

The effect of hermaphrodite density and frequency at three spatial scales on the pollen receipt and seed set of gynodioecious *Geranium richardsonii* (Geraniaceae)

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Abstract

Gynodioecy is a mode of sex expression where male sterile (hereafter female) plants and hermaphroditic plants coexist within a population. In order for the females to be maintained by natural selection, they must have experienced an increased fitness. Fitness is defined as the ability of genotype or phenotype to contribute genes to the pool of seeds for the next generation. Since females only transmit their genes through seed production, their inability to produce pollen has to be compensated for. Experimental evidence from a variety of gynodioecious species have not found the theoretically required fitness advantage for females. This is in part may be due to interactions of the plant with its local frequency and density and not the global population characteristics. Females in particular may become pollen limited as the density and frequency of hermaphrodites declines. I present the results of a study that examined the effect of hermaphrodite density and frequency at three spatial scales on pollen receipt of *Geranium richardsonii* in four populations in Gothic, CO. In the lower density, patchy populations the smaller spatial scales seem to be more important to female pollination success. As the density of the populations increased the total hermaphrodite density and female frequency become able to explain more of the variation in female pollen receipt. The small spatial scales did not seem to determine the hermaphrodites pollination success as a large portion of the variation could be explained by the total hermaphrodite density.

Introduction

Gynodioecy is a mode of sex expression where male sterile (hereafter female) plants and hermaphroditic plants coexist within a population. Of interest since this term was defined by Darwin (1877), gynodioecy has been found in almost 7% of the 121 492 species surveyed by Yampolsky and Yampolsky (1922).

Gynodioecy is thought to be the evolutionary intermediate toward dioecy; it is unlikely that the two mutations occurred simultaneously to eliminate both ovule and pollen production. It is thought that the initial step was the occurrence of a mutation that abolished pollen production producing female plants (Charlesworth and Charlesworth, 1978). In order for the females to be maintained in the population and allow for the subsequent evolution of dioecy, they must have been evolutionarily favored. Hermaphroditic plants are able to transmit their genes to the next generation through male and female function producing pollen and seeds; whereas female plants are only able to transmit their genes through seed production. For females to be maintained in a

population by natural selection, their inability to produce pollen has to be compensated for by an increase in female fitness surpassing hermaphrodites by up to two times depending on the mode of sex determination. This means that the females must experience increased fitness relative to hermaphrodites (Lewis, 1941; Lloyd, 1975; Charlesworth and Charlesworth, 1978; Agren and Wilson, 1991; Delph, 1996).

Fitness is determined by the ability of a phenotype or genotype to contribute genes to the pool of seeds for the next generation (McCauley and Taylor, 1997). There are two main hypotheses that have been formulated to explain potential sources of the increase in female fitness. The first hypothesis states that females are at an advantage because their flowers are all outcrossed while hermaphrodites have the potential to self-fertilize and thus incur inbreeding depression (Lewis, 1941; Lloyd, 1975; Charlesworth and Charlesworth, 1978; Agren and Wilson, 1991; Delph, 1996, Sakai et al, 1997). If a population displays inbreeding depression, females can be established even if they have the same seed fertility because of the increased fitness of outcrossed progeny (Bawa, 1980). The second hypothesis states that more resources can be allocated to seed production since females don't have to put resources and energy into the production of costly male reproductive organs such as pollen, anthers, and attractive structures such as petals (Lewis, 1941; Lloyd, 1975; Charlesworth and Charlesworth, 1978; Agren and Wilson, 1991; Delph, 1996, Sakai et al, 1997). This reallocation of floral resources from male reproductive function (pollen production and pollinator attraction) to female reproductive function (seed production) may allow the females to compensate for the loss of male reproductive success if the smaller flower size does not result in pollen limitation (Charlesworth and Charlesworth, 1987). The sources of increased production of seeds therefore may be a result of a consistent annual difference in seed production, greater hermaphrodite mortality, or differing

patterns of resource allocation (Sakai et al, 1997). Experimental evidence from *Geranium* and other gynodioecious species supports the hypotheses for increased female fitness but does not often find the theoretically required two-fold fitness advantage for females (Agren and Wilson, 1991; Eckhart, 1992; Pettersson, 1992; Maki, 1993).

One possible explanation for the failure to find the required fitness increase in females may be that population structure is playing an important role in the process of evolution. In a population subdivided into local groups, the individual fitness of a given phenotype or genotype may depend more strongly on the composition of the local group in which it interacts rather than the composition of the entire population. Inherent in this idea is the assumption that individual fitness is a function of the local frequency and not the global frequency. This results in a frequency dependence that influences the fitness trait creating a population structure that results in groups varying in genetic and phenotypic composition (McCauley & Taylor, 1997).

McCauley and Taylor (1997) stated that the sex expression in gynodioecious plants is a trait that can be expected to be influenced by local fitness and display a population structure with considerable variation among local subunits in sex frequency. This is supported by the observation that natural gynodioecious populations within a short distance of one another vary greatly in female frequency (pers. obs., Table 1). Therefore in gynodioecious plants, a portion of the selective pressures that determine the number of females and hermaphrodites could be frequency-dependent (McCauley and Brock, 1998). If this is true, natural populations should be found where female fitness is negatively frequency-dependent, due to the fact that pollen is maximally available when females are rare, whereas hermaphrodite fitness is positively frequency-dependent due to maximum pollen availability when hermaphrodites are common (McCauley and Taylor, 1997).

