

Impacts of climate change on the maintenance of gynodioecy: the pattern, mechanism, and demographic processes underlying population level sex ratio

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Research Proposal

Abstract: One area that has confounded scientists since the 1800's^{1,2} is the maintenance of gynodioecy, a mating system characterized by female and hermaphrodite individuals. While hermaphrodite plants can contribute offspring through both seed and pollen, females only contribute genes to subsequent generations through seed production. Hermaphrodites also have the capacity to self-fertilize, allowing reproduction when the population density is low, or pollen is limited. On the other hand, females avoid inbreeding, and may have an advantage where resources are limited. Since these factors vary with environmental conditions¹, the relative fitness of each sex may also vary across species' ranges. The operational sex ratio (OSR; hermaphrodite:female) has been related to both abiotic (geographic patterns and climate severity) and biotic (pollinator availability) conditions in several species with forms of dioecy³⁻⁶. Given that climate change is shifting many aspects of local environments, populations of gynodioecious species could be indirectly influenced through sex-specific responses to environmental change⁴. I will address these questions in *Silene acaulis* (Caryophyllaceae) by examining the pattern of OSR, identifying the underlying mechanisms driving OSR, investigating the influence of OSR on demographic dynamics, and examining how climate differentially affects the fitness of female and hermaphrodite individuals.

Conceptual Background: *Silene acaulis* is a long-lived, gynodioecious, cushion plant, with a range spanning the arctic and alpine tundra of North America, Europe, and Eastern Russia. Females in this species consistently produce more and higher quality offspring than hermaphrodites^{1,7} though the mechanism driving this advantage is not clear. Females reallocate resources from pollen production to produce more flowers and fruit^{1,8-10} and seeds with higher establishment rates than hermaphrodites¹. However, there is no evidence that seed provisioning differs between females and hermaphrodites⁸ or that seed quality is fully explained by inbreeding depression in hermaphrodites¹. Differences in seed establishment have instead been attributed to the timing or quality of pollen receipt^{1,11}, and other unknown differences in seed quality^{1,8,9}. No study has linked the magnitude of these effects to sex ratio differences in natural populations and climate conditions. In Alaska (cold and wet), female *S. acaulis* plants have four times the lifetime reproduction as hermaphrodites⁷, while studies in more southern areas found that female reproduction was only two or three times that of hermaphrodites^{1,10}.

Regardless of the mechanisms underlying sex-specific fitness differences, the (OSR) in *Silene acaulis* has been related to elevation¹² and latitude³ in Sweden and Norway respectively. Variation in OSR indicates the potential for sex-specific niche differentiation. As of yet, there are no studies in North America on the broad patterns of OSR variation in *S. acaulis*. In pilot studies, I used citizen science data and a field survey to establish preliminary patterns in OSR. Using over 4,500 iNaturalist images, I identified a stark geographic pattern in which female occurrence increases with latitude. In field surveys, I found a corresponding trend where female frequency increases with elevation at Niwot Ridge, Colorado Rockies. Given that OSR varies with latitude and elevation, what are the demographic consequences and the abiotic or biotic variables driving this broad geographic pattern?

Demographic modeling in plants rarely includes sex, despite the power of this approach for linking sex-specific environmental responses to patterns of population dynamics, OSR, and even range shifts. For example, Petry et al⁴. found that sex-specific differences in water use efficiency for a dioecious species were driving elevational shifts in OSR under climate change, with male dominated populations moving upward in elevation in response to changes in soil moisture. Similarly, Miller and Compagnoni⁵ found that niche differentiation between sexes of a different dioecious species could explain patterns of OSR and species' range limits across a moisture gradient in the southern Great Plains. By using demographic models, these two studies have yielded great insights into how OSR variation drives demographic dynamics through abiotic and biotic environmental changes. Yet OSR is more constrained in dioecious species (such as these examples), since both sexes are required for reproduction. It is less clear why females are maintained in populations of gynodioecious species or how this may be impacted by climate.

My dissertation addresses three broad objectives: 1) determine the geographic and climate patterns that drive OSR throughout the *S. acaulis* range using field surveys, 2) determine the mechanisms underlying fitness advantages for females and hermaphrodites through pollination experiments in populations with high vs. low female frequency, and 3) examine the demographic consequences of gynodioecy dependent on climate by building a sex and size structured integral projection model (IPM)^{4,5} and incorporating climate variables. In this proposal, I am requesting funding for my third objective, in which I strive to answer these three questions:

1) How does sex affect vital rates and demography; 2) How does the OSR affect population growth (λ) in different environments; 3) How does climate affect sex-specific performance and predicted OSR?

