NATURAL THREATS TO THE RARE ARCTIC PRIMROSE, *PRIMULA TSCHUKTSCHORUM*: GOOSE GRAZING AND REPRODUCTIVE INTERFERENCE WITH ITS SISTER SPECIES

Primula tschuktschorum – Seward Peninsula, Alaska

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ABSTRACT

We studied the impact of goose herbivory on the fecundity of two arctic primroses and the potential for reproductive interference between these two primroses in northwestern Alaska. The two species are sister taxa; *Primula eximia* is a common species from eastern Siberia throughout Alaska and *P. tschuktschorum* is a rare species known only from the Bering Strait region. Herbivory by geese was identified as a potential threat to the persistence of populations of the rare species in an earlier report. At one *P. tschuktschorum* site at Kuzitrin Lake the population appears to have declined dramatically in ten years to a few thousand individuals, with the rare species largely be replaced by its common congener. Non-breeding, molting Canada geese were observed grazing heavily on both species at the lake margin. Populations of *P. tschuktschorum* and *P. eximia*, to a lesser extent, are present away from the lake, which do not face grazing pressures. Two treatments were used at the lake edge: plots open to grazing and those where grazing was excluded. We found that goose grazing reduces the probability of a reproductive plant producing offspring by over 50% in both species. Further, grazing appears to influence the population structure. The number of seedlings per plot was substantially lower for plots that were exposed to grazing for both species, but this was particularly dramatic for *P. tschuktschorum*. These results indicate that natural ecological interactions are severe enough to threaten population persistence of the rare species. The two species differ dramatically in their reproductive ecologies and these differences appear to put the rare species at a competitive disadvantage, especially in the context of grazing. Last, we revealed evidence of hybridization between the two species.

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INTRODUCTION

The causes and patterns of rarity are particularly poorly studied and understood in the Arctic. In most cases rarity is not due to anthropogenic alterations such as outright habitat loss or competition by invasive species, instead natural factors are likely the cause, such as extreme habitat specialization of uncommon and unusual substrates, neospeciation, stochastic processes, and negative ecological interactions with other native species. Studying rare and common species in the Arctic gives us a unique insight into natural forms of rarity, which are largely obscured by more extreme anthropogenic effects at lower latitudes (see Carlson et al. 2006).

In particular, seed predation and herbivory can be locally intense at high latitudes during the short growing season. Herbivory may be partially responsible for one Arctic primrose's rarity. The narrow endemic chukchi primrose, *Primula tschuktschorum* in northwestern Alaska (Fig. 1.) suffers from extensive grazing that may threaten population persistence (Kelso 1995). At one site
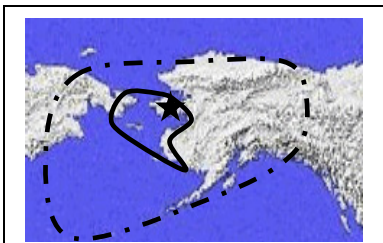

Figure 1. Global distribution of *Primula tschuktschorum* (solid line) and *P. eximia* (dashed line). The black star represents the location of the study site.

the ground was highly disturbed by geese and very few plants were able to mature fruits as most scapes were clipped off several centimeters above the ground (Kelso 1992). However, Kelso (1995) also suggests that moderate levels of grazing may benefit the rare plant by reducing competition from other plant species, but that continual and intense grazing might begin to negatively impact the growth and recruitment of new individuals. The genus *Primula* in particular is known to be a poor competitor and tends to be restricted to low competition habitats (Bullard et al. 1987, Kéry et al. 2000, Kelso pers. comm.).

Grazing effects on other species –

For a number of other plant species, the direct and indirect effects of herbivory have been shown to impact population dynamics. The removal of reproductive structures is substantially more damaging to *Primula veris* population growth than herbivory to vegetative structures (García & Ehrlén 2002). The intensity of sheep grazing and year-to-year viability in herbivory was a critical determinant of population growth of *Anthyllis vulneraria* (Bastrenta et al. 1995). In *Haplopappus radiatus*, seed production, seedling recruitment, and other demographic functions are affected by cattle grazing, herbivory by grasshoppers, seed predation by insect larvae, as well as seasonal precipitation (Kaye 2001). In that long-term study, cattle grazing negatively affected population growth rate (λ) in some years. In a population matrix analysis of *Lathyrus vernus*, grazing reduced the proportion of larger, reproductive individuals and the effects of herbivory resulted in decreased probability of individuals increasing in their size from one year to the next (Ehrlén 1995). Among several populations of the rare *Astragalus tyghensis* tracked for 10 years and modeled with a stochastic approach, low growth rate and high extinction probability were documented in populations exposed to grazing by cattle or deer, but protected sites had high growth rates and low extinction risks (Carlson and Kaye 2001). Herbivory was shown to be more

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important than pollen limitation and it affected numerous vital rates, causing population declines in *Trillium grandiflorum* (Knight 2004). Grazing can also be an important factor reducing interspecific competition, as the genus *Primula* is generally quite sensitive to competition (e.g., Bullard et al. 1987, Kéry et al. 2000,). The rare *P. scotica* is limited by a reliance on coastal sites with few competitors, and has been shown to respond positively to grazing when fertilizer inputs through feces are minimal (Bullard et al. 1987). Whale (1984) observed negative impacts on three species of *Primula* when growing in thick stands of the grass *Brachypodium sylvaticum*, and observed significant negative effects of grazing on seed production.