Population density is another factor that has been found to have a strong effect on reproductive success. Density is broadly defined as the number of individuals per area. This definition limits the use of density as a measurement to populations that are spatially uniform. Often naturally occurring populations are patchy at a variety of spatial scales. To be more precise Kunin (1997) suggests the use of local density, the spacing between neighboring individuals, and population size, the number of individuals in a local population, as measures of population characteristics. When local density and population size can be differentiated, they are often found to have very different effects on the species interactions and population dynamics (Kunin, 1997). Kunin (1993) found that local population density influences seed set in self-incompatible plants which results in significant declines in per flower reproductive success at low density. The results of studies of population size are often confounded by the fact that naturally small populations are usually also low density. Experimentally, when population size has been manipulated while holding the density constant, there has been no effect on the pollination and reproductive success. The number of flowers visited in a population was affected by the total flower number so that almost all of the pollinators preferentially visited the high density plots. Therefore it appears that population density, not necessarily size, had a strong effect on the attraction of pollinators (Kunin, 1997). This evidence supports the hypothesis that reproductive declines at low density are due to pollination failure (Kunin, 1993).

In several studies, plant reproductive success has been found to be strongly influenced by local population density (Widen and Widen, 1990; Kunin, 1992; Karron et al, 1995; Bosch and Waser, 1999). As females increase in density and frequency in a population, the population can become pollen limited resulting in a reduced seed set (Lloyd, 1975; McCauley and Taylor, 1997). Preliminary studies show a strong negative correlation between pollination success and

female frequency in *G. richardsonii* populations (Williams et al 2000, unpublished). Like most gynodioecious species, *G. richardsonii* are insect-pollinated which can play a part in determining the fecundity of females when pollen production and dispersal is restricted (Widen and Widen, 1990). Females may also be limited in that most hermaphrodite flowers are larger than females in gynodioecious species, which has been found to be less attractive to pollinators resulting in females significantly receiving less pollen than hermaphrodites (Williams et al, 2000). This may result in females becoming pollen limited at a high frequency or when located spatially distant from hermaphrodites. This demonstrates a negative frequency-dependent response (Williams et al, 2000). Williams et al (2000) found that females, on average, receive less pollen than hermaphrodites and total pollen receipt is weakly positively correlated with the total hermaphrodite population density. They also found that relative female success, the ratio of mean pollen receipt by female flowers to mean pollen receipt by hermaphrodites, of females is negatively correlated with female frequency (Williams et al, 2000). Male-sterility in *Geraniums* is most likely controlled by a combination of cytoplasmic genes producing male sterility and nuclear genes restoring male function which results in less than a two fold increase in female fitness being required in order for female maintenance. Even with this decreased requirement for increase in fitness, the increase in female fitness has been found to be only marginally greater (Williams et al, 2000).

Previous studies have used the global frequency and density of females as the population characteristics. They have failed to take into account the local frequency and density of females in which the individual plants interact. Kunin (1997) has shown that the local floral environment and the global floral environment can have very different effects on the fitness of a phenotype or genotype. In this study, I examine which spatial scale (0.5m radius, 2x2 m quadrant, or

population) has the most predictive power in determining the fitness of each sex. I hypothesize that the populations will display density dependence. Under the assumption that the foraging behavior of pollinators varies at the three different spatial scales I predict that the strength of the correlation between pollen receipt and density will vary. As the proportion of females increases, the populations will have a lower pollen receipt resulting in a negative correlation but as the population density increases, the female frequency may become less important. Therefore since the females must outcross and hermaphrodites may self-pollinate, I would expect the females to display a stronger density dependence than hermaphrodites.

Materials and Methods

Study Organism- *Geranium richardsonii* Fischer and Trautvetter (Geraniaceae) is a perennial herb, native to moderately disturbed habitats in subalpine zones. *Geraniums* produce multiple stems that produce radially symmetrical white flowers with pink to purple veins (Weber, 1987). This is a gynodioecious species in which plants produce either hermaphroditic flowers or female flowers (Williams et al, 2000). The perfect flower of a typical hermaphrodite consists of ten stamens in two whorls with filaments as tall as or taller than the style with large purple anthers. Each anther will contain hundreds of large (75-100 μm in diameter) pollen grains. There is a temporal separation of the male and female phases in the hermaphrodites. The flowers remain in the male phase for one to two days prior to the stigma lobes opening and becoming exposed. The flower will then remain in the female phase for approximately one to two days before the stigma closes and the petals wilt and drop off. Typical female flowers contain stamens with small yellow anthers on filaments shorter than the style with no pollen or little viable pollen produced in the anthers. Female flowers' stigma lobes will open and be exposed soon after flowering and remain open for two to three days until the petals wilt and drop. There is no

synchrony among different flowers on a plant, allowing for geitonogamy, selfing between flowers of the same plant. *G. richardsonii* typically flower from late June to early August producing tens to greater than a 100 flowers per plant.

