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Natural history of Maguire primrose, *Primula cusickiana* var. *maguirei* (Primulaceae)

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NATURAL HISTORY OF MAGUIRE PRIMROSE, *PRIMULA CUSICKIANA* VAR. *MAGUIREI* (PRIMULACEAE)

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ABSTRACT.—Natural history information for rare plants can help land managers better understand the threats to extinction that a taxon may face. Our focus is on the natural history of Maguire primrose (*Primula cusickiana* var. *maguirei*, Primulaceae), an endemic, threatened plant found along a narrow corridor within a single canyon in northern Utah. We examined floral morphology, air temperature, relative humidity during flowering, dichogamy, blooming period, and visits from flying insects. As with most *Primula*, Maguire primrose displays distinct floral distyly. Within the distylous flowers, 17% of our samples had a timing difference in the maturation of anthers and stigmas, a trait not previously recorded in any other *Primula* species. Temperatures during the early-spring blooming period fluctuated widely between recorded minima below 0 °C and maxima above 33 °C. We captured 8 different species of flying insects visiting Maguire primrose flowers in air temperatures ranging from 6 to 15 °C. Bloom timing was not well synchronized between different canyon locations. Between different canyon locations, we observed only a small number of plants that overlapped in their flowering phenology. This threatened primrose variety has a cool, early-season blooming period, a dependence on visiting insects for outcrossing, and disjunct populations throughout the canyon, resulting in the potential for serious challenges to reproduction.

RESUMEN.—La información sobre la historia natural de plantas raras puede ayudar a los coordinadores del manejo de tierras a comprender mejor los peligros de extinción que pueden amenazar un taxón. Nos enfocamos en la historia natural de la prímula Maguire (*Primula cusickiana* var. *maguirei*, Primulaceae), una planta endémica amenazada que sólo se encuentra a lo largo de un corredor angosto dentro de un solo cañón en el norte de Utah, EUA. Examinamos su morfología floral, la temperatura del aire y la humedad relativa durante la floración, la dicogamia, el período de floración y los insectos voladores que visitan esta variedad. Tal como sucede con la mayoría de especies del género *Primula*, la prímula Maguire exhibe distilia floral marcada. De la flores dístilas, en el 17% de nuestros muestreos las anteras y estigmas maduraron en distintos momentos, un rasgo que no se había observado en ninguna otra especie de *Primula*. La temperatura registrada durante el período de floración a principios de la primavera fluctuó ampliamente entre mínimas de bajo 0 °C y máximas de más de 33 °C. Capturamos 8 especies distintas de insectos voladores que visitaban las flores de la prímula Maguire a temperaturas ambientales entre 6 °C y 15 °C. La floración no estuvo bien sincronizada entre las plantas de distintas partes del cañón. Observamos sólo un reducido número de plantas en distintas partes del cañón cuyos períodos de floración coincidían. Esta variedad amenazada resiste las temperaturas bajas de un temprano período de floración, una dependencia de las visitas de insectos para el cruzamiento y las poblaciones fragmentadas a lo largo del cañón, todo lo cual puede presentar desafíos graves para su reproducción.

Plants with restricted distributions are especially at risk of extinction because locally adverse conditions can be more detrimental for them than for widespread species. Furthermore, narrowly restricted plants usually have smaller effective population sizes, resulting in fewer individuals available for mating. Managers mandated to conserve rare and narrowly distributed plants rely on sufficient natural history information to make critical management decisions.

Here we examine a primrose known only from 2 populations within a 20-km corridor of a river canyon in northern Utah. Despite its being listed as a threatened plant by the U.S. Fish and Wildlife Service (1985), fundamental biological information about Maguire primrose (*Primula cusickiana* var. *maguirei* L.O. Williams)

has yet to be recorded (U.S. Fish and Wildlife Service 1990). Our examination of *P. cusickiana* var. *maguirei* focused on 5 main questions: (1) Is there flower distyly, as seen in most primrose species? (2) Do populations at different canyon locations experience different temperature regimes? (3) Do anthers and stigmas mature at different times within a flower (i.e., is dichogamy present)? (4) Do populations differ in flowering phenology? (5) What insects and other animals visit the flowers?

Distribution and Taxonomy

Primula species have a widespread global distribution in a variety of terrestrial ecosystems (Guggisberg et al. 2006), with western North American *Primula* found primarily in alpine and

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subalpine mesic habitats (Kelso et al. 2009). A group of 7 North American primroses in subgenus *Auriculastrum* section *Parryi* exhibits involute leaf venation, syncolpate pollen, and heterostyly (Richards 2002, Mast et al. 2006). Section *Parryi* is composed of *Primula parryi*, *Primula capillaris*, *Primula rusbyi*, *Primula angustifolia*, and 4 varieties of *P. cusickiana*. Each *P. cusickiana* variety is separated by hundreds of kilometers, with variety *maguirei* found only in northern Utah on limestone, dolomitic limestone, and quartzite outcrops of Logan Canyon (Kelso et al. 2009). *Primula cusickiana* var. *maguirei* is differentiated by its glabrous leaves, white farinose calyx, and a corolla tube length 2 times the length of the calyx (Heil and Porter 2003). Despite their geographic differences, all *P. cusickiana* varieties are found in moist habitat pockets within their ranges.

