Reproductive biology of island and mainland populations of *Primula mistassinica* (Primulaceae) on Lake Huron shorelines

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Abstract: To investigate the influence of insularity on plant reproductive biology at a local geographic scale, we examined aspects of reproduction in distylous *Primula mistassinica* Michx. (Primulaceae) on Lake Huron shorelines of the Bruce Peninsula and adjacent Tobermory Islands in Ontario, Canada. A total of 7 mainland and 13 nearshore island populations were compared. Controlled pollinations demonstrated that *P. mistassinica* possesses a dimorphic incompatibility system with intermorph crosses setting significantly more seeds than self or intramorph crosses. Floral morphology, population style-morph ratios, and seed fertility were compared in mainland and nearshore island populations to determine whether there was evidence for differences in reproductive traits between these areas. Style-morph ratios did not differ significantly from equilibrium expectations, and there were no consistent differences between island and mainland populations in floral morphology or fertility. Rather, the generalized pollination system of *P. mistassinica* and extensive historical opportunities for colonization appear to have mitigated insular effects so that proximate ecological factors are more relevant to the current reproductive biology of populations.

Key words: distyly, insularity, pollination, reproductive biology.

Résumé : Afin d'étudier l'influence de l'insularité sur la biologie reproductive des plantes à l'échelle géographique locale, les auteurs ont examiné des aspects de la reproduction chez le *Primula mistassinica* Michx. (Primulaceae) distyle, venant sur les rives du lac Huron bordant la péninsule de Bruce et sur les îles Tobermory adjacentes, en Ontario, au Canada. Ils ont comparé au total 7 populations continentales et 13 populations insulaires riveraines. La pollinisation contrôlée démontre que le *P. mistassinica* possède un système d'incompatibilité dimorphe, les croisements intermorphes donnant naissance à un nombre significativement plus élevé de graines que les autocroisements ou les croisement intramorphes. Ils ont comparé la morphologie florale, les rapports style-morphe des population et la fertilité des graines dans les populations continentales vs. les populations insulaires riveraines, afin de déterminer s'il y a des preuves confirmant les différences des caractères reproductifs entre ces deux sites. Les rapports style-morphe ne diffèrent pas significativement des équilibres attendus, et il n'y a pas de différences congruentes entre les populations continentales et insulaires au niveau de la morphologie florale et de la fertilité. Au contraire, le système de pollinisation généralisé du *P. mistassinica* et les opportunités historiques importantes semblent avoir estompé les effets insulaires de sorte que les facteurs écologiques immédiats sont plus pertinents à la biologie reproductive usuelle des populations.

Mots clés : distylie, insularité, pollinisation, biologie reproductive.

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Introduction

The reproductive biology and genetics of plant populations on islands may differ from mainland populations in several respects (reviewed in Ehrendorfer 1979; Barrett 1996). First, adaptations for self-fertilization are likely in island populations as they increase the probability of establishment following dispersal. Second, island colonization may lead to a loss of genetic variation because of founder effects and genetic drift in small founding populations. Finally, island pollinator faunas are often depauperate, so fertility may decline in island populations unless countered by the evolution of selfing mechanisms. Although recent studies have supported the second prediction by comparing the genetic diversity of island and mainland populations (reviewed in Frankham 1997 and see Affre et al. 1997), there have been relatively few island–mainland comparisons of breeding systems and pollination. Existing comparisons typically test Baker's (1955) prediction that self-compatible species are more likely to colonize islands and have mostly involved interspecific comparisons at large geographic scales (Barrett 1996, and references therein). Intraspecific studies at small scales that would allow explicit comparisons of reproductive traits in mainland and island populations are generally lacking.

The paucity of intraspecific studies may reflect the assumption that gene flow at small geographic scales will prevent evolutionary divergence (e.g., Halkka and Halkka

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1974). It seems unlikely, however, given the evidence for local adaptation at even more restricted spatial scales in plant populations (Snaydon 1970; Antonovics 1976; Turkington and Aarssen 1984), that colonization of islands within regional archipelagoes will fail to cause significant changes to plant reproductive biology. Recent intraspecific investigations have indeed shown that insular effects can be present at a local scale, in terms of lowered reproductive success (Linhart and Feinsinger 1980; Spears 1987) and adaptive reduction of dispersal ability (Cody and Overton 1996). Nonetheless, studies that examine patterns of floral morphology and breeding-system variation between numerous islands and the nearby mainland are rare.

To investigate the possible effects of insularity on island plant populations at a local scale, we compared 7 mainland and 13 nearshore island populations of *Primula mistassinica* Michx. (Primulaceae) on Lake Huron shorelines along the Bruce Peninsula and Tobermory Islands (Fig. 1), paying particular attention to aspects of the species' floral morphology and breeding system. The islands vary in size from about 1 ha (Middle and Harbour Islands) to 875 ha (Cove Island) and are located between 0.5 km (Doctor Island) and 6.3 km (Bear's Rump Island) from the Bruce Peninsula. *Primula mistassinica* is distylous, with populations containing both long-styled (or "pin"; hereafter L-morph) and short-styled (or "thrum"; hereafter S-morph) individuals that differ reciprocally in stigma and anther heights. The floral morphs in distylous species are normally self-incompatible, and at equilibrium occur at a ratio of 1:1 unless there is frequent self-fertilization (Ganders 1979; Richards 1986; Barrett 1992). Rare, self-compatible homostylous phenotypes occur in most heterostylous taxa, particularly in association with ecologically or geographically marginal environments, where they are best documented in the genus *Primula* (Charlesworth and Charlesworth 1979; Richards 1986, 1993).