Study Sites

The research was conducted in the vicinity of the Rocky Mountain Biological Laboratory (RMBL) in the East River Valley near Gothic, Colorado (2900 m). In this subalpine region, the snowmelt usually occurs from late April to early June. The *G. richardsonii* at this elevation are found at the margins of aspen and willow stands in moderately disturbed areas. Research in the summer of 2001 was conducted on four spatially discrete populations, Pumphouse (PH), Aspen, Research Meadow (RM), and Virginia (VA), within the vicinity of RMBL that spanned a range of habitats, plant densities and sex ratios (Table 1).

Protocol

Two of four spatially discrete populations were censused each week from June 26 through July 30, 2001 on a rotation that continued until three censuses were completed for each population. At the beginning of each week, sixty to ninety flowers were tagged with small paper jewelry tags tied below the desired flower for stigma collection later in the week. At the same time, twenty to thirty flowers were tagged for collection at the end of the flowering season to assess seed set. Eligible flowers included open flowers that had not yet lost their anthers and floral buds that were about to open. If the sample size was not achieved, the population was tagged the following week in addition to the other scheduled populations.

Flowers marked for stigma pollen counts were collected two to three days after marking, after the petals had wilted and dropped. In the lab, the stigmas were removed with fine forceps and squashed on microscope slides in basic fuchsin gel (Kearns, and Inouye, 1993). The stained

pollen grains adhering to the stigmas were counted under a compound microscope at 100x. The flowers marked to assess seed set were collected at the beginning of August. The tagged fruits were placed in coin envelopes and allowed to dry three to four days prior to counting the number of mature seeds produced by the fruit.

At the time of floral tagging, the number of open hermaphrodite flowers and female flowers within a 0.5 m radius were counted to determine the local mating environment of each target flower. For each population, a weekly census of the number of open flowers was conducted for each 2x2 m quadrant within the population which were summed to determine the overall population density and sex ratio.

For each census period in each population, the differences in pollen receipt in females and hermaphrodites was analyzed with an ANOVA. Standard deviation was the measure of variability. ANOVA was also used to generate means used in the correlations with population density and sex ratio. Linear regressions were used to determine the affect of 0.5m and 2x2 m local density on pollen receipt. The mean pollen receipt for each census period was analyzed with linear regression to examine the effect of total floral density and total hermaphrodite density on mean pollen receipt by hermaphrodites and females. A multiple regression of the mean stigma pollen receipt on the local 0.5m radius hermaphrodite density, 2x2 m quadrant density, total population hermaphrodite density, and female frequency for each population was used to determine which factors and scales explain the most variation in pollen deposition. All analyses were carried out using StatView (v. 4.53 Abacus Concepts, 1996).

Results

Pollen deposition

On average hermaphrodites received more pollen than females although the difference was only

significant at $p < 0.05$ in 3 out of 12 censuses (Table 2). The amount of pollen varied during the flowering season so that it was highest at the highest flowering plant density (Table 1).

Density- and frequency-dependent pollination success

There was a tendency for stigma pollen receipt to increase in both females and hermaphrodites as the density of the hermaphrodites increases. In each population, there was a trend for a positive correlation between hermaphrodite density at 0.5m and 2x2m spatial scales and stigma pollen receipt on female and hermaphrodite flowers (Fig. 1, 2). Although the correlation was significant at $p < 0.05$ in only 5 of 46 cases (Table 4), all censuses in each population showed a weak positive correlation between hermaphrodite density at the two lower spatial scales and stigma pollen receipt. The contribution that each spatial scale and female frequency make in explaining the variation seen in pollen receipt shows no strong trends (Table 5). It appears that in the lower density, patchy populations (Aspen and PH) the smaller spatial scales seem to be more important for the females. However, as the density increases, the total population density for females becomes more important (VA and RM). In contrast, in hermaphrodites the small scale doesn't seem to provide much explanatory power, total population density explains most of the variation in pollen receipt.

When the mean stigma pollen loads were calculated for each sex for each populations census, there were several significant trends. There was a significant, positive correlation between population hermaphrodite density and the mean stigma pollen loads for females ($N=12$, $P < 0.001$, $R^2=0.842$) and hermaphrodites ($N=12$, $P < 0.005$, $R^2=0.603$) during all censuses (Fig. 3). The correlation between total floral density and the mean stigma pollen loads of both sexes during all censuses was significantly positive ($N=23$, $P < 0.005$, Fig. 4). Contrary to previous studies (Williams et al, 2000) and preliminary data (Williams, unpublished) there was no

significant correlation between female frequency and the stigma pollen loads of both sexes ($N=23$, $P>0.05$, $R^2=0.002$) or between female frequency and relative female pollination success ($N=12$, $P>0.05$, $R^2=0.026$, Fig. 5).

