

Variation in interaction zone size and influence of sex on fitness components of *Valeriana edulis*

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ABSTRACT

Sex and size allow for many different types of individuals within one species. These individuals can have different needs, which can influence responses to interaction, as well as what interactions take place between species members. We modeled how the sex and size of individuals of *Valeriana edulis*, a dioecious sub-alpine herb found across the western United States, influences the ways that they interact with neighboring members of their own species. This research could contribute to our ecological understanding of the role of sex and size in intraspecific plant interactions, which could have implications for species conservation under climate change.

INTRODUCTION

Individuals interact with members of their own species via shared resources, mutualists, and natural enemies in ways that can profoundly affect the individual's fitness. These shared intermediaries result in interactions that lead to worse or better fitness for the conspecifics involved. For example, Adler et al. (2018) found that intraspecific interactions were 4 to 5 fold stronger than interspecific interactions in their review of 39 previous plant competition studies. The fitness impacts of intraspecific interactions can range from positive to negative and may impact one or multiple components of fitness. For example, in the budding hydromedusa *Eleutheria dichotoma*, neighbors positively impacted reproductive rates by increasing access to gametes, while negatively impacting survival through a reduction in resources within a neighborhood (Daňko et al. 2018). The reason for this variation in sign and strength among different fitness components is that the intermediaries of the interactions differ. Therefore anything that directly impacts the resource, mutualist, or natural enemy intermediary of an intraspecific interaction will alter the sign or strength of the interaction.

Environmental conditions mediate the sign and strength of intraspecific interactions by altering the availability of resources, mutualists, and natural enemy intermediaries. Specifically, the stress gradient hypothesis posits that interactions will become positive as environmental stress increases (Adams et al. 2021). In the case of the coastal grass *Phragmites australis* the environmental stressor of salt water cyclically washes over groups of the grass; in freshwater conditions the interactions trend towards competition, but as salinity increases the roots of individuals facilitate the survival of the group through increased rainwater infiltration into dense rootmats, lowering the salinity concentration (Reijers et al. 2019). Individuals can have direct impacts on how a neighborhood responds to the environment in the present, but they can also affect future environmental conditions through plant-soil feedbacks. Organisms condition the soil through what nutrients they take out and put back in, which can change the biotic and abiotic contexts for conspecific members in ways that stabilize or destabilize community-level dynamics (Smith-Ramesh and Reynolds 2017, Van Nuland et al. 2017). These plant-soil feedbacks can affect access to soil nutrients like nitrogen. This access can be contingent on the density of neighbors. In studies done with *Arabidopsis thaliana* the same quantity of nitrogen in the soil

would reduce growth in low-density neighborhoods, but these reductions would be alleviated in high-density conditions (Yan et al. 2023). Intermediaries often exist along gradients of low to high availability. These gradients can exist along many different axes, such as longitude, latitude, and elevation (Seyfried et al. 2011, Bründle et al. 2020, Croy et al. 2022, Miller and Compagnoni 2022). Gradients of access lead to many possible environments that members of a species must survive in.

Although individuals within a species overlap strongly in their ecological niche, they can have important ecological differences based on their life stage or sex that change their interaction strengths and responses to the environment. Seedlings will be susceptible to different enemies than a mature adult will. Females will need slightly different resources to become reproductively successful than males will. Individuals can thrive in one kind of soil as a juvenile but can be restrained by resource availability in the same soil as an adult (Duddenhöffer et al. 2018). Females of a species can thrive in wetter areas, outcompeting males, but struggle to survive as the environment dries (Correia and Diaz-barradas 2000, Miller and Compagnoni 2022). It is not surprising that environments can be better for one kind of species member than another, due to intermediary needs changing as individuals reach reproductive maturity, and there being different sexes within one species, whose needs can also differ. The limiting resource nitrogen can be used at different rates by the sexes (Harris and Pannel 2008), and by different life stages (Bhadra and Cai 2019). Interactions are altered as a part of organisms moving through different stages and identities. Overlaying these identities with density of neighbors can massively change how fitness is impacted, such as the Conn and Blum (1981) study which found that females and males of the short-lived perennial herb *Rumex hastatulus* had different responses to the same density and nutrient treatments, with the greatest differences between the sexes at lower densities. Sexual identity leads to different life histories within one species, not all life stages necessarily being equivalent.

Populations do not function with only juveniles, or just females; there is an interdependency between all ages and sexes, which come together to make a “species”. When intraspecific interactions differ along axes of individual variation, ecological patterns such as population growth and extinction risk will respond to changes in population composition in complex ways, depending on what directions, for example more male or older, the composition is changing. We have few examples that jointly consider how life stage and sex affect the strength of intraspecific interactions. Based on the theory of Spatial Segregation of the Sexes: when males and females experience different fitness impacts in the same environments, then selection favors the abundance of the sex that is more fit in that area (Bierzychudek and Eckhart 1988), and findings from Miller and Compagnoni (2022) we know that these different kinds of identity must be working together to affect range distributions and viability. One of the few studied examples of combinations of sex and age is the earlier flowering times in males (Forrest 2014, Richardson et al. 2023) but we need more studies that explore the effects of identity on the many kinds of interactions that plants are involved in. We get a richer story when we bring age and sex together, letting us better predict range limits and individual-level response to

environmental change. These understandings will also help us apply better management techniques on rare and invasive plants by giving fuller answers to questions such as: do we plant adults of the same sex right next to each other? Do juveniles need to be planted far from each other? Upon reaching maturity does an invasive species contribute to their own decline at certain densities? By gaining a fuller understanding of the ways that plants of different ages and sexes respond to the environment, we will learn what it truly means to support all members of a species.