Grazing by geese in the Arctic –

The effect of grazing by geese on arctic and subarctic plant communities has had some attention (see Hik et al. 1991, Gathier et al. 1995, Person et al. 1998, Mulder and Ruess 2001, Zacheis et al. 2001). However, overall patterns are not obvious, results appear to be very species and case specific, and last, these studies have been largely ignored actual demographic consequences to individual plant species.

Field studies have indicated that the responses of plant species are highly species specific, with the biomass of some species being reduced for some and increasing for others in the presence of grazing (Zacheis et al. 2001). In arctic graminoids, grazing by geese significantly reduced aboveground biomass and the geese consumed as much as 113% of the net aboveground primary production (Gathier et al. 1995). While, Person et al. (1998) found that excluding brant geese on the Yukon-Kuskokwim delta, Alaska, did not affect growth or primary productivity of *Carex subspathacea*.

The variable responses of arctic and subarctic plants to goose grazing appears to be largely the result of an interaction of negative and positive effects. The removal of growing biomass by grazing is clearly a negative impact on plant growth and viability (although temporary, compensatory growth is common). This negative effect appears to often be ameliorated by increased nutrient addition through fecal input and reduced plant-plant competition. Additionally, unexpected positive feedbacks are possible under high grazing pressure that result in serious degradation of plant communities. Specifically, experimental treatments mimicking the effects of grazing and fecal input on the arctic grass, *Puccinellia phryganodes*, showed that the presence of geese results in a net neutral outcome (Hik et al. 1991). The grazing had a detrimental effect on shoot growth and net primary production, while the addition of nutrients through feces ameliorated the effects of clipping (Hik et al. 1991). However, Beaulieu et al. (1996) found that while goose grazing, reduced overall plant height, above-ground net primary productivity was not negatively impacted. Furthermore, there was an absence of an effect of feces on plant growth in Beaulieu et al's. (1996) study.

In sum, current research on plant responses to goose grazing in the arctic and subarctic indicates very case specific results and offers little predictive power for species not examined. Under some intensities of grazing, particular species are benefited by reduced competition and increased nutrient input, while other species suffer. Thus, predicting the particular outcome is

questionable of *P. tschuktschorum* to the intensity of grazing from the published literature. Additionally, there is an increased risk to rare arctic species such as *P. tschuktschorum* to substantial increases in North American goose populations.

The increase in Canada goose populations in the U.S. has elevated many problems ranging from aircraft and drinking water safety issues to over-fertilization of city park lawns. The concerns have caused the U.S. Fish and Wildlife Service to adopt a nation-wide strategy to reduce Canada goose populations (Tollefson, 1999). Increases in Snow and Ross Geese populations are clearly impacting their arctic breeding habitat. In a small area of the Canadian high arctic, the snow goose colony was estimated at 17,000 in 1965 and by 1996 the population had jumped to more than 650,000 nesting geese. The nesting geese cause serious destruction of the vegetation and the Canadian Wildlife Service has been able to confirm the conversion of plant communities to exposed peat and mineral soil; in some cases, over a 50% conversion of tundra plant communities to exposed peat has occurred (see www.arctic.uoguelph.ca/cpl/arcticnews/articles/Geese/Geese.htm).
The continued increase in nesting goose populations in the arctic is clearly a concern for overall ecosystem health, in addition to particular species of conservation concern.

Comparative Reproductive Ecologies –

The genus *Primula* is well known for its high proportion of distylous species. Distyly is a reproductive system of two morphological types that have reciprocal positions of anthers and stigmas. A diallelic incompatibility system is generally present that allows reproduction only between one of two genotypes. This dimorphic reproductive system, where populations are composed of two mating types that are highly intramorph and self incompatible, typically ensures that on average, an individual may mate successfully with only half the other individuals in a population.

Distyly and the Reproductive Assurance Model –

Successful distyly depends on reliable pollination; reproductive failures through climatic or anthropogenic perturbations that impact requisite pollinator numbers or diversity should give self-fertile homostyles (recombinant distylous forms that produce anthers and stigmas at the same height and are self-fertile) an advantage over heterostyles with diminishing seed production (Charlesworth & Charlesworth 1979, Piper et al. 1984). Fertility assurance can allow homostyles to become established, perhaps to outcompete their less fecund progenitors or to spread into new territory when colonization opportunity exists, a scenario present in the Bering Strait region at various times during the last glaciation (Elias et al. 2001, Kelso unpublished manuscript). Matthews (1974) documented loss of insect taxa since the late Tertiary and other studies (Short et al. 1992, Elias 2000) show migrations and range shifts during the late glacial and postglacial periods. If pollinator disruptions led to lessened fertility for distyles, pollinator-independent homostyles with ecological opportunity in newly open habitats would have had an advantage for range expansion with ongoing climatic amelioration in the Holocene. Examples of the distylous

Primula tschuktschorum and the homostylous *P. eximia*, its sister taxa in sect. Crystallophlomis (Primulaceae) (Mast et al. 2001) illustrate the reproductive assurance model of homostyle success (Kelso, pers. comm.).