Discussion

Pollen Deposition

Reallocation of floral resources from male function (pollen and petals) to female function (seed and fruit production) may allow females to compensate for the loss of pollen production if the smaller flower size does not reduce pollen receipt to the point of pollen limitation (Charlesworth and Charlesworth, 1987). In *G. richardsonii* on average, hermaphrodites received 1.4 times more pollen than females (calculated as the ratio of the average number of pollen grains received by hermaphrodites to the female receipt in each census, Table 2). This is considerably lower than the 2.2 times increase found by Williams et al (2000) in the same populations in 1997 and 1998. This may in part be due to a higher pollinator abundance (Williams, pers. observ.). Higher pollinator abundance may remove pollen limitation in some years despite high female frequencies. As the pollinators in a population increase, the amount of pollen being moved from hermaphrodite flowers to female flowers increases, resulting in increased stigma pollen receipt.

There are two aspects to increased pollen receipt, the quality of the pollen and the quantity of the pollen. An increase in pollen may not be particularly beneficial if it is geitonogamous self-pollen. Although there is temporal separation of the male and female phases in *G. richardsonii* flowers, there is no synchrony in the blooming among flowers of the same plant allowing for geitonogamy (selfing between flowers of the same plant). Williams et al (2000) found a majority (between 66% and 93%) of the increase in pollen receipt for hermaphrodites relative to the females was due to geitonogamy. Hand pollination experiments

have found that *G. richardsonii* can self and subsequently suffer from inbreeding depression in fruit and seed set (K. O'Malley, C. Williams, and M. Kruchenreuther, unpublished data). With the geitonogamous self pollination, pollen receipt is not necessarily the best indicator of plant fitness, the fruit production and seed set would have to be examined to determine if there is a positive relationship between pollen receipt and seed set, and if the seeds from geitonogamously self-pollinated seeds were just as viable as the outcrossed hermaphrodite and female seeds.

Density- and frequency-dependent pollination success

Kunin (1997) showed that the local floral environment and the global floral environment can have very different affects on the fitness of a phenotype or genotype. In examining three different spatial scales (local, intermediate, and global), all three spatial scales showed a weak-positive correlation (although significant at $p < 0.05$ in only 5 of the 46, Table 2, 3) between hermaphrodite density and stigma pollen receipt (Fig. 1,2). The density of the populations affected which spatial scale was best able to explain the variation in the pollen receipt for females. In populations that were lower in density and spatially patchy, such as Aspen and PH, the local and intermediate spatial scales were able to best explain the variation in female pollen receipt (Table 5). As the density of the populations increased, RM and VA, the total population hermaphrodite density became more important in explaining the variation in pollen receipt (Table 5). In the low density and spatially patchy populations, pollinators are going to be attracted to the densest patches within the population. As the hermaphrodite density within a patch increases, the more pollen that will be available to the plants in that patch. This is especially important for females who are unable to produce their own pollen but rely on the pollen of the surrounding hermaphrodites. But as the density of the population increases, the determining factor in pollen receipt will be the pollinator abundance and the pollination success

will behave much like the hermaphrodites mentioned below.

Hermaphrodite pollination success does not seem to be affected by the local and intermediate spatial scales. Most of the variation in pollen receipt could be explained by the global hermaphrodite density (Table 5). As the total population hermaphrodite density increased, the stigma pollen receipt increased (Fig. 3). Kunin (1997) found that population density had a strong effect on the number of pollinators present in a population. He found that almost all categories of pollinators preferentially visited high density plots (Kunin, 1997). *G. richardsonii* is an insect-pollinated plant that is facultatively outcrossing at the flower level due to temporal separation of the male and female phases. This means that most pollen receipt on the stigma requires an insect intermediate to transfer the pollen to a receptive stigma. As the hermaphrodite density increased, there were more flowers present in the population perhaps resulting in increased recruitment of pollinators. The same trend was present when effect of total floral density on mean pollen receipt was examined (Fig. 4). This supports the idea that as the pollinators in a population increase, the amount of pollen available and being moved between flowers increases, resulting in increased stigma pollen receipt. The increase in stigma pollen receipt with increasing hermaphrodite density and total floral density could reflect the relationship between high floral densities and high levels of pollinator recruitment.

The pollinators were present in a higher abundance than in previous years which could explain some of the weak correlations at the local and intermediate spatial scales (Williams et al, 2000). With an increased pollinator abundance there is going to be increased overlap between spatially discrete populations and pollen will be brought in from farther distances. This is going to result in less reliance on the immediate environment in pollination success.

The two most successful predictors of stigma pollen receipt for hermaphrodites and

females is the total hermaphrodite density (Fig. 3) and the total floral density (Fig. 4) when looking at the mean pollen receipt for each sex during each census period. A rather surprising result was that female frequency of the populations did not seem to have an effect on the stigma pollen receipt (Fig. 5). Williams et al (2000) found a strong negative frequency dependence in females and this was also found in other gynodioecious species (Widen and Widen, 1990; McCauley and Taylor, 1997). The frequency dependence of the populations this summer may have been confounded by changes in floral densities and pollinator abundance. To attempt to tease apart these two effects it may be beneficial in the future to experimentally manipulate the female frequencies in arrays while maintaining a constant density and to more closely monitor pollinator abundance and activity between populations, censuses, and years.

