Weakening selection by pollinators for large corollas in an alpine wildflower, *Polemonium viscosum*

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Introduction

- The sweet-smelling morph of *Polemonium viscosum* is pollinated by large, long-tongued bumblebee queens.[1]
- Historically, larger sweet-smelling flowers were favored by bumblebees, having higher seedset than smaller flowers.[2]
- However, warming temperatures in Colorado alpine meadows are favoring smaller bumblebees with wider diet breadth.
- These shifts in bumblebee morphology may influence the strength of selection for flower size, which is a heritable trait, in sweet-smelling *Polemonium viscosum*.

Methods

1. We surveyed six populations of *Polemonium viscosum* across two habitats on each of three mountains in the central Colorado Rocky Mountains in 1985 and 2017 (Fig. 1A).
2. Floral measurements (Fig. 1B) were recorded from fresh flowers of sweet and skunky scent morphs for a total of 53 and 67 individuals for 1985 and 2017, respectively. Skunky morph flower size is smaller than that of the sweet morph, driven by ant predation and drought prevalence at lower altitudes where skunky individuals are more common. We would not expect bumblebee driven evolutionary change in the skunky morph; therefore, it acts as a control for potential direct effects of climate on flower size.

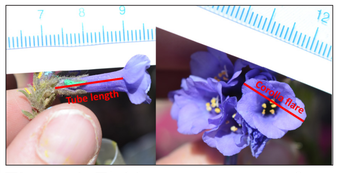


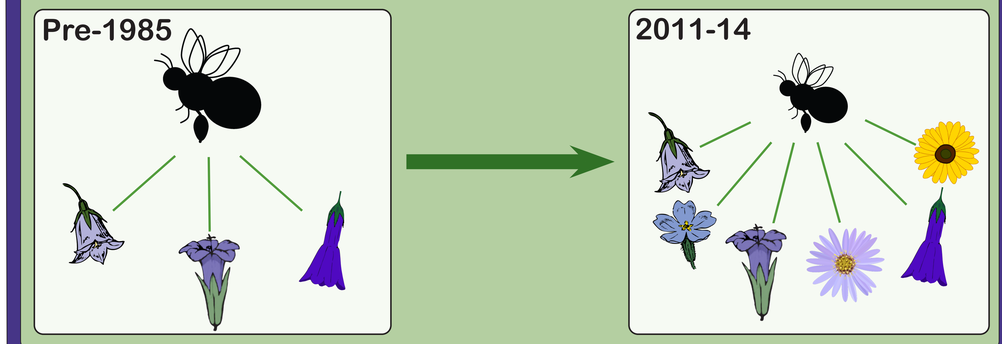
Figure 1. Field measurements of flower size (A) and locations of the surveyed *P. viscosum* populations in the Colorado Rocky Mountains (B).

3. All seeds produced per individual were counted upon maturation to measure reproductive success. To test for a current (2017) selection regime, we regressed seed set on flower size (PC1 of corolla flare, tube length, lobe length, lobe width) using a mixed effects analysis of covariance via *lme* in the R package 'nlme' with scent morph and flower size as fixed effects and site and habitat as random effects.
4. In 2017, we used pollen supplementation experiments to test if the plants were pollen-limited (N = 11 and 9 supplemented and N = 19 and 24 controls in the skunky and sweet morphs, respectively). Seeds were counted following fruit maturation.
5. We then tested for a change in flower size using fresh flower measurements collected in 1985 and 2017 via linear mixed effects models with scent morph and year as fixed effects and site and habitat as random effects.

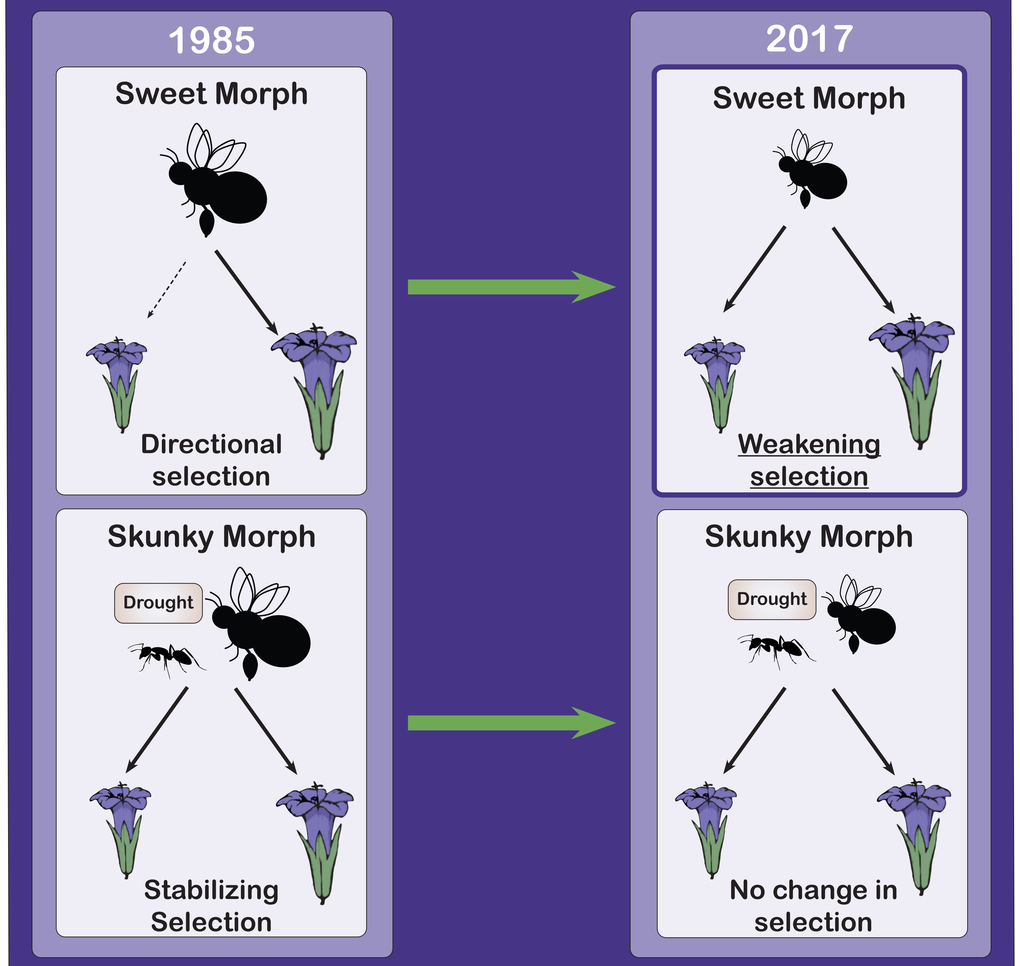
Citations:

[1] Galen, C. (1989). *Evolution*, 43(4), 882–890.
[2] Galen, C., Zimmer, K. A., & Newport, M. E. (1987). *Evolution*, 41(3), 599-606.
[3] Miller-Struttmann, N. E., Geib, J. C., Franklin, J. D., Kevan, P. G., Holdo, R. M., Ebert-May, D., ... & Galen, C. (2015). *Science*, 349(6255), 1541-1544.

Background: Warming has led to smaller alpine bumblebees that forage across more diverse floral morphologies (shallow & deep flowers)[3], with potential consequences for flower size evolution.



Hypothesis: As alpine bumblebees have become smaller and more generalized, they favor smaller flowers in the sweet morph of *Polemonium viscosum*, weakening historical selection regimes.



Selection is no longer favoring large flowers of *Polemonium viscosum*.

Results

- In 2017, neither scent morph of *P. viscosum* was pollen limited (Fig. 3), and indiviudal seedset was relatively high.

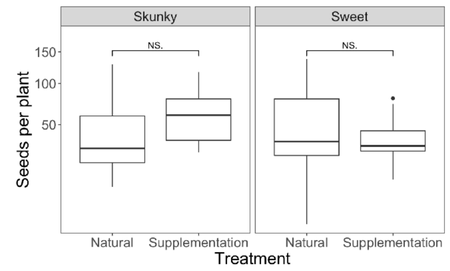


Figure 2: All *P. viscosum* individuals sampled in 2017 had similar seedset - both those that were pollen-supplemented and those left open to natural pollination (sweet morph: $F_{1, 28} = 0.74$, $p = 0.40$; skunky morph: $F_{1, 21} = 2.64$, $p = 0.12$).

- Unlike historical patterns, reproductive success (i.e., seedset) does not increase with flower size for the sweat morph, indicating weakening selection for large flowers.

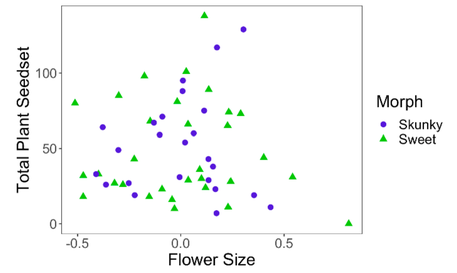


Figure 3: Flower size had no significant relationship with total plant seedset in *P. viscosum* individuals of either scent morph sampled in 2017 (sweet morph: $F_{1, 26} = 0.17$, $p = 0.68$; skunky morph: $F_{1, 20} = 0.010$, $p = 0.92$).

- As predicted, sweet smelling flowers were smaller in 2017 relative to 1985, whereas skunky morph flower size has not changed.

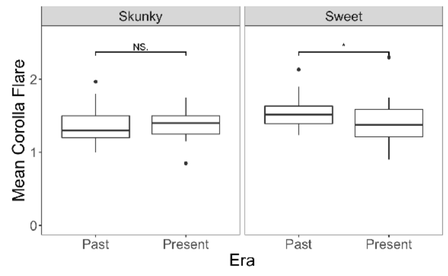


Figure 4: Flowers of the sweet morph significantly decreased in mean corolla flare, while flowers of the skunky morph did not change in size (interaction between era and scent morph: $F_{1, 111} = 6.3834$, $p = 0.0129$).

Discussion

- Flower size in the sweet smelling morph of *P. viscosum* is decreasing, as predicted if smaller bees are foraging more broadly and no longer favoring large flowers.
- While selection for large flowers is weakening, it has not reversed direction, indicating other factors may favor smaller flowers. For instance, ant predators, which are known to favor smaller, narrower flowers in *P. viscosum*, may have a more prominant role in the current evolutionary landscape experienced by the sweet smelling flowers. Alternatively, alpine environments are resource-limited and may experience more frequent droughts with climate change.
- Future studies should investigate these alternative hypotheses to determine the underlying mechanims favoring smaller flowers in *P. viscosum.* Additional changes in selection regimes on flower size over a larger number of years is required to predict the long-term trajectory of evolutionary change in flower size.

Acknowledgments

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