

# Dynamics of male inconstancy in *Valeriana edulis* in the abiotic and mating environment

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## Abstract

This study investigated inconstancy in the sex-expression of male flowers across populations of Edible Valerian (*Valeriana edulis*) as well as potential drivers of its variation. Though *Valeriana edulis* is dioecious (individuals typically have separate sexes), plants showing dominant male sex-expression may also produce female reproductive structures (stigmas). As such, we aimed to (1) characterize variation in male inconstancy in *V. edulis* populations and explore the influence of the (2) abiotic environment and (3) mating environment on the distribution of inconstant sex expression in what is considered a dioecious system. To address these goals, we conducted flower surveys in multiple populations to determine the degree, frequency, and variation in expression of inconstancy (*i.e.* how inconstancy varies between individuals or flowers). We also tested potential abiotic drivers of inconstancy using remotely sensed datasets for growing degree days as a proxy for temperature and snowmelt date to represent soil moisture. Finally, we obtained operational sex ratios (proportion of flowering individuals that are primarily male-expressing) through demographic surveys of the populations to examine its effect on male inconstancy. These results have implications for potentially reclassifying *Valeriana edulis* as a dioecious species, exploring the limitations of binary thinking, and gaining a better understanding of how differential effects of the environment on individuals may in turn affect population biodiversity, performance, and persistence.

**Key words:** Dioecy, subdioecy, sex ratios, labile sex-expression, binary thinking, climate change, elevation gradient, *Valeriana edulis*

## Introduction

Most angiosperms produce perfect (hermaphrodite) flowers with both female and male reproductive function (Thompson, 1986). However, approximately 5-6% of flowering plants have a dioecious sexual system, with male and female reproductive organs in separate individuals (Renner, 2014). Dioecy is hypothesized to have primarily evolved from a hermaphroditic ancestral state through a gynodioecious (hermaphrodites and pure females) pathway relatively recently (Billard et al., 2005; Barrett, 1992). The female reproductive function in hermaphrodites was evolutionarily lost much more recently, such that the ability to suppress male function is older than ability to suppress female function. Accordingly, sex expression is labile in many otherwise dioecious plant species, and males are more often observed to exhibit “leaky” dioecy (Lloyd, 1975; Delph & Wolf, 2005; Ehlers & Bataillon, 2007).

Male and female reproductive functions require different resource currencies (e.g. carbon, nitrogen, water) that mediate the costs and fitness benefits of a plant's sex expression strategy (Tonnabel et al., 2017). The net benefits of any particular strategy will be context-dependent. Adopting a pure female or male sex-expression strategy allows for specialized allocation of resources into developing either more/higher quality male or more female gametes, rather than maintaining both functions (Ehlers & Bataillon, 2007). For example, plants allocating more to female reproductive function can allocate less energy to male function, and thus produce a seed set greater in quality and quantity (Vamosi et al., 2008; Queenborough et al., 2009).

However, more resources, such as carbon and nitrogen, are required to support female function, which imposes a higher energetic cost for females (Antos & Allen, 1990; Geber et al., 1999). In contrast, it is often “cheaper” to be a male, and males may thus be able to reallocate resources to survival, vegetative growth, as well as to high quality pollen production (Tonnabel et al., 2017). Though not as constrained by resources as females, average male fertility may be reduced by male-male competition even when the average seed set in the population is not pollen limited (Stanton, 1994).

Energetic costs and reproductive payouts in males and females are distinct and sensitive to resource availability and intraspecific interactions, and conditions that reduce tradeoffs in male and female functions favor the persistence of hermaphroditism in dioecious and subdioecious populations (Crossman & Charlesworth, 2014). Having both male and female reproductive function as well as the ability to self-fertilize enables hermaphrodites the advantage of self-assurance in highly variable, new, or limited environments pertaining to resources or mates (Schoen, 1982; Lloyd & Schoen, 1992; Wolfe & Shmida, 1995; Ehlers & Bataillon, 2007). Even when pollinator services fluctuate (Cossard & Pannell, 2019; Ehlers & Bataillon, 2007), or when there are few mates available (Cossard & Pannell, 2021), it is beneficial to at least be capable of producing some seeds, even if both seed set and pollen quantity and quality is diminished. The same is true for when resources needed to sustain pure female reproductive costs are limited (Ehlers & Bataillon, 2007). Self compatibility also allows hermaphrodites to be good colonizers and persist in populations characterized by cycles of extinction and re-colonization since they do not need to rely on the presence of the other sex to reproduce (Cossard & Pannell, 2021). As such, having both female and male reproductive functions is favored through self-fertilization, especially in unstable habitats regarding mates, resources, fragmentation, or disturbance.