Conclusion

This study was able to confirm that hermaphrodites on average do receive more pollen than females. Both hermaphrodites and females of *G. richardsonii* demonstrated a weak-positive correlation between hermaphrodite density at all three spatial scales and stigma pollen receipt. With increasing floral density, the spatial scale that could explain a majority of the variation in female pollen receipt increased from the local to global scale. The local and intermediate spatial scales for hermaphrodites were able to explain very little of variation in pollen receipt. Most of the hermaphrodite pollen receipt variation can be explained by the global hermaphrodite density.

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Table 1. Characteristics of *Geranium richardsonii* populations studied in 2001 near RMBL.

Population	Census	Date	Area (m ²)	Frequency			Density (m ⁻²)		
				Hermaph flowers	Female flowers	% Female	Hermaph flowers	Female flowers	Total Flowers
PH	1	6/25	120	109	41	27.3	0.908	0.342	1.250
	2	7/9	120	205	127	38.3	1.708	1.058	2.767
	3	7/23	120	58	27	31.8	0.483	0.225	0.708
Aspen	1	7/2	80	197	80	28.9	2.463	1.000	3.463
	2	7/15	80	86	29	25.2	1.075	0.363	1.436
	3	7/30	80	8	2	20.0	0.100	0.025	0.125
RM	1	6/26	56	175	108	38.2	3.125	1.929	5.054
	2	7/10	56	1180	741	38.6	21.071	13.232	34.304
	3	7/24	56	706	354	33.4	12.607	6.321	18.929
Virginia	1	7/3	80	61	89	59.3	0.763	1.113	1.875
	2	7/16	80	37	195	84.1	0.463	2.438	2.900
	3	7/30	80	11	18	62.1	0.138	0.225	0.363

Table 2. The mean stigma pollen receipt ($\pm$ 1 std. dev.) for each sex during each 2001 census for each population.

Population	Census	Pollen Receipt		P	N Plants
		Hemaphrodite	Female		
PH	1	50.8 ($\pm$ 38.1)	19.5 ($\pm$ 15.1)	0.0464	17
	2	48.4 ($\pm$ 39.9)	29.6 ($\pm$ 17.7)	0.0259	90
	3	34.6 ($\pm$ 52.9)	23.0 ($\pm$ 27.1)	0.4029	68
Aspen	1	41.3 ($\pm$ 24.3)	35.7 ($\pm$ 20.4)	0.3652	67
	2	34.8 ($\pm$ 35.8)	35.4 ($\pm$ 37.7)	0.9575	59
	3	4.9 ($\pm$ 7.5)	NO FEMALES	0.5618	9
RM	1	41.4 ($\pm$ 26.4)	37.7 ($\pm$ 23.7)	0.5800	55
	2	106.8 ($\pm$ 63.8)	99.8 ($\pm$ 56.0)	0.6593	92
	3	37.5 ($\pm$ 35.3)	45.5 ($\pm$ 42.4)	0.3731	82
Virginia	1	24.7 ($\pm$ 34.4)	16.3 ($\pm$ 13.7)	0.1550	76
	2	50.1 ($\pm$ 59.5)	22.3 ($\pm$ 16.3)	0.0036	72
	3	10.5 ($\pm$ 11.2)	10.3 ($\pm$ 12.6)	0.9761	29

Table 3. The linear regression results for stigma pollen receipt versus hermaphrodite density at the 0.5m spatial scale and the 2x2m quadrants. There was no 2x2m quadrant data collected for Research Meadow during census 1. * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Population	Census	0.5 m Regression Results						2x2 m Regression Results					
		F			H			F			H		
		R	P-Value	N	R	P-Value	N	R	P-Value	N	R	P-Value	N
PH	1	0.186	0.6595	8	0.471	0.2007	9	0.465	0.2453	8	0.740	0.0227	9
	2	0.128	0.5422	25	0.084	0.5054	65	0.033	0.8767	25	0.053	0.6762	65
	3	0.074	0.7847	16	4.933×10^{-4}	0.9972	52	0.044	0.8713	16	0.045	0.7515	52
Aspen	1	0.283	0.2140	21	0.100	0.5098	46	0.494	0.0228	21	0.105	0.4858	46
	2	0.302	0.2097	19	0.090	0.5806	40	0.754	0.0002	19	0.303	0.0575	40
	3	-----	-----	0	0.183	0.6382	9	-----	-----	0	0.222	0.5665	9
RM	1	-0.134	0.5128	26	-0.043	0.8252	29	-----	-----	-----	-----	-----	-----
	2	0.403	0.0744	20	-0.104	0.3826	72	0.260	0.2692	20	-0.135	0.2592	72
	3	0.342	0.8680	26	-0.052	0.7011	56	0.260	0.1991	26	0.160	0.2397	56
Virginia	1	0.109	0.4974	41	0.286	0.9630	35	-0.153	0.5440	18	-0.020	0.9428	16
	2	0.104	0.4846	47	0.180	0.3894	25	1.420×10^{-4}	0.9992	47	0.390	0.0539	25
	3	0.124	0.0082	19	0.340	0.8258	11	0.588	0.0082	19	0.075	0.8258	11

Table 4. A summary table of the significance of the linear regressions of hermaphrodite density at the 0.5m and 2x2m spatial scales and pollen receipt. + denotes a positive correlation between the variables.