Methods: I will compare the fitness of females vs. hermaphrodites in populations of *S. acaulis* using a sex and size structured integral projection model (IPM)^{4,5}. I will use data from a long-term demographic dataset with sites in New Mexico (2 populations), Colorado (4 populations), Southern Alaska (5 populations), and Arctic Alaska (4 populations)¹³. In 2001, plots were established by mapping and tagging 100-300 plants per population. Each year (2001-present), the survival, size, and number of fruits is recorded for each plant and subplots are searched for an estimate of seedling establishment. Since these censuses occur after flowering, the sex of most plants is unknown. I am requesting funding to travel to each site during flowering to sex all the individuals. Since *S. acaulis* is extremely long-lived, most individuals mapped in 2001 are still alive. I will then construct an IPM which uses regression models to predict vital rates (survival, growth, and reproduction) as a function of plant size and sex¹⁴⁻¹⁶. I will also incorporate climate variables as covariates to determine if and how climate influences vital rates of each sex¹³. From the IPM, I will get the long-term population growth rate (λ) and stable stage distribution (SSD; proportion of individuals in each size and sex class at population equilibrium)¹⁴⁻¹⁶.

Analysis: I will use a life table response experiment (LTRE), a type of demographic analysis, to determine the contributions of females and hermaphrodites to changes in λ across sites and environmental conditions⁵. I will use the SSD to predict population sex ratios as a function of climate^{4,5} and compare predictions to observed OSR from field surveys to validate the model. Finally, I will link the predicted OSR to population growth rate and climate variables. Together, these analyses will allow me to examine the sex-specific responses to climate that have occurred over the last 25 years and predict how climate scenarios could shift OSR in the future with forecasting¹⁷.

Predictions: I expect that females contribute to population growth through superior seed production^{1,10} and seedling survival¹, and that this effect is strongest in cooler and wetter climate conditions. I predict that shifts in the OSR are related to temperature^{6,13} and potentially precipitation patterns^{4,5}, with female frequency increasing in northern latitudes^{3,10}. Lastly, I expect that female vital rates will contribute strongly to changes in λ across the range and with respect to climate, if pollen is not limited⁵.

Contribution to Plant Ecology: This research will determine how gynodioecious species respond to and persist (or not) in changing environmental conditions and build on our understanding of mating system maintenance and evolution in plants. My proposed work also uses novel approaches, as sex is rarely incorporated in demographic models and species distribution models of plants. My approach has applications in the management of species with unique mating systems that are of conservation concern.

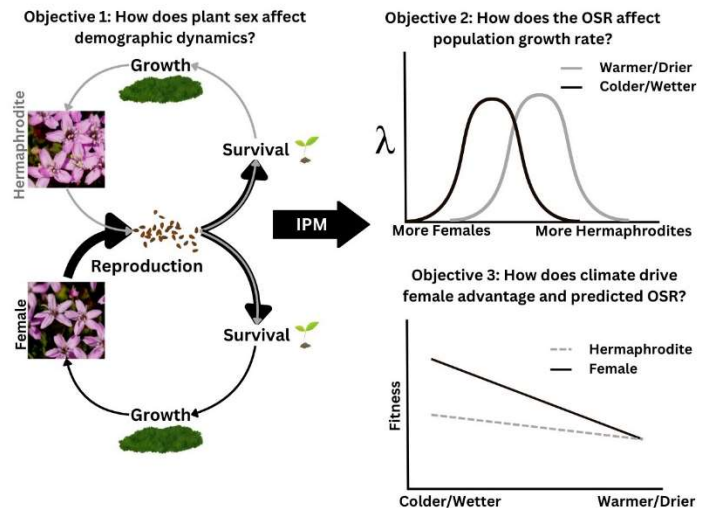


Figure 1. Conceptual diagram outlining the three proposed objectives. Lifecycle with vital rates: arrow thickness indicates the hypothesized contribution of hermaphrodites (grey) and females (black) to each vital rate.

Bibliography

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Budget:

I plan to use this award for travel and as pay for one undergraduate research assistant. Travel to Niwot Ridge, Colorado Mountain Research Station and McCarthy, AK is covered by a grant awarded to Megan DeMarche (advisor) for collection of long-term demographic data. Demography data are typically collected after the plants produce fruit. To sex plants when flowering, I require travel funds outside of travel for demographic data collection. Travel from Colorado to New Mexico will only require gas, as I will be using a lab truck. In Alaska, I will rely on public transportation in the form of various shuttle services. Additionally, I am asking for student pay of \$17 per hour, which is \$2 per hour over the student wage at the University of Georgia. In doing so, I hope to attract a diverse applicant pool for research assistantship positions, by reducing potential financial obstacles.

