

Observational Support for Reduced Herbivory in the Perfoliate Bracts of *Mimulus glaucescens* (Shield-bracted Monkeyflower)

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Introduction

Mimulus glaucescens (syn. Erythranthe glaucescens) is a regional endemic plant restricted mainly to Butte and Tehama Counties in northern California, and it is aptly named the shield-bracted monkeyflower to describe its unique perfoliate leaf morphology. Perfoliation describes leaves that are completely fused around the stem, creating a cup or disk shape, and it has evolved independently in numerous other plant species, such as in miner's lettuce (Claytonia perfoliata) or honeysuckles (Lonicera sp.). Since perfoliate bracts are produced after a plant species has transitioned to flowering, and generally subtend developing flowers or inflorescences, researchers have hypothesized an adaptive function for a physical plant defense mechanism against floral herbivory. In accordance with the optimal defense hypothesis, researchers have previously hypothesized that perfoliate bracts serve to impede or restrict movement by crawling herbivores, providing extra protection to the high fitness-value reproductive organs.

A study on *Mimulus glaucescens* by Katherine Toll, 2023 found that perfoliate bracts had lower probabilities of herbivory than basal leaves and could deter crawling herbivores, such as caterpillars, from reaching the floral apex of the plant. In concurrence with the findings from Toll 2023, preliminary results from this field study find observational support that perfoliate bracts experience reduced herbivory in *Mimulus glaucescens*.



Figure 1. Image from Toll 2023 showing observed within-plant variation in herbivory in *M. glaucescens.*

Study System

Mimulus glaucescens is an annual plant in the 'yellow monkeyflower' species complex, and it is known only from the foothills of the southern Cascade Range and adjacent northern Sierra Nevada. Seedlings begin to emerge in the winter, where a rosette of basal, petiolate leaves form initially. In early spring, M. glaucescens begins bolting and transitions to flowering, where it produces perfoliate inflorescence leaves (perfoliate bracts) and glaucous epicuticular leaf waxes on the stem and perfoliate bracts.

Species in the 'yellow monkeyflower' complex can share herbivores including *Mimulus* specialist caterpillars of the variable checkerspot (*Euphydryas chalcedona*) and the closely related common buckeye (*Junonia coenia*) (Toll 2023). These caterpillars usually feed primarily on reproductive structures and are commonly found spending time near the apices of *Mimulus* plants (Toll 2023).

Methods

 Resurvey dozens of CSU Chico Ahart Herbarium M. glaucescens records to find study populations.

- In spring 2024, collected plant trait and herbivore data of *Mimulus glaucescens* spanning an elevation gradient across its range. Surveyed 30-50 plants from 10 populations with low elevation sites (0-1,000 ft) near Upper Bidwell Park, middle elevation sites (1,001-2,000 ft) near the Big Chico Creek Ecological Reserve, and high elevation sites occurred up to 4,000 feet elevation into the Sierra foothills.
- On each plant, record presence/absence of herbivore damage, and categorize damage as general chewing/caterpillar, aphid, leaf miner, spittle bug and record location of damage (basal rosette leaves, perfoliate bract, floral).
- Subset plants with herbivore damage and perform Chi-square test to determine if plant organs (rosette, bracts, or flowers) differ in their proportion of damage.

Results

Plant organs differed in the proportion of herbivore damage received. Perfoliate bracts had significantly less damage than rosette leaves and flowers χ2(df = 2,N = 173)=23.7, p<0.0001. Rosette leaves and flowers had roughly equivalent incidents of herbivory; of the plants with herbivore damage present, 54% and 56% had rosette and/or floral damage, respectively. Only 32% of plants sustained damage to perfoliate bracts.

Figure 2. Herbarium record of *M. glaucescens* showing basal rosette leaves and perfoliate bracts.



Conclusions

Similar to the findings from Toll 2023, this study shows observational support for reduced herbivory in the perfoliate bracts of *M. glaucescens*. Toll collected herbivory and leaf type data from 5 *M. glaucescens* populations in the field and fit the data in a binomial mixed model. Across all 5 populations, perfoliate bracts had a lower probability of damage than basal leaves. Toll performed an additional comparison with the co-occuring monkeyflower species, *Mimulus nasutus*, which lacks perfoliation, to show that variation in herbivory was due to perfoliate bracts and not plant developmental timing. Reiterating the Toll 2023 findings, this Chi-square analysis shows perfoliate bracts sustained significantly less herbivory, while basal rosettes and flowers had roughly equivalent rates of herbivory.

Glaucous wax secretion has been implicated in anti-herbivore defense in other plant species, which could be a driving factor in the reduced herbivory on perfoliate bracts. Perfoliate bracts may have an adaptive function to deter floral herbivory by crawling herbivores as the plant transitions from growth to reproduction. For example, the turnip sawfly (*Athalia rosae*), a specialist on Brassicaceae, feeds on leaves during early instars but later moves to flowers (Wetzel et al. 2023). Additionally, variable plant environments challenge the behavioral and information-processing abilities of whiteflies and other herbivores in ways that lead to reduced herbivore performance and increased vulnerability to predators (Wetzel et al. 2023). Perfoliation may increase the variability and complexity of the plant habitat, reducing herbivore performance and deterring floral herbivory.

References

Toll, K. 2023. Perfoliate Leaves Reduce Herbivory in the Shield-Bracted Monkeyflower (*Mimulus glaucescens*). *Ecology* 104(1): e3876.

Wetzel, W.C., Inouye, B.D., Hahn, P.G., Whitehead, S.R., Underwood, N. 2023. Variability in plant-herbivore interactions. *Annual Review of Ecology, Evolution, and Systematics*, 54, 451-474.