Here we document for the first time the reproductive biology of *P. mistassinica* and pose three questions that explicitly compare mainland and nearshore island populations:

(1) Does floral morphology differ between mainland and island populations? In particular, is there any evidence for the occurrence of floral adaptations in island populations that promote self-pollination?
(2) Do populations exhibit biased style-morph ratios, and is this correlated with insularity?
(3) Is fertility reduced in island populations in comparison with those on the mainland?

Methods

The study species

Primula mistassinica, commonly known as bird's-eye primrose, is a variable diploid member of *Primula* section *Aleuritia*. It is typically distylous and may be differentiated from other Nearctic *Primula* by its lavender (rarely white) corollas and heavily yellow farinose or efarinose leaves (Kelso 1991). It is distributed across boreal North America, reaching its southern limit in the Great Lakes region and New England (Soper et al. 1965; Kelso 1991). In southern Ontario, peak flowering of the cymose inflorescences occurs during late May; the flowers are scented and last as long as 10 days.

Reproductive biology

To document distyly in *P. mistassinica*, measurements of stigma and anther height, and pollen size and number were made in a population at Cape Hurd on the Bruce Peninsula (see Fig. 1). Stigma and anther height were measured on single flowers sampled from 25 plants per style morph, using camera lucida and Sigma-Scan (version 2.6, Jandal Scientific 1986) connected to a digitizing tablet. Ten pollen grains from six plants of each morph were measured using Northern Exposure image analysis software (release 2.9X, Empix Imaging 1995), and their sizes compared using ANOVA, with morph and plant nested within morph as main effects. To compare pollen production of the floral morphs, anthers from twelve flowers per morph were acetolyzed (Kearns and Inouye 1993) and the pollen grains suspended in lactophenol–glycerin with cotton blue stain before four replicate counts were made using a hemacytometer. Pollen counts for the style morphs were compared using a Student's *t* test. All statistical analyses were conducted using JMP (version 3.0.2; SAS Institute Inc. 1994).

The compatibility of the floral morphs was investigated by using plants transplanted to a glasshouse prior to flowering. Three flowers on 10 plants of each style morph were randomly allocated to separate treatments conducted on the same day: self-pollination, intramorph cross-pollination, and intermorph cross-pollination. The calyx and corolla tubes were slit to facilitate treatments using short-level organs. Seed set was quantified when fruits matured 2 months later, and treatments were compared using a Kruskal–Wallis nonparametric test. Seed set in the two style morphs was compared for each treatment using one-way ANOVA or Kruskal–Wallis tests, depending on whether ANOVA assumptions were met.

To determine the most frequent visitors to flowers of *P. mistassinica*, collections were made during visits to populations at peak flowering. Voucher specimens of taxa collected are deposited in the insect collection of B.M.H.L. The degree of pollen limitation in the Cape Hurd population was determined by adding supplemental pollen to stigmas of 2 flowers on 12 plants per morph, marking them, and later comparing their seed set to 2 unmanipulated flowers on the same plant. Other flowers on each plant were removed. A two-tailed paired *t* test was used to compare mean seed set of the pollen-supplemented flowers with those of the control flowers in each morph.

Island–mainland comparisons

Floral morphology

Seven floral characters (Table 1) were measured, as described above, on single flowers sampled from 25 plants per style morph (fewer in small populations) in six mainland and seven island populations. Stigma–anther separation was derived from these measurements as the distance between the stigma and the apex or base of the anther in the L- and S-morphs, respectively. Inflorescence samples were also collected from four mainland and eight island populations to assess variation in the total number of flowers per inflorescence. Measurements were analyzed using a mixed-model nested ANOVA, with region (island or mainland) and style morph as fixed effects, and population nested within region as a random effect. *F* tests for the effect of region used a denominator constructed from $\mathrm{MS}_{\mathrm{population(region)}}$ and $\mathrm{MS}_{\mathrm{error}}$ and those for morph and region × morph similarly used a composite of $\mathrm{MS}_{\mathrm{morph\times population(region)}}$ and $\mathrm{MS}_{\mathrm{error}}$. In each of these cases, degrees of freedom were derived from the Satterthwaite approximation (SAS Institute 1994; Sokal and Rohlf 1995). The effects of population(region) and morph × population(region) were tested using $\mathrm{MS}_{\mathrm{morph\times population(region)}}$ and $\mathrm{MS}_{\mathrm{error}}$ as denominators, respectively. Ovary height was log transformed to meet ANOVA assumptions. A sequential Bonferroni test (Rice 1989) was used to determine tablewide ANOVA probabilities.

