinated, or control treatment. Individual flowers were caged in the bud stage with a modified gelatin capsule. The cage was removed on controls as the flower opened, but was not removed in the other treatments. For the hand-pollination treatment, outcross pollen from 2-3 donors was applied by a small brush to receptive stigmas and the cage was replaced. Less than 20 % of the stems produced any fruit from the experimental flowers. We suspect that the caging and/or hand-pollination treatments may have damaged experimental stems. In 2004, we switched to a different bagging method that enclosed entire stems in a mesh bag rather than individual flowers. Hand pollinations with self-pollen were done to test for the potential for geitonogamy. In August 2005, 40 female and 42 hermaphrodite stems were sampled along a 100 m north-south transect through the Bluff Lake meadow. One bud on each stem assigned to either a control or bagged treatment.

Results

Results of bagging whole stems and hand-pollinations in 2004 were more successful. Of 25 hermaphrodite stems bagged and hand-pollinated with self-pollen, nine stems produced fruit. Of 25 hermaphrodite stems that were bagged only, two stems produced fruits. No bagged female stems produced any fruits. In 2005, results were consistent with 2004 bagging treatments. Three of 21 caged hermaphrodite flowers produced fruit (1 or 2 seeds/fruit). About half of the control hermaphrodite flowers produced fruit (11 of 21), which is consistent with the overall fruit set rate at this site. None of the caged female flowers produced fruits; however, 17 of 19 control female flowers produced fruit (1-7 seeds/fruit). These results suggest that autogamous selfing is not a common mode of reproduction in *S. pedata*. Bagging in combination with hand-pollination with self-pollen indicated that geitonogamous selfing can occur in *S. pedata* (via the services of insect pollinators).

F. Compare estimates of fruit set and or seed set between female plants and hermaphrodite plants in 3-4 populations.

Methods

Stems or racemes were sampled in 2004 and 2005 along linear transects at Bluff Lake, Lot K, Taco Bell, Civic Center, and Ski Beach sites. Populations of *S. pedata* at Ski Beach, Taco Bell and Bluff Lake were sampled in 2004, while Lot K, Civic Center, and Bluff Lake populations were sampled in 2005. We sampled 16-30 stems per morph per site. We recorded the presence or absence of a fruit along the stem and its position on the stem (1-15), with position 1 as the most basal flower. The absence of a fruit is easily detected by visual inspection as the flower and pedicel do not persist on the stem if no ovules have developing seed. The base of the pedicel, where it joins the stem, remains as a persistent ”stub” that marks the flower location on the stem. The number of ovules per flower or fruit and the number of viable seeds per fruit were measured for positions 11-15 along racemes at three sites: Bluff Lake, Taco Bell, and Ski Beach. In 2004, only hermaphrodite stems were sampled at Bluff Lake because sampling occurred after most females had matured and dispersed their seeds. Only hermaphrodites were sampled at Civic Center because nearly all the mature female stems had been cut down by the City of Big Bear in the yearly mowing of herbaceous vegetation that occurs consistently at this site. Data were statistically analyzed with t-tests and two-factor analysis of variance. For the analysis of variance, fruit positions were grouped into three regions, 1-5, 6-10, and 11-15 and percent fruit set was calculated for each region.

Results

At all sites where both morphs were sampled, the average female fruit set was almost twice the average fruit set of hermaphrodite plants (Figure 4). Analysis of variance revealed a highly significant effect of sex morph on the rate of fruit set of positions 1-15 ($p < .0001$ for all sites, Table 1). Average female fruit set ranged from 70% - 94% whereas the average hermaphrodite fruit set ranged from 26% - 56%. Individuals from the two larger meadow sites, Bluff Lake and Lot K, had somewhat greater fruit set values than those from the smaller sites, Ski Beach and Taco Bell. Analysis of variance also revealed a highly significant effect of fruit position at all sites sampled. At all sites except Bluff Lake in 2005, hermaphrodites, and to a lesser extent females, exhibited a strong trend of increasing fruit set with increasing apical position along the stem (Table 1, Figure 4). Average fruit set of hermaphrodites in positions 1-5 was very low; values ranged from 9% - 43%. Average fruit set of females in positions 1-5 was much greater: values ranged from 43% - 88%. A significant interaction between sex and fruit position occurred at just one site, Lot K, indicating that females did not exhibit the same trend of increasing fruit set with increasing apical position. (Table 1).

Population	n (F)	n (H)	Sex Morph	p value	Position on stem	p value	Sex x Position	p value
Bluff Lake 04	-	22	-	-	6.2	.0034	-	-
Bluff Lake 05	23	23	69.6	<.0001	2.1	.12	.87	.42
Civic Center	-	30	-	-	12.7	<.001	-	-
Lot K	16	16	67.9	<.0001	26.6	<.0001	14.8	<.0001
Ski Beach	16	18	44.7	<.0001	14.6	<.0001	1.6	.21
Taco Bell	19	20	49.9	<.0001	6.3	.0025	.77	.46

Table 1. F and p values from ANOVA of fruit set data. Sample size given for each morph as n(F) and n(H)

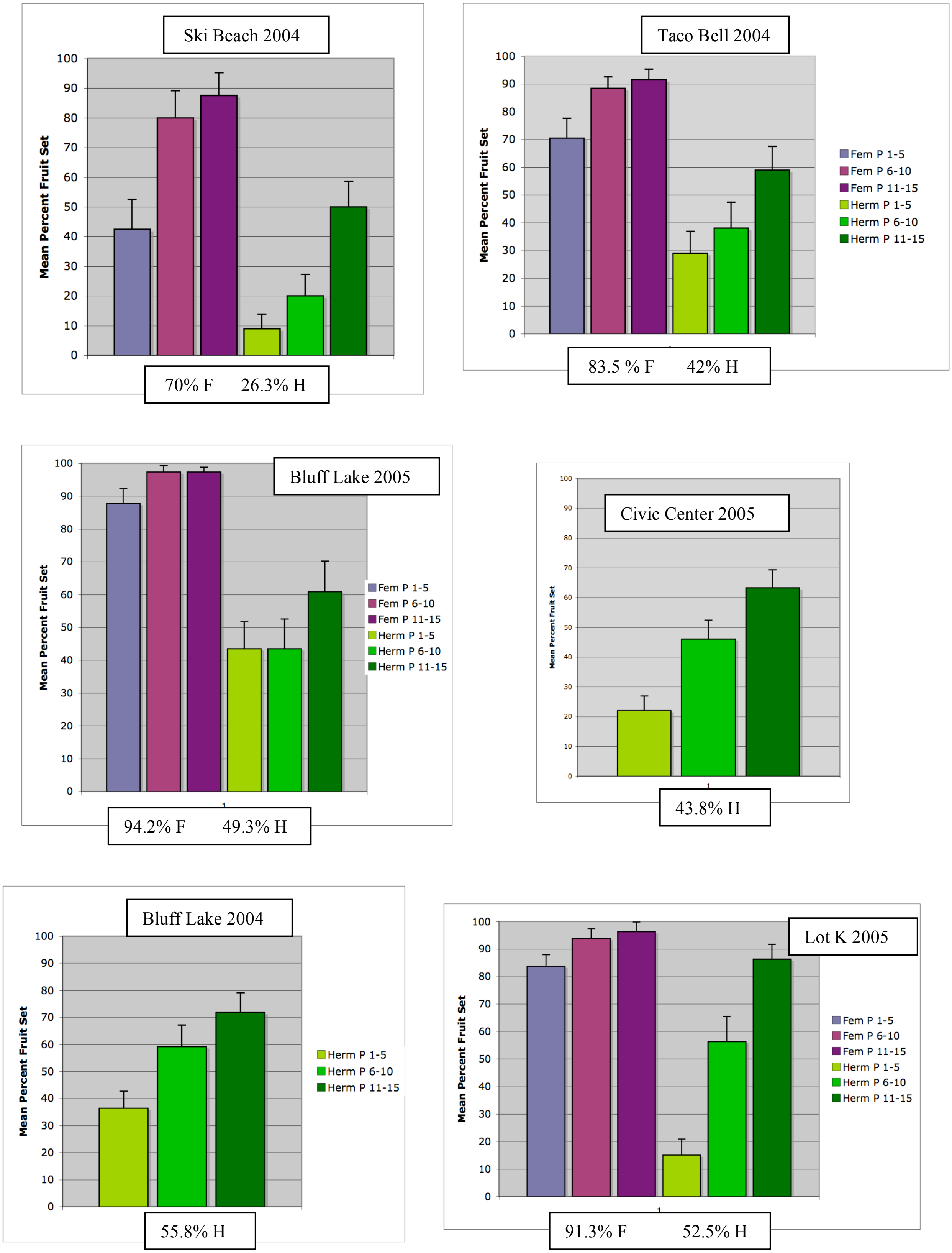

Figure 4. Fruit set of female and hermaphrodite stems at positions 1-15 at five sites. The overall fruit set average for each morph is indicated below the bars.

The number of seeds and ovules per fruit did not vary as dramatically as the fruit set data but did show some significant differences. Although female flowers are significantly smaller than hermaphrodite flowers, they bear significantly more ovules than hermaphrodites (Figure 5A, Table 2). Unlike the other two sites, the morph comparison was marginally significant at Taco Bell. The average number of ovules per fruit ranged from 6.1 – 6.4 in females and 5.3 – 5.9 in hermaphrodites. The number of viable seeds produced per fruit or flower was not consistently different between the two sex morphs at the three sites (Figure 5B, Table 2). The average number of viable seeds per fruit ranged from 4 – 5 in females and 4.2 – 4.5 in hermaphrodites. We analyzed fruits in positions 11-15 for ovule and seed number because earlier positions tended to have low rates of fruit set, so there were fewer fruits available for analysis.