      Primula tschuktschorum is a rare species of the Bering Strait Region of northwestern Alaska and northeastern Asia (Fig. 1; Kelso 1987) with small populations, few flowers per plant, and low seed set. It is listed as globally rare (G3) by the Alaska Natural Heritage Program, University of Alaska Anchorage (see http://aknhp.uaa.alaska.edu/ Botany_tracking_page.htm).

      In comparison, homostylous *P. eximia* is relatively widespread in western Alaska and northeastern Asia (Fig. 1), mountains of coastal southeastern Alaska, and into the Yukon, covering a region also only recently ice-free (Manley & Kaufman 2002). Populations of *P. eximia* are typically large and plants are robust, floriferous and abundant seed set, well marked genetically and morphologically, it appears to have exploited opportunities in open terrain and is perhaps now locally outcompeting its presumptive progenitor (M. Carlson, T. Kaye pers. obs.).

Objectives –

      We conducted a study that 1) identified the impacts of grazing on fecundity and population structure of both the rare *P. tschuktschorum* and the common *P. eximia*, 2) gain insight in the natural biological status, i.e., population growth or decline, of *P. tschuktschorum*, 3) understand the reproductive ecologies of these two species and how they may interact with grazing pressures.

METHODS

HERBIVORY

We conducted our research at Kuzitrin Lake
(65º23'N, 163º13'W) at the northern edge of the Bendeleben
Mountains on the Seward Peninsula, Alaska (Figs. 1., 2., &
3.). We first visited the site 15 to 20 days after ice-out on 25
June 2004 for six days to erect exclosures and conduct
hand-pollinations. The site was revisited from 26-31 July to
collect data on the treatments and remove the exclosures.

Upon arrival at Kuzitrin Lake, we surveyed the entire
lake margin where populations of both *P. tschuktschorum*
and *P. eximia* had been identified (Kelso 1992, 1995). We
mapped the distribution and noted the approximate
population sizes of all patches of both species (Fig. 3). The
surveys revealed that *P. tschuktschorum* was very

Figure 2. Kuzitrin Lake, Seward Peninsula. A population of *P. tschuktschorum* is in the frost boil in the foreground.

uncommon along the eastern margin of the lake, where many thousands were observed in 1995
(Kelso, 1995). We detected less than 500 *P. tschuktschorum* individuals in this area that now
had well over 10,000 *P. eximia* plants. Population sizes of *P. eximia* were not that robust in 1995,
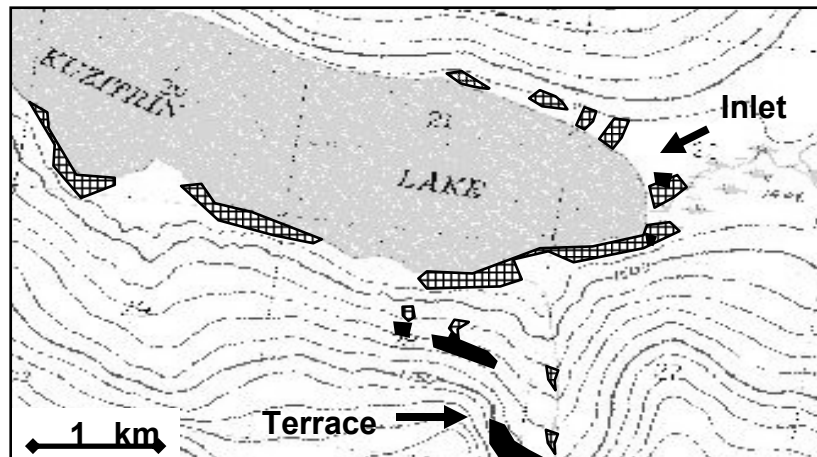although no data were taken (Kelso pers. comm.).

Figure 3. Population distribution of *P. tschuktschorum* (black polygons) and *P. eximia* (cross hatching) on the eastern end
of Kuzitrin Lake (65º23'N, 163º13'W), Seward Peninsula, Alaska. Arrows indicate the location of established monitoring
plots.

The habitat of the region is composed of gelifluction terraces, dominated by *Carex* spp.
and low *Salix* spp. that transition into largely open, saturated mud boils and coarse sand at the
lake margin (Figs. 2., 5., & 6.). Both species of *Primula* co-occur along the lake margin just below
the *Dodecatheon*-zone and along the north-facing slope of Mt. Boyan in wet sedge habitats.

Molting, non-breeding Canada geese were observed upon our arrival in late June on the lake and grazing along the lake margin.

Monitoring plots –

We were unable to locate enough individuals in June of *P. tschuktschorum* that were in the area subject to grazing to warrant the construction of exclosures. We therefore established 40 monitoring plots to obtain demographic data on *Primula eximia* along a 100 m section of the lake margin. The plots were randomly located and assigned one of two treatments, grazing excluded or open to grazing. If an assigned random location did not possess any plants another location was assigned. The monitoring plots along the lake were erected in a portion of the population that had not yet been visited by geese.

Figure 4. Monitoring plots, exclosures and plots open to grazing.

At higher elevations, 2 km from the lake we established 20 monitoring plots of *P. tschuktschorum*. When we returned in late July, we established 20 additional plots of *P. tschuktschorum* near the lake inlet that had been subjected to intense herbivory. No exclosures were constructed around the *P. tschuktschorum* plots but the high elevation (terrace site) was not grazed and the inlet site was grazed.