Reproduction and Outcrossing

Some plant species exhibit distinctly distylous flowers with consistent di- or trimorphisms. Primroses typically are characterized by flowers with 2 different forms, each with anthers and stigmas in "reciprocal" placement (Mast and Conti 2006). "Pin" morphs have recessed anthers and long styles that reach the corolla tube mouth, while "thrum" morphs have anthers in the corolla tube mouth and shorter, recessed styles. Insect visitors that move between flower morphologies have pollen deposited on their bodies in a way that is thought to promote "legitimate" outcrossing, which is the reproduction resulting from intermorph pollen transfer (Darwin 1877).

Intermorph outcrossing in *Primula* is also promoted by self-incompatibility systems present in stigmas of both pin and thrum plants, which select for pollen from the opposite morph (Richards 1993). Although most *Primula* species are distylous, some species can occasionally self-fertilize (Kelso 1992, Richards 2002). Carlson et al. (2008) examined the breeding system of *P. tschuktschorum*, a distylous North American arctic species, and found both weak self-incompatibility and intramorph incompatibility that allow for some self-fertilization, perhaps as a reproductive assurance in an occasionally pollinator-limited arctic environment. Additionally, a few distylous *Primula* species exhibit a homostyle flower morphology that is a combination of pin and thrum characteristics. These individuals are usually able to self-fertilize because of a breakdown in the self-incompatibility system

(Richards 2002). Dichogamy, the temporal offset of anther and stigma maturation, is another mechanism that may lessen the possibility of self-fertilization (Barrett 2002a) and decrease sexual interference (Barrett 2002b). However, to our knowledge, dichogamy has not been reported in any *Primula* species.

Considering the 2 floral morphologies and incompatibility constraints common among *Primula* congeners, rare *Primula* species may face outcrossing challenges. The combination of heterostyly and self-incompatibility systems results in reproductive constraints that reduce the number of potential mates, such that, for each individual plant, only about half of an entire population is available for legitimate outcrossing. The number of potential mates is further reduced for *P. cusickiana* var. *maguirei* due to its geographic distribution, where individuals are found in 2 disjunct populations along a narrow canyon. Additionally, bud break and development of *P. cusickiana* var. *maguirei* are likely temperature dependent (Karlsson 2002), resulting in blooming times that are only partially synchronous with one another and likely differ between populations.

Phenology and Temperature

Cool temperatures during emergence and blooming can pose multiple reproductive hurdles for spring-blooming *Primula* and their pollinators. Plants must be able to develop and reproduce in cool temperatures and have receptive flowers available for pollination when it is warm enough for the pollinators themselves. Additionally, expected future climate changes may disrupt selfing rates, as well as the synchronicity of bloom timing with insect emergence, a critical factor in outcrossed reproduction for pollinator-dependent *Primula* (McKee and Richards 1998, Price and Waser 1998). We examine these critical insect interactions, the timing of blooming at different canyon locations, and the temperature conditions during blooming and development for *P. cusickiana* var. *maguirei*. These natural history details will hopefully assist management agencies charged with protecting this threatened variety.

METHODS

Study Area

Fieldwork took place exclusively in Logan Canyon, which is located within the Bear River
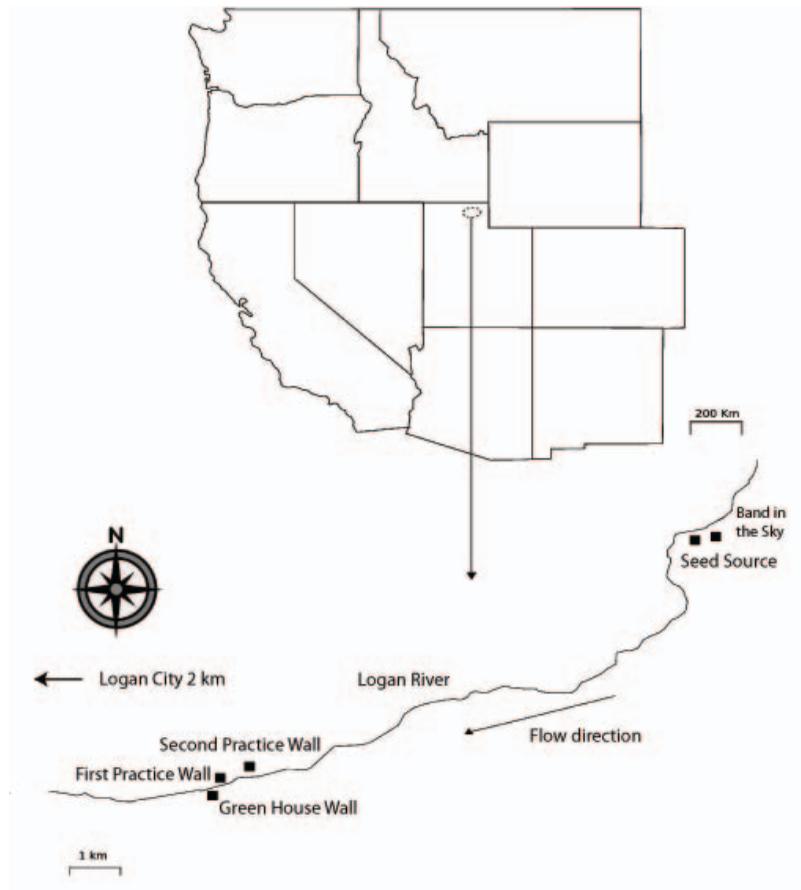
Fig. 1. The western United States and Logan Canyon, Utah, study locations for *Primula cusickiana* var. *maguirei*.