Population	0.5 m			2x2 m		
	N	F	H	N	F	H
PH	3	0	0	3	0	1 (+)
Aspen	3	0	0	3	2 (+)	0
RM	3	0	0	2	0	0
VA	3	1 (+)	0	3	1 (+)	0
Total	12	1 (+)	0	11	3 (+)	1 (+)

Table 5. The standardized partial regression coefficients denoting the contribution that each spatial scale and female frequency makes in explaining the variation in stigma pollen receipt.

Population	Standardized Partial Regression Coefficients				Standardized Partial Regression Coefficients			
	F		H		F		H	
	0.5 m	2x2 m	Total	% F	0.5 m	2x2 m	Total	% F
Aspen	0.272	0.707**	-0.468	-0.033	-0.123	-0.07	0.4*	-0.063
PH	-0.264	0.245	-0.078	0.247	0.034	-0.024	0.266	-0.135
RM	0.286*	-0.064	0.425*	0.244*	-0.076	-0.137	0.517***	0.268**
VA	0.024	-0.05	0.305	0.294*	0.156	0.143	0.006	0.216

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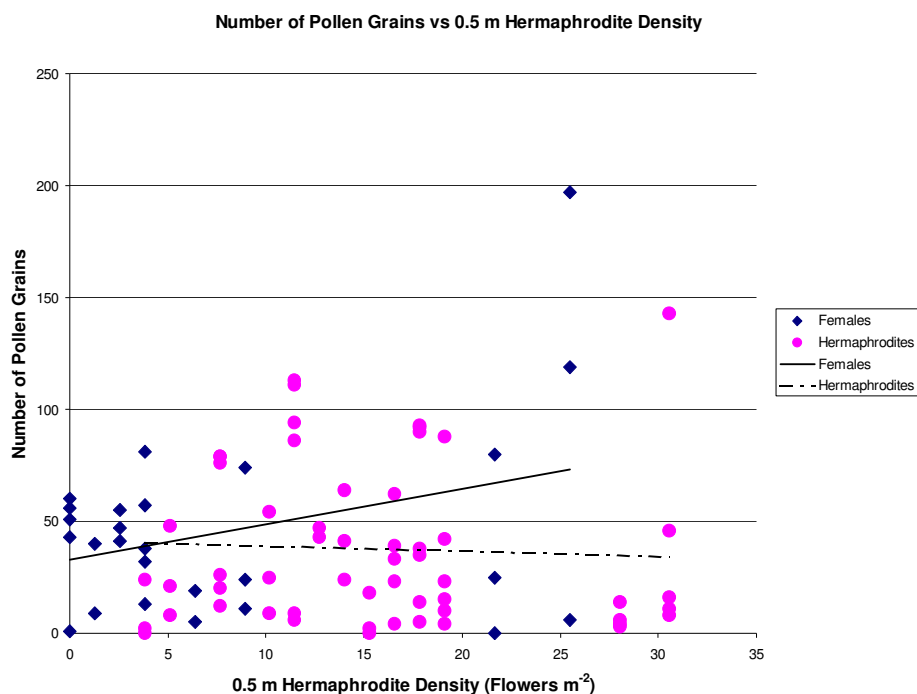


Figure 1. The stigma pollen receipt for each sex compared to the 0.5m hermaphrodite density in Aspen population during census 2. Hermaphrodites: $y = -0.2429x + 41.321$; $R^2 = 0.003$. Females: $y = 1.595x + 32.645$; $R^2 = 0.117$. This is representative of trend of all of the linear regressions for each population census for the 0.5 hermaphrodite density.