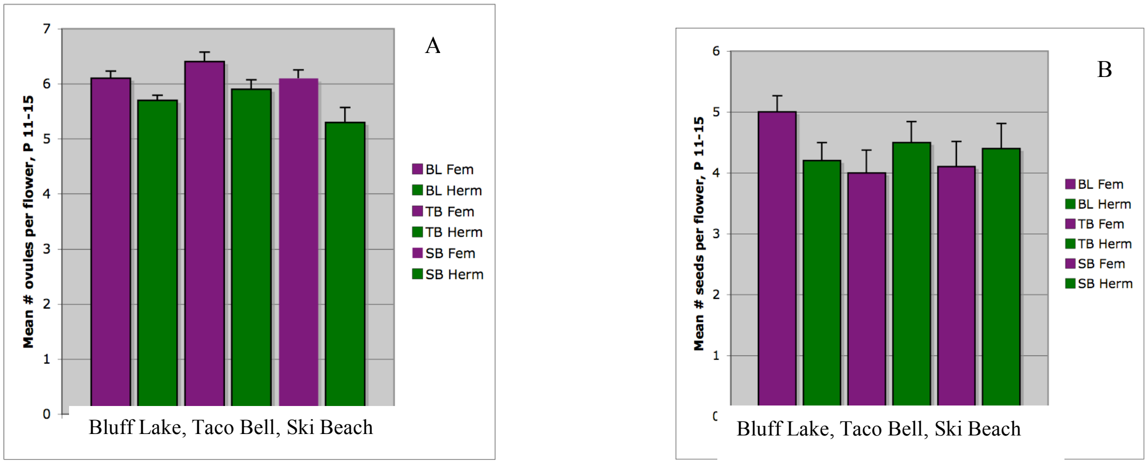

Figure 5. Comparison of the numbers of seeds and ovules per flower between *S. pedata* females and hermaphrodites. A. Number of ovules. B. Number of viable seeds.

Population	n(F)	n(H)	Ovules/ fruit	p value	Seeds/fruit	p value
Bluff Lake	24	25	2.5	.017	2.2	.034
Ski Beach	18	11	-2.7	.01	.5	.62
Taco Bell	19	16	-1.76	.087	.97	.34

Table 2. Statistical t and p values from t-test analysis of seed/ovule data. Sample size given for each morph as n(F) and n(H).

G. Document each study population with a standard herbarium collection of Sidalcea pedata, to consist of a portion of one plant (not a whole plant) with reproductive structures. These voucher specimens will be deposited at a herbarium approved by the Contract Manager.

For the two sites with large population sizes, voucher specimens of a hermaphrodite and a female individual were collected and pressed, and were deposited at the combined Herbarium of the Rancho Santa Ana Botanic Garden and Pomona College. A total of 4 specimens were deposited: 1 hermaphrodite stem and 1 female stem from Lot K (Eagle Point), collected on May 22, 2004; 1 hermaphrodite stem and 1 female stem from Bluff Lake, collected on July 13, 2005.

(2) Conduct studies to assess the identity of insect visitors to *Sidalcea pedata* flowers.

A. Identify potential study populations for experiments and observations. Selection criteria will include: size of population, size of meadow remnant, nature of the surrounding land use, geographical location. Four to seven populations will be selected.

See under 1A above.

B. Observe and collect insect visitors to *Sidalcea pedata* flowers in 3-7 populations. Pollen loads of specimens collected will be analyzed. Those with significant amounts of *Sidalcea pedata* pollen will be classified as potential pollinators.

Methods

Insect floral visitors of *Sidalcea pedata* and co-flowering species were collected at seven sites during the 2002-2005 flowering seasons. Floral visitors were netted on a total of 48 days during the four flowering seasons. Netting of insects was more intensive in 2003 (18 sampling days), than in the other years (about 10 sampling days/ year). Of the seven sites (Lot K, Bluff Lake, Taco Bell, Ski Beach, Civic Center, Presbyterian Center, and Coldbrook), netting of floral visitors was most intensive at the Lot K and Bluff Lake sites. A total of 643 insect visitors to *S. pedata* or neighboring meadow species (Appendix 1) were netted, pinned, labeled and identified to family and or genus level. Of these, 590 insects were caught on flowers of *S. pedata*. The amount of *S. pedata* pollen on pinned specimens was scored as either none, few (approximately 10 pollen grains or less) or many (greater than 10 pollen grains). The presence of other kinds of pollen on insect specimens was noted as well to document the degree of foraging generalization among visitor taxa. Identification keys in Michener (2003) and Michener et al. (1992) were used to identify bees to family and genus level.

Results

The vast majority of floral visitors netted were insects in the order Hymenoptera, in the families Apidae, Halictidae, and Megachilidae (Table 3). A few bees were in the families Andrenidae and Colletidae. Common floral visitors included *Anthophora* sp., *Apis mellifera*, *Bombus* spp., *Lasioglossum* spp., and *Osmia* spp. See Appendix 2 for a more detailed list of the bee floral visitors netted and sites where they were captured. Honey bees and bumble bees were commonly observed and netted floral visitors at the Bluff Lake site but were uncommon at the remaining six sites. A diversity of smaller-sized bee species such as *Ceratina* sp., *Lasioglossum* spp., *Halictus* spp. and *Osmia* spp. comprised most of the floral visitors caught at the other six sites (Appendix 2). *Ceratina* sp., *Lasioglossum (Dialictus)* spp. and *Osmia* species were the most widespread genera of bee visitors, occurring at six of the seven sites sampled. The *Sidalcea* specialist, *Diadasia nigrifrons*, occurred at four sites. Lot K had almost as many bee visitor genera (15) as Bluff Lake (17) even though there were far fewer sampling dates at Lot K (Appendix 2). The Civic Center and Taco Bell sites also showed a relatively high number of bee genera (11-12) given the number of sampling dates. Conservatively, at least 41 bee species were caught foraging on checkerbloom flowers (Appendix 2). This estimate is likely to rise as more species level identifications are completed.

Order	**Family**	**Genus**	**No pollen**	**Few grains**	**Many grains**	**Total**	**Other pollen**
Hymenoptera	Andrenidae	*Andrena*	0	0	2	2	1
	Apidae	*Apis*	1	3	36	40	15
		Bombus	5	14	40	59	34
		Anthophora	0	12	15	27	9
		Diadasia	0	7	10	17	5
		Xeromelecta	0	0	1	1	0
		Nomada	0	2	2	4	1
		Svastra.	0	0	1	1	1
		Ceratina	4	7	1	12	6
	Colletidae	*Hylaeus*	0	1	0	1	0
	Halictidae	*Lasioglossum*	5	20	22	47	15
		Halictus	0	3	15	18	6
		Agapostemon	0	5	7	12	4
	Megachilidae	*Osmia*	7	28	51	86	47
		Megachile	1	0	6	7	3
		Stelis	0	6	4	10	9
		Ashmeadiella	0	7	0	7	3
		Coelioxys	0	0	1	1	0
		Anthidium.	0	0	2	2	1
		Heriades	0	1	0	1	1
		Hoplitis	0	2	0	2	0
		Chelostoma	0	1	0	1	0
	Formicidae		0	0	1	1	0
	Misc. Wasps		3	4	4	11	7
Hymenoptera Total			26 (7.1)	123 (33.2)	221 (59.7)	370	165 (44.6)
Coleoptera Total			25 (33.3)	27 (36.0)	23 (30.7)	75	29 (38.7)
Diptera Total			34 (43.6)	32 (41.0)	12 (15.4)	78	25 (32.1)
Lepidoptera Total			34 (81.0)	8 (19.0)	0 (00.0)	42	0 (00.0)

Table 3. Number of floral visitors caught with *Sidalcea pedata* on their bodies. Amount of *S. pedata* pollen on specimens was scored as no pollen grains, few pollen grains (1-10 grains) or many pollen grains (10+ grains). Other pollen refers to the number of netted specimens with heterospecific pollen on their bodies. Numbers in parentheses refer to percentage of the total.

Less common non-hymenopteran floral visitors caught included various beetles in the order Coleoptera, butterflies in the order Lepidoptera, and flies in the order Diptera

(Table 3). Coleoptera caught include the families Buprestidae, Coccinellidae, Curculionidae and several unidentified families. Butterflies in the families Hesperiidae, Lycaenidae, Nymphalidae and Pieridae were caught on flowers; lycaenids were common visitors to many flowering species at Bluff Lake. Dipteran visitors netted included the families Bombyliidae (bee flies), Syrphidae (flower flies), Muscidae, Tachinidae, Anthomyiidae, and Conopidae.

Almost all of the bee and wasp visitors netted carried *S. pedata* pollen (~93%), while the non-hymenopteran visitors caught evidenced much lower frequencies of pollen presence (Table 3). Only 19% of lepidopterans netted carried *S. pedata* pollen, while flies and beetles had about 56% and 66% of individuals with *S. pedata* pollen, respectively. Floral visitors frequently carried heterospecific pollen as well. Almost half of all bees and wasps, 39% of beetles, and 32% of flies carried other types of pollen on their bodies in addition to *Sidalcea* pollen. While the presence of checkerbloom pollen on insects does not imply that said insect is effective at depositing pollen on stigmas of *S. pedata*, it does suggest which kinds of insects are more likely to be potential pollinators. See section 3A for experimental results on pollen deposition abilities of common visitors. The occurrence of heteropecific pollen on 17 of the 22 bee genera suggests that most bee visitors to *S. pedata* are generalist foragers. This result is consistent with observations that all bees closely observed were foraging for nectar within *Sidalcea* flowers rather than pollen, with the possible exception of *Diadasia nigrifrons* females.

C. **Observe and collect weevils in flowers as they may be seed predators or foliovores of *S. pedata*. Infested flowers will be observed and dissected to determine if significant seed predation occurs.**

Methods

Lot K Weevil survey. In 2005, the presence and number of weevils on *S. pedata* plants were established by counting the number of weevils found on *S. pedata* plants with open flowers along 24 – 30 meter transect lines. A total of five transect lines were established. Transect lines 1-4 were 24 meters long while the fifth was 30 meters long. Lines 1 – 3 ran parallel to one another 6 meters apart. Lines 4 and 5 were established 6 meters perpendicular to line 3. All lines were located in the northeast end of Lot K. Every 3 meters along each line the presence and the number of weevils was noted. Only plants with open flowers lying 1 meter to either side of the line were inspected. Observations (between 1030-1530 h) were taken once for every transect line on 5/27/05, 6/3/05, 6/6/05 and 6/8/05 during the peak of the flowering season.