The plots were 10 cm X 50 cm and contained approximately 20 plants per plot on average, with some plots of over 100 plants. The exclosures were constructed of wire fencing 0.5 m tall and 1.0 x 0.7 m (Fig. 4.). The exlosures were larger than the plots to avoid grazed edge effects. The plots were marked with large nails and tacked flagging. All exclosures were removed at the end of July when the plants had senesced and the geese were gone.

Data collection –

All *Primula* plants were mapped and assigned an individual number and data was collected on the number and size of basal leaves, number of flowers, and number of fruits. Mapping and numbering plants in this will allow us to track individual plants through time and develop the data necessary for constructing models for grazed vs. protected populations in the future.
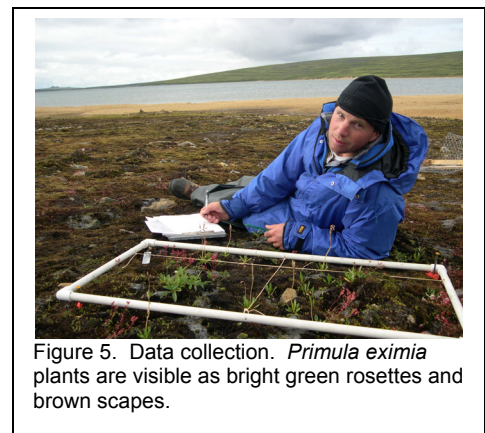

Figure 5. Data collection. *Primula eximia* plants are visible as bright green rosettes and brown scapes.

To determine to what extent *P. tschuktschorum* was morphologically distylous and the potential for reproductive interference due to similar floral morphologies we measured ten characters from separate, randomly selected individuals. Measurements were made using digital calipers to 0.00 mm under 10 X magnification from carefully dissected pressed voucher specimens. We measured total flower number (buds + flowers + fruits), leaf length and width, corolla diameter, aperture width, corolla tube length, calyx length, stigma position, and proximal and distal positions of the anthers.

Ovule and pollen counts were made from dissected buds under 20 X. The buds were collected from one flower per individual and preserved in alcohol in the field. Numbers and proportions of ovules and pollen were used to determine potential maximum female and male fitness and relative degree of outcrossing.

Figure 6. Hand-pollinations of *Primula eximia*.

Assessment of self, intra- and intermorph compatibility –

To determine the nature of self, intra-, and intermorph compatibilities in *P. tschuktschorum* we emasculated in bud and subsequently pollinated approximately 15 flowers each for six treatments. The treatments were short-style self, long-style self, short-style X short-style, long-style X long-style, short-style♂ X long-style♀, and long-style♂ X short-style♀.

For *P. eximia* self compatibility and autonomous seed set was determined by exposing three receptive flowers to one of three treatments: unmanipulated, self-pollinated, and cross-pollinated.   Self and cross-pollinated flowers were emasculated in bud in late June and pollinated 24 to 36 hours following emasculation (intact buds the size we emasculated opened and began dehiscing pollen in this time frame). Self-pollination was conducted by within plant (geitonogamous) crosses. Plants were caged with window screen material around wire frames to prevent insect visitation.

The level of pollen limitation in both species was determined by exposing flowers of a single plant to an unmanipulated, open pollination treatment and to pollen augmentation treatment (pollen was transferred to a stigma from another individual by using pollen from another individual to coat the ball-tip of an insect pin; see Miller et al., 1994). A second control group was used in *P. eximia* to test for the effect of the pollen transfer technique. This treatment involved touching the stigma with a clean ball-tip of an insect pin and leaving the flower open for pollination. All treatments were marked using colored nylon string tied around the pedicles. Fruits of all treatments were collected four weeks following pollination when capsules were becoming dry, but remained closed.

RESULTS

HERBIVORY

Observations of grazing –

We observed grazing by 200-250 molting Taverner's Canada geese (*Branta canadensis* ssp. *taverni*) on both *Primula* species and co-occurring *Carex ursina* at the lake margin in late

Figure 6. Molting Canada geese flocks on Kuzitrin Lake.

June 2004 (see Fig. 6.). The geese had been foraging for at least two weeks prior to our arrival, judging from the amount of vegetation disturbed and feces. Local residents have observed the geese arriving on the lakes on the Seward Peninsula as the ice melts, generally in early June. The geese continued to forage for the week we were there and were gone by late July/early August when we returned.

Flocks of geese would forage intensively within 40 m of the lake shore, clipping off a large percentage of reproductive scapes, but not removing *Primula* leaves (Fig. 7.). They fed on *Carex ursina* leaves, while other co-occurring species such as *Saxifraga nudicaulis* and *Salix pulchra* were not grazed. Trampling by geese in the saturated soils and feces inputs were extensive in lakeside *Primula* populations. Small numbers of free-ranging reindeer (*Rangifer tarandus*) or reindeer-caribou hybrids were observed in June and late July at the site. We did not observe them grazing on *Primula*.

Effects of grazing –

Grazing was clearly severe for both species near the lake margin.   The exclosures were erected a few weeks after the arrival of the geese, and the cages appeared to be effective in eliminating geese with 11.7% of individuals in exclosure treatments showed evidence of grazing, which occurred prior to the construction of the exclosures. While in the open treatment 42% of *P. eximia* plants were grazed.   For *P. tschuktschorum* individuals in open treatments next to the lake (Inlet site), 66% of were grazed, while none were grazed at the upper terrace site.