Mountains of northern Utah (Fig. 1). Logan Canyon is a sinuous chasm containing the Logan River, and is characterized by extensive limestone cliffs. *Primula cusickiana* var. *maguirei* has only been observed along a 20-km section of Logan Canyon in 2 distinct populations at exposed cliff areas, most of which are on north-facing slopes within approximately 1 km of the Logan River (U.S. Fish and Wildlife Service 1985). Plants are found at elevations between 1400 m and 1800 m in exposed areas with small limestone cracks and ledges containing shallow soils. We used 5 locations of plants for our study, 3 of which are in the lower canyon population (Greenhouse Wall [GHW], First Practice Wall [FPW], and Second Practice Wall [SPW]), and 2 of which are in the upper canyon population (Seed Source [SS] and Band In The Sky [BITS]; Fig. 1). These 2 populations are approximately 12 km apart and have different associate plants:

Juniperus and *Artemisia* dominate the lower canyon population, while *Pseudotsuga* forest dominates the upper canyon population. At the upper canyon, we have observed *P. cusickiana* var. *maguirei* growing with multiple moss species, including *Tortula princeps* and *Weissia* spp. (Pottiaceae). We selected locations based on the number of plants available, accessibility of plants, and safety considerations.

Clones, Distyly, and Dichogamy

During our field experiments, we noted plants with similar flower morphologies clumped together, suggesting a clonal nature in *P. cusickiana* var. *maguirei*. Clonal growth of *P. cusickiana* var. *maguirei* may pose additional outcrossing challenges if pollinators only visit pockets of flowering plants instead of moving between them. Kelso et al. (2009) recently reported clonal growth in section *Parryi*. To see if clonal growth

is occurring, we delicately excavated 2 groups of plants growing in shallow loose soil to examine stems and roots.

To determine if *Primula cusickiana* var. *maguirei* is distylous, we collected flowers from upper and lower canyon populations to measure floral features. Topmost flowers from 116 individuals (similar sample sizes from upper and lower canyon sites) were randomly collected from plants growing >1 m apart to ensure independence among individuals. Sampled flowers were then longitudinally sectioned in the laboratory. Dissected flowers were photographed with a micrometer scale for reference, and we used Carnoy software (Biovolution, Belgium) to measure 5 distances from the pistil base to the nearest 0.01 mm. We measured 4 commonly dimorphic characters: pistil length, maximum and minimum anther height, and corolla tube length. In addition, sepal length was measured to explore whether this character is diagnostic of flower morphology at the bud stage. Sepal length has occasionally varied by morph in other *Primula* (Carlson et al. 2008). We used 2-sample *t* tests assuming unequal variances to test for differences between morphologies.

We tested for the presence of dichogamy, the temporal offset of stigma and anther maturation, from topmost flowers at different ages (unopened flowers to withering flowers) from each population. Flower age was determined by flower color, size, and shape because young flowers were brightly colored, smaller, and less ragged than older flowers. We determined these age-dependent characteristics by observing many plants on a daily basis and noting changes through time. Twenty-four individual flowers (6 from the lower canyon [SPW] in 2008, 11 from the lower canyon [FPW and GHW] in 2009, and 7 from the upper canyon [BITS] in 2009) were collected and dissected to isolate their stigmas and anthers. We immersed stigmas in H_2O_2 and examined them microscopically for the evolution of bubbles as evidence of stigma maturation (Kearns and Inouye 1993).

Phenology

To examine variation in timing of bloom along Logan Canyon, we repeatedly visited designated sites (one or several per location) to count the number of open intact flowers. We also recorded the morphology (pin or thrum) of the flowers. Typical monitoring sites were pockets of plants composed of multiple flowering scapes. We picked a diversity of accessible plant pockets throughout each population to comprise monitoring sites that were representative of the habitats present. We monitored upper and lower canyon populations in 2008 and 2009. In 2008, 152 monitoring sites were observed (101 lower canyon, 51 upper canyon), and in 2009, 159 monitoring sites were observed (98 lower canyon, 61 upper canyon). Each monitored site had vegetative rosettes that produced between 0 and 40 flowering scapes. We monitored sites every 2–6 days in 2008 and every 5 days in 2009. We monitored flowering as early in the season as was safely possible, and continued until the bloom ended at the designated sites. Our counts of flower numbers included both the natural blooming and withering of flowers, as well as the removal of intact flowers due to herbivory.

Temperature and Insect Visitors

To document temperature and relative humidity during early bloom of *P. cusickiana* var. *maguirei*, we placed Hobo field sensors (Onset Computer Corp., Bourne, MA) among populations to record conditions every 30 minutes from 19 April to 14 July 2008, and from 22 March to 30 June 2009. We placed 7 sensors in the lower canyon population, and 3 sensors in the upper canyon population in concert with monitoring efforts by the USDA Forest Service (Torti 2008). Our disproportionate sensor distribution aimed to document the greater habitat variability found within lower canyon sites. Sensors were placed adjacent to existing plants.

We collected insect visitors via aerial net when possible. Date, time, and location of collection specimens were recorded. Collections were deposited and accessioned in the USDA–ARS U.S. National Pollinating Insect Collection at Utah State University (Logan, UT).