Fruit dissection. On 6/24/05, 10 stems of each morph were collected every 3 meters along transects 4 and 5 in order to assess weevil predation of fruits. These stems were collected in an area no larger than 220 sq. meters. Mature fruits from each stem were dissected. Seeds were put into three condition categories. The condition categories were as follows: predated, viable and nonviable. Predated seeds were seeds that showed any evidence of being eaten. Viable seeds were non-predated, plump, hard brown or black large seeds. Nonviable seeds were, flat, papery, light colored small seeds. Mann-Whitney U tests were used to analyze seed data. Any weevil larva, pupae, or adults found in seeds were collected and counted. Weevils were identified as *Macrorhoptus niger* Hatch by weevil systematist, Dr. Horace Burke, Texas A & M University.

Results

Weevil survey. *Macrorhoptus* weevils were infrequently observed on *S. pedata* stems in all transects for the four days (except transect 5 where there was 2 days of observation) observations were made. All observed weevils were seen in flowers of different hermaphrodite individuals. No weevils were observed on *S. pedata* stems along transects 1 and 2 on any of the 4 days weevil presence data was collected. A total of two weevils were observed along transect 3, seven weevils were observed along transect 4 and three weevils were observed along transect 5. Weevil surveys at Lot K were not a reliable indicator of weevil activity or seed predation, as many more weevils were found while dissecting the fruits than were observed during the survey.

Fruit dissection. The number of predated seeds per fruit was not significantly different between the sex morphs ($p > 0.1$). For female stems, the mean number of predated seeds per fruit was 0.62 ± 0.19, while the mean for hermaphrodite stems was 1.08 ± 0.34 predated seeds per fruit. The percentage of predated seeds per stem was not particularly high: about 11% for females and 19% for hermaphrodite stems. A total of 16 dead weevil larvae and 11 adult weevils were found in fruits borne on female stems. In fruits on hermaphrodite stems, a total of 31 dead weevil larvae, 2 weevil pupae, and 19 weevil adults were found. A non-weevil seed predator attacked 22 seeds on two different female stems and the observed seed damage was atypical of weevil seed predators. Regardless of seed predation, female stems produced more viable seeds per fruit than hermaphrodite stems. The average number of viable seeds per fruit on female and hermaphrodite stems was 3.89 ± 0.26 vs. 2.1 ± 0.28. This difference between the morphs was statistically significant ($p < .05$). The percentage of viable seeds per stem was also significantly higher for female than for hermaphrodite stems (61% vs. 39%; $p < .01$). Appendix 3 contains a table of the seed predation data.

D. Once the major kinds of insect floral visitors are known, systematic observations of floral visitors will be conducted in 3-5 populations. Timed transects or plots within each population will be observed at least three times (days) during the flowering season. Weather data such as wind speed, relative humidity, and temperature will be recorded as well.

Methods

Two large meadow sites (Bluff Lake and Lot K) were sizeable enough for observations of floral visitors at replicate plots. At one small meadow fragment, Ski Beach, only one2m by 8m visitation plot could be established. Systematic, repeated observations of *S. pedata* floral visitors were conducted at Bluff Lake on 6, 9, 16, and 23 July 2004. Floral visits were observed and recorded to six 2m by 9m plots within the meadow during 10 minute observation periods. On each date, two observers recorded visits to each plot. An observer walked slowly around the periphery of the plot at an even pace and recorded all visits observed in the field of view. Observations were done during the mid-day when activity is the highest, with a total of 1244 floral visits observed during 48 observations periods. Similar observations were made to three 4m by 8 m plots at Bluff Lake in 2005 on the following dates: 6, 10, 13, and 20 August. Data comprise a total of 821 visits in 36 observation periods, divided into morning (100-1130 h), mid-day (1230-1400 h), and afternoon (1500-1630 h) periods.

Floral visit observations were conducted at Lot K on 28 May 2005, and 2, 3, 6, 8, and 12 June 2005. Visits were recorded to three 4m by 8m plots during 15 min. observation periods between 1000 – 1600 h. A total of 430 floral visits were observed in 48 observation periods at Lot K. At Ski Beach, floral visitors were observed within a 2 m by

8 m plot on 11, 13, and 15 July 2005. Observations were conducted similar to Lot K. A total of 50 floral visits were observed in six observation periods: three were during mid-day and three were in afternoon. We categorized the identity of floral visitors by size, color, and species, if possible in the field, for bees and by order or family for the non-bee floral visitors. For all sites, we endeavored to count a floral visit by an individual once, rather than recording multiple visits by the same individual. By recording visits in this manner, our data reflect more accurately the frequency of individual visitors at flowers. At Bluff Lake and Lot K sites, the number of flowering stems within the observation plots were estimated on each date visitation data was recorded.

Results

All three sites differed in the number and kinds of floral visitors to *S. pedata*. Higher floral visitation rates were observed at Bluff Lake, with bumble bees (*Bombus* spp.) and honey bees (*Apis mellifera*) the most frequent visitors in both years (Figures 6A and 6B). At Lot K, the most common floral visitors were small to medium sized bees (Figure 6C), mostly in the families Halictidae and Megachilidae. No visits were observed from bumble bees or honey bees although a few were netted from Lot K. At Ski Beach, floral visitation rates were the lowest of all three sites. Medium sized bees in the families Halictidae and Megachilidae were the most frequent floral visitors. Bumble bees were infrequent visitors to *S. pedata* flowers, but were frequently observed on other nearby flowering species. Density of *S. pedata* flowering stems for Bluff Lake and Lot K is shown in Figure 7.

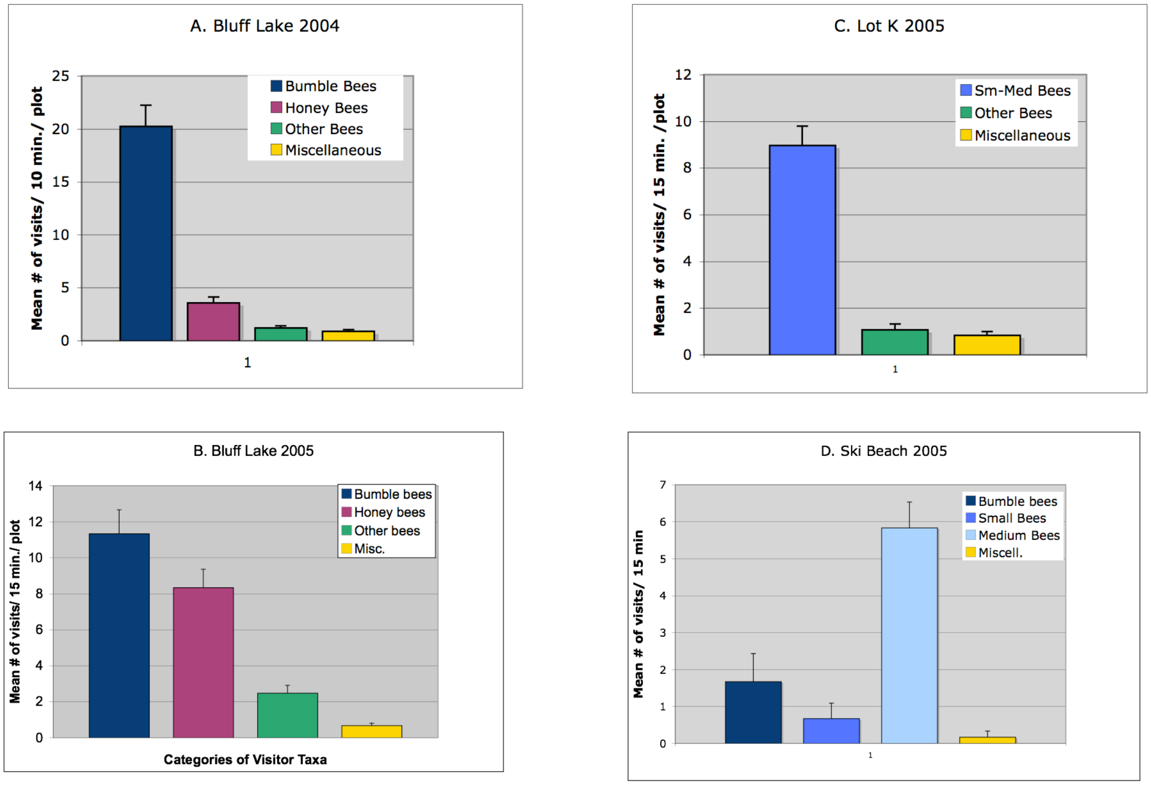

Figure 6. Floral visitation to *S. pedata* plots at Bluff Lake (A & B) and Lot K (C), and Ski Beach (D) sites. Other bees include the families Megachilidae, Halictidae, and

Anthophoridae and miscellaneous visitors include the orders Coleoptera, Lepidoptera, Diptera, Othroptera, and Hemiptera.

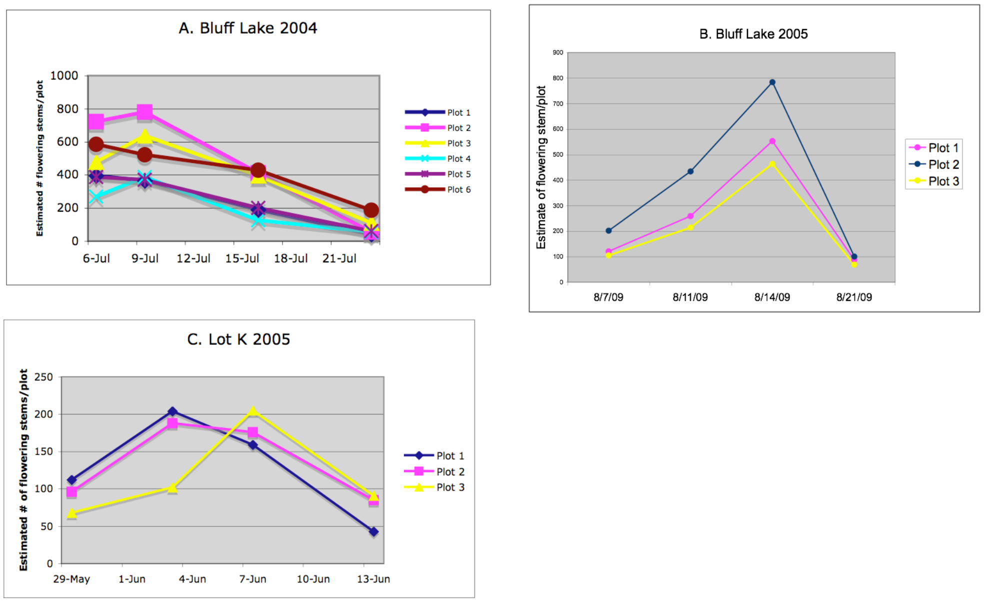

Figure 7. Estimates of flowering stem densities in visitation plots at Bluff Lake (A & B) and Lot K (C). Dates shown are actual dates when visit observations occurred.