Fig. 1. Location of 7 mainland and 13 island populations of *Primula mistassinica* sampled on Lake Huron shorelines in Ontario, Canada. The lower panel shows the study area and the location of the mainland Bruce Peninsula populations, with lines along the left margin corresponding to 5 min of latitude, ranging from 44°50′ in the south to 45°20′ in the north. The upper panel is an enlargement of the Tobermory Islands showing the location of the island populations. ◆, Small-sized populations (<100 individuals); ■, medium-sized populations (100–1000 individuals); ●, large-sized populations (>1000 individuals).

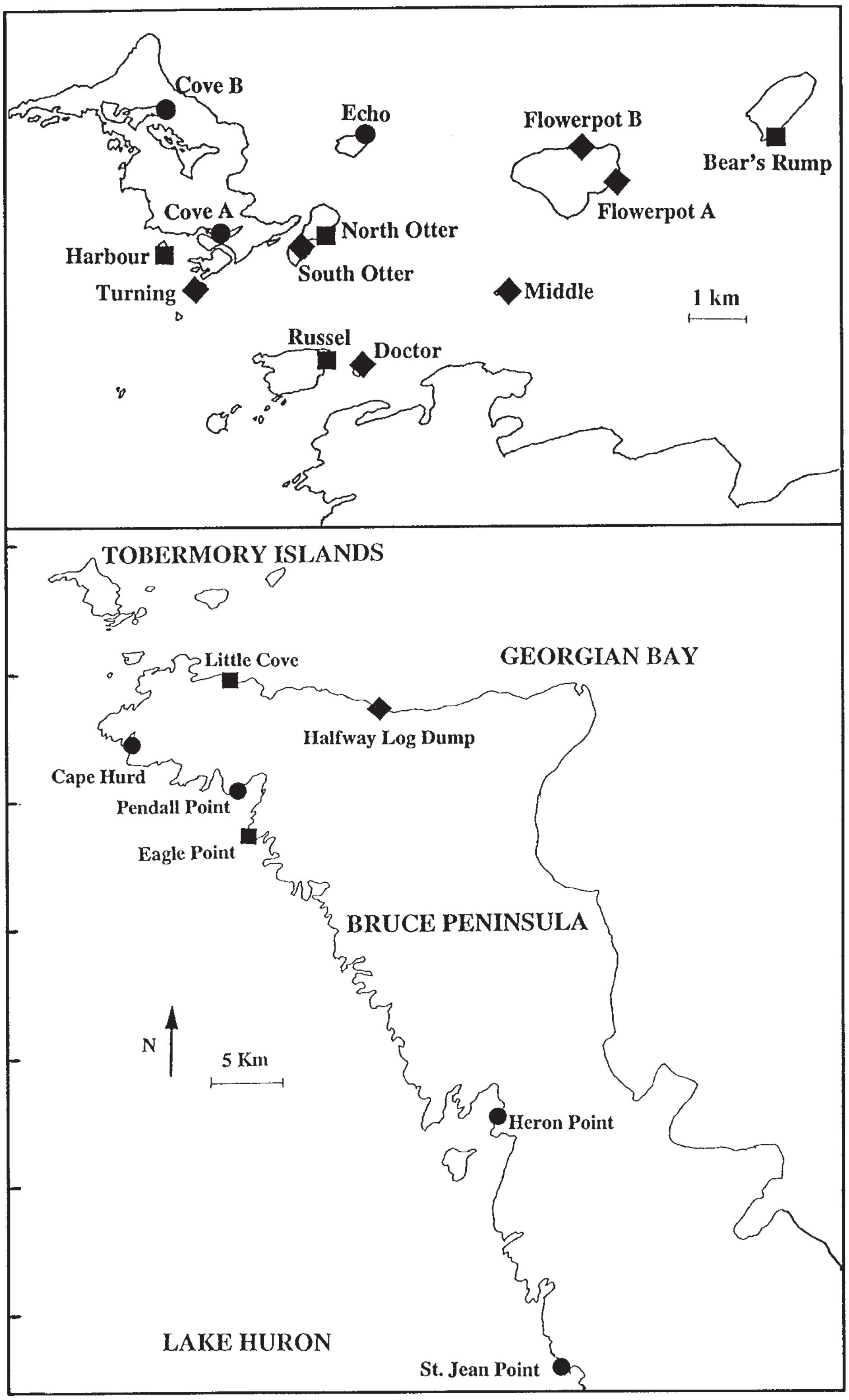
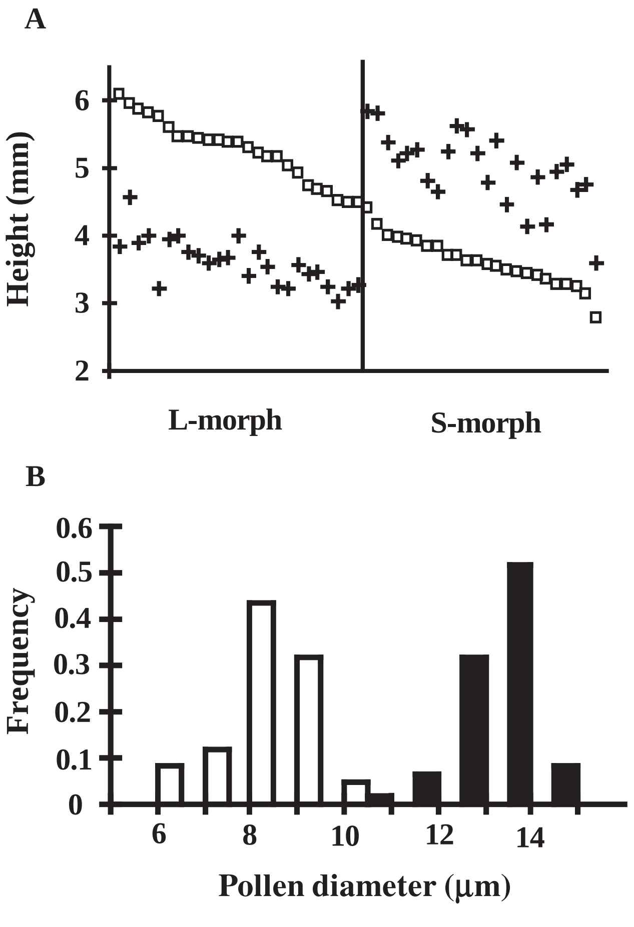