RESULTS

Clones, Distyly, and Dichogamy

Excavations in 2008 indicate that *P. cusickiana* var. *maguirei* can be clonal. We observed rhizomes, 9 cm in length, connecting 2 plants of the same flower morphology. The specimen is deposited in the Intermountain Herbarium in Logan, Utah (UTC#250355). This evidence, coupled with our field observations of small pockets of plants with the same flower morphology, suggests that this variety is often naturally clonal. Additionally, a previously collected
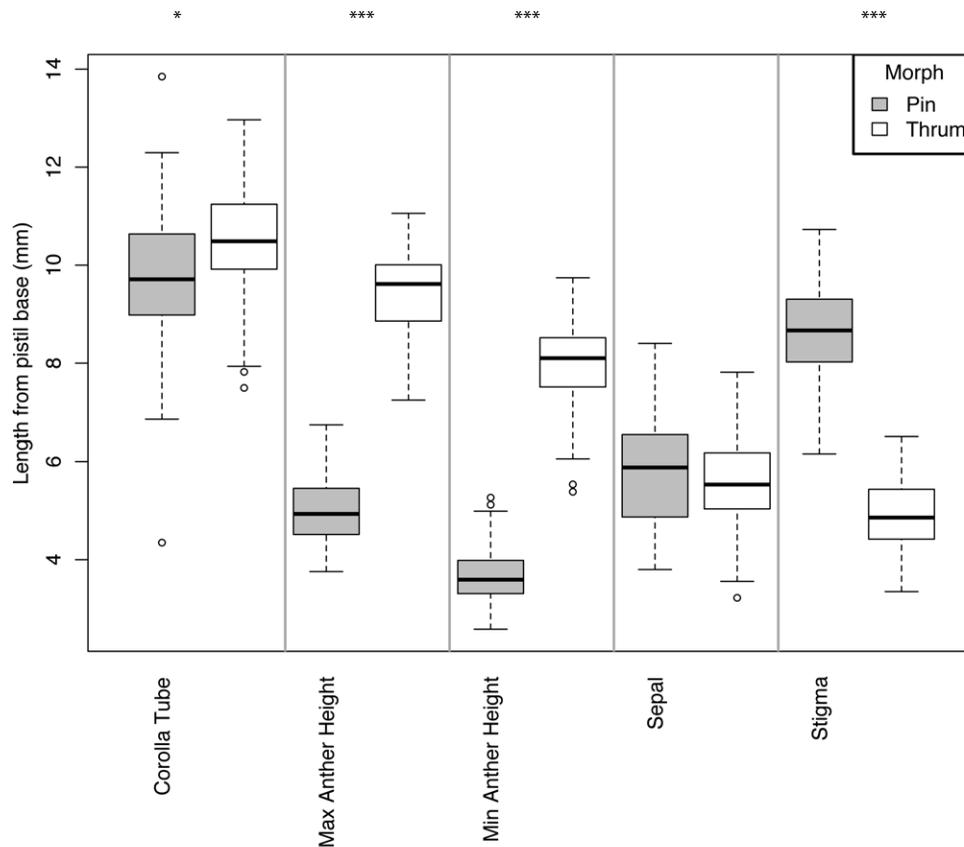
Fig. 2. Measurements of *Primula cusickiana* var. *maguirei* pin and thrum flowers. All length measurements were taken from the pistil base. Max Anther Height is the measurement to the anther apex, whereas Min Anther Height is the measurement to the anther nadir. Differences between morphologies were tested using 2-sample *t* tests assuming unequal variances (*$P < 0.05$, ***$P < 0.001$).

Intermountain Herbarium specimen also demonstrates clonal growth (UTC#00184462).

We observed clear separation of floral characters into pin and thrum categories (Fig. 2). All sampled flowers had distinct morphology membership with 62 pin plants and 54 thrum plants. Of the floral characters measured, only 2 characters had overlapping ranges between morphologies: sepal length and corolla tube length. Sepal length was the only character that did not show significant morphology-specific differences ($P = 0.294$); all other characters were significantly different between morphs.

Of the 24 flowers measured for dichogamy, 4 individuals (3 thrum and 1 pin) had mature stigma surfaces but anthers that were not dehisced (protogyny). Flowers of the 20 other individuals matured anthers and stigmas concurrently or had not yet reached maturity. Flowers lacking mature stigmas did not produce bubbles in H_2O_2 immersion.