Figure 7. Grazed *P. eximia* plants.

The impacts of grazing on overall fecundity were significantly negative. Open plots typically produced 1.29 fruits while plots excluding grazing produced 2.50 fruits for *P. eximia*. No fruits were matured for *P. tschuktschorum* subjected to grazing, while plots at the higher elevation terrace site 1.33 fruits on average (Fig. 8.)
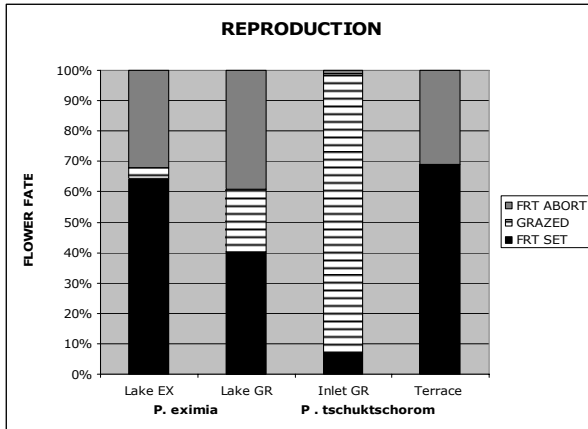
REPRODUCTION

Figure 8. Relative percentage of flowers maturing to fruits, grazed, and aborted for *P. eximia* with grazing excluded (Lake EX) and open to grazing (Lake GR) and for *P. tschuktschorum* at a site grazed (Inlet GR) and a site not grazed (Terrace). Percentage of grazed fruits was significantly different between grazed and grazing excluded treatments in *P. eximia* (p = 0.01; Mann-Whitney U test) and between the two *P. tschuktschorum* sites (p < 0.001; Mann-Whitney U test).

Grazing also appeared to influence the overall structure of populations in both species (Table 1., Fig. 9.). Seedlings were more common and made a significantly larger component of the population structure in *P. eximia* protected grazing and the inlet population of *P. tschuktschorum* exposed to grazing had very few seedlings relative to the terrace site.

Table 1. Mean number of individuals per plot and percent of reproductive plants grazed for *P. tschuktschorum* (PRTS) and *P. eximia* (PREX) in late July 2004. N = 20 for each treatment. At the Lake site exclosures were constructed in late June around 20 plots; the remaining 20 plots were subject to grazing throughout July. The *P. tschuktschorum* Inlet site is 300 m from the Lake site and was heavily grazed in 2004. The Terrace site is 2 km from the Lake site and was not grazed.

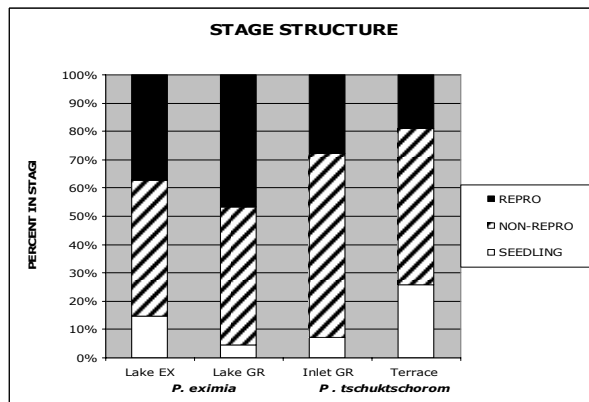| Species	Site	Treatment	Seedling	Non-reproductive	Reproductive	Total	% Grazed
PREX	Lake	exclosure	4.60	7.30	4.50	16.45	11.8
PREX	Lake	grazed	0.74	6.84	5.95	13.53	41.9
PRTS	Inlet	grazed	1.05	6.40	2.40	9.85	65.7
PRTS	Terrace	not grazed	7.30	14.35	3.10	24.75	0.0

STAGE STRUCTURE

Figure 9. Relative percentage of seedlings, non-reproductive, and reproductive plants for *P. eximia* with grazing excluded (Lake EX) and open to grazing (Lake GR) and for *P. tschuktschorum* at a site grazed (Inlet GR) and a site not grazed (Terrace).
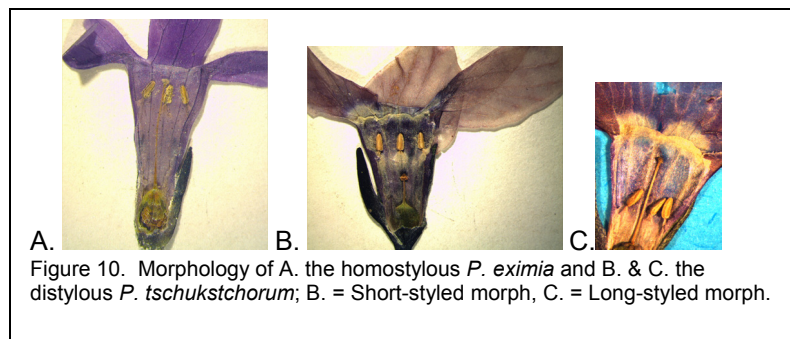
The two species were found to differ dramatically in their reproductive ecologies, as suggested by Kelso (1987). The breeding system of *P. tschuktschorum*, however, is a very loose form of distyly.