Despite the known profound effects of both the mating (Cossard & Pannell, 2019; Cossard & Pannell, 2021; Barrett, 2021) and abiotic environment (Bawa & Lloyd, 1984; Barrett et al., 1999; Delph & Wolf, 2005) on the persistence of hermaphrodites, it is unclear how variation in sex inconstancy at the individual level may affect population performance and persistence. Especially in light of climate change, it is important to understand the effects of a changing environment on sex allocation strategies that have the potential to influence the trajectory of the population or species. Ultimately, the patterns and consequences of leaky sex-expression must be considered in order to gain a more comprehensive understanding of sexual systems, which has historically been restricted by culturally deep-seated binary thinking (Glick et al., 2016; DuBois & Shattuck-Heidorn, 2021).

*Valeriana edulis* (Edible Valerian) is a slow-growing, dioecious, and perennial flowering plant in the family Caprifoliaceae that grows over a steep elevational gradient of ~1,980- 3810 m in western Colorado (Petry et al., 2016). Sex is likely genetically determined, and *V. edulis* does not reproduce vegetatively. *Valeriana edulis* is known to experience sex-specific responses to climate change where aridification promotes male frequency in the population at increasingly higher elevations (historically female biased) and in turn reduces pollen limitation and increases seedset (Petry et al., 2016). Consequently, it is plausible to believe that the climate plays an important role in sex-expression and composition. While Petry and colleagues (2016) examined sex ratios and population performance at a broad (population) scale, the role of male inconstancy at a finer (flower, individual, and intra-population) scale has not yet been investigated in *V. edulis*. As such, *V. edulis* provides a unique opportunity to study how inconstant sex-expression varies across the abiotic environment compared to the mating environment, how this dynamic

may affect population range expansion in the face of climate change, and how a binary way of thinking limits our understanding of a dioecious system in the real world.

Thus, we aim to answer (1) what is the range in variation of male inconstancy, (2) does male inconstancy in *V. edulis* vary by spatial patterns of resource availability, and (3) does the mating environment (mate and pollen availability) influence the frequency of hermaphroditism?

