Maintenance of a deceitful reproductive strategy in *Begonia involucrata* by a male-biased sex ratio

Justin E. Campbell, Rafael D. Rosengarten, and Dora J. Sugar

Abstract: Begonia involucrata is a monoecious perennial herb that has rewardless female flowers that mimic the pollen-producing male flowers. We quantified the male-biased sex ratio among open flowers, and showed that this ratio is maintained across inflorescence generations. We counted the number of open flowers, large buds, small buds, and seeds on 291 inflorescences, and distinguished florets as being male or female. Open male flowers were three times more abundant than open female flowers in the current and next generation. Though male and female florets are initially produced in equal numbers, maintaining a male-biased sex ratio of mature florets may confer a benefit of increased pollination.

Key Words: bee pollinator, deceit, Monteverde, reproductive strategy

Introduction

Begonia involucrata is a monoecious perennial herb that has rewardless female flowers that mimic the pollen-producing male flowers. Pollinating bees are deceived into visiting the female mimics because their stigmas resemble the male anthers and they produce identical odors (Ågren and Schemske 1991). For the mimicry to succeed, the mimic flower must be less common than its model. *B. involucrata* accomplishes this inequality through delayed development of its monoecious flowers. Male flowers of *B. involucrata* develop before female flowers and have a longer phase as a mechanism to keep reward flowers more abundant (Ågren and Schemske 1991). We quantify the male-biased sex ratio of open flowers, and demonstrate that this bias is stable across inflorescence generations.

Methods

We sampled begonias along all trails at the Monteverde site. Each flowering plant was categorized as solitary or within a patch (3 or more plants), and we counted the number of inflorescences, open flowers, large buds, small buds, and seeds. We distinguished each flower and bud as being either male or female. We counted 291 inflorescences from 15 solitary plants and 12 patches. Large buds were assumed to represent the next generation of open flowers. We calculated the sex ratio of open flowers in the current and the next generation, and determined the replacement probabilities of male, female, and mixed inflorescences using a chi-squared contingency table.

Results

Open male flowers were three times more abundant than open female flowers in the current (paired-t = 4.96, df = 290, P = 0.0001) and next generation (paired-t = 8.44, df =208, P = 0.0001; Fig. 1). The sex ratio in the next generation was not significantly different from that of the current (paired-t = 0.44, df = 11, P = 0.67). The sex ratio did not differ significantly between patch plants and independent plants for either the current generation (t = -0.31, df = 238, P = 0.76) or the next generation (t = 0.70, df = 236, P = 0.48). Fifty-seven percent of current inflorescences had all male open florets, 18% had all female, and 25% were mixed (Fig. 2). Sexes of inflorescences change non-randomly over time; males either remain male or become female or mixed, and females either remain female or go to seed (χ^2 = 97.6, df = 291, P = 0.0001; Fig. 2).

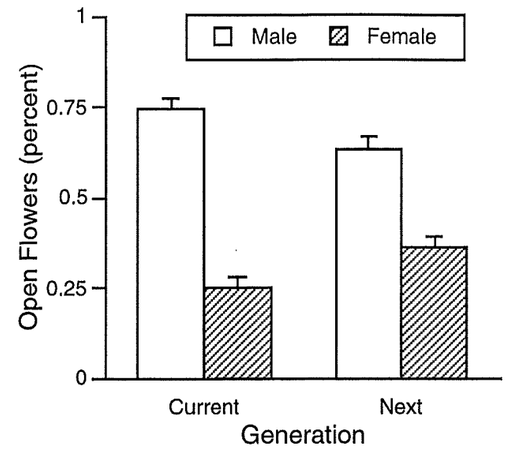

Fig. 1. A greater proportion of open flowers, averaged across all inflorescences, are currently male. The next generation of open flowers will also be male-biased. (Means ±1 SE, n = 291).

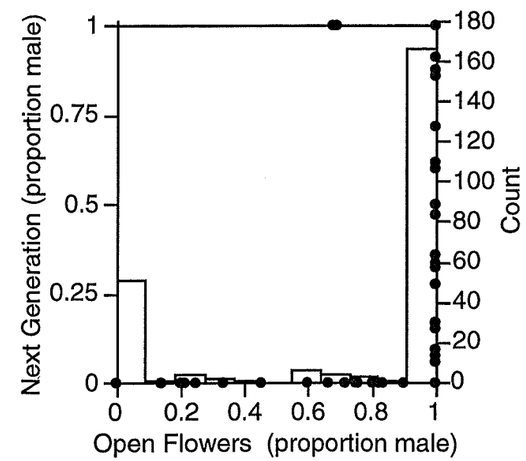

Fig. 2. All-male inflorescences may be all-male, all-female, or mixed in the next generation. Points represent the proportion of open flowers on an inflorescence that are currently male and the proportion that will be male in the next generation. The histogram shows the number of all-male, all-female, and mixed-gender inflorescences for open flowers.

Discussion

Begonias may be genetically constrained to produce equal ratios of immature male and female florets but have evolved other mechanisms to maintain a male-biased sex ratio of its open florets. Ågren and Schemske (1991) found an even sex ratio in inflorescence buds. We quantified a male-biased ratio that was stable over two generations. This result is consistent with the assumption that in a deceit system, the mimic must be rarer than the model in order for the pollinator to continue visiting similar flowers.

We showed that inflorescences with all-male open florets will either remain all-male or begin the transition to all female, whereas all-female inflorescences are terminal and will either remain female or go to seed. Ågren and Schemske (1991) suggest that for the success of *B. involuncrata*'s deceit system, the female phase of an inflorescence should be short relative to the male phase, to reduce the time pollinators have to learn the position of the rewardless females. The spatial turnover of females, resulting from buds opening and maturing at different times, may help maintain the unpredictability of their location to pollinators.

We are interested in the fate of the immature female florets that initially equal males in number. If all florets eventually mature, then the sex-ratio must become female-biased at the end of the flowering season. This would result in a drastic decline in pollination success in the last generation. Alternatively, female florets may have high mortality before maturation. The benefit of increased pollination by maintaining the male-biased sex ratio may outweigh the cost of dropping immature flowers. Future research could reveal the duration of the male-biased sex ratio. Also, comparison with other *Begonia* species may show the sex ratio found in *B. involuncrata* exists across the genus, and potentially in other taxa with similar deceit strategies.

Literature Cited

Ågren, J., and D. W. Schemske. 1991. Pollination by deceit in a neotropical monoecious herb, *Begonia involucrata*. Biotropica 23(3): 235-41.