Phenology

Plants at the lower canyon population bloomed from 28 April to 25 May 2008, and slightly earlier in 2009 (12 April–19 May). The upper canyon population bloomed from 15 May to 20 June 2008, and from 4 May to 3 June 2009. Upper and lower canyon blooming differences were clearly observed during both field seasons (Fig. 3), with 10–15 days of overlap. The overlap was a brief window of time where a small number of late-blooming lower canyon individuals were flowering concurrently with a few early-blooming upper canyon plants (12 km away). Additionally, the numbers of pin and thrum flowers available at given times were somewhat variable but generally followed overall bloom cycles that were
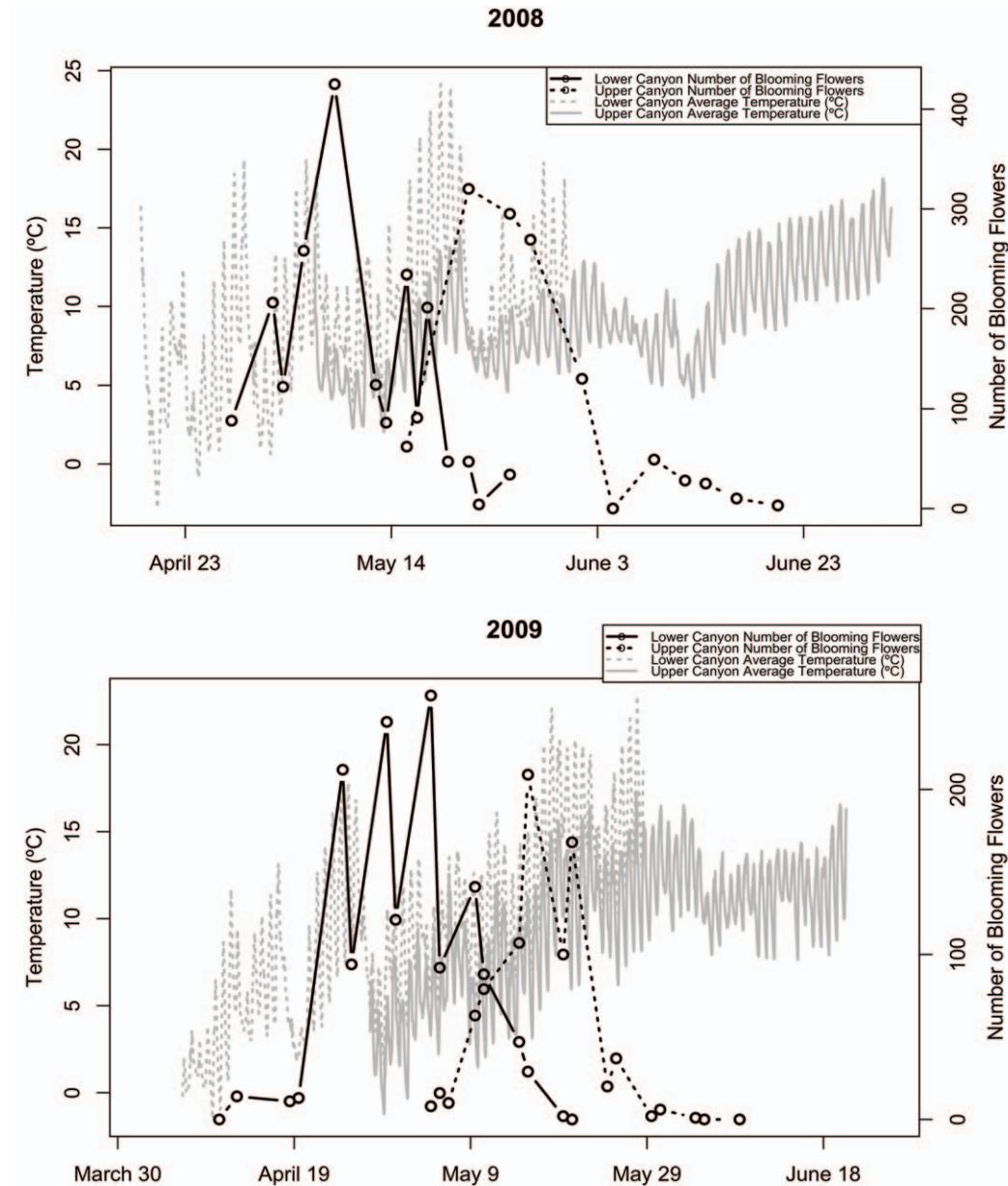
Fig. 3. *Primula cusickiana* var. *maguirei* phenology and average air temperature at different Logan Canyon, Utah, locations in 2008 and 2009. Average temperatures (light gray solid and dashed lines) were calculated from 7 HOBO monitors at the lower canyon and 3 HOBO monitors at the upper canyon, and scaled to the left y-axis. Temperatures were averaged across monitors within each canyon location and plotted by 30-minute intervals. The numbers of flowers present at lower canyon populations (solid black line) and upper canyon populations (dashed black line) are scaled to the right y-axis. Scales of y-axes differ between graphs.