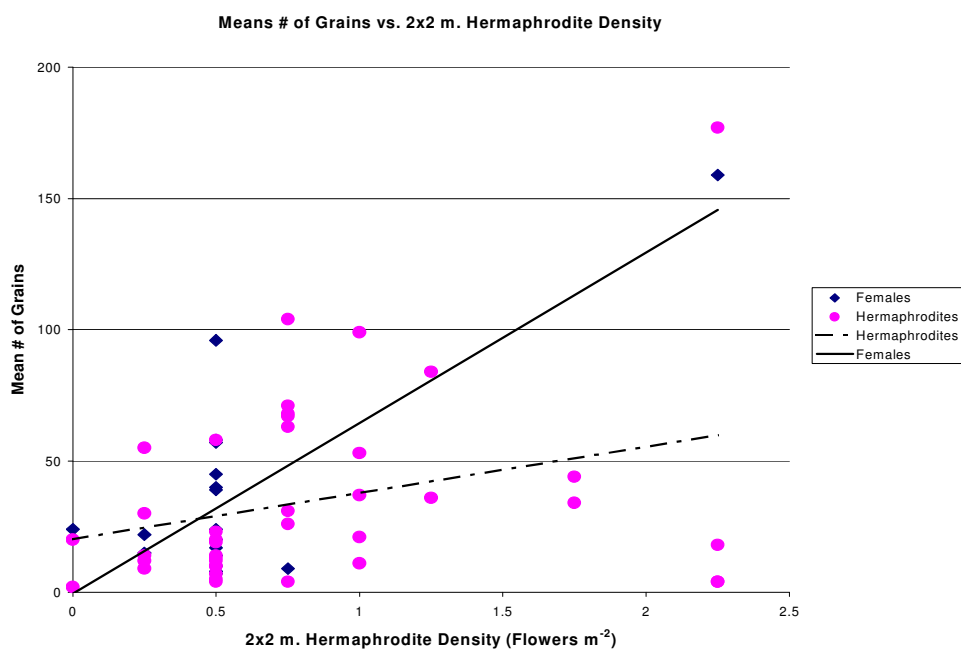


Figure 2. The stigma pollen receipt for each sex compared to the 2x2 m hermaphrodite density in Research Meadow census 3. Hermaphrodites: $y = 17.673x - 20.135$; $R^2 = 0.092$. Females: $y = 64.943x - 0.521$; $R^2 = 0.568$. This is representative of trend of all of the linear regressions for each population census for the 2x2m quadrant hermaphrodite density.

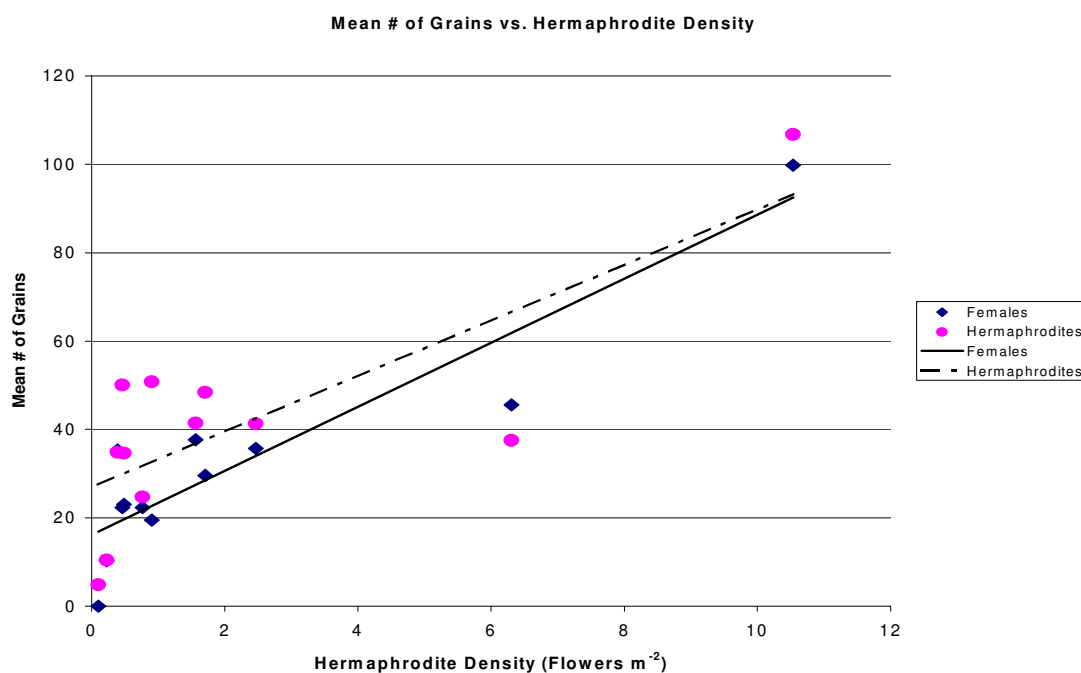


Figure 3. Mean number of grains received by flowers of each sex in populations of varying total hermaphrodite densities in 2001 censuses. Mean number of grains was calculated by taking the average pollen receipt for each sex during each census. Hermaphrodites: $y = 26.867x + 6.307x$; $R^2 = 0.603$. Females: $y = 16.106 + 7.251x$; $R^2 = 0.842$.