Table 1. Mean squares from mixed-model ANOVAs of the effect of region (island or mainland), morph, and population nested within region on floral characters measured on an average of 25 plants per morph from six mainland and seven island populations of *Primula mistassinica*.

Source of variation	df	No. of flowers	Calyx length	Corolla tube length	Petal length	Log ovary height	Style length	Filament length	Anther length	Stigma–anther separation
Region	1	8.31	0.001	2.49	4.85	0.05	0.43	0.49	0.58	0.70
Morph	1	4.18	1.41**	15.52***	4.81*	0.006	387.06***	229.60***	2.66***	42.34***
Region × morph	1	0.10	0.008	0.0008	0.42	0.007	0.016	0.17	0.02	0.06
Population (region)	11	40.65***	2.22***	4.97***	5.37**	0.03**	0.93*	1.18*	0.36***	0.75
Morph × population (region)	11	2.68	0.099	0.19	0.48	0.004	0.21*	0.25**	0.009	0.58***
Error	566	2.97	0.22	0.27	0.34	0.003	0.087	0.083	0.023	0.10

Note: Tablewide probabilities after a sequential Bonferroni test are indicated by asterisks (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$). For flower number there were 10 and 916 degrees of freedom for the effect of population (region) and error, respectively.

Fig. 2. (A) Variation in stigma (□) and anther (+) height for 25 plants of the L- and S-morphs of *Primula mistassinica* from the Cape Hurd population, ranked by stigma height. (B) Distribution of pollen size for plants of the L- ($N = 60$, open bars) and S-morph ($N = 60$, solid bars) of *P. mistassinica* from the Cape Hurd population. Mean sizes of pollen grains in the two morphs are presented in Table 2 and are significantly different (see text).



Style-morph ratios

A random sample of inflorescences from each of the 20 populations was used to determine style-morph ratios. *G* tests were employed to test for significant deviation from an equilibrium style-morph ratio (1:1) within populations and when populations were pooled (Sokal and Rohlf 1995).

Fertility

Mature inflorescences (20 per morph) were collected from six mainland and five island populations in mid-July to assess female fertility. Fruit set was not assessed because the vast majority of flowers set fruit, as in other *Primula* species (e.g., Baker et al. 1994). Mean seed set was estimated as the average number of seeds counted in two randomly chosen capsules per plant. Mean seed set was multiplied by the number of flowers on a plant to give an estimate of total fertility. Seed set was analyzed with the same mixed-model nested ANOVA described above for analysis of floral measurements. Total fertility was square root transformed to meet ANOVA assumptions. A Tukey–Kramer HSD test was used to contrast mean seed set in populations pooled over morphs. To investigate potential predictors of female fertility, mean fertility for each population was regressed on the mean value for several morphological and ecological parameters from the populations, including population size, mean number of flowers per inflorescence, and both island isolation and area. Population size was obtained by counting the total number of plants (small populations) or by averaging two independent estimates of population size (large populations).

Results

Reproductive biology

The pattern of floral variation in the Cape Hurd population demonstrates that *P. mistassinica* possesses a conventional distylous floral syndrome. Plants can be grouped into two distinct morphological groups on the basis of differences in stigma and anther height and pollen size (Fig. 2). Stamens and pistils were usually entirely within the corolla tube, but the tips of anthers in the S-morph and terminal section of the style in the L-morph were sometimes exserted. Flowers of the L-morph had significantly smaller pollen grains produced in greater numbers than flowers of the S-morph (Table 2; pollen size: morph $F_{1,108} = 1527.2$, $P < 0.0001$, plant (morph) $F_{10,108} = 10.76$, $P < 0.0001$; pollen number: $t_{22} = 3.88$, $P < 0.001$).