not morph-specific (Fig. 4). We also observed herbivory at some of our monitoring sites. Snails of the *Oreohelix* genus were directly observed chewing on the fleshy leaves of seedling and mature *P. cusickiana* var. *maguirei*. Other her-bivory damage was likely caused by small rodents, such as the bushy-tailed woodrat (*Neotoma cinerea*, Muridae) as reported by Bjerregaard and Wolf (2008). In 2009, we observed herbivory at about 21% of the monitoring sites, with
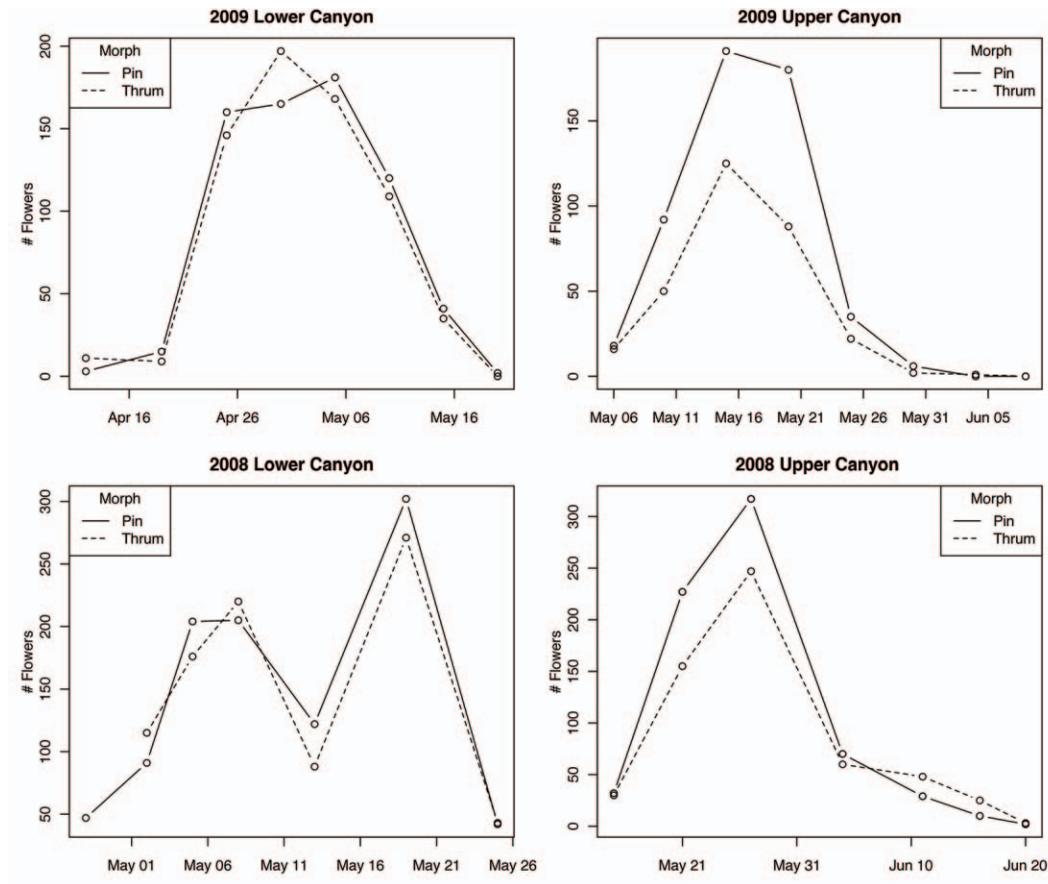
Fig. 4. Phenology of *Primula cusickiana* var. *maguirei* by location, year, and morphology.

damage ranging from the removal of single flowers to the removal of all aboveground plant structures. In 2009, we observed more herbivory damage at lower canyon monitoring sites (24.5%) than at upper canyon monitoring sites (18.5%). Our 2008 data set did not consistently record herbivory damage and, therefore, was not considered.

Temperature and Insect Visitors

The phenology and development of established *P. cusickiana* var. *maguirei* plants is likely tied to microsite temperatures, as has been shown with other *Primula* species (Karlsson 2002). We observed that the lower canyon was warmer (in average and maximum temperatures) than the upper canyon, and plants there bloomed much earlier than upper canyon populations (Fig. 3). Lower canyon plants also experienced larger temperature fluctuations (maximum °C –

minimum °C) relative to upper canyon plants. Lower canyon temperature fluctuations were 27 °C in 2008 and 34 °C in 2009. Upper canyon plants experienced temperature fluctuations half that range: 14 °C and 18 °C in 2008 and 2009, respectively (Table 1). Figure 3 represents the mean temperatures every 30 minutes across sites (HOBO® data loggers, Onset Computer Corporation, www.onsetcomp.com) within each of the 2 locations. Although there was variation among these HOBO monitors, the variation was considerably less than the daily temperature fluctuation for any one monitor.

Among the visitors to *P. cusickiana* var. *maguirei* flowers, we captured 8 insect species (Table 2) and made 67 visual observations (Table 3). Air temperature at insect collection times ranged from 6.6 °C to 15.4 °C, with a mean of 11.7 °C. In 2008, we observed white-lined sphinx moths

TABLE 1. Temperature and relative humidity during *Primula cusickiana* var. *maguirei* flowering periods. Averages were calculated across sites from multiple monitors. Temperature minima and maxima were from individual monitors placed within populations.

	2008		2009	
	Lower Canyon	Upper Canyon	Lower Canyon	Upper Canyon
Average temperature (°C)	10.2	8.8	9.4	10.0
Minimum temperature (°C)	–0.2	3.0	–0.2	0.6
Maximum temperature (°C)	26.9	16.8	33.7	18.8
Range (maximum–minimum)	27.1	13.9	34.0	18.2
Average relative humidity	65.5	82.3	64.9	76.0
Minimum relative humidity	19.9	33.0	14.9	27.3

TABLE 2. Insects captured visiting *Primula cusickiana* var. *maguirei*, and collection information. All specimens are deposited in the U.S. National Pollinating Insects Collection at Utah State University, Salt Lake City, Utah.