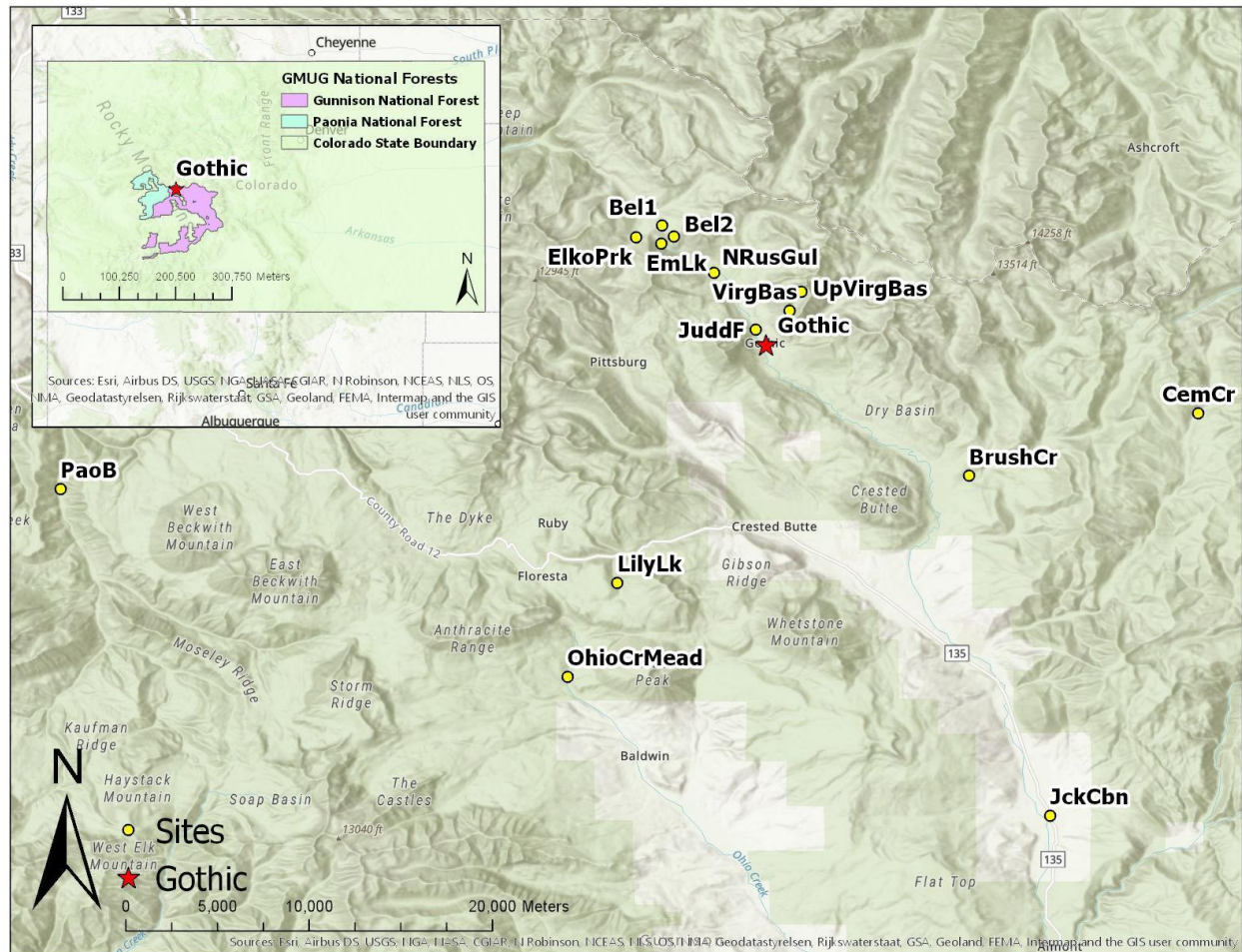
## Methods

### Study Site

*Valeriana edulis* grows across a broad elevational gradient in the Gunnison National Forest, providing an opportunity to conduct a comprehensive study on male inconstancy and its variation and spatial distribution. We focused my study on 13 *V. edulis* populations in Gunnison County (Fig. 1). Sites were stratified by climate and elevation to separate the common associations between the two, in which high elevation correlates with lower temperature and higher precipitation (Table 1).

**Table 1.** Elevation and geographic location of study sites.

| Name                  | Abbreviation | Elevation (m) | Coordinates            |
|-----------------------|--------------|---------------|------------------------|
| Paonia B              | PaoB         | 2040          | 38.88857, -107.33597   |
| Jack's Cabin Cemetery | JckCbn       | 2511          | 38.72878, -106.8504    |
| Ohio Creek Meadow     | OhioCrMead   | 2730          | 38.79676, -107.08731   |
| Brush Creek Range     | BrushCr      | 2780          | 38.89512, -106.89028   |
| Judd Falls Trailhead  | JuddF        | 2918          | 38.96649, -106.99473   |
| North Rustlers Gulch  | NRusGul      | 2989          | 38.99451, -107.01538   |
| Lily Lake Trailhead   | LilyLk       | 3075          | 38.84271, -107.06286   |
| Emerald Lake          | EmLk         | 3185          | 39.00886, -107.04117   |
| Cement Creek          | CemCr        | 3195          | 38.92582, -106.77765   |
| Elko Park             | ElkoPrk      | 3230          | 39.01177, -107.05346   |
| Virginia Basin        | VirgBas      | 3350          | 39.75948, -106.97809   |
| Bellview II           | Bel2         | 3429          | 39.01763, -107.04102   |
| Bellview I            | Bel1         | 3440          | 39.01240, -107.03490   |
| Upper Virginia Basin  | UpVirgBas    | 3650          | 38.985131, -106.972510 |



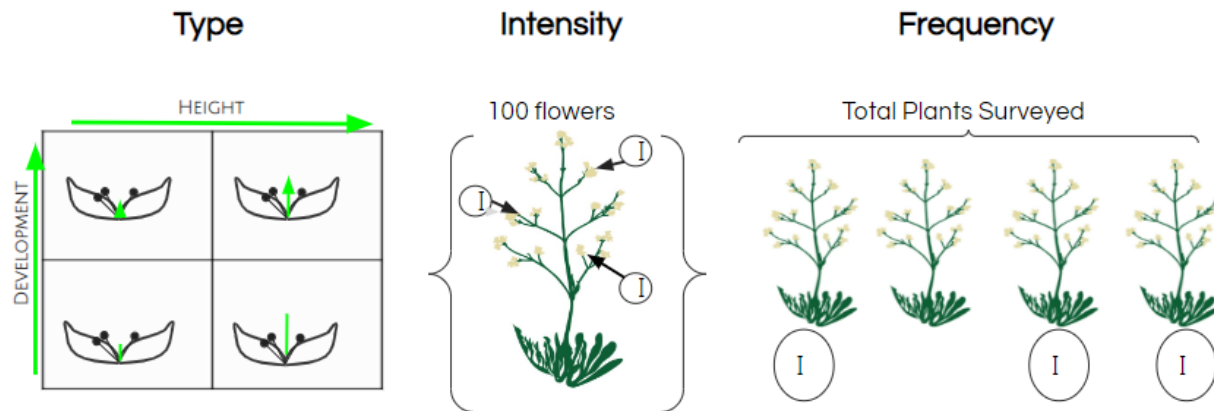
**Figure 1.** Field sites where anatomical male inconstancy was measured in *Valeriana edulis* populations.

### Characterizing Inconstancy

We measured how inconstancy in *Valeriana edulis* manifests anatomically at the flower, individual, and population levels by conducting flower surveys for male plants, stratified by size, in each population, examining up to 100 flowers on each individual (Fig. 2). Size of the individual was controlled for and measured as the perimeter of the rosette clusters. Inconstancy (the presence of a female reproductive structure in an otherwise male expressing plant) at the scale of individual flowers was scored by the height of the style, and the development of the stigmatic surface. The height of the style was categorized by relative height to the mouth of the corolla (below, above), and the development of the stigmatic surface was designated based on the distinction of a clefted, trifid- shaped stigma present (developed or undeveloped).