Controlled self and cross-pollinations of the two morphs demonstrated that *P. mistassinica* possesses a dimorphic self-incompatibility system. Self and intramorph pollination resulted in low levels of seed set, whereas intermorph polli-

Table 2. Mean (mm), SE, and sample sizes (N) of floral characters measured on an average of 25 plants per morph from six mainland and seven island populations of *Primula mistassinica*.

	Long-styled morph			Short-styled morph		
Character	Mean	SE	N	Mean	SE	N
No. of flowers	3.89	0.085	475	3.69	0.086	465
Calyx length*	4.48	0.029	297	4.37	0.030	295
Corolla tube length*	5.39	0.032	297	5.71	0.038	293
Petal length*	5.51	0.040	297	5.29	0.037	295
Ovary height	1.83	0.014	297	1.80	0.014	295
Style length*	3.72	0.022	297	1.99	0.015	295
Filament length*	1.34	0.014	297	2.64	0.023	295
Anther length*	1.17	0.009	297	1.31	0.011	295
Stigma–anther separation*	1.20	0.019	297	0.65	0.022	295
Pollen number*	30 315	2 382	12	16 667	2 586	12
Pollen size*	8.69	0.12	60	13.12	0.09	60

Note: Pollen size (µm) and number measurements are from the Cape Hurd population (see text).
*Significant difference between the morphs (Table 1 and see text).

nation increased seed set significantly (Fig. 3; Kruskal–Wallis test: H = 14.05, 14.84 for L- and S-morphs, respectively, df = 2, $P < 0.001$). The strength of self-incompatibility was stronger in the S-morph than the L-morph (Fig. 3).

Remarkably few individuals of insect species were seen visiting the flowers of *P. mistassinica*. Flower flies (Syrphidae) were the most prevalent visitors and particularly noticeable on warm, sunny days. Species of *Eristalis* (*E. arbustorum* (L.), *E. bardus* (Say), *E. dimidiatus* Wiedemann, *E. tenax* (L.), and *E. transversus* Wiedemann) and *Platycheirus* (2 species) were most common, but *Eupeodes americanus* (Wiedemann), *Helophilus fasciatus* Walker, *Lejops stipatus* Walker, *Orthonevra* sp., and *Parhelophilus rex* Curran & Fluke were also collected. Other visitors to flowers included six additional families of Diptera (mosquitoes (Culicidae), fungus gnats (Sciaridae), soldier flies (Stratiomyiidae), blow flies (Calliphoridae), muscid flies (Muscidae), and dung flies (Scathophagidae)), locally common thrips (Thysanoptera) and sap beetles (Nitidulidae, *Carpophilus* sp.), and rarely, the halictid bee *Augochlorella striata* (Provancher).

In the Cape Hurd population, there was no significant difference between seed set in pollen-supplemented flowers and control flowers in either the L-morph (supplemented 93.5 ± 6.6; control 84.6 ± 9.0; t_9 = 1.34) or the S-morph (supplemented 95.7 ± 6.4; control 101.8 ± 9.2; t_{10} = 0.51). Preliminary studies with smaller samples at St. Jean Point and Little Cove on the mainland and in the Flowerpot B island population corroborated these results.

Island–mainland comparisons

Does floral morphology differ?

Comparison of floral traits failed to reveal any significant differences between mainland and island populations. This was indicated by the absence of a significant region effect in the ANOVA (Table 1). Morph and population main effects accounted for most variation in floral characters. Plants of the L-morph had longer calyces and petals but shorter corolla tubes and anthers than the S-morph (Table 2). Differences between the two morphs in style and filament length were those expected for a distylous species. Despite thorough searches at all sites, no homostylous plants were encountered in any of the populations.

