The effect of population sex ratio on fitness in the gynodioecious *Geranium maculatum*

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Introduction

Gynodioecy is a breeding system in which female and hermaphroditic individuals coexist within populations. Although only 7% of plant species have this form of sex expression, gynodioecy has been of interest to scientist dating back to Darwin because despite losing half of their potential nuclear fitness, females are maintained within populations.

In order for females to be maintained, they must produce more seeds than hermaphrodites. Many factors influence the relative seed fitness of females including pollen availability, inbreeding depression and pollinator preference. This study focuses on the affect of pollinator preference on female fitness. Because females depend on pollen from other individuals for seed production, pollinator preferences may affect them more than hermaphrodites, who can produce self fertilized seeds. In most species, pollinators prefer the larger flowered, pollen-producing hermaphrodites to females. This may lead to females producing fewer seeds, thereby affecting the maintenance of females.

Pollinator preference itself may be affected by the female frequency. Often in polymorphic species, whether in flower color or sex expression, pollinators specialize on the most common type. In this case, at low female frequencies, females may receive fewer visits, which may decrease their seed fitness while at higher frequencies they receive more. This frequency dependant preference may influence how common females are in populations. To examine the affect of pollinator preference and female frequency on the fitness advantage of females, we created experimental populations with varying female frequencies.

Hypothesis 1: Females will receive fewer visits than hermaphrodites and thus will produce fewer seeds.

Since females produce smaller flowers and no pollen, pollinators will not be as attracted to them, resulting in lower seed production.

Hypothesis 2: Pollinator discrimination will decrease as the female frequency increases, leading to higher seed production.

Since pollinators tend to visit the most common type, as the female frequency increases, so will the relative visitation rate and thereby the seed production.

Materials and methods

Geranium maculatum is a native herbaceous perennial that flowers in early spring. Females have smaller flowers and small, non-functional anthers (Fig 1).

Fig 1. Flowers of hermaphroditic (left) and female (right) individuals.

To test the effect of sex ratio, experimental populations with varying sex ratios were designed. Three sex ratios, 13%, 26% and 42% female, were obtained using plants transplanted from a local population with a sex ratio of ~50%. Thirty one plants were used in each experimental population and randomized among sex ratios after three days of pollinator observations. Each sex ratio was replicated three times. In addition to pollinator observations (~6 hours for each replicate), the flower number, number of seeds, petal size and pollen number were also recorded.

Acknowledgments

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Results

The pollinators: A variety of pollinators were observed - the most common were halictid bees or similar sized insects. Others included carpenter bees, beeflies and butterflies.

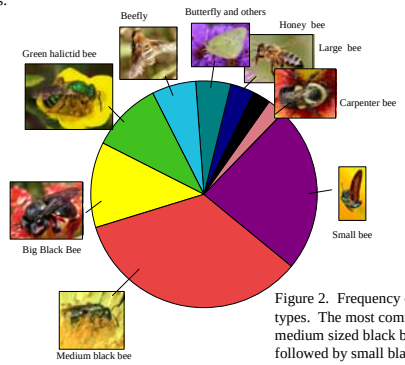
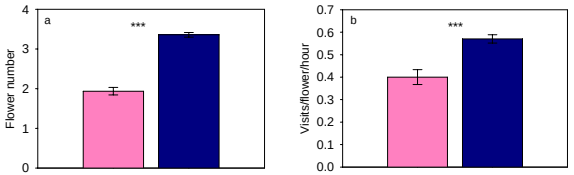


Figure 2. Frequency of pollinator types. The most common were medium sized black bees, followed by small black bees.

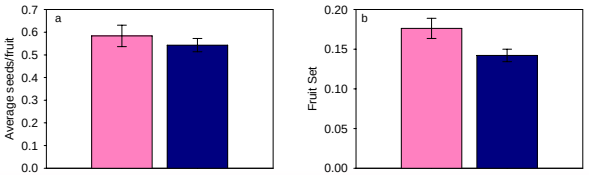
Gender differences: Females produced significantly fewer flowers than hermaphrodites (Fig 3a). As expected, pollinators preferred hermaphrodites, with females receiving ~30% fewer visits (Fig 3b).

Figure 3. Females (pink bars) had fewer flowers (a) and fewer pollinator visits (b) than hermaphrodites (blue bars).



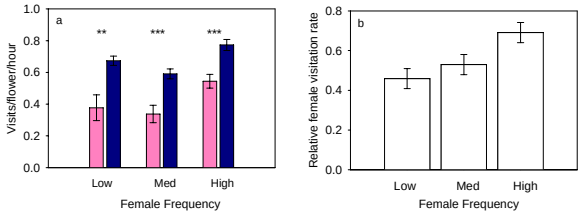
Despite receiving fewer visits, females produced the same amount of seeds per fruit (Fig 4a) and the same percentage of fruit (Fig 4b). The similar seed and fruit production may indicate that females are not pollen limited. The slightly higher fruit set in females may be due to greater resource availability or a lower selfing rate, which may cause fewer fruit abortions.

Figure 4. Females produced the same number of seeds per fruit (a) and developed the same proportion of fruit (b) as hermaphrodites.



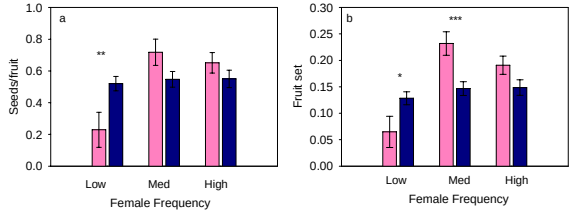
The effect of female frequency: The female frequency did not significantly affect the visitation rate (Fig 5a). However, discrimination against females was slightly stronger at the lowest female frequency compared to the highest female frequency (Fig 5b, p=0.08).

Figure 5. The female frequency did not affect the visitation rate (a), however as the female frequency increased, females received proportionally more of the visits (b).



Although the visitation rate did not differ, the seed and fruit production were affected, at least for females (p=0.0001, p=0.0042 respectively). Females at the lowest female frequency produced fewer seeds (Fig 6a) and fewer fruits (Fig 6b) than at the higher female frequencies.

Figure 6. Females at the lowest female frequency produced significantly fewer seeds (a) and fewer fruits (b) compared to the medium and high female frequency.



Conclusions

As hypothesized, females received fewer visits from pollinators. This however did not result in fewer seeds being produced. This indicates that female seed production is not pollen limited. The expected decrease in seed production may occur in times where there are fewer pollinators or a more limited supply of pollen.

The female frequency did not significantly affect pollinator preference though there is some evidence that discrimination against females is especially pronounced at the lowest female frequency. Although there was little difference in visitation rate, the seed set and fruit set were affected. At the lowest female frequency, females produced significantly fewer seeds and fruits. The cause of this result is not clear and will be investigated further.

This study suggests that pollinator discrimination does not affect the seed production of females, as long as pollinators and pollen are abundant. However, at lower female frequencies, discrimination against females may be strong enough that females suffer a reduction in seed production. This suggests that in order to become established in a population, females must compensate for the effect of pollinator discrimination through another means.

While this study isolates the affect of pollinator preferences, it demonstrates that the maintenance of females in populations is influenced by many factors. Other factors must play a part in the establishment and maintenance of females. Several other factors are currently being studied including the effect of flowering frequency, life span and clonality, the effect of sex ratio on selfing rate, and population genetic structure.