The degree, or intensity, of inconstancy ( $d$ ) represents how much a plant diverges from its dominant sex, and is the allocation of resources to producing the sexual organs of the other sex. (Barrett, 1992). We measured the degree of intensity by the number of flowers out of the total number of flowers surveyed that show any type of inconstancy, to get a ratio for each individual. Each 100 flowers surveyed for a measure of intensity of inconstancy was given a type according to the scheme laid out previously.

Finally, the frequency of male inconstancy ( $r$ ) for each population will be a proportion of plants of a particular sex showing any production of flowers of the other sex (Cossard & Pannell, 2019). We determined the proportion of plants out of the total number of male plants that showed any indication of inconstancy in its sex expression for each population.



**Figure 2.** Characterizing male inconstancy at the flower, individual, and population levels.

### Effects of the Abiotic and Mating Environment

To study the effects of the abiotic environment on male inconstancy, we included 2020 and 2021 raster datasets from the RMBL Spatial Data Platform for growing degree days (GDD) and snowmelt date (proxies for “temperature” and “soil moisture”, respectively). Raster datasets cover the Upper Gunnison River (UGR) domain at a 9m spatial resolution. For GDD, 0 °C was used as the threshold temperature.

To study the effects of the mating environment on male inconstancy, we obtained the operational sex ratios (OSRs) for populations in 2022, which represents the proportion of flowering individuals that are male (Petry et al., 2016). Once all inflorescences have open flowers, flowering plants within an arm’s length was sexed and counted as male or female using zig-zag transects within a designated area until at least 200 of the rarer sex (usually males) have been tallied.

### Analysis

A regression-based path analysis was used to determine the separate direct effects of the abiotic and mating environments on patterns of male inconstancy. The abiotic environment is known to bias sex ratios in *V. edulis* (Petry et al., 2016), and there is also evidence that sex ratios, which are informative of mate and pollen limitation, influences the frequency of hermaphrodites in a dioecious or subdioecious population (Cossard & Pannell, 2021). As such, environmental conditions affect sex ratios in *Valeriana*, which may in turn affect patterns of inconstant sex expression. Since we are interested in the direct effects of the mating environment, a regression-based path analysis was necessary to parse out and control the indirect effects that the abiotic environment has on sex ratios. Size dependence of inconstancy was also considered as larger and older plants tend to have greater access to resources, or that there may be a higher energetic requirement for plants to allocate resources towards producing anatomical structures and gametes of the opposite sex (Barrett et al., 1999). To determine the effects of our predictors

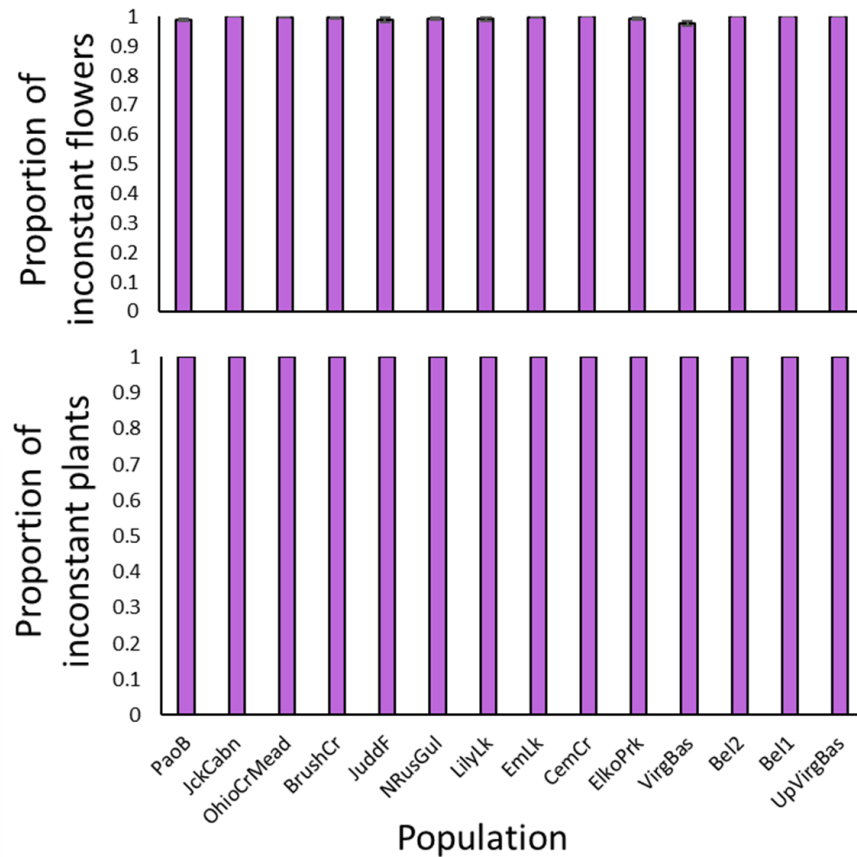
(plant perimeter, GDD, snowmelt date, and OSR) on the total incidence of inconstancy at the population (frequency of male inconstancy;  $r$ ) and individual level (degree of inconstancy;  $d$ ), we ran a logistic regression using a Bayesian approach to fit the model. Since multiple flowers were surveyed for each individual, and flowers on the same plant were not expected to be statistically independent, a “random effect” of individual plants was included. With the same predictors, a multinomial regression was used to see what drives the variation in the composition of inconstancy types at the flower level.