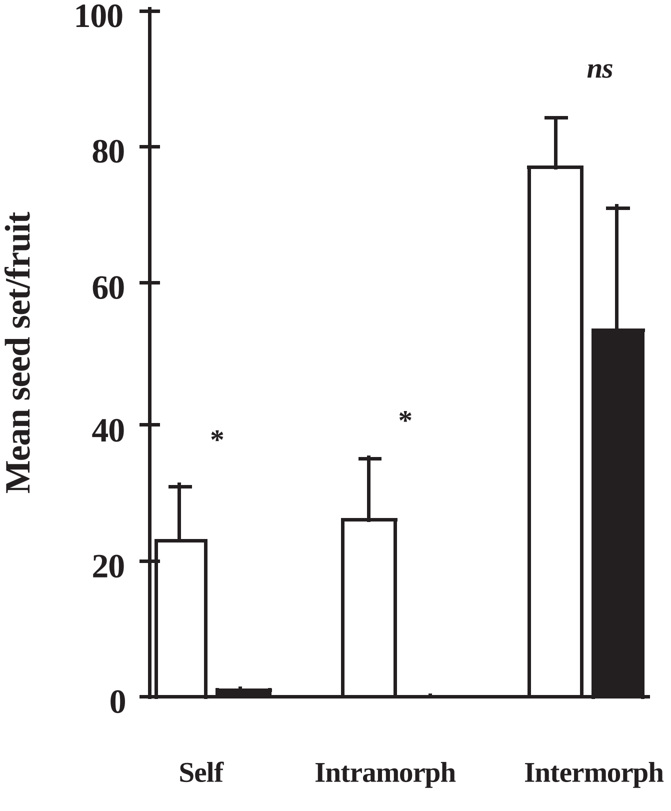


Fig. 3. Mean seed set per fruit (± SE) in *Primula mistassinica* flowers of the long-styled (N = 10, open bars) and short-styled (N = 6, solid bars) morphs after self-pollination, intramorph cross-pollination, and intermorph cross-pollination treatments in the glasshouse. Probabilities after nonparametric Kruskal–Wallis test are indicated by asterisks (*, $P < 0.01$; Kruskal–Wallis H = 8.54, 9.36 for self and intramorph pollination, respectively, df = 1). ns, not significant after one-way ANOVA ($F_{1, 14}$ = 2.00).

Table 3. Mixed-model ANOVAs of the effect of region (island or mainland), morph, and population nested within region on female fertility in six mainland and five island populations of *Primula mistassinica*.

		Mean seeds		Square root of total fertility	
Source of variation	df	Mean square	*F*	Mean square	*F*
Region	1	7283.87	0.58	253.05	0.50
Morph	1	3057.18	10.06*	38.19	1.14
Region × morph	1	87.77	0.29	6.82	0.20
Population (region)	9	13 461.6	46.22***	537.07	15.66**
Morph × population (region)	9	291.24	0.61	34.29	1.50
Error	360	475.56	475.56	22.99	22.99

Note: *, $P < 0.01$; **, $P < 0.001$; ***, $P < 0.0001$.

Fig. 4. Mean seed set per fruit (± SE) in six mainland and five island populations of *Primula mistassinica*. Within these two regions, population size generally decreases from left to right. ◆, Long-styled morph; ■, short-styled morph. Mean seed set between populations sharing the same letter is not significantly different ($P < 0.05$) after Tukey–Kramer HSD test pooled over morphs. Mainland sample sites are as follows: (1) Heron Point; (2) Cape Hurd; (3) St. Jean Point; (4) Eagle Point; (5) Little Cove; (6) Halfway Log Dump. Island sample sites are as follows: (1) Echo; (2) Bear's Rump; (3) Flowerpot B; (4) South Otter; (5) Turning.

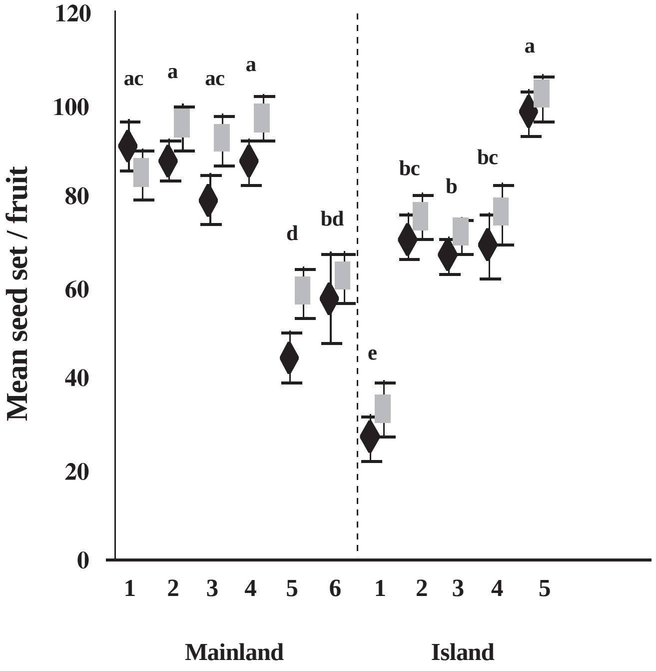
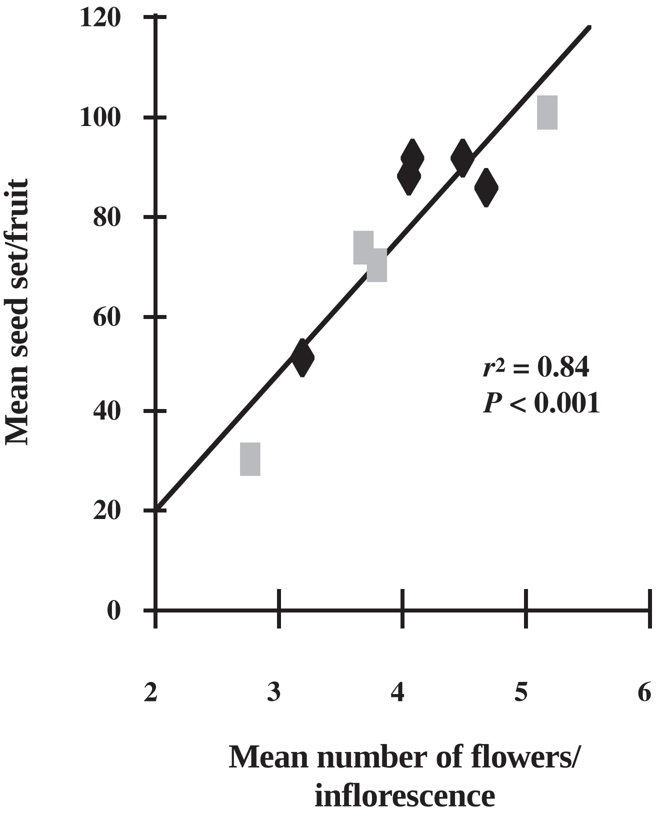


Fig. 5. Relation between mean seed set per fruit and mean number of flowers per inflorescence in five mainland (◆) and four island (■) populations of *Primula mistassinica*. Seed set and flower number were counted on separate random samples from the populations.