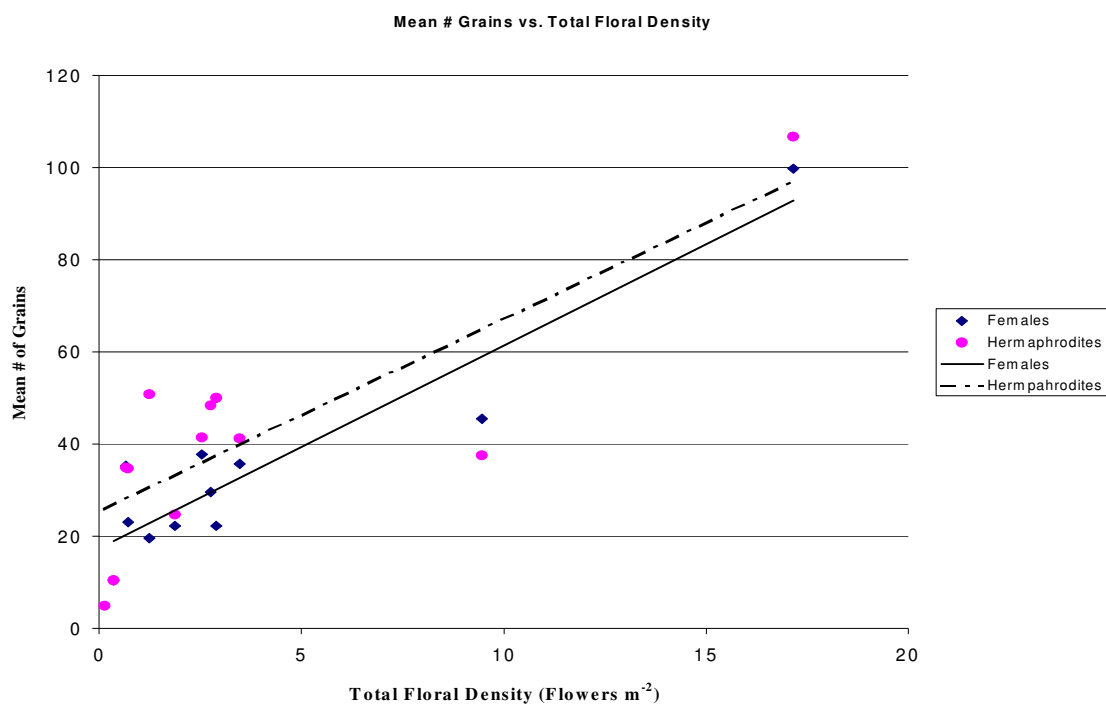


Figure 4. Mean number of grains received by flowers of each sex in population of varying total floral densities in 2001 censuses. Mean number of grains was calculated by taking the average pollen receipt for each sex during each census. Females: $y = 15.053 + 4.6345x$; $R^2 = 0.853$. Hermaphrodites: $y = 25.388 + 4.187x$; $R^2 = 0.658$.

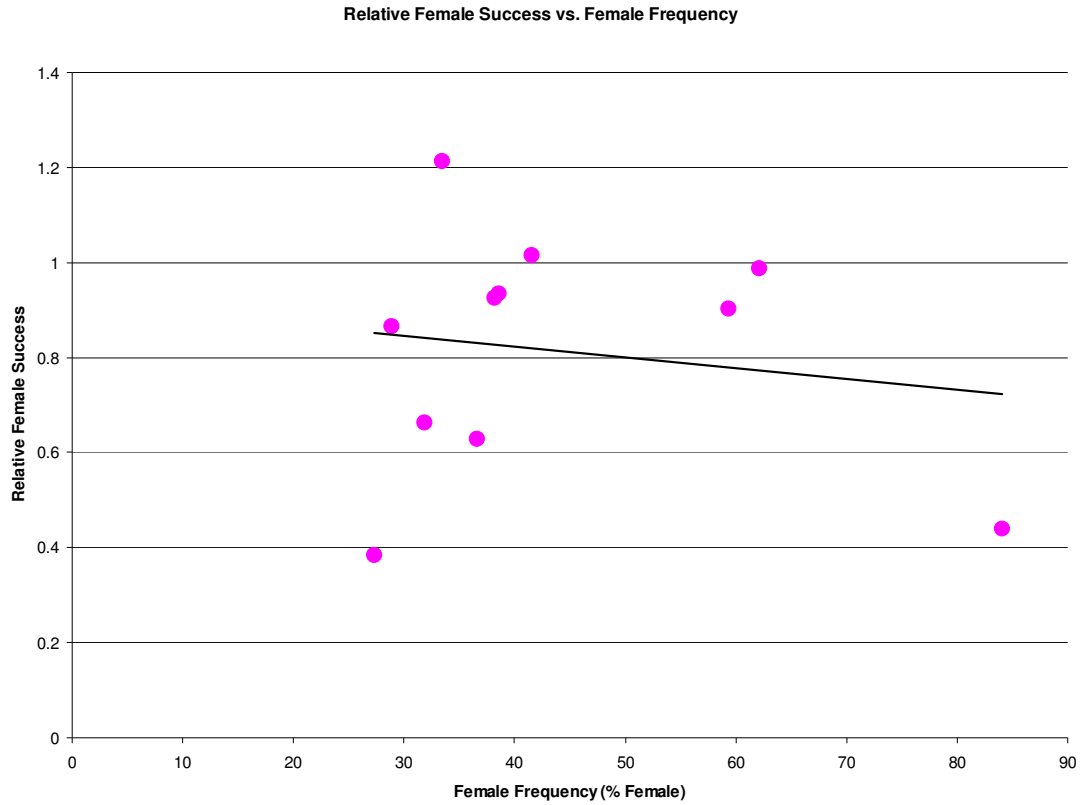


Figure 5. Relative success of female flowers compared to hermaphrodite flowers at receiving pollen in populations of different female frequency in 2001 censuses. Relative female success was calculated as the ratio of mean pollen receipt by female flowers to mean pollen receipt by hermaphrodites in each census. $y = 0.621 + 0.003x$; $R^2 = .026$