A survey of floral visitation activity at Bluff Lake in the evening, 1900-2100, did not reveal any nocturnal floral visitation to *S. pedata*.

E. From the detailed visitation observations and pollen load analysis, determine if there is an oligolectic bee pollinator associated with *Sidalcea pedata*. Other species of *Sidalcea* are known to be associated with the oligolectic bee species, *Diadasia nigrifrons*.

Diadasia nigrifrons (Anthophoridae) is an infrequent floral visitor to *S. pedata*. We rarely observed individuals foraging and have collected only twelve individuals from Lot K, Presbyterian Center, Civic Center and Taco Bell sites. As it is not abundant and rarely observed, we do not have enough information to determine if females are truly oligolectic on *S. pedata* at these sites. In addition, five individuals of a different *Diadasia* species were caught from Bluff Lake and Lot K. All *Diadasia* specimens do carry *Sidalcea* pollen and five individuals bear pollen of other species. The other common bee species observed foraging on checkerbloom flowers appear to be generalists, rather than specialists.

F. Determine if insect visitors have any apparent preference for one floral morph by conducting choice tests in 2-3 populations.

Methods

At Bluff Lake and Lot K sites, insect visitor preference for hermaphrodite or female *S. pedata* flowers was assessed by using a “choice” stick, which was basically a stick with cut stems of both sexes in vials at the end of the stick (Figure 8A). We placed two stems, one of each sex in vials to the left and right sides of the stick, and trimmed the stems to keep the number of open flowers equal between the female and hermaphrodite stems. Most stems had two or three open flowers per stem. Stems were put in vials filled with a dilute sucrose solution. When stems in the vials wilted, they were replaced with freshly cut stems. An observer offered the stems to insects foraging in the Bluff Lake or Lot K meadow, at the height of existing racemes and recorded visits by insects to the flowers on the cut stems. Once a visit sequence was complete, and the insect flew off, the observer relocated to a different part of the meadow for the next sequence. At Bluff Lake, choice tests were conducted in 2003 and 2005. Dates of choice tests were seven days between 2-22 July 2003, (with approximately 1-2 hours or observations each day) and 30 July, 5 and 10 August 2005. At Lot K, choice tests were conducted on 28 May 2005 and 2, 6, and 12 June 2005.

Results

Bluff Lake 2003. A total of 123 visit sequences were observed on choice stick or (experimental) stems, with the majority of visits made by bumble bees and honey bees. A few butterflies, bombyliid and syrphid flies, as well anthophorid bees were also observed on the choice stick stems. Most insects visited 1 to 4 flowers on the choice stick stems before flying away. About 80% of all insects visited a hermaphrodite flower first on the choice stick. Of the 54 bumble bee visit sequences, 90% landed on a hermaphrodite flower first. Of the 39 honey bee sequences observed, about 67% visited a hermaphrodite first (Figure 8B). About half of the bumble bee and honey bee sequences observed were composed of visits to 2 or more flowers on at least two experimental stems. For these multiple stem sequences (n=41), half of these involved switching, where the bumble bee or honey bee switched at least once between the two floral morphs (Figure 8B).

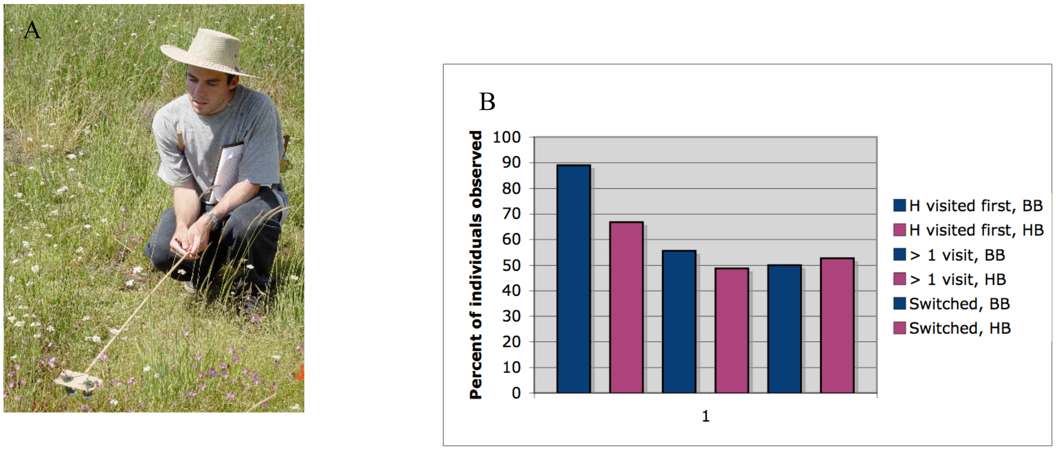

Figure 8. Testing insect preferences for *S. pedata* hermaphrodite and female flowers. A. Choice stick used in observations of insect preference. B. Bluff Lake 2003 bumble bee and honey bee visit sequences.

Bluff Lake 2005. Similar to 2003, a high proportion of bee floral visitors switched between the two floral morphs despite an initial preference for hermaphrodite flowers. Of the 46 insects visitors observed, 36 individuals were bumble bees (n = 22) and honey bees (n = 14). 91% of bumble bees and 93% of honey bees visited a hermaphrodite flower first on the experimental stems even though there were equal frequencies of both floral morphs on the choice stick. 86% of bumble bees and 76% of honey bees visited more than one flowering stem. Of the bumble bees and honey bees that made multiple stem visits, 89% of these bumble bees and 90% of these honey bees switched morphs (Figure 9B).

Lot K 2005. Results from this site were generally similar to those from Bluff Lake albeit with different floral visitors. Of the 61 foragers that visited the experimental choice stems, 48 individuals were small black bees (n = 34) and medium black bees (n = 14). A bee, black in color and less than 1 cm, was categorized as a small black bee and any black bee greater than 1 cm was categorized as a medium black bee. 94% of small black bees and 57% of medium black bees visited a hermaphrodite flower first on the choice stick. Only 50% of the small black bees visited more than one stem whereas 100% of the medium black bees visited two or more experimental stems. Furthermore, of the small black bees that made multiple stem visits, 41% switched floral morphs. The frequency of switching for medium black bees that visited multiple stems was considerably higher: 100% of these individuals switched floral morphs (Figure 9A).

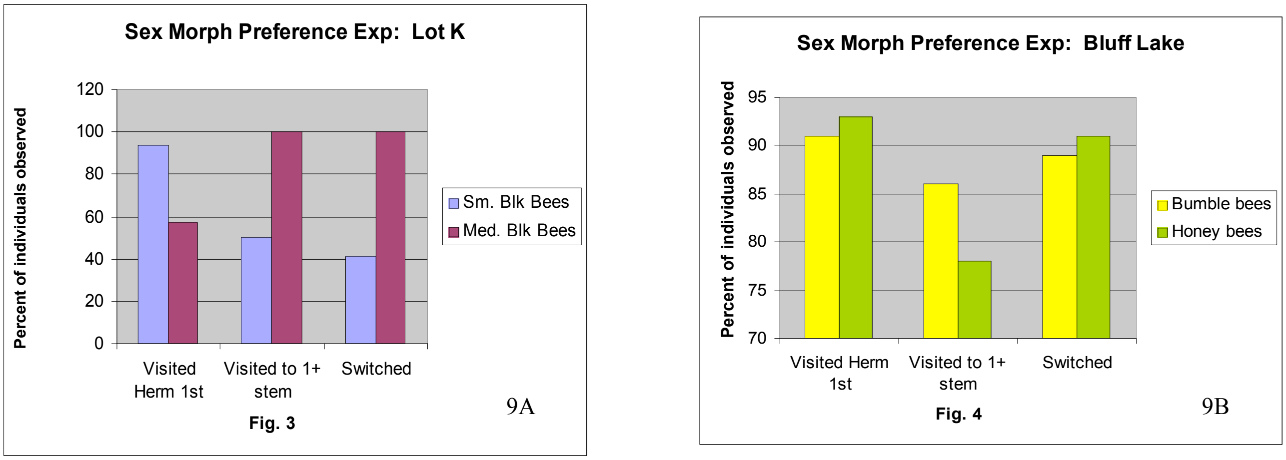

Fig. 3

9A

Fig. 4

9B

Figure 9. Floral visitor choices to experimental stems. A. Lot K 2005. B. Bluff Lake 2005.

G. Properly labeled specimens of insect visitors will be sent to taxonomic specialists to confirm the genus and species, if possible. Vouchers will be deposited at the UC Riverside Entomology Museum.

All insects collected have been pinned and labeled with locality and floral species information and given a unique number. All information associated with each floral visitor has been entered into an Excel spreadsheet. Identification of many bee species are currently underway and when identification is complete, selected voucher specimens will be deposited at either the UC Riverside Entomology Museum or at the UC Davis Entomology Museum.

H. The contractor will assemble a pollen reference collection from common simultaneously flowering species in or near the study populations in order to analyze pollen loads found on specimens.

A pollen slide collection was created for the Bluff Lake site. Pollen of common co-flowering species such as yarrow, cinquefoil, lupine, Parish's yampah, buckwheat, wild rose and several composites were mounted on slides. Pollen on stigmas and on the pinned specimens were compared to these reference slides.

(3) Conduct studies to evaluate the effectiveness of potential pollinators of *Sidalcea pedata*.

A. Conduct detailed observations of the foraging behavior of potential pollinators (as determined above) in 1-2 populations. Examine patterns of visitation between successively visited flowers (inter-and intraplant) for different kinds of pollinators. This will provide an assessment of the degree of pollinator fidelity to each *S. pedata* floral morph as well as to the species.