Are population style-morph ratios biased?

A total of 1243 plants from 7 mainland populations and 869 plants from 13 island populations were sampled to determine style-morph ratios. When populations were pooled, there was no significant departure from equilibrium expectations on the mainland (L-morph 0.511: S-morph 0.489; $G_{\text{pooled}} = 0.59$, df = 1) or the islands (L-morph 0.487: S-morph 0.513; $G_{\text{pooled}} = 0.61$, df = 1). Style-morph ratios were homogeneous among both mainland and island populations (mainland: $G_{\text{het}} = 7.18$, df = 6, $p > 0.05$; islands: $G_{\text{het}} = 10.51$, df = 12, $p > 0.05$). There was a significant deviation from an equilibrium style-morph ratio in only one population (Heron Point on the mainland, where L-morph 0.61: S-morph 0.39; $N = 100$, $G = 4.88$, df = 1, $P < 0.05$).

How does fertility vary?

Comparisons of female fertility in mainland and island populations failed to detect any significant difference between the two regions (Table 3). Fruits of the S-morph had significantly greater seed set (78.3 ± 2.0; $N = 195$) than those of the L-morph (70.6 ± 2.2; $N = 187$), but total fertility was not associated with style morph. The effect of population accounted for most of the variation in seed set and total fertility (Table 3). Within regions, seed set varied greatly among populations but was not correlated with simple predictors of fertility such as population size (Fig. 4). Female fertility within island populations was unrelated to either island isolation or area. The only morphological trait associated with seed set per fruit was inflorescence size. Among nine populations, there was a significant positive relation between mean number of flowers per inflorescence and mean seed set per fruit (Fig. 5). This association was unrelated to region.

Discussion

Our comparisons of the reproductive biology of distylous *P. mistassinica* in mainland and nearshore island populations on Lake Huron shorelines in Ontario found no evidence for consistent differences in their floral morphology, style-morph ratios, or fertility. This finding probably results from a synergism between aspects of the life history and floral biology of the particular species investigated and the geographic scale of our study. Below we discuss in more detail the reproductive ecology and biogeography of *P. mistassinica* to account for our results.

The differences in floral morphology detected in *P. mistassinica* were those befitting the two morphs of a distylous species. Other characters may have been expected to vary between populations from mainland and island areas, but only population-level differences were found. For example, if pollinators were less abundant or reliable on the islands, flower size and stigma–anther separation may have decreased, as these transitions are correlated with increasing self-fertilization and have been documented in other mainland–island comparisons (Barrett 1985; Inoue et al. 1996). Our results indicate that these changes are more responsive to local conditions found within populations than to larger scale ecological factors related to insularity.

The absence of self-pollinating homostyles within populations of *P. mistassinica* is not entirely unexpected, because homostyles are generated rather infrequently (on the order of 10^{-3}) through crossovers within the supergene controlling heterostyly (Charlesworth and Charlesworth 1979). Furthermore, in *Primula* the evolution of homostyly tends to be associated with polyploidy, so homostyly may be less likely in a diploid species such as *P. mistassinica* (Kelso 1991, 1992; Richards 1993). Even if rare homostyles were present in the populations we surveyed, it does not appear that the reproductive assurance provided by self-fertilization has been a strong enough selective pressure to permit their spread (Charlesworth and Charlesworth 1979) whether or not this is in association with island colonization.

The observed style-morph ratios in populations of *P. mistassinica* suggest that self-fertilization occurs rarely, regardless of insularity. Significant selfing rates are undoubtedly prevented by the dimorphic incompatibility system of this species. The leaky self-incompatibility in the L-morph, which is not unusual (see Barrett and Cruzan 1994), could provide some capacity for self-fertilization. However, the equilibrium style-morph ratios consistently found in populations of *P. mistassinica* cast doubt on whether this occurs. In addition, offspring resulting from self-fertilization would likely have limited survivorship because of inbreeding depression in this predominately outcrossing species (Charlesworth and Charlesworth 1987). It is important to note that, in the absence of self-fertilization, founder effects (e.g., overrepresentation of one style-morph among founders) alone cannot bias population style-morph ratios in a distylous species. After a single generation of disassortative mating within a founding population a 1:1 style-morph ratio would be restored, because intermorph cross-pollinations produce seeds of the two morphs at equal frequencies (Barrett 1992).