Here we studied the effects of sex and size on intraspecific interactions within the dioecious, polycarpic, sub-alpine herb *Valeriana edulis*. We used 15 years of observational census data which tracks over 3000 individuals. We modeled the effects so that predictions can be made about how the species will respond to changing population compositions. Through this project we sought to answer the following questions:

1. Do different fitness components have different neighborhood sizes?
2. Does accounting for neighbor trait variation improve predictions of focal fitness components?

METHODS

Study system

Valeriana edulis is a perennial herb that grows across a wide range of environmental conditions from xeric shrublands to mesic alpine environments. It is dioecious with suspected genetically fixed sex expression (Petry et al. 2016). After *V. edulis* seeds germinate they remain a vegetative rosette for several years. Once they reach sexual maturity they flower most years (Soule 1981). The species grows very large taproots, with little to no lateral root branching, thus they are expected to have small zones of underground influence. Aboveground, the inflorescences are often browsed by deer and in some populations, and in some populations there is a white mildew that transfers between plants covering the leaves. The plants are pollinated by generalists at distances of up to 10 meters apart (Petry et al. 2016), and seeds from female plants are wind dispersed.

A few effects of intraspecific interaction within *Valeriana edulis* have already been studied. Petry et al. 2016 explored the effects of OSR (Operational Sex Ratios) on female seedset. The authors found that in high elevation populations with the proportion of males at 22.8% had seedsets of 76%, compared to low elevations with seed sets of 95%. Studying the effects of density at distances of 1 meter, excluding sexual differences, revealed that survival and flowering probability decreased with increasing density, and found no effects on seed production and growth (Davis and Petry. 2023). From these previous studies we know that there are sex ratio biases across populations (Petry et al. 2016), but the amount of neighbors does not systematically change as you go up in population (Davis and Petry. 2023) and within populations there's no evidence for spatial segregation of the sexes (Petry et al. 2016). It is important for this study that

there may be population level sex bias, but no grouping of the sexes within populations. It would be difficult to study the effects of neighbor sex on focal fitness if we only saw dense neighborhoods of females and males.

Table 1. Locations and properties of study populations,

Site	Elevation (m)	Coordinates	Approximate population size
Paonia Meadow	1967	38.923873, -107.33737	200
Paonia B	2040	38.88857, -107.33597	200-400
Spring Creek	2653	38.77058, -106.76467	20
Ohio Creek Meadow	2730	38.79676, -107.08731	>300
Mt. Crested Butte	2757	38.87534, -106.90848	300
Brush Creek Range	2780	38.89512, -106.89028	>500
Judd Falls Trailhead	2918	38.96649, -106.99473	150
North Rustler's Gulch	2989	38.99451, -107.01538	>500
Lily Lake TH	3075	38.84271, -107.06286	200
Burro Park	3082	38.12299, -106.7913	50
Emerald Lake	3185	39.00886, -107.04117	>500
Cement Creek	3195	38.92582, -106.77765	>500
Rocky Brook	3219	38.86939, -106.6633	>300
Gothic/Baldy Saddle	3270	38.97699, -107.02518	200
Virginia Basin	3350	38.97594, -106.97809	>300
Bellview II	3429	39.01763, -107.04102	>500
Bellview I	3440	39.01240, -107.03490	150-300
Mexican Cut	3440	39.02656, -107.06679	<100
Cottonwood Pass	3450	38.84618, -106.42587	<100
Yule Pass East	3500	38.99706, -107.08272	>500

East Maroon Pass	3587	39.01057, -106.94295	200
Triangle High Meadow	3790	39.00084, -106.92500	>300
Frigid Air Pass	3790	39.05310, -107.02190	200-400

Study Populations

This study took place in sites across Gunnison county, Colorado (Table 1). A handful of these populations were chosen because they were a part of Judy Soule's 1981 dissertation. Additional ones have been added to the study over time with a focus on finding sites across the elevational range of this species, all the way from 1967m to 3790m. Sites were selected not just on the basis of elevation, but also with a lens for different average temperatures and precipitation so that analysis of these demographic studies will not be biased by only using populations found in high elevations or in hotter areas. This selection of sites creates a very full picture of all the environments within which *V. edulis* can live and interact with each other.

Demographic census

We conducted an annual demographic census of 50-250 tagged plants in each population. We measured individual size as the perimeter of the rosette where the leaves insert into the soil with just enough tension applied to begin pulling the leaves inward. We standardized size measurements across observers to reduce bias. We counted the number of flowering stems and estimated the number of seeds following Petry et al. (2016). Survival is based on comparing the current year status, to what was found in the past year, notated as simple binary, either alive (0) or dead (1), we measured flