Fitness consequences of divergent selection on clonal reproduction in a perennial plant

Kaitlyn Dawson

PI: Dr. Jannice Friedman
Department of Biology, Queen's University, Canada
First year MSc student

Affiliated sections within BSA: Ecological, Genetics

Abstract
Most plants can reproduce both sexually and clonally, and the maintenance of dual strategies remains a fundamental dilemma in evolutionary biology. Because organisms have finite resources, investment in clonal reproduction is likely to trade off with investment in sexual reproduction. While it is well-established that the optimal balance between strategies favoured by natural selection depends on local environmental conditions, the fitness consequences and evolutionary outcomes of altering reproductive strategies are less clear. The goal of this study is to quantify selection and the fitness consequences of manipulated investment in divergent reproductive strategies using the plant *Erythranthe guttata*. This predominately outcrossing species reproduces sexually via seed and clonally via horizontal vegetative shoots called stolons. Here, I will measure selection and fitness in a common garden in the natural environment in California by growing lines of *E. guttata* that have been subjected to five generations of divergent selection for high or low stolon number. Throughout the summer, I will measure components of individual fitness to estimate the strength of selection on stolon number. Understanding the fitness consequences of differential investment in clonal reproduction will help inform how plants within a population can shift reproductive strategies and patterns of allocation under heterogeneous or changing environmental conditions.

Background
A central goal in evolutionary biology is to understand how organisms adapt to changing environmental conditions. Abiotic conditions can have strong effects on life history strategies. In plants, one of the most dramatic changes in life history strategies is observed through differential allocation to clonal versus sexual reproduction. Vegetative clonal reproduction provides an immediate benefit for colonization and persistence, but sexual reproduction increases genetic variation among offspring and seeds can escape harsh conditions, both of which are favourable in heterogeneous environments (Lei et al., 2010; Smith & Maynard-Smith, 1978). Because these strategies are thought to compete for limited resources, investment cannot be maximized for both clonal and sexual reproduction (Stearns, 1989). It has been demonstrated that the balance between clonal and sexual reproduction favoured by natural selection strongly depends on local ecological conditions (Zhang et al., 2023). That said, very few studies have investigated how selection on reproductive traits affects fitness in nature which is crucial to understanding how populations will respond to a rapidly changing and heterogeneous environment.

Here, I aim to quantify selection on plant reproductive strategies in natural conditions. A challenge of quantifying selection in nature is that the pool of traits present in a natural population is a relic of past selection (Endler, 1986). I will resolve this issue by reintroducing plants that experienced selective breeding in a greenhouse back into their native environment. Over five generations, plants from a single population were selected for either high or low investment in clonal reproduction (Steinecke, 2023). By using artificial selection lines, I know the previous targets and strength of selection (Connor, 2003). Furthermore, it would be impossible to investigate selection on reproduction if the population does not include adequate phenotypic variation. With artificial selection, I can create individuals that display broader variation in reproductive traits than seen in the founding population yet using the existing standing genetic variation (Walsh & Lynch, 2018). Returning these individuals to their natural environment will reveal how selection on different reproductive modes affects fitness.

Methods

To examine the fitness consequences of selection on clonal reproduction I will grow artificial selection lines of a perennial plant, *Erythranthe guttata* (syn: *Mimulus guttatus*) in a common garden field experiment. *Erythranthe guttata* is a predominantly outcrossing species that reproduces sexually via bee-pollinated flowers and clonally via horizontal vegetative stems called stolons. Stolons are key for perennials because they root in the soil and form overwintering rosettes (Demarche et al., 2016; Friedman et al., 2015). In the spring, I will plant seed from plants that have been subjected to five generations of directional selection for either high or low stolon number (Figure 1). I will plant individuals from replicate high, low, and control selection lines (N = 4000 plants) in Sequoia National Forest, California and monitor plants throughout the summer. By returning plants to their native environment, I can measure selection and fitness consequences of divergent reproductive strategies.

I will use three approaches to broadly estimate the strength and type of selection. First, I will determine whether the high and low artificial selection groups differ in total fitness. I will use a composite measure of fitness that incorporates sexual (e.g., flower number, flower size) and clonal traits (e.g., stolon number, stolon length). Next, I will test whether individuals with greater stolon investment survive longer than those with lower investment. To do this, I will record survival throughout the summer and measure overwinter survival by returning to the field site in the following spring and recording the presence and size of new rosettes. Finally, to explore whether investment in clonal reproduction decreases investment in sexual reproduction, I will test if plants that produce more stolons also tend to make fewer flowers and look for evidence of correlational selection. In addition to measuring plant phenotypic traits, environmental data on soil moisture, precipitation, and temperature will be collected throughout the growing season to quantify habitat heterogeneity.

Significance

This study will employ a novel methodological approach that compares artificial selection lines in a natural environment. Using artificial selection lines allows for fitness estimates on a broader range of phenotypes that may not be present in the source population, and yet still uses the existing standing genetic variation. This experimental design allows me to investigate a longstanding yet fundamental question of how and why natural selection has maintained variation in reproductive strategies within a single population.

Quantifying the direction and strength selection of selection on clonal reproduction in nature will also provide valuable insight into species conservation amidst an era of rapid environmental change. In western North America, less winter precipitation is falling as snow, and snowpack is melting earlier in the spring, substantially reducing water available to terrestrial ecosystems during the dry summer months (Overpeck & Udall, 2020). Such rapidly changing soil moisture patterns are likely to impose strong natural selection for altered growth and reproduction on plant species. Assessing the fitness consequences of altering life histories using *E. guttata* can inform how populations may respond to these shifting environmental conditions.

Budget

Description	Cost (USD)
Equipment Tools used for common garden experiment (soil moisture probes, plant tags, calipers, rulers)	$200
Accommodations Camping fees at Sequoia National Forest	$1280 ($32/night × 5 nights/week × 8 weeks)
Total	$1500

Figure 1. Image contrasting *Erythranthe guttata* that has been selected for high stolon number (left) and low stolon number (right). Stolons are horizontal stems that grow along the soil and form roots.

Bibliography

Connor, J. K. (2003). Artificial selection: a powerful tool for ecologists. *Ecological Society of America*, 84, 1650–1660. https://doi.org/10.1890/0012-9658(2003)084[1650:ASAPTF]2.0.CO;2

DeMarche, M. L., Kay, K. M., & Angert, A. L. (2016). The scale of local adaptation in *Mimulus guttatus*: comparing life history races, ecotypes, and populations. *New Phytologist*, 211, 345–356. https://doi.org/10.1111/nph.13971

Endler, J. A. (1986). *Natural Selection in the Wild*. Princeton University Press.

Friedman, J., Twyford, A. D., Willis, J. H., & Blackman, B. K. (2015). The extent and genetic basis of phenotypic divergence in life history traits in *Mimulus guttatus*. *Molecular Ecology*, 24, 111–122. https://doi.org/10.1111/mec.13004

Lei, S. A. (2010). Benefits and costs of vegetative and sexual reproduction in perennial plants: a review of literature. *Journal of the Arizona-Nevada Academy*, 42, 9–14. https://doi.org/10.2181/036.042.0103

Overpeck, J. T., & Udall, B. (2020). Climate change and the aridification of North America. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 11856–11858. https://doi.org/10.1073/pnas.2006323117

Smith, J. M., & Maynard-Smith, J. (1978). *The evolution of sex* (Vol. 4). Cambridge: Cambridge University Press.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3, 259– 268. https://doi.org/10.2307/2389364

Steinecke, C. (2023). *Selection and genetic constraints on clonal investment in a perennial plant*. [Master's thesis, Queen's University, Canada]. ProQuest Dissertations Publishing.

Walsh, B. and Lynch, M., (2018). *Evolution and selection of quantitative traits.* Oxford University Press.

Zhang, H., Chen, S.-C., Bonser, S. P., Hitchcock, T., & Moles, A. T. (2023). Factors that shape large-scale gradients in clonality. *Journal of Biogeography*, *50*, 827–837. https://doi.org/10.1111/jbi.14577

Biogeographical sketch – Kaitlyn Dawson

EDUCATION

Master of Science student, Queen's University Biology Department. **Sept 2023 – present**
Bachelor of Science, Honours, Queen's University, Kingston, ON **2019 – 2023**

- Earned Dean's list recognition for every term completed, with a cumulative GPA of 3.83 on a 4.3 scale.

WORK EXPERIENCE

Teaching assistant, Department of Biology, Queen's University **Sept 1 2023 - present**
BIOL 212 – Scientific methods in biology

- Facilitated three-hour lab sessions per day for three course sections.
- Graded lab activities and reports for 50 students.

BIOL 343 – Advanced statistics for biologists

- Marked 30 assignments on a weekly basis for four months.
- Assisted in weekly tutorials to help students with statistical analyses in R-Studio

Student mentor, Queen's University Desert Ecology Field Course **May 1 – May 14, 2023**

- Participated as a student leader on a two-week long desert ecology field course through the Ontario Universities Program in Field Biology (OUPFB) in California and Arizona, USA.
- Led class exercises and group research projects to investigate biological hypotheses concerning desert wildlife.

Field/Lab Technician, Eckert Lab, Queen's University **May-Sept 2022**

- Worked under the supervision of a master's student to execute controlled greenhouse experiments.
- Duties consisted of data collection and entry, counting seeds, performing experimental crosses, and assaying various components of plant growth and reproduction.

CONFERENCE PRESENTATIONS

"Using viral-induced flower colour change to study turnip mosaic virus prevalence in *Hesperis matronalis*," *Joint Annual Meeting of the Canadian Society for Ecology and Evolution and the Canadian Botanical Association.* Winnipeg, Manitoba. June 2023.
"Viral-induced flower colour change reveals that turnip mosaic virus increases with stand size and human disturbance in *Hesperis matronalis*," *53rd Ontario Ecology, Ethology, and Evolution Colloquium*. London, Ontario. May 2023

AWARDS

Best student talk award, 2023 CSEE-CBA Meeting in Winnipeg, MB **June 2023**

- Awarded a $600 prize at the joint meeting of the Canadian Society for Ecology and Evolution (CSEE) and the Canadian Botanical Association (CBA) for my podium talk discussing my undergraduate Honours thesis project.

VOLUNTEER EXPERIENCE

Peer Advisor, Peer Academic Support Services, Queen's University, Kingston, ON **Dec 2022- April 2023**

- Volunteered once a week as an advisor for a first-year academic advising service.
- Responded to questions about academic policies and program selection and provided referrals to additional resources and support services.

PROFESSIONAL DEVELOPMENT

Anti-oppression in STEM workshop, Queen's University **September 25th, 2023**