## Results

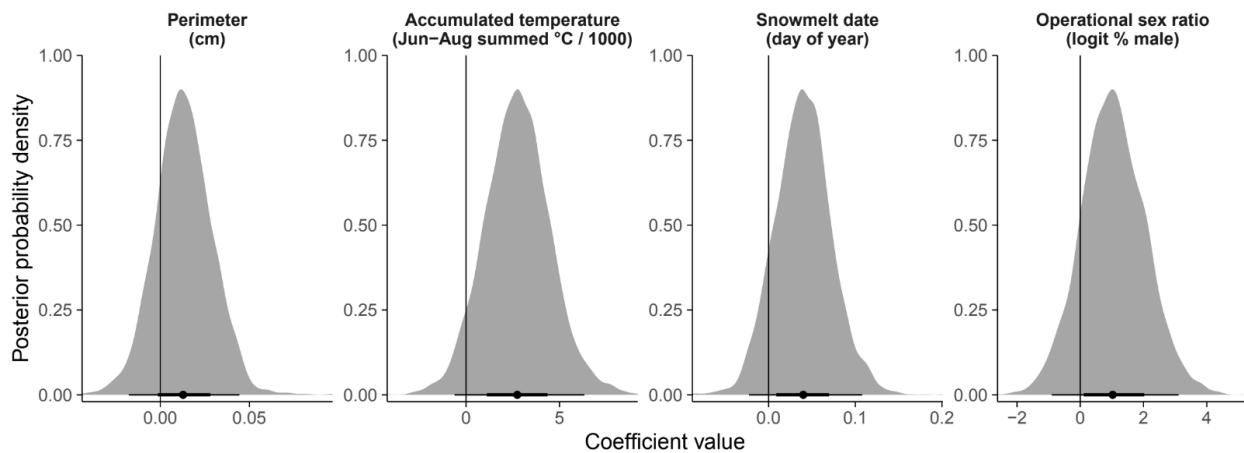
We analyzed the effect of size, GDD, snowmelt date, and operational sex ratios on incidence of anatomical male inconstancy at the population and individual level using a logistic regression with a Bayesian approach. We found that incidence of inconstancy in different populations was present and extremely high in all populations ( $r = 1$ ; Fig. 3). Similarly, incidence of inconstancy at the individual level was also exceptionally high ( $d = 0.995$ ). Accordingly, no effect was detected for size (Estimate = 0.01; 90% CI = -0.02 - 0.04), GDD (Estimate = 2.76; 90% CI = -0.86 - 6.43), snowmelt date (Estimate = 0.04; 90% CI = -0.03 - 0.11), or OSR (Estimate = 1.06; 90% CI = -0.93 - 3.11) on the average male inconstancy incidence across populations and individuals within each population (Fig. 4). The credible interval of 90% of the distribution overlaps zero in the posterior distributions of the coefficients, and so we have interpreted that as having no effect. Composition of inconstancy types at the flower level was variable (Fig. 5).

To test the same predictors as potential drivers of variation in types of anatomical male inconstancy, a multinomial regression analysis was performed. We detected no effect of size (Estimate<sub>Short/Devel</sub> = 0.02; 90% CI<sub>Short/Devel</sub> = -0.00 - 0.04; Estimate<sub>Short/Undevel</sub> = -0.00; 90% CI<sub>Short/Undevel</sub> = -0.01 - 0.00; Estimate<sub>Long/Devel</sub> = 0.00; 90% CI<sub>Long/Devel</sub> = -0.02 - 0.02; Estimate<sub>Long/Undevel</sub> = 0.01; 90% CI<sub>Long/Undevel</sub> = -0.00 - 0.02) or snowmelt date (Estimate<sub>Short/Devel</sub> = -0.02; 90% CI<sub>Short/Devel</sub> = -0.08 - 0.03; Estimate<sub>Short/Undevel</sub> = 0.01; 90% CI<sub>Short/Undevel</sub> = -0.01 - 0.03; Estimate<sub>Long/Devel</sub> = 0.00; 90% CI<sub>Long/Devel</sub> = -0.04 - 0.05; Estimate<sub>Long/Undevel</sub> = 0.02; 90% CI<sub>Long/Undevel</sub> = -0.01 - 0.05) on any of the types of inconstancy (Fig. 6). However, we did find that GDD had a positive effect on incidence of long and undeveloped pistils (Estimate<sub>Short/Devel</sub> = -1.72; 90% CI<sub>Short/Devel</sub> = -4.69 - 1.14; Estimate<sub>Short/Undevel</sub> = 0.04; 90% CI<sub>Short/Undevel</sub> = -0.96 - 1.06; Estimate<sub>Long/Devel</sub> = 0.99; 90% CI<sub>Long/Devel</sub> = -1.51 - 3.59; Estimate<sub>Long/Undevel</sub> = 1.51; 90% CI<sub>Long/Undevel</sub> = 0.06 - 3.08).