Captured visitors	Location	Sex or type	Date, time collected	Average temp. at collection (°C)	Accession number
Osmia austromaritima	FPW	Male	19 Apr 2009, 14:40	11.2	BBSL771069
Anthophora pacifica	FPW	Male	19 Apr 2009, 14:24	11.2	BBSL771070
Dialictus sp.	FPW	—	19 Apr 2009, 14:45	11.4	BBSL771071
Anthophora pacifica	SPW	Male	21 Apr 2009, 11:56	12.8	BBSL771072
Anthophora pacifica	SPW	Male	21 Apr 2009, 12:02	12.8	BBSL771073
Anthophora pacifica	SPW	Male	21 Apr 2009, 13:35	14.2	BBSL771074
Anthophora pacifica	SPW	Female	22 Apr 2009, 09:40	11.1	BBSL771075
Anthophora pacifica	SPW	Female	22 Apr 2009, 12:24	15.4	BBSL771077
Bombus centralis	SPW	Worker	22 Apr 2009, 12:05	14.9	BBSL771076
Anthophora pacifica	SPW	Female	27 Apr 2009, 14:45	8.9	BBSL771081
Anthophora pacifica	SPW	Male	27 Apr 2009, 11:20	6.6	BBSL771079
Anthophora pacifica	SPW	Male	27 Apr 2009, 11:33	6.6	BBSL771080
Bombyliidae (Family)	SPW	—	27 Apr 2009, 10:32	6.9	BBSL771078
Habropoda cineraria	BITS	Female	11 May 2009, 14:25	11.8	BBSL771082
Anthophora pacifica	BITS	Female	17 May 2009, 11:24	11.1	BBSL771085
Habropoda cineraria	BITS	Female	18 May 2009, 15:13	14.8	BBSL771088
Bombus bifarius	BITS	Worker	18 May 2009, 14:52	14.8	BBSL771087
Osmia lignaria propinqua	BITS	Male	18 May 2009, 14:46	14.8	BBSL771086

[a]FPW = First Practice Wall, SPW = Second Practice Wall, and BITS = Band in the Sky.

(*Hyles lineata*, Sphingidae) visiting upper canyon populations at dusk but did not see them at all in 2009. We twice observed broad-tailed hummingbirds (*Selasphorus platycercus*, Trochilidae) visiting *P. cusickiana* var. *maguirei* (11 and 19 May 2008). Large *Anthophora pacifica* bees (both sexes) were the most abundant visitor that we captured.

DISCUSSION

Distyly

About 91% of all *Primula* species are distylous, which usually promotes outcrossing (Richards 2002). However, distyly reduces the number of potential plants with which an individual may successfully mate (Barrett 2002a). This reduction of potential mates could be a substantial reproductive cost for a rare, patchily distributed species, and reproduction may de-pend on the neighbor density and morphology, as observed in *P. sieboldii* (Ishihama et al. 2006). We measured 4 floral characters of *P. cusickiana* var. *maguirei*. Sepal lengths did not differ between pin and thrum morphologies, meaning this character cannot be used as a prebloom proxy for flower morph. The corolla tube depths of each morph were not entirely dissimilar from one another, but averages were statistically different. It is unclear what the role of longer corolla tubes in thrum morphs may be. Perhaps there are maternal advantages to entice visiting pollinators to reach nectaries at the base of deeper flowers and, in doing so, make better stigmatic contact (Nishihiro et al. 2000). There is probably no such maternal selective pressure in pin morphs because any pollinators near the corolla tube opening are more likely to contact the stigma than are pollinators in thrums. It seems, however, that pin anthers would similarly

TABLE 3. Observed number of visitors to *Primula cusickiana* var. *maguirei* by location for combined 2008 and 2009 field efforts.

Observed visitors	Location	Observations
Andrena sp.	FPW	1
Anthophora sp.[a]	FPW	1
Andrena sp.	GHW	1
Anthophora sp.[a]	GHW	4
Bombus centralis	GHW	1
Bombus spp.	GHW	7
Bombyllidae (Family)	GHW	2
Anthophora sp.	SPW	11
Bombus spp.	SPW	5
Lepidoptera	SPW	2
Anthophora sp.[a]	SS	1
Bombus nevadensis	SS	1
Bombus spp.	SS	1
Hyles lineata	SS	3
Selasphorus platycercus	SS	2
Anthophora sp.[a]	BITS	14
Bombus spp.	BITS	8
Osmia spp.	BITS	2

[a]*Anthophora* sp. and *Habropoda* sp. were not distinguishable in visitation observations.
[b]FPW = First Practice Wall, GHW = Greenhouse Wall, SPW = Second Practice Wall, SS = Seed Source, and BITS = Band in the Sky.

benefit from deeper corolla tubes, but selective pressure may be stronger toward female fitness, as pollen is relatively abundant and easily transferred. The 6 other congeners in section *Parryi* also display clear distyly (Kelso et al. 2009). Additionally, we observed no homostyles in our samples or during field observations.

Dichogamy

Contrary to expectations, our tests suggest that stigmas of *P. cusickiana* var. *maguirei* may become receptive 1–2 days before anthers dehisce within the same flower. Evidence of dichogamy in *Primula* has not been demonstrated as far as we know and could be a novel finding here. Dichogamy can minimize self-fertilization (Barrett 2002a) and help to avoid sexual interference through reduced gamete wastage and fitness reduction (Barrett 2002b). However, earlier stigma maturation is probably not very influential for *P. cusickiana* var. *maguirei*, as anthers mature only a short time after their stigmas and 83% of our sampled flowers did not show dichogamous tendencies. Additionally, our tests suggest that stigmas of old withering flowers might remain receptive. Having receptive stigmas throughout the bloom could give *P. cusickiana* var. *maguirei* more opportunity to outcross, assuming a pollen selection or self-incompatibility mechanism is present (Richards 1993). However, stigmas of late-stage flowers

that are dusted with pollen could give a false positive result; occasionally pollen can react with H_2O_2 and give results that suggest stigma receptivity (Kearns and Inouye 1993). Further testing of this trait is required to confirm or negate the results of our experiment. Because distylous *Primula* already have spatial separation of their reproductive structures (herkogamy) and usually have self-incompatibility systems, evolutionary forces selecting for dichogamy are not expected to be strong in *Primula* (Barrett 2002b).