Item	Price per	Count	Total
Gas for round trip travel from Colorado to New Mexico in lab truck (per gallon)	\$2.62	37	\$96.94
Round trip from McCarthy, AK to Glennallen, AK (per route)	\$150.000	2	\$300.00
Round trip from Glennallen, AK to Tok, AK (per route)	\$65.000	2	\$130.00
Round trip from Tok, AK to Fairbanks, AK (per route)	\$90.000	2	\$180.00
Research Assistant (per hour)	\$17.000	45	\$765.00
		Sum	\$1,471.94

EDUCATION

Current PhD, Plant Biology Department *University of Georgia (UGA)*
2020-2022 MS in Environmental and Conservation Sciences, *North Dakota State University (NDSU)* 4.0/4.0 GPA
2016-2020 BA, in Biology and ACS Chemistry *Concordia College*, Moorhead, MN, 3.95/4.0 GPA

RESEARCH AND TEACHING EXPERIENCES

2023-Current Maintenance of gynodioecy in *Silene acaulis*, Department of Plant Biology, UGA
2023-Current Biology Teaching Assistant: Introductory Organismal Biology, PhD work, University of Georgia, GA
2020-2022 Temperature tolerance in *Solanum carolinense*, MS work, Biological Sciences Department, NDSU
2020-2022 Biology Teaching Assistant: Anatomy and Physiology Lab, North Dakota State University, ND
2020 Phenology of prairie forbs, MS work, Biological Sciences Department, NDSU
2019 Honors thesis, "Ecophysiology of cultivar and native prairie plants", Biology Dept, Concordia College
2019 Biology Teaching Assistant: Ecology, Concordia College, Moorhead, MN
2019 Biology Teaching Assistant: Evolution and Diversity, Concordia College, Moorhead, MN
2018-2020 Greenhouse Technician, Concordia College, Moorhead, MN
2018 Research assistantship, Carbon dynamics at Long Lake Field Station, MN, Concordia College
2017, 2020 Research Intern, Aquifer and groundwater analysis, Bureau of Mines and Geology, Montana Tech

PUBLICATIONS AND PRESENTATIONS

Papers E.K. Chandler, S.E. Travers. 2021. The timing of snowmelt and amount of winter precipitation have limited influence on flowering phenology in a tallgrass prairie. *Botany*. 100(3): 301-311.
Talks Ecological Society of America, Montreal, Canada (2022); Student Research Day, NDSU (2022, **2nd place**); Northern Plains Biological Symposium, NDSU (2021); Botany Conference, Virtual (2021); Evolution Conference, Virtual (2021); Environmental and Conservation Sciences Virtual Seminar Series (2021); PSU Biology Department Seminar Series, co-talk with Dr. Steve Travers (2021); Celebration of Student Scholarship (CSS), Concordia College (2020); Chemistry Senior Seminar, Concordia College (2020);
Posters CSS Poster, Concordia College (2019; 2018, **Best Representation of Data on a Poster**)

FELLOWSHIPS AND GRANTS

2021 Shockey-Scooby Summer Fellowship (3000 USD), Shockey-Scooby Travel Award (250 USD)

MENTORING EXPERIENCE

NDSU Kirsten Warcup (2022), Danielle Wright (2022), Todd Pottinger (2021), Marian Taiwo (2021), April Fahrendorff (2021)

PROFESSIONAL DEVELOPMENT

Research Wilderness First Aid Training (2022); Careers in plant science workshop (2022); Think Like a Modeler: A Tutorial on Building Dynamic Ecological Models for Early-Career Ecologists (ESA, 2022); Data Science for Ecologists and Environmental Scientists (2021); Presenting Science Effectively – Where things stand (Botany, 2021); Scientific Communication Workshop (2021); Marine Community Sampling Methods Workshop (2020); LEAF training for LI-6400XT infrared gas analyzer, Li-COR Headquarters (2019)
Teach/Mentor Graduate Teaching and Learning Conference (2021); USGS Bystander Intervention Workshop (2020)

OUTREACH AND SERVICE

Planting Science Mentor (2021-current); Treasurer of Plant Biology Graduate Student Association (2023-current); Department of Plant Biology Representative, Graduate Student Association, DEI Committee (2023-current); Georgia State Science Fair Judge (2023); Hilsman Middle School Science Fair Judge (2024); Undergraduate Research Ambassador, Concordia College (2018-2020); Riverkeepers Water Festival, Moorhead, MN (2019); High Impact Leadership Training Trip, Salt Lake City and San Francisco (2019); Mississippi Delta Justice Journey, Plaquemines Parish, LA (2018); Conservation Days Event for Middle Schoolers Outreach, MT (2017)

MEMBERSHIP IN ASSOCIATIONS

Botanical Society of America (2021-current), Torrey Botanical Society (2024-current), Ecological Society of America (2022-current), UGA Plant Biology Graduate Student Association (2022-current), NDSU Environmental and Conservation Sciences Graduate Student Association (2020-22), NDSU Biological Sciences Graduate Student Association (2020-22)