Methods

In 2003 and 2004, we observed individual insects foraging on *S. pedata* flowers at Bluff Lake to determine how often individual foragers switch between floral morphs and to determine if patterns of floral visitation (within and between flowering stalks) differed among floral visitors. Insect visitors that switch frequently between floral morphs are likely to be more effective at depositing pollen on female flowers than those that are more constant to either morph. Furthermore, insect visitors that tend to visit many flowers on a single hermaphrodite stalk or raceme are more likely to contribute to geitonogamous selfing than visitors that forage on only one flower per hermaphrodite flowering stalk. The latter foraging pattern is more likely to promote outcrossing between *S. pedata* individuals.

A total of 80 insect foragers were observed in diverse areas of the Bluff Lake meadow on 11 and 15 July 2003 and a total of 49 foragers were observed on 2, 6, and 9 July 2004. Observers followed the foraging sequence of an individual *S. pedata* visitor from flower to flower in the meadow as long as possible and recorded the time of each sequence, the floral morphs visited, the number of flowers and stems visited, and the type of insect visitor. For the majority of individuals, at least a four stem sequence was observed. Observers moved to a new location for the next foraging sequence (at least 20 m away) to minimize the probability of observing the same individual again. Bumble bees and honey bees were the most commonly observed *S. pedata* foragers. Foraging observations were conducted in areas of the meadow where there was a mixture of both morphs. At Lot K, a total of 37 insect foragers were observed 28 May, 2 June, and 6 June 2005. Most of the foragers observed were small and medium sized black bees and the majority of foraging sequences observed ranged from 2-4 stems before the insect flew away.

Results

In both years at Bluff Lake, approximately one-third of the bumble bee and honey bee foragers observed switched at least once between the floral morphs during the recorded foraging sequences (Figure 10). Insect foragers were nearly always constant to hermaphrodites if there were no switches during the recorded sequence. Several individuals of bumble bees and honey bees were observed to be inconstant to *S. pedata* flowers during a foraging sequence, switching to other co-flowering species in the meadow once or several times. Analysis of intra-stem visitation patterns in 2003 indicates that bumble bees visit significantly more flowers on a raceme than honey bees (t=2.3; p=0.022; df=58). Bumble bees visited an average of 1.29 ± .05 s.e. flowers/stem, while honey bees visited an average of 1.16 ± .03 s.e. flowers/stem. In 2004, bumblebees (n=37) visited an average of 1.32 ± .04 flowers/stem, whereas honey bees (n=9) visited an average of 1.04 ± .02 flowers/stem. Statistical comparison of the two was not calculated in 2004, due to few honey bees observed. On an individual basis, differences between bumble bees and honey bees in the number of flowers visited per stem may not be very large, yet when hundreds of workers of both types are foraging in the meadow, this difference could imply that bumble bee and honey bee colonies provide different pollination services to *S. pedata*.

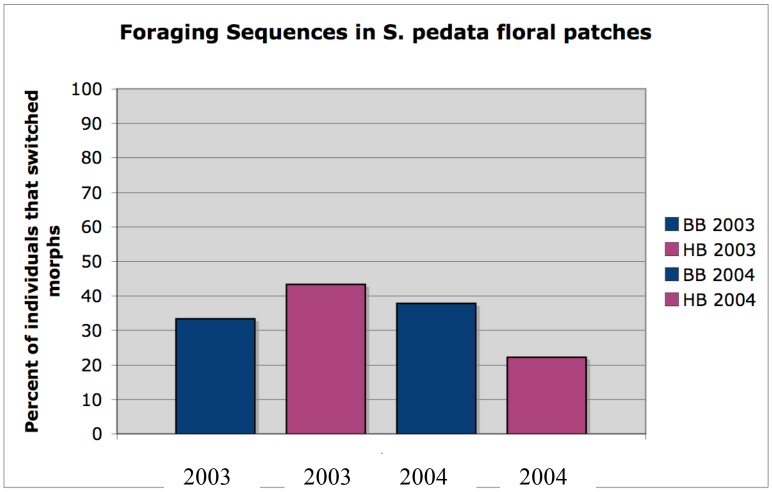

Figure 10. Frequency of switching between floral morphs in recorded foraging sequences of bumble bees and honey bees at Bluff Lake.

Slightly more than half (55%) of the *Sidalcea* foragers at Lot K that visited at least two stems switched between the morphs during the recorded sequences. A few individuals were observed to be inconstant to *S. pedata* flowers during a foraging sequence, switching to other co-flowering species and then returning to checkerbloom flowers. Small and medium sized bees pooled together (n=28) visited an average of 1.62 ± .09 flowers per raceme. Only five individuals, of the 28 observed, visited one flower per stem consistently during a sequence. The small and medium bees, the predominant floral visitors at Lot K, tended to visit more *S. pedata* flowers per stem, than either honey bees or bumble bees at Bluff Lake.

B. Assess pollen deposition on unvisited or virgin flowers from a single visit made by different kinds of pollinators. In 1-2 populations, a cut flower stem will be presented to a foraging pollinator for one visit only. The amount of

pollen deposited on the stigma will be assessed either in the field or in the lab. Approximately 30 –40 individual flower stems will be used per population, with only one flower stem removed per plant.

Methods

At Bluff Lake in 2004, pollen deposition by a single visit from various bee visitors was assessed by presenting unvisited or “virgin” female flowers to foragers at the end of a choice stick. Only female flowers were used as hermaphrodite flowers have intrinsic pollen that could obscure or bias the counting of pollen grains deposited. Hermaphrodite stems were placed in neighboring vialsof the choice stick. After the one visit, pollen grains were counted on the stigmatal surfaces by examining the stigma with a hand lens. Female flowering stems were collected early in the morning, before much visitation activity occurred, and were kept in vials, covered by netting, to prevent any insect visitation. Individual flowers on the cut stems were checked to ensure that no pollen was present on the stigmas before use on the choice stick. Pollen deposition was examined from 25 bee floral visitors on 16 and 20 July 2004.

Results

Pollen deposition data indicated that bumble bees and honey bees can be highly effective pollinators of *S. pedata*. Observers were more successful in obtaining visits from bumble bees than from honey bees. Twenty-one bumble bees visited experimental female flowers, whereas only three honey bees and one anthophorid bee visited experimental flowers. Four bumble bees visited two female flowers; the other individuals visited just one. All bee visitors except one bumble bee deposited one pollen grain or more on the stigmas of female flowers. Figure 11 shows that a visit from bumble bee and honey bee visitors deposited a variable amount of pollen: from just a few *S. pedata* pollen grains to more than 40 pollen grains. As most checkerbloom flowers have a maximum of 6 or 7 ovules, it is theoretically possible that one bee visit that deposits stigmatal pollen load of 6+ pollen grains is enough to achieve full fertilization of the *S. pedata* flower.

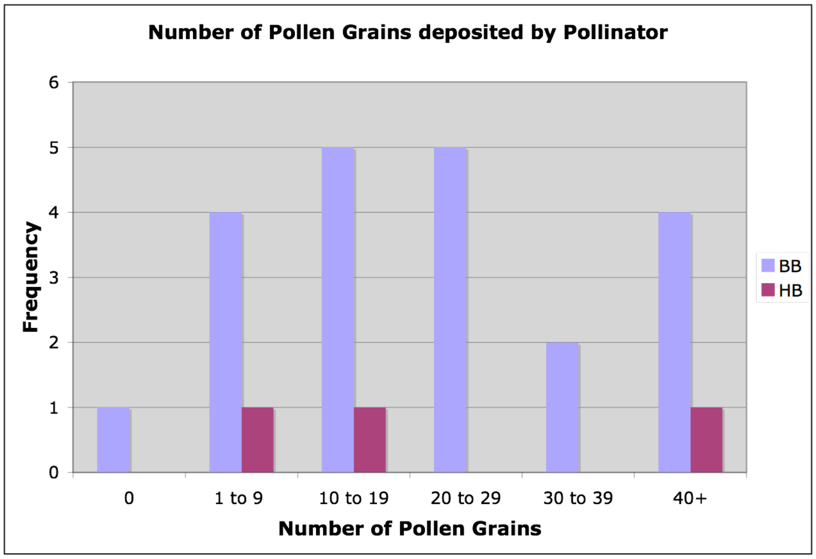

Figure 11. Number of pollen grains deposited on the stigma of female S. pedata flowers by a single visit from bumble bees and honey bees.

In addition to the bumble bees and honey bees, one *Anthophora* sp. bee visited an experimental female flower and deposited approximately 55 *S. pedata* pollen grains from the single visit.

C. Review the existing pollination literature on pollinators that potentially contribute to significant seed and fruit production of *Sidalcea pedata.*

See the next section.

(4) Literature Review: Biology/Ecology of other *Sidalcea* species

Evolutionary Relationships

Checker mallows or checkerblooms are found primarily in the western U.S. and the genus is comprised of 25 species of annuals and perennials (Hill 1993). *Sidalcea* is known to be a difficult group due to complex morphological variation and suspected hybridization. Most species are diploid, but different ploidy levels can occur. Annual species appear to have significantly higher rates of molecular evolution than perennial species (Andreasen and Baldwin 2001). Using nuclear ribosomal DNA sequences, Andreasen and Baldwin (2003) re-examined relationships among *Sidalcea* species. They found that there is a strongly supported *malviflora* clade that consists of all seven of the *S. malviflora* subspecies, *S. neomexicana*, *S. pedata*, and *S. covillei*. *S. pedata* is most closely related to *S. neomexicana*, and the six *S. malviflora* subspecies except *S. malviflora sparsifolia*, which is basal to *S. pedata*. *S. covillei*, another endangered species, is basal to *S. malviflora sparsifolia*.

Breeding system

Published literature indicates that at least eight other species of *Sidalcea* are gynodioecious, so it is not surprising that *Sidalcea pedata* is gynodioecious as well. This suggests that gynodioecy is a common reproductive trait among *Sidalcea* species. Gynodioecious *Sidalcea* species include *S. malviflora malviflora* (Graff 1999), *S. hendersoni* (Marshall & Ganders 2001; Gisler & Love 2005), *S. oregana spicata* (Ashman and Stanton 1991; Ashman 1992), *S. hirtipes* (Schultz 2003a,b), *S. malviflora sparsifolia* (Leong, unpublished data), *S. nelsoniana* (Gisler and Meinke 1997, Halse et al. 1989) as well as *S. cusickii, S. campestris,* and *S. virgata* (Halse et al. 1989). Dimling (1992) studied the reproduction of clonal *S. malviflora elegans* but did not report that it was gynodioecious.