Assessment of homostyly and distyly –

Primula eximia was found to possess a classical homostylous breeding system, composed of a single, self-compatible morphological type (Table 2.). All morphological features were significantly different from both morphs of *P. tschuktschorum*. *Primula tschuktschorum* is clearly morphologically distylous; however, it has a very weak self- and intramorph incompatibility system (Table 2., Figs. 10. & 11.).

Table 2. Comparative morphology of *P. eximia* and the long- (LS) and short-styled morphs (SS) of *P. tschuktschorum*. Means are followed by (SE); N = 40, 29, and 18 for *P. eximia*, LS, and SS, respectively, except for pollen and ovule numbers (n = 10, 7, and 8). Homogeneous groups (Student-Newman-Keuls) are represented by shared letters, following 1-way ANOVA.

Character	*P. eximia*	LS *P. tschuktschorum*	SS *P. tschuktschorum*
Flower/plant	4.38 (0.27) a	2.79 (0.20) b	2.28 (0.18) b
Leaf ln	33.27 (1.46) a	71.71 (3.58) b	65.08 (3.53) b
Leaf wd	6.85 (0.41) a	5.65 (0.31) b	5.48 (0.30) b
Corolla wd	15.54 (0.30) a	21.21 (0.43) b	20.79 (0.56) b
Aperture wd	4.41 (0.10) a	5.18 (0.17) b	5.25 (0.11) b
Tube ln	9.69 (0.15) a	8.77 (0.15) b	9.35 (0.13) b
Calyx ln	5.59 (0.11) a	7.75 (0.16) b	6.95 (0.20) c
Stigma pos	8.39 (0.27) a	7.50 (0.13) b	4.92 (0.13) c
Anther pos a	8.89 (0.15) a	5.71 (0.10) b	8.10 (0.11) c
Anther pos b	7.87 (0.15) a	4.61 (0.15) b	6.90 (0.11) c
Pollen num	40,625 (5,459) a	85,393 (11,398) b	55,812 (5,582) a
Ovule num	123 (14.57) a	46 (4.90) b	53 (3.58) b

A.　　　　　　B.　　　　　　C.

Figure 10. Morphology of A. the homostylous *P. eximia* and B. & C. the distylous *P. tschukstchorum*; B. = Short-styled morph, C. = Long-styled morph.

Primula eximia is fully self-compatible, it produces twice the number of flowers, and twice the number of ovules as both the long-styled and short-styled morphs of *P. tschuktschorum* (Fig. 12). This translates to roughly 5 to 6 x the number of seeds produced per plant by the homostyle in both open pollinated and pollen augmentation experiments (Fig. 13).

The long-styled *P. tschuktschorum* shows some indication of pollen limitation with pollen augmentation increasing seed set by 2 x (Fig. 13). Preliminary data suggest that, *P. tschuktschorum* morphs may have a low level of intramorph or self compatibility. As illegitimate (self and within-morph) pollinations for both long- and short-styled morphs resulted in a few seeds (Fig. 11.). However, seedset of legitimate intermorph pollinations were double those of illegitimate crosses.
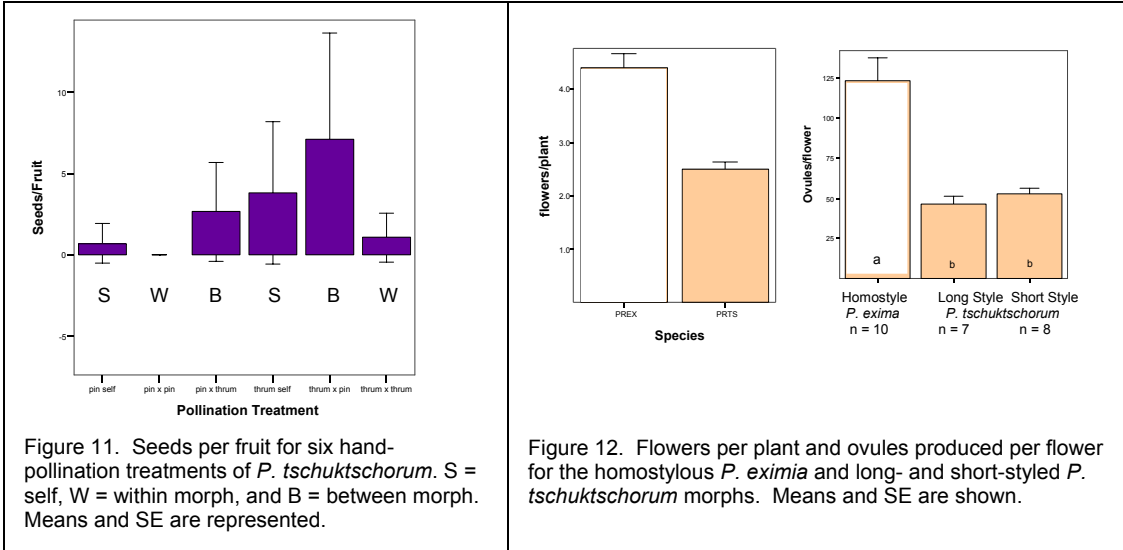

Figure 11. Seeds per fruit for six hand-pollination treatments of *P. tschuktschorum*. S = self, W = within morph, and B = between morph. Means and SE are represented.