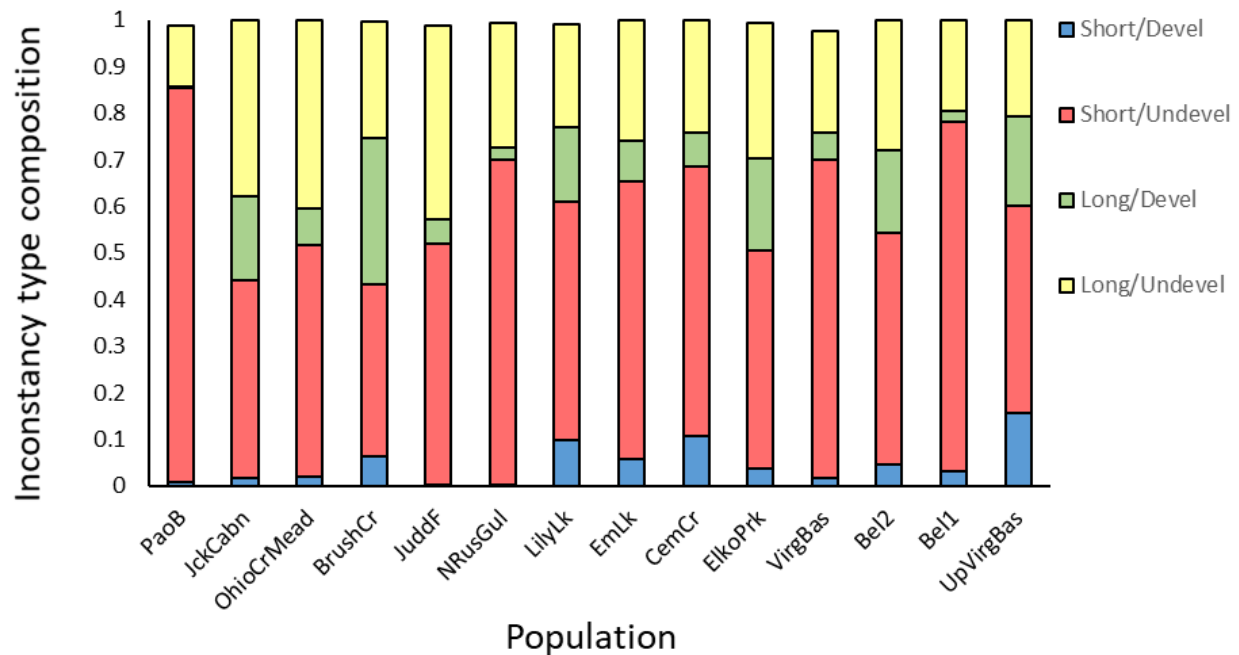
We also did not detect an effect of OSR (Estimate<sub>Short/Devel</sub> = 1.08; 90% CI<sub>Short/Devel</sub> = -0.52 - 2.78; Estimate<sub>Short/Undevel</sub> = 0.19; 90% CI<sub>Short/Undevel</sub> = -0.41 - 0.72; Estimate<sub>Long/Devel</sub> = 0.04; 90% CI<sub>Long/Devel</sub> = -1.27 - 1.47; Estimate<sub>Long/Undevel</sub> = -0.38; 90% CI<sub>Long/Undevel</sub> = -1.16 - 0.40) on the types of inconstancy (Fig. 6).



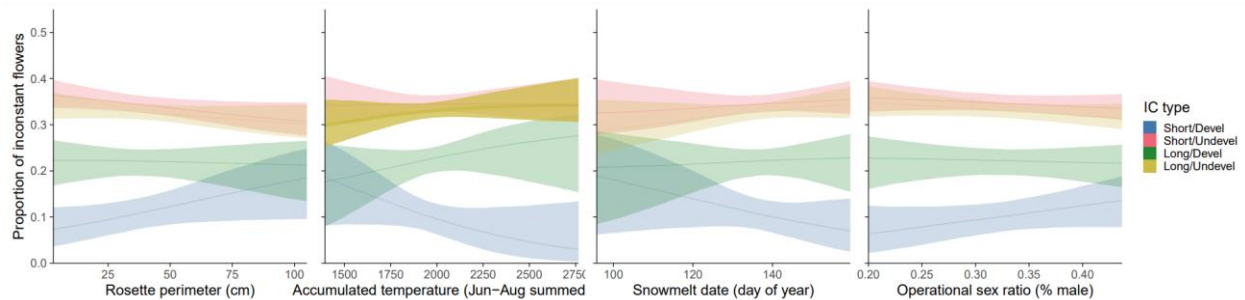
**Figure 3.** Comparison of average proportions of inconstant male flowers (top) examined that showed any anatomical inconstancy out of up to 100 flowers for every individual in each population and inconstant male plants (bottom) that showed any anatomical inconstancy out of the total number of plants surveyed for each population. Populations are ordered by increasing elevation. Mean  $\pm$  SE;  $n = 1889$  flowers and 199 individuals respectively. Absence of error bars indicate no variation in the mean across replicates.