Selfing is likely to occur in several species. Hermaphrodites have been found to be self-compatible and protandrous in *S. hendersoni* (Marshall & Ganders 2001), *S. oregana spicata* (Ashman and Stanton 1991) and *S. malviflora malviflora* (Graff 1999). Hermaphrodite flowers of *S. hirtipes* are protandrous as well (Schultz 2003b). Graff (1999) states that selfing (by geitonogamy) in *S. malviflora malviflora* requires the services of a pollinator due to protandry of hermaphrodites. In contrast, *S. malviflora elegans* has been reported as an obligate outcrosser (Dimling 1992).

The genetic basis of gynodioecy or male sterility has been examined in *S. hendersoni* and *S. oregana spicata*. Marshall & Ganders (2001) did a series of crosses between *S.*

hendersoni morphs and found that crosses of hermaphrodites to female mothers produced a hermaphrodite to female offspring ratio not significantly different from 1:1. Crosses of hermaphrodite mothers produced hermaphrodite offspring only. Marshall & Ganders (2001) concluded that male sterility is controlled by a nuclear gene, not by cytoplasmic genes or factors. Alternatively, they proposed that if male-sterile cytoplasmic factors have become fixed in the populations studied, then male sterility could appear to be controlled by nuclear genes. Ashman (1992) did similar greenhouse crosses with *S. oregana spicata* that resulted in female mothers producing very female-biased progenies and hermaphrodite mothers producing either all hermaphrodite offspring or a mixture. Ashman (1992) stated that a combination of nuclear and cytoplasmic genes controls inheritance of male sterility in *S. oregana spicata*.

Fitness Comparisons Between the Sex Morphs

Fitness components have been measured from greenhouse-grown progenies of outcrossed females, selfed hermaphrodites, and outcrossed hermaphrodites. These *Sidalcea* studies provide evidence for female advantage due to maternal sex effects and outcrossing benefits. In *S. hendersoni*, progenies from outcrossed females produced more viable seeds/fruit, produced more flowers, and had greater germination rates than offspring of outcrossed hermaphrodites (Marshall & Ganders 2001). Offspring from selfed hermaphrodites had the lowest fitness values. In *S. oregana spicata*, seeds of female mothers, compared to seeds from hermaphrodite mothers, had greater germination success and the seedlings had a faster growth rate (Ashman 1992). The level of inbreeding had no effect on these early developmental processes. Effects of inbreeding were noted at the reproductive adult stage in terms of reduced adult growth rates and smaller adult sizes at first flowering. In addition, Ashman (1992) reported higher seedling growth rates for female offspring that were transplanted to field sites.

Various components of fitness have been measured in natural populations of *Sidalcea* species. Some studies have found differences in the fecundity of female and hermaphrodites. Females of *S. hirtipes* produced 43% more seeds/fruit on average than hermaphrodites, but no difference was found between the two in the number of fruits/stem or seed mass. Graff (1999) documented in *S. malviflora malviflora* that open-pollinated female focal plants produced more than twice as many seeds/flower than open-pollinated hermaphrodite focal plants, regardless of the surrounding morph neighborhood. In *S. hendersoni*, however, no consistent differences in fecundity were detected between the sex morphs (number of fruits per raceme, number of viable seeds per fruit in the six populations studied (Marshall & Ganders 2001; Gisler & Love 2005). Ashman (1994) found that *S. oregana spicata* females allocated more of their reproductive resources to seeds compared to hermaphrodites. Hermaphrodites allocated fewer resources to seeds, because of necessary competing allocations to pollen and larger floral structures.

Aspects of Pollination Biology

Floral characteristics. Details of the floral biology of *S. oregana spicata* were reported by Ashman and Stanton (1991). In hermaphrodite flowers, the male phase lasts about one day, and styles become exerted the second day. Female flowers exert styles on first day of anthesis. The life span of female flowers was longer (about a day) than the female phase of hermaphrodite flowers. Flowers produce very small amounts of viscous nectar that is florescent and appears blue under UV radiation. As in many gynodioecious species, the petal length of females is significantly shorter than in hermaphrodites, but female stems had more open flowers at a time. Halse et al. (1989) examined the pollen of four *Sidalcea* species in the Willamette Valley, *S. nelsoniana, S. cusickii, S. campestris,* and *S. virgata*. The pollen of all four species was similar in appearance using scanning electron microscopy. Grains were 60-70 microns in diameter, spiny, and the presence of pollenkit was detected. Dobson (1988) reported the presence of pollenkit from several other species of *Sidalcea*.

Floral visitors. Studies have reported that a variety of insects visit *Sidalcea* flowers, but bees tended to be the major floral visitors. Bumble bees were the primary pollinators of *S. oregana spicata* and *S. hendersoni* flowers (Ashman 1992; Marshall and Ganders 2001), while the major pollinators observed visiting *S. malviflora malviflora* flowers were bees in the Andrenidae, Anthophoridae, Colletidae, and Halictidae (Graff 1999). Gisler and Meinke (1997) found that floral visitors to *Sidalcea nelsoniana* included native bees, wasps, syrphid flies, and lepidopterans. Both Ashman and Stanton (1991) and Graff (1999) found that nectar was the primary pollinator reward. However, one native bee species was observed collecting pollen on *S. oregana spicata. Diadasia nigrifrons* females were the primary pollen collectors, but a variable and infrequent visitor to *S. oregana spicata* (Ashman and Stanton 1991). Sipes and Tepedino (2005) concluded that *D. nigrifrons* is oligolectic on *Sidalcea*, based on evidence from many pollen load analyses, which is consistent with the earlier observations of Linsley and MacSwain (1957). Only one study tested for floral morph preferences among insect visitors. Ashman and Stanton (1991) concluded that there was no significant preference for either inflorescence type, but pollinators did visit individual hermaphrodite flowers more frequently than female flowers.

Spatial and Temporal Distribution of Morphs. Spatial and temporal heterogeneity of *Sidalcea* sex morphs reportedly influenced patterns of pollen flow in two species studied. Graff (1999) found that at a neighborhood level, genders of *S. malviflora malviflora* vary spatially in their degree of association. The neighborhood hermaphrodite frequency was lower around focal female plants than around focal hermaphrodite plants. Both genders were equally pollen limited and both were more pollen limited when surrounded by female, rather than hermaphrodite neighborhoods. Temporal heterogeneity in gender distribution was observed by Ashman and Stanton (1991). Females of *S. oregana spicata* flowered first and so the population was female biased early in the flowering season; much later in the season hermaphrodites were 80% of the flowering individuals.

Seed Predation

Several *Sidalcea* species host weevil seed predators that can significantly limit the number of viable seeds produced. Marshall and Ganders (2001) found sex-biased seed predation in *S. hendersoni* populations where the weevil *Anthonomus melancholicus* predated upon the developing fruits of hermaphrodites more frequently. Another weevil species, *Macrorhoptus sidalceae* was not found to be a selective predator. If seed predation was taken into account in natural populations, then female *S. hendersoni* realized a significantly higher rate of seed production than hermaphrodites. Weevil seed predation in *S. nelsoniana* populations resulted in damage to 0-84% of the total ovules on sampled stems (Gisler and Meinke 1997). *Macrorhoptus sidalceae* infestation levels among other *Sidalcea* species varied considerably: numbers of weevils observed per plant was significantly greater for S. *nelsoniana* than for S. *campestris* or S. *virgata*. Dimling (1992) reported weevil predation of *S. malviflora elegans* by *Macrorhoptus. niger.* Weevil seed predation rates for two years were 39% and 26% of all ovules scored. *Sidalcea malviflora sparsifolia* also hosts the weevil *Macrorhoptus. niger* and weevils have been reared from fruiting stems (De Anda & Leong, unpublished ms). The larvae of *Macrorhoptus* weevils feed on developing seeds, pupate within the hollowed out seeds, and adults emerge by chewing an exit hole in the carpel wall (Burke 1973).

(5) Summary and Conclusions

Breeding System. *Sidalcea pedata* is obviously gynodioecious, with female flowers typically almost half the size of hermaphrodite flowers. Both sex morphs were present at all five primary sites plus two other sites visited, a lot at the corner of Park and Oriole, and the Presbyterian Conference Center. Results from field experiments involving caging and hand-pollination of flowers indicate that hermaphrodites can produce fruits and seeds through geitonogamy, or neighbor selfing. This type of selfing requires the services of insect pollinators, as opposed to autogamous selfing, which does not require insect pollinators. Data suggest that hermaphrodites may be capable of an extremely low rate of autogamous selfing; alternatively, very small insects such as thrips or ants may occasionally act as pollinators. Results from Bluff Lake demonstrate that females, as one might expect, cannot produce seed from autogamous selfing and therefore require the services of insect pollinators. Consequently, seed reproduction by *Sidalcea pedata* morphs, whether through selfing or outcrossing, requires the pollination services of insects.

Reproductive Output. The fecundity of *S. pedata* females was almost twice that of hermaphrodites in the populations sampled. Specifically, average percent fruit set of flower positions 1-15 was 70-90% in females and 26-56% in hermaphrodites. Number of seeds per fruit was not consistently different between the two morphs. It is possible that for some hermaphrodites, fruit set of more apical regions (beyond positions 1-15) might converge towards typical female values. The high fruit set of females suggests that females are not pollen-limited to any great extent. A notable finding of this study is the trend of increasing fruit set with increasing apical position of the flower. This trend is manifested more strongly in hermaphrodites than females. Perhaps most of the earlier, basal hermaphrodite flowers function primarily as males. This interpretation is consistent with the observation that a number of early season closed-up hermaphrodite flowers at Bluff Lake had either no stigmas exerted or only partial stigma exertion. As females tend to finish fruiting earlier than hermaphrodites at the same site, it may be advantageous for hermaphrodites to allocate more resources to male function earlier in the season, and then to increase allocation to female function as the flowering season progresses.