Figure 12. Flowers per plant and ovules produced per flower for the homostylous *P. eximia* and long- and short-styled *P. tschuktschorum* morphs. Means and SE are shown.

Between species crosses were compatible, but only crosses from *P. tschuktschorum* short-styled (thrum) males to *P. eximia* females produced seeds (Fig. 14.). DNA evidence suggests that morphologically intermediate individuals along the lake margin are in fact hybrids (Whittall, unpublished data).
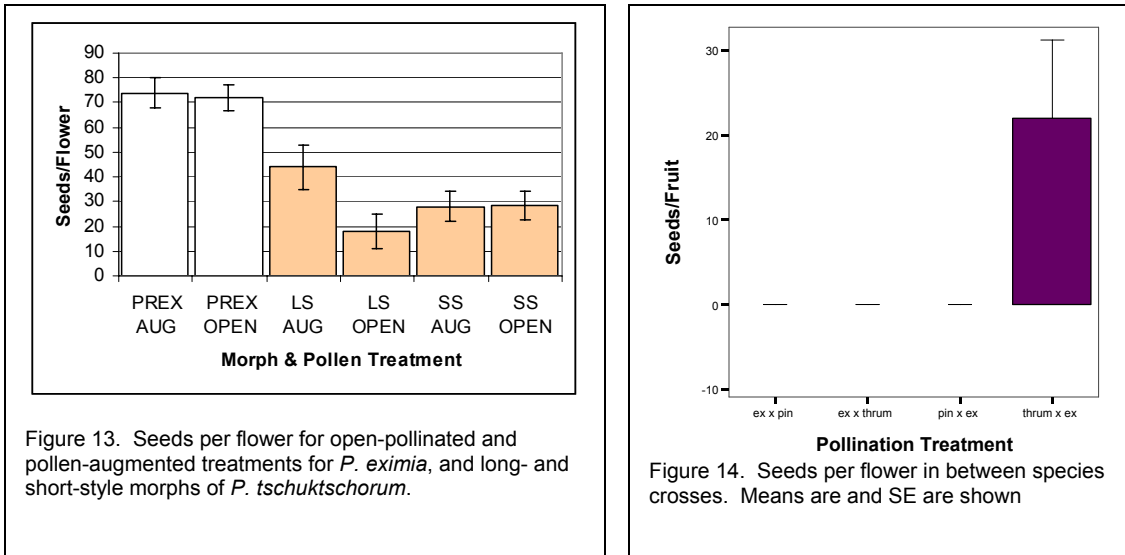

Figure 13. Seeds per flower for open-pollinated and pollen-augmented treatments for *P. eximia*, and long- and short-style morphs of *P. tschuktschorum*.

Figure 14. Seeds per flower in between species crosses. Means are and SE are shown

Moderately large flocks of molting, non-breeding Canada geese appear to be summer residents on Kuzitrin Lake in most years based on past reports (Kelso 1992, 1995) and observations of local residents. The geese selectively forage on above-ground portions of *Primula eximia* and *P. tschuktschorum*, and of sedges (primarily on *Carex ursina*, and *C. aquatilis*), intensively foraging within 40 m of the lake margin. Most of the other dominant plant species were not grazed. The geese's activity is very localized and intense, with some areas completely denuded and others untouched. In addition to the direct grazing impacts, the geese may influence the plant community due to trampling, removal of competing sedge biomass, and nutrient inputs through feces. The geese were actively foraging by early to mid June and were gone by late July.

Our results indicate that grazing by geese has a strong immediate impact on reproductive output of both the common and rare species of *Primula* at Kuzitrin Lake. The fecundity of plants exposed to grazing pressure was reduced by over 50% for both species, with nearly all the reproductive structures removed of the rare *P. tschuktschorum* at the lake margin.

Additionally, grazing by geese also affects the population structures of both species. Seedlings are very uncommon when populations are exposed to grazing. It is likely that the impact on juveniles is occurring by two mechanisms: seedlings are being directly removed by grazing (evidenced by the differences within a season in open vs. grazing excluded treatments of *P. eximia*) and also because few mature seeds are entering the seed bank. The upper *P. tschuktschorum* site matured significantly more fruits and produced over seven times the number of seedlings relative to the site subjected to grazing at the lake margin. It is probable that fruit set has historically been higher for the upper site since it is not suitable goose habitat, and that the higher seed production is directly reflected in a higher number of seedlings.

The severe fitness consequences and reduction of recruitment indicates that grazing is a serious threat to the population persistence of *P. tschuktschorum* as suggested by Kelso (1995). It is likely that the reduction of competition and nutrient additions through feces do not outweigh the drastic losses of reproductive structures and seedlings. The apparent precipitous decline of *P. tschuktschorum* over the last decade may be a direct result of goose herbivory, especially considering that *Primula* are generally not long-lived species (ca. 10 years). It is curious that populations of *P. eximia* did not decline as well, and may have increased in fact. Differences in the reproductive ecologies of the two primroses may provide the answer.