**Figure 4.** Posterior probability distributions of each of the model's predictor coefficients. Horizontal black lines below each distribution represent 50% and 90% confidence intervals.



**Figure 5.** Comparison of the anatomical male inconstancy type composition observed in each population, in order of increasing elevation. Each bar represents the average proportion of each type of inconstancy out of the total number of open flowers surveyed that showed any degree of male inconstancy.



**Figure 6.** Marginal effect plots for rosette perimeter (Size), accumulated temperature (GDD), snowmelt date, and OSR with all other predictors controlled for at their mean value. Ribbons represent the proportion of inconstant flowers of each inconstancy type. Bolded ribbons indicate an effect was detected, while relatively transparent ribbons indicate that no effect was observed, and the width represents the degree of uncertainty.

## Discussion

Male inconstancy in populations of *Valeriana edulis* across an elevational gradient was analyzed for incidence at the population (frequency,  $r$ ) and individual level (degree,  $d$ ), composition of anatomical inconstancy types at the flower level, and response to plant size, growing degree days, snowmelt date, and operational sex ratios. Contrary to our expectations, we found that incidence of male inconstancy was exceedingly high, at least anatomically. Our results are inconsistent with previous studies that have reported low frequencies of sex inconstancy in different dioecious species: less than 1% in *Deprea paneroi* (Sawyer & Anderson,

2000); up to 45% fruiting males in the tropical tree *Jacaratia mexicana* (Aguirre et al., 2007); 2% in *Diospyros egrettarum* (Venkatasamy et al., 2007); and 1.3% - 4.7% in male *Mercurialis annua* plants (Cossard & Pannell, 2019). It is important to distinguish that our study only reports anatomical inconstancy as any presence of female reproductive structures in male plants, so it is unclear how this result changes if stigmatic functionality was accounted for. However, it is evident that anatomical male inconstancy was much more common than previously believed to be (Petry et al., 2016), and is almost certain to be present in every circumstance since all of our predictor variables for male inconstancy had no effect. Thus, *Valeriana edulis* has biologically no mechanisms to shut down development of the female reproductive pathway.

At the flower level, inconstancy type is variable along two axes of style height and development of the stigmatic surface. Our findings support that inconstant males were more likely to have undeveloped stigmas, which may suggest that there is a lower frequency of functional hermaphrodites, if anatomical inconstancy correlates with functional inconstancy. We would have expected to see a lower proportion of long and developed pistils if this were the case. However, anatomical and functional inconstancy do not always correlate. The relative fitness of male or female function in a hermaphroditic individual may be quantitative along a continuum (Leigh et al., 2006), and so allocation towards development of the physical structure required for female function does not always translate to reproductive payout. As such, it is also necessary to map the correlation between anatomical and functional male inconstancy to understand which types are relevant to the individual's fitness, and how each type of inconstancy contributes to the population's reproductive investment in the next generation.

Our finding of no size effect on both incidence of inconstancy and composition of inconstancy types, was unexpected. Patterns of resource allocation tied to male and female functions are driven by differences in strategies to achieve fitness: male fitness depends on access to mates, whereas female fitness is determined by acquisition of resources to bear the cost of producing offspring (Bateman, 1948). Since the cost to produce female gametes is generally higher than for male gametes (Bawa, 1980; Antos & Allen, 1990; Geber et al., 1999), we expected to see a higher incidence of inconstancy in larger plants, since age and size allude to an advantage in resource acquisition and accumulation (Barrett et al., 1999). Larger plants would then have a superior energetic capacity to produce seeds, since they would have resources to allocate towards reproduction of the other and more costly sex, rather than towards vegetative growth and survival. This is especially important considering the long life history of this species, characterized by high early mortality rates, so survival is critical for young and small plants (Petry, 2016). This may suggest that more research is needed and the anatomical inconstancy is intrinsic to reproduction in individual plants, and could be due to a genetic component.

Surprisingly, we also found that a longer growing season increases long and undeveloped styles. We might have expected an increase in both height and development of the pistil considering plants experiencing a longer growing season would have more time to grow and accumulate resources, which may then be allocated towards producing seeds (Gonsamo & Chen, 2016; Gonsamo et al., 2018). It was also surprising that the trend observed of the effect of accumulated temperature (GDD) on male inconstancy types was not reflected with snowmelt date as a predictor variable, of which no effect on male inconstancy types was found. Patterns of temperature and precipitation often correlate predictably with elevation (Morán-Tejeda et al., 2013), so our results indicate that a greater diversity of field sites may be necessary to explore the differential effects of GDD and snowmelt date, as proxies of temperature and precipitation respectively, on anatomical male inconstancy types.