Floral Visitors/ Pollinators. A diversity of insects in the orders Hymenoptera, Coleoptera, Diptera, Lepidoptera, Hemiptera, Orthoptera and Odonata were either caught or observed on *S. pedata* flowers. A total of 643 insect visitors were netted on checkerbloom flowers or nearby flowering species. Bees in the families Apidae, Halictidae, and Megachilidae were the most frequently observed/caught floral visitors to *S. pedata* and 93% of bees caught carried *S. pedata* pollen on their bodies. Preliminary identification of bees suggests that there are at least 41 species of bee visitors or potential pollinators of *S. pedata* in the Big Bear region. Most of the bee visitors netted were generalist pollinators as many bee taxa had pollen of other species on their bodies. A specialist bee species on *Sidalcea*, *Diadasia nigrifrons*, was not abundant, but occurred at four sites. Bees in the genera *Ceratina*, *Lasioglossum (Dialictus)* and *Osmia* were the most geographically widespread of the bee visitors, occurring at six of the seven sites sampled. *Osmia* bees were the most abundant genus caught; it is estimated that at least seven *Osmia* species were found to visit *S. pedata* flowers. Surprisingly, the European honey bee, *Apis mellifera*, was a common checkerbloom floral visitor at one site only, Bluff Lake. Systematic floral visitation observations at the Bluff Lake and Lot K sites revealed that bumble bees and honey bees were the most frequent floral visitors at Bluff Lake. In contrast, small and medium sized bees in the Halictidae and Megachilidae were the predominant floral visitors at Lot K. Numerous, repeated observations of bees at checkerbloom flowers indicated that virtually all individuals were foraging for nectar rather than pollen. Findings suggest that *S. pedata* and its bee floral visitors/ pollinators are part of larger, plant-pollinator interaction webs at the montane meadow sites sampled.

Pollinator Effectiveness. Experimental tests of single visit pollen deposition to "virgin" female flowers yielded data that indicate that one pollinator visit can deposit enough pollen to achieve full fertilization of a flower. Pollen deposition from a single visit to a female phase hermaphrodite flower is likely to deposit even a larger amount as hermaphrodite flowers contain more nectar (M. Jones unpubl. data) and thus bees tend to forage in hermaphrodite flowers longer. Honey bees and bumble bees deposited a variable number of *S. pedata* pollen grains on stigmas (1-40+) in a single visit. The one *Anthophora* bee that visited experimental flowers deposited about 55 pollen grains of *S. pedata* in one visit. Experimental tests of pollen deposition were not done at Lot K, so the pollinator effectiveness of the small and medium sized bees is not known. Some of the smallest bees (~0.75 cm in length or less) may be able to avoid touching the stigma lobes while foraging for nectar at the bottom of the corolla. Thus, the very small-sized bees could end up depositing little on no pollen. Different intra-stem foraging patterns by bees suggest that certain bees may be more effective at promoting geitonogamy than others. Bumble bees visited significantly more flowers per stem than honey bees at Bluff Lake. The small and medium sized bee taxa at Lot K appeared to visit even more flowers per stem than bumble bees. Finally, recorded foraging sequences of individual bees in natural populations, as well as choice tests using an experimental "choice stick" indicated that larger-sized bees, such as honey bees and bumble bees, as well as small and medium-sized bees were preferentially attracted to hermaphrodite flowers at a distance. But once at a focal hermaphrodite flower, bees commonly switched between floral morphs in the local vicinity 30-90% of the time. The documented differences in bee foraging behavior imply that the pollination services provided to *S. pedata* by these generalist bee species are likely to be functionally different from one another.

Seed Predation. *Macrorhoptus niger* weevils were found on *S. pedata* at the Lot K site. Adults were infrequently observed on flowers, yet larvae and pupae were commonly dissected out of fruits in the lab, and numerous adults emerged from collected fruits. The number of predated seeds per fruit was not significantly different between the morphs sampled. The percentage of predated seed per stem was fairly low: approximately 11% for females and 19% for hermaphrodites.

Recommendations for Future Management of *Sidalcea pedata*

Research findings indicate overwhelmingly that female and hermaphrodite plants differ significantly in their reproductive biology and pollination ecology. The amount and pattern of fruit set are markedly different between the morphs, and the timing of fruiting and seed dispersal is divergent as well. Hermaphrodites can produce offspring through outcrossing and geitonogamy, whereas females appear to produce offspring solely through outcrossing. Bee pollinators appear to distinguish between the two morphs and were more highly attracted to hermaphrodite flowers when initially flying to a new group of stems. **These unambiguous results argue strongly for the need to recognize the differing biology and ecology of *Sidalcea pedata* sex morphs in any future management or conservation actions.** Specific suggestions for future management actions are listed below.

1. **The long-term persistence and recovery of *S. pedata* populations depends upon the continuing existence of both female and hermaphrodite individuals in a**

population. Females have higher fecundity then hermaphrodites, and studies of other *Sidalcea* species indicate that the offspring of female mothers have greater germination, seedling, and flowering success than offspring of hermaphrodite mothers (Ashmann 1992; Marshall and Ganders 2001). Available data thus suggest that females and their offspring are most likely to succeed in the remaining meadow fragments in the Big Bear region. Hermaphrodites, though lower in fecundity, are indispensable to female reproductive success and consequently are essential to continued population persistence. Vegetation clearance or mowing that disproportionately reduces female fecundity is highly detrimental to the persistence of *S. pedata* populations. Such a situation occurred at the Civic Center site last year as the timing of mowing by the City of Big Bear coincided with the fruiting of female stalks. It is unclear if the fruiting stems had enough time to mature any viable seeds when they were cut down. Only three female stalks were found that were not cut down. Hermaphrodites were able to regrow parts of stems lost as most were still in the flowering stage at the time of mowing.

2. **Any individuals participating in scientific research, consulting, or implementation of conservation or management actions in the field must be able to recognize the two sex morphs of *S. pedata*.** The flowers of the two morphs are easily distinguishable based on size and anther morphology. It is unclear why previous work on this species did not recognize such an obvious difference in floral morphology. When past flowering, female and hermaphrodite plants are difficult to distinguish. Preliminary data suggest that a combination of measurements on fruit size and sepal width may allow morphometric separation of the sex morphs based on field measurements. As mentioned previously, the timing of fruiting could also be used in the identification of *S. pedata* fruiting stalks as females tend to fruit earlier and release their seeds earlier than hermaphrodites.

3. **Collection of *S. pedata* seeds, for mitigation or conservation purposes, must be done in a manner that guarantees that seeds are collected from both female and hermaphrodite fruiting stems.** Depending on the genetic basis of male sterility in *S. pedata*, collection of seed from just one sex morph can result in a highly sex-biased seed collection. If genetic control of male sterility is like *S. hendersoni* (Marshall and Ganders 2001), then seeds collected from hermaphrodite stems only will produce only hermaphrodites. On the other hand, if the genetic basis of gynodioecy in *S. pedata* is similar to *S. oregana spicata* (Ashmann 1992), then seeds collected from hermaphrodites will produce both hermaphrodites and females. As the genetic basis of male sterility is not known for *S. pedata*, the prudent method of seed collection would be to collect seed from approximately equal numbers of female and hermaphrodite fruiting stems. As females tend to fruit and disperse their seeds earlier than hermaphrodites, seed collection from any particular population must be done on multiple dates throughout the fruiting period. Early dates will collect mostly offspring from females while later dates will be biased towards the offspring of hermaphrodites. The added complexity of trying to identify sex morphs in the post-flowering stage of *S. pedata* argues even more strongly in favor of a careful, systematic collection of mature seeds at weekly intervals throughout the entire fruiting period. This would be the most expeditious method for ensuring adequate representation of genetic variation, as well as an adequate sex ratio of both sex morphs in the seed collected. Under no circumstances should seed be collected from *S. pedata* populations on only one date if such seed is intended for mitigation purposes.

4. **Pollination and seed production of *S. pedata* females and hermaphrodites depends upon the pollination services of a diversity of generalist bee species.** Consequently, continued persistence of bird-foot checkerbloom populations within meadow sites requires the continued persistence of local bee populations. Preliminary identification to morphospecies indicates that at least 41 bee species provide pollination services to *S. pedata* in the Big Bear region. As these generalist bee species visit numerous other co-flowering meadow species (some similarly endangered, such as *Thelypodium stenopetalum*), it is clear that the birdfoot checkerbloom- bee interactions examined in this research are part of a larger web of meadow plant-pollinator interactions. Within such a web of generalist pollination interactions, changes in one plant or pollinator species can have direct and indirect effects on many parts of the web. Furthermore, findings suggest that pollination services provided by bee species are not completely redundant. So it is important to maintain a high diversity of bee pollinators, in order to promote a diversity of mating opportunities between and within *S. pedata* plants. Long-term stability and recovery of *S. pedata* populations (an appropriate goal within protected areas), thus requires that a diverse, multi-species, generalist plant-pollinator web of interactions exist in *S. pedata* meadow habitats.

5. **Floral resources required by the diverse generalist bee pollinator assemblage associated with *S. pedata* meadow habitats need to be adequately maintained to ensure long-term persistence of bee populations.** Little is known about the specific resource requirements of most of the bee species associated with Big Bear meadows, as these habitats have been little studied. However, information of a more general nature is known for family or genus level floral requirements. Except for the *Diadasia* bees, most of the other bee pollinators of *S. pedata* are polylectic generalists that will visit a diversity of flowering meadow species. As honey bees and bumble bees maintain long-lived colonies compared to the other bees species, these eusocial bees have the greatest requirements for a diversity of floral resources, over a relatively long temporal period. Other smaller-sized bees, such as *Ceratina* or *Lasioglossum* (*Dialictus*), may have two generations per year in Big Bear. This means that the amount of floral resources available to the second generation in late summer (after *S. pedata* flowers) is likely to determine strongly bee abundance in the following spring or early summer, when *S. pedata* flowers. In other words, the diversity and abundance of other flowering species in meadow habitats, present both before and after *S. pedata* flowers, can directly facilitate bee pollination of *S. pedata* flowers. In the absence of specific knowledge of the floral requirements of the generalist bee pollinators of Big Bear checkerbloom, the best course of action would be to maximize the diversity and abundance of native flowering species in meadow habitats that contain *S. pedata* populations.