Phenology

Although 12 km separates upper and lower canyon populations, our study confirms a disparate blooming period (Bjerregaard and Wolf 2008). The lower canyon population is in a wide section of Logan Canyon that receives long periods of direct sunlight each day during early spring. The upper canyon population, however, remains shaded for most of each day, and is located in a steep and narrow stretch of the canyon, about 100 m higher than the lower canyon population. Due to elevation, landform, and sun exposure differences, upper canyon snowpack lasts longer than lower canyon snowpack. Although both populations face north, we suspect that landscape features explain the temperature differences and therefore bloom-timing differences observed in *P. cusickiana* var. *maguirei*.

Historical impacts from humans do not seem to explain the current distribution of disparate *P. cusickiana* var. *maguirei* populations in Logan Canyon. Humans have altered the landscape of Logan Canyon through widespread grazing and timber harvesting in the late 19th and early 20th centuries (English 1971, Speth and Peterson 1980, Gore 1998). However, 2 previous studies of *P. cusickiana* var. *maguirei* (Wolf and Sinclair 1997, Bjerregaard and Wolf 2008) reported strong genetic differentiation between upper and lower canyon populations, suggesting isolation and subsequent divergence long before humans began affecting Logan Canyon. Genetic differentiation in *P. cusickiana* var. *maguirei* may be influenced by physical and biotic location characteristics through differing selection pressures. Furthermore, genetic differences will likely be maintained if phenology continues to reduce the opportunity for gene flow between upper and lower canyon populations (Fig. 3). Future studies to understand the complex interactions of these factors might benefit from a

direct measure of gene flow among plants (Ishihama et al. 2005).

Our observed number of *P. cusickiana* var. *maguirei* pin and thrum flowers at monitoring sites generally followed the overall pattern of bloom cycles (Fig. 4). Although a previous study found a 1:1 ratio of pin and thrum plants (Bjerregaard and Wolf 2008), there still may be a difference in the number of pin and thrum flowers blooming at a given time. The slight differences in pin and thrum flowers blooming concurrently makes outcrossing constraints possible for *P. cusickiana* var. *maguirei*. Outcrossing success in patchy subpopulations with few individuals would likely be negatively affected by morph-specific flower pulses. However, as outcrossing rates for both morphologies were not diminished for naturally pollinated plants (Davidson 2010), we conclude that the morphology ratio is approximately equal, as is expected for most distylous *Primula* species (Richards 1993).

The *P. cusickiana* var. *maguirei* phenology in the 2008 and 2009 field season seemed to be adequately synchronized with pollinator occurrence. *Primula cusickiana* var. *maguirei* was an early bloomer in the Bear River Range, and was visited by early emerging bees, especially *Anthophora* species. Although the *P. cusickiana* var. *maguirei* blooms experienced freezes, days were often warm enough for biotic pollen vectors to visit the plant, and polylectic generalist bees seemed to be the main pollinators of Maguire primrose. Generalist pollinators rely on a wide diversity and abundance of blooming plants, making generalist pollinators a relatively stable vector for this threatened primrose (Gibson et al. 2006, Carvalheiro et al. 2008, Ebeling et al. 2008), barring any drastic flower timing shifts (Miller-Rushing and Inouye 2009).

Temperature

McKee and Richards (1998) grew 5 *Primula* species under controlled greenhouse conditions and, as expected, found that early blooming species (*Primula vulgaris*, *Primula veris*, and *Primula scotica*) were able to tolerate near-freezing temperatures much better than late-blooming species (*Primula frondosa* and *Primula farinosa*). It is likely that *P. cusickiana* var. *maguirei* is similarly adapted to low temperatures but may still be affected by early spring conditions. Unusually cool spring temperatures may prevent or discourage insect visitations

(Lundberg 1980), whereas unusually warm conditions may provide more consistent insect visitors but result in changed selfing rates. McKee and Richards (1998) showed that early blooming *Primula* species exposed to warmer temperatures during blooming periods resulted in increased selfing and illegitimate xenogamy rates via breakdown in the self-incompatibility system. However, it is unknown whether plant development, bud break, and flowering occur at a fixed date or whether they are temperature-dependent. Therefore, future climate change may alter the pollination ecology and reproduction system in an unpredictable way.

Visitors

Our pollinator observations and collections were intended to give an important first glance at the diversity of visitors on *P. cusickiana* var. *maguirei*. Identifying even a small number of visitors to *P. cusickiana* var. *maguirei* is an important first step in understanding its relationship with pollinators. The observed visitors included a limited diversity of animals, all of which are floral generalists. Future quantitative studies focusing on visitation rates and pollen transfer success would provide more important information about this outcrossing species.

Conclusions

Basic natural history information on a species can provide important details for land managers, and an understanding of those details is critical to conservation and management efforts and, ultimately, to protection of rare organisms. Although no Maguire primrose management activities are currently underway, the mandated recovery plan calls for mapping and reintroduction of this threatened plant, despite a fundamental gap in the understanding of its natural history. Regrettably, our understanding of the natural history of many other threatened and endangered plants in the Intermountain Region of western North America is also lacking. *Primula cusickiana* var. *maguirei* has a role that appears to be dependent on the early blooming local flora for pollinator support and also has a response to temperature that warrants further study. Other aspects of the *P. cusickiana* var. *maguirei* life cycle—particularly its breeding system, germination conditions, seedling establishment, and longevity—are also important to understanding its population dynamics and, ultimately, its viability.

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