The *P. tschuktschorum* site of 500-1,000 individuals is surrounded by more extensive numbers of *P. eximia*. These observations suggest that there has been a dramatic replacement of the rare species by the common species. Dramatic declines have been observed in other species of *Primula*, associated with natural and anthropogenic perturbations (Endels et al. 2002, Brys et al. 2004). We were able to relocate large populations of *P. tschuktschorum* at higher elevations

as well as populations of the closely related *P. eximia*, outlined by Kelso (1995) that were free from grazing.
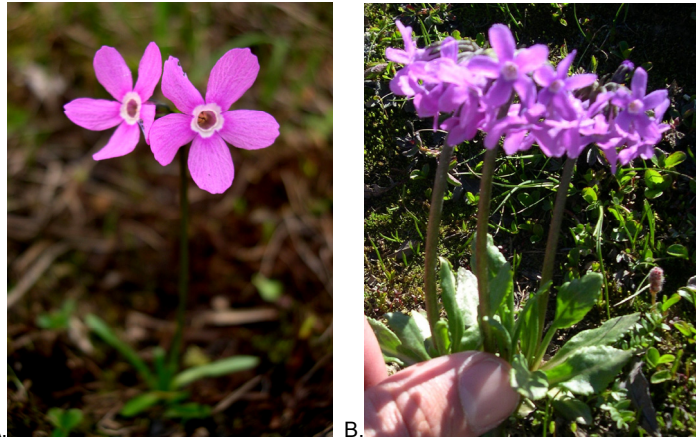

Figure 15. A. *Primula tschuktschorum* and B. *P. eximia*

REPRODUCTIVE ECOLOGY

Successful distyly depends upon sufficient population size, equal morph ratios, and adequate insect facilitation of pollen transfer. Disruptions from climatic or anthropogenic perturbations, or natural factors, such as herbivory may cause negative impacts. Under these condtions, homostyle morphs or homostylous sister taxa may prosper and utilize opportunities for territorial expansion, migration, or exploitation of novel habitats (Kelso unpublished manuscript).

The larger range and population sizes of *P. eximia* relative to *P. tschuktschorum* has been suggested to be evidence of the successful strategy of reproductive assurance in a habitat where pollinators are rare (Kelso 1987). Contemporary support for the reproductive assurance model comes from studies on *Primula sieboldii*, a distylous species suffering from extreme pollinator limitation as urbanization has reduced its chief pollinator, queen bumblebees. Studies show (summarized in Washitani et al. 2005) that the loss of a single important pollinator can cause reproductive distress but that under these conditions, fecundity of the self fertile homostyle morphs is several times greater, providing an atypical reproductive advantage. These results parallel those of Piper et al. (1986) for *P. vulgaris* and are in alignment with general conclusions about the detrimental effects of diminishing population sizes and habitat fragmentation on European Primulas (e.g., Kéry et al. 2000, Jacquemyn et al. 2002, van Rossum et al. 2002, Lienert & Fischer 2003, Brys et al. 2004). Conjoined factors produce negative reproductive impacts quickly while extended impacts may induce local extirpation or promote the establishment of mutant homostyles. Loss of pollination and reduced distyle population sizes, coupled with opportunities for migration and ecological expansion may be the most potent recipe for recombinant homostyle success: this combination increasingly exists today in high latitudes where ice retreat and climatic warming are prominent (see Kelso 1987).

We found *P. eximia* to be fully self-compatible and not pollen limited. It is able to produce 5 to 6 x the number of seeds per plant as *P. tschuktschorum*, putting it at a substantial competitive advantage. The long-style morph of *P. tschuktschorum* does produce significantly more pollen than *P. eximia*, but this is unlikely to translate into any competitive reproductive advantage in siring success for the rare species and stigmatic clogging of its common congener. *Primula tschuktschorum* only produces half the number of flowers per plant, so that the total export and receipt of pollen (male fitness) would not be greater than for the common species.

Interestingly, *P. tschuktschorum* has a low level of self- and intramorph incompatibility. Illegitimate (self and within-morph) pollinations for both long- and short-styled morphs resulted in seed production; however, seedset of legitimate intermorph pollinations were double those of illegimate crosses. This indicates a very leaky system that may be the result of selection for reproductive assurance in the face of low pollinator abundance and activity (bumblebee pollinators were uncommon on *P. tschuktchorum*, even in good weather in 2004).

Last, hybridization was revealed where the two species co-mingled at the lake margin. Pollination treatments show that compatibility is asymmetrical, with successful seed set possible only via pollen from the short-styled *P. tschuktschorum* to the stigma of *P. eximia*. This presence of hybrids indicates that these species are in fact very closely related and that pollinators do not distinguish between the species. The lack of pollinator discrimination increases the potential for negative reproductive interactions between the species and may partially explain the decline of *P. tschuktschorum*.

CONCLUSIONS

Our results indicate that natural ecological interactions of herbivory and reproductive interference are severe enough to threaten population persistence of the rare *P. tschuktschorum*. The distylous breeding system of *P. tschuktschorum* reduces levels of reproductive assurance relative to its common sister species, despite a somewhat "leaky" compatibility system. This appears to put the rare species at a competitive disadvantage. Populations of *P. tschuktschorum* insulated from herbivory and the presence of *P. eximia* are expected to be of less threat and thus greater conservation value. Long-term, life-table experiments are required to understand the importance of different forces on population growth rates.

Midnight - Kuzitrin Lake, Seward Peninsula, Alaska

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