6. **Nesting resources required by the diverse generalist bee pollinator assemblage associated with *S. pedata* meadow habitats need to be adequately maintained to ensure long-term persistence of bee populations.** Bees in the family Megachilidae generally nest in preexisting cavities of various sizes. For example, holes in wood or trees made by beetles or other animals, spaces in old plant stems, crevices between stones, fence boards, or other building materials are commonly utilized by megachilid bees. In contrast, the anthophorid (*Anthophora* and *Diadasia*) and halictid bee pollinators observed in this study construct nests in the ground, either in banks or in flat soil. Found at almost all sites, the genus *Ceratina* nests in pithy dead stems or in dead twigs. Michener (2000) does report a few deviations in these general nesting

habitats for a few groups. Bumble bees commonly nest in old rodent burrows or bird nests, or in spaces under vegetation. Honey bee colonies are often located in the hollow limbs or trunks of mature trees. Based on the nesting habits discussed above, the following recommendations can be made: a diversity of sizes of old/dead plant stems, twigs, as well as larger living shrubs and trees should be within flight distance of *S. pedata* populations for use as potential nesting habitats for bee pollinators. Meadow sites that support robust rodent populations (i.e. Bluff Lake) will also provide nesting habitat for bumble bee pollinators.

7. **Current levels of fruit and seed production are fairly high for *S. pedata* females, which suggests that pollination services are not limiting reproduction to any large extent in the sites examined. Less clear, however, is whether the conditions exist for successful germination of seeds and seedling recruitment into the study populations.** Because *S. pedata* is a perennial species, it is not always obvious by casual inspection of sites whether there is a high frequency of successful seedling establishment in existing *S. pedata* populations. If funding becomes available to support continued research on *Sidalcea pedata* biology and ecology, the next studies should focus on the requirements needed for successful germination and seedling establishment. Ashman and Stanton (1991) reported that *S. oregana spicata* seedlings were commonly observed where gophers had disturbed the soil. Halse and Mishaga (1988) found that part of the seed coat of *S. nelsoniana* needed to be removed in order for a high frequency of germination to occur. It is likely that future studies of *S. pedata* germination and seedling establishment will implicate the significance of other animal-mediated processes in maintaining conditions for germination and seedling growth.

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Appendix 1. Floral visitors netted on co-flowering meadow species, listed by insect taxa.

Flower	Location	Order	Family	Genus	Species
Eriogonum. Sp	Bluff lake	Diptera	Bombyliidae		
Eriogonum. Sp	Bluff lake	Diptera	Bombyliidae		
grass	Lot. K	Diptera	Bombyliidae		
Sm. Yellow flwr	Bluff Lake	Diptera	Bombyliidae		
yel. Mustard	Lot. K	Diptera	Syrphidae		
yel. Mustard	Lot. K	Diptera	Syrphidae		
Eriogonum. Sp	Bluff lake	Diptera	Tachinidae		
Eriogonum. Sp	Bluff lake	Diptera	Tachinidae		
Sm. Yellow flwr	Bluff Lake	Diptera	Tachinidae		
Ratail flwr	Lot. K	Hymenoptera	Andrenidae	Andrena	
Yellow flwr	Bluff Lake	Hymenoptera	Andrenidae	Andrena	
Eriogonum. Sp	Bluff lake	Hymenoptera	Anthophoridae	Nomada	
Thelypodium	Lot. K	Hymenoptera	Anthophoridae	Xeromelecta	
Eriogonum. Sp	Bluff lake	Hymenoptera	Apidae	Apis	mellifera
Eriogonum. Sp	Bluff lake	Hymenoptera	Apidae	Apis	mellifera
Eriogonum. Sp	Bluff lake	Hymenoptera	Apidae	Apis	mellifera
Sm. Yellow flwr	Bluff Lake	Hymenoptera	Apidae	Apis	mellifera
Sm. Yellow flwr	Bluff Lake	Hymenoptera	Apidae	Apis	mellifera
Sm. Yellow flwr	Bluff Lake	Hymenoptera	Apidae	Apis	mellifera
Dodecatheon	Ski	Hymenoptera	Apidae	Bombus	vosnesenkii
Lupinus. sp	Bluff lake	Hymenoptera	Apidae	Bombus	vosnesenkii
Yellow flwr	Bluff Lake	Hymenoptera	Apidae	Bombus	vosnesenkii
Thelypodium	Lot. K	Hymenoptera	Halictidae	Agapostemon	
Thelypodium	Lot. K	Hymenoptera	Halictidae	Lasioglossum (Dialictus)	
yel. Mustard	Lot. K	Hymenoptera	Halictidae	Lasioglossum (Dialictus)	
Eriogonum. Sp	Bluff lake	Hymenoptera	Halictidae	Lasioglossum (Lasioglossum)	
Eriogonum. Sp	Bluff lake	Hymenoptera	Halictidae	Lasioglossum (Lasioglossum)	
Sm. Yellow flwr	Ski	Hymenoptera	Halictidae	Lasioglossum (Lasioglossum)	
Thelypodium	Lot. K	Hymenoptera	Halictidae	Lasioglossum (Lasioglossum)	
Thelypodium	Lot. K	Hymenoptera	Halictidae	Lasioglossum (Lasioglossum)	
Thelypodium	Lot. K	Hymenoptera	Halictidae	Lasioglossum (Lasioglossum)	
Purple flwr	Ski	Hymenoptera	Megachilidae	Ashmeadiella	
Eriogonum. Sp	Bluff lake	Hymenoptera	Megachilidae	Osmia	
Eriogonum. Sp	Bluff lake	Hymenoptera	Megachilidae	Osmia	
Eriogonum. Sp	Bluff lake	Hymenoptera	Megachilidae	Osmia	
Eriogonum. Sp	Bluff lake	Hymenoptera	Megachilidae	Osmia	
Pinecone nest	TB	Hymenoptera	Megachilidae	Osmia	
Scroph?	Lot. K	Hymenoptera	Megachilidae	Osmia	
Thelypodium	Lot. K	Hymenoptera	Megachilidae	Osmia	
Thelypodium	Lot. K	Hymenoptera	Megachilidae	Osmia	
Eriogonum. Sp	Bluff lake	Hymenoptera	Megachilidae	Stelis	
Eriogonum. Sp	Bluff lake	Hymenoptera	Megachilidae	Stelis	
Eriogonum. Sp	Bluff lake	Hymenoptera	Megachilidae	Stelis	
Eriogonum. Sp	Bluff lake	Hymenoptera	Sphecidae		
Eriogonum. Sp	Bluff lake	Hymenoptera	Sphecidae		
yel. Mustard	Lot. K	Hymenoptera	Sphecidae		
yel. Mustard	Lot. K	Hymenoptera	Vespidae		
yel. Mustard	Lot. K	Lepidoptera	Hesperiidae		
Eriogonum. Sp	Bluff lake	Lepidoptera	Lycaenidae		

Appendix 2. Bee visitors netted on *Sidalcea pedata* flowers by taxa and site. Number of species estimated as number of morphospecies. Site abbreviations and # sampling dates per site are: Bluff Lake (BL) 25, ColdBrook Campground (CB) 1, Civic Center (CC) 5, Lot K (LK) 14, Presbyterian Conference Center (PC) 1, Ski Beach (SB) 2 and Taco Bell (TB) 5.

Family	**Genus/ species**	**# species**	**BL**	**CB**	**CC**	**LK**	**PC**	**SB**	**TB**
Andrenidae	*Andrena*	2				x			
Apidae	*Anthophora*	1	x			x			x
	Apis mellifera	1	x			x			x
	Bombus californicus	1	x						
	Bombus edwardsii	1	x			x			
	Bombus vandykei	1	x						
	Bombus vosnesenskii	1	x						
	Ceratina	1		x	x	x	x	x	x
	Diadasia nigrifrons	1			x	x	x		x
	Diadasia	1	x			x			
	Nomada	1	x			x			
	Svastra.	1	x						
	Xeromelecta	1	x						
Colletidae	*Hylaeus*	1							x
Halictidae	*Agapostemon*	2	x	x	x	x			
	Halictus	1			x	x		x	x
	Lasioglossum (Dialictus)	2	x	x	x	x		x	x
	Lasioglossum (Evylaeus)	1				x			
	Lasioglossum (Lasioglossum)	2	x		x	x			x
Megachilidae	*Anthidium*	1	x		x				
	Ashmeadiella	1	x		x	x		x	
	Chelostoma	1			x				
	Coelioxys	1	x						
	Heriades	1			x				
	Hoplitis	2	x						x
	Megachile	3	x		x	x			x
	Osmia	7	x	x	x	x		x	x
	Stelis	1	x						

Appendix 3. Seed predation data from Lot K 2005.

Morph	% predated seeds/stem	% viable seeds/stem	% non-viable seeds/stem
F1	24%	63%	13%
F2	2%	50%	45%
F3	9%	71%	16%
F4	0%	73%	19%
F5	8%	47%	44%
F6	0%	69%	26%
F7	4%	77%	11%
F8	11%	66%	11%
F9	15%	60%	26%
F10	33%	34%	30%
F avg.	**11%**	**61%**	**24%**
H1	18%	33%	40%
H2	6%	55%	38%
H3	0%	47%	51%
H4	31%	34%	45%
H5	21%	47%	20%
H6	10%	43%	38%
H7	23%	35%	32%
H8	8%	56%	35%
H9	62%	5%	14%
H10	15%	40%	40%
H avg	**19%**	**39%**	**35%**

morph	#fruits/stm	ave seeds/frt/stm	predated seeds/frt/stm	viable seeds/frt/stm
F1	19	4.95	1.21	3.10
F2	36	6.25	0.14	3.13
F3	12	6.25	0.58	4.42
F4	14	6.5	0	4.71
F5	27	6	0.48	2.81
F6	27	7.14	0	4.96
F7	9	6.3	0.22	4.89
F8	34	6.29	0.68	4.18
F9	10	6.2	0.9	3.70
F10	24	5.95	1.96	3.04
F avg.	**21.2**	**6.18**	**0.62**	**3.89**
H1	18	3.72	0.67	1.22
H2	22	6.55	0.41	3.6
H3	16	4.5	0	2.12
H4	17	5.82	1.82	2
H5	18	5.28	1.11	2.5
H6	22	5.05	0.5	2.18
H7	20	5.1	1.15	1.8
H8	10	5.2	0.4	2.9
H9	14	6.07	3.79	0.29
H10	21	6	0.9	2.38
H avg	**17.8**	**5.33**	**1.08**	**2.10**