Lastly, we detected no effect of OSR on development or height of the pistil. In the case that development of anatomical male inconstancy is tied to functionality, this result is inconsistent with previous research that found higher proportions of inconstant male plants with increasing female frequency (Lloyd, 1976; Barrett, 1992). Population settings that would maximize the reproductive payout for a hermaphrodite would dictate an environment that does not limit mates. We would expect the reproductive benefit of being an inconstant male to increase with increasing male frequency, as mating opportunities and probability of successful pollination would increase (Alonso, 2005). It could be that the mating environment truly has no effect on male inconstancy and variations in anatomical inconstancy types, and further research is needed to explore additional abiotic candidate drivers that were not considered in this model, such as nutrient availability, that may better determine this observed pattern. However, it could also be that our model is unable to detect the effect due to limited OSR data available.

Overall, it was surprising to find that there was a much higher frequency and degree of male inconstancy as well as variation in anatomical male inconstancy types in *Valeriana edulis* than was expected. Furthermore, neither of the predictor variables for the abiotic environment nor the mating environment showed any clear effects on our metrics of anatomical male inconstancy, despite GDD having a positive effect on the long and undeveloped inconstancy type. There is also a lot of uncertainty with how strong of an effect GDD actually may have on this type of anatomical male inconstancy. It is unknown what ecological and genetic controls are underlying this variation observed within males showing inconstancy in dominant sex expression. What is clear however, is that there are many future directions to better understand this system and how differences in individual experiences, particularly when sex expression plays such a large role, scale up to affect the population through reproductive fitness of individuals as a collective.

Ultimately, the findings of this study indicate the importance of questioning assumptions and categorization schemes. Historically, we have largely ignored this plasticity in sex expression and our reliance on categorizing individuals as males or females likely limits our understanding of the biology of systems that show more variation than we are led to believe from typological descriptions of sexual conditions based on botanical terminology (Barrett, 1992). Male inconstancy in *Valeriana edulis* shows considerable variation in sex phenotypes on a continuous scale, from flowers with highly developed pistils to those with pistils that are essentially non-existent, but still present. While studies on the functionality of the different types of inconstancy in *V. edulis* are required to determine their relative contributions to the next generation, this study reveals how complexity from sex expression limits the usefulness of binary discrete categorizations, which may lead to potentially enormous misconceptions about a phenomenon that is actually quite common in the system. This has strong implications to rethink how the use of arbitrary classification schemes that depend on binary labels to describe systems that are much more diverse can obscure exploration of biological phenomena that may have profound impacts for the individual. No effect was found for many of the chosen factors to represent the abiotic and mating environment. However, this study serves as a baseline for future studies on male inconstancy in *Valeriana edulis*, as well as demonstrates the unique opportunity this system provides to study the importance of a more comprehensive understanding of sexual systems, particularly how our binary thinking of sex expression may constrain our ability to describe and understand the natural world.

### **Major Professional Objectives**

The objectives of my research program are to learn how to conduct field biology, learn interesting biology that I can use to further my education, collect preliminary or baseline data for a long-term study, contribute to a global network studying alpine organisms, and collaborate with other scientists.

### **Projected Outcomes**

I plan to complete a study this summer that I will present orally and as a final paper to add to the RMBL publications database.

### **Data Archiving, Curation, and Vouchers**

As part of the RMBL Data Archiving, Curation, and Vouchers, I will participate in workshops and training for spatial and non-spatial metadata and archiving. My Data Management Plan includes a description of the datasets being archived, the dissemination methods, and the timeline for data-sharing. I will use the RMBL template metadata form. I will use the default data repository Environmental Data Initiative (EDI), <https://environmentaldatainitiative.org/> unless my mentors request a different repository.

### **Environmental Impacts**

Disturbances include trampling and light soil disturbances in and around study sites as well as harvesting inflorescences outside of designated study plots. Overall, this project will have no long-term environmental consequences. Since *V. edulis* is a long-lived perennial flowering plant, one-time harvesting will not have significant negative impacts on its survival or fitness. Other disturbances can be mitigated by reducing the number of times a site is visited and avoiding making new trails.

### **Relationship to Existing Research**

This study fits into current research with how variation in *V. edulis* in a changing environment affects the population and feedbacks into individual performance, as well as how that may affect our ability to predict the fates of *V. edulis* populations. It builds on the importance of sex expression for the way that an individual in a dioecious system experiences environmental cues. Existing research has shown that individuals experience sex-specific effects of both the abiotic environment and the mating environment, mostly regarding mate and pollen limitation. This study seeks to fill in gaps in knowledge about how important male inconstancy may be for the individual and the population by being the first to document this phenomenon in this study system, and explore potential drivers. This study will also address questions of how science is conducted, and what the limitations or consequences of imposing a binary perspective of sex expression are.

### **Importance of RMBL to Research**

*Valeriana edulis* populations are found across a large elevational gradient in Gunnison National Forest. RMBL is not only important for this study in terms of proximity to the study sites, but also for the long-term datasets available for this species. Previous research done on this

species with demography, as well as long term climate data are also especially important. The demographic data will be used for analyzing the effects of the mating environment on male inconstancy, and datasets for climate and soil properties will be pertinent for the analysis pertaining to the hypothesized abiotic drivers of inconstant sex expression in *V. edulis*.

## Declaration of Interests

The author declares no conflicts of interest.

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