The lack of any consistent differences between the fertility of mainland and island populations of *P. mistassinica* indicates that intermorph pollen transfer by pollinators must be effective in both areas. Anecdotal reports of butterfly pollination of *P. mistassinica* occur in the literature (Soper et al. 1965), but syrphid flies were the predominant visitors to flowers in the populations we investigated. Syrphid flies are generalist pollinators that visit flowers to consume pollen grains (Proctor et al. 1996) and their hairy bodies give them some capacity for intermorph cross-pollination. Small bees were observed infrequently, but this may simply reflect their more restricted foraging during the inclement weather conditions that often occur on the Bruce Peninsula in May. Bees may be significant pollinators during the instances within the lengthy flowering period of *P. mistassinica* when weather is more amenable to their activity. Syrphid flies (*Helophilus groenlandicus* O. Fabricius) were reported as the most important pollinators of homostylous *P. laurentiana* Fern. in Maine, even though it was visited frequently by bumblebees (Campbell et al. 1986). Intermorph pollen transfer by the beetles and thrips observed in *P. mistassinica* flowers is probably relatively insignificant, but little is known regarding their patterns of inter-plant movement and potential for pollen transfer.

The generalized pollinators of *P. mistassinica* probably account for successful cross-pollination of the species even on small, isolated islands. In instances where insular effects on the pollination of island plants have been detected (Spears 1987; Inoue et al. 1996), the species involved were dependent on specialized bee pollinators that have more restricted larval substrates than flies and hence are less able to inhabit small islands. The larvae of *Eristalis* species, in particular, breed in substrates ranging from shallow water and muck to decaying vegetable matter (Gilbert 1986), habitats that are available on both the mainland and islands. Bumblebees and moths are often reported as pollinators of larger-flowered *Primula* species (Schou 1983 for *P. elatior* (L.) Hill; Boyd et al. 1990 for *P. vulgaris* Huds.; Antrobus and Lack 1993 for *P. veris* L.; Miller et al. 1994 for *P. angustifolia* Torrey and *P. parryi* Gray; Washitani et al. 1995 for *P. sieboldii* E. Morren), which might make these taxa more susceptible to pollinator declines, as has been documented for the rare *P. sieboldii* in isolated Japanese populations (Washitani et al. 1994).

Island size and isolation and population size were not good predictors of fertility within individual populations, indicating that local ecological factors were more important in governing reproductive success. The strongest association detected in our data was between mean seed set per fruit and the number of flowers per inflorescence (Fig. 5). If inflorescence size is influenced by resource status, for example through variation in soil nutrients, microhabitat differences or length of growing season, then this correlation would suggest that fertility may be resource limited. This hypothesis was invoked to explain the increase in seed set per capsule with capsule number per inflorescence in *Primula farinosa* L., but the alternative hypothesis of greater pollinator visitation to larger inflorescences could not be excluded (Baker et al. 1994). Low seed set in some of the populations most exposed to offshore winds (Little Cove, Halfway Log Dump and Echo Island) suggests that exposure may be a significant factor limiting fertility in *P. mistassinica* populations. To the extent that weather conditions are less severe as the flowering season progresses, the flowering time of populations may also influence the probability of pollinator visitation. Studies of pollinator visitation and the intensity of pollen limitation in populations exposed to varying microclimatic conditions would be necessary to evaluate these ideas.

Even if ecological factors associated with insularity were capable of causing character divergence between mainland and island populations, historical and biogeographical factors may have mitigated their effects. The northern section of the Bruce Peninsula and all of the Tobermory Islands, except the higher elevation portions of Flowerpot and Bear's Rump, were submerged at least until Nipissing-phase lake levels began to fall about 4000 years ago (Morton and Venn 1987). When lake levels receded, colonies founded on both the mainland and the islands would have been equally insular, and there may not yet have been enough time for subsequent evolutionary adjustment to conditions in contemporary island and mainland environments. Furthermore, the high floatation capacity of *P. mistassinica* seeds (category A of Morton and Hogg 1989: more than 50% of seeds remain afloat after 1 week with periodic mechanical shaking; B. Larson, unpublished data) may allow periodic gene flow between populations and constrain evolutionary divergence. Fluctuating lake levels provide an opportunity for seeds to be washed from shoreline environments and to be dispersed among the network of small islands that surround the tip of the Bruce Peninsula. Recurrent migration through seed dispersal between the populations studied is aided by the relatively close proximity of *P. mistassinica* populations on the Lake Huron shoreline. Frequent gene flow was similarly invoked by Halkka and Halkka (1974) to explain the consistent equilibrium style-morph ratios found in island populations of tristylous *Lythrum salicaria* L. in southern Finland.

Our results indicate that the ecological and evolutionary consequences of insularity to plant populations depend on the particular species and spatial scale investigated. It appears that the reproductive versatility of *P. mistassinica* and limited isolation of the Tobermory Islands buffer island populations from the effects of insular selective forces on their reproductive biology. Further examination of microevolutionary patterns and processes in small insular environments are worth conducting since they have the potential to reveal significant evolutionary changes to plant reproductive biology accompanying island colonization. Island plant populations represent a naturally fragmented system, so our results also illustrate the reduced susceptibility of species with effective dispersal and generalized pollination systems to pollinator declines in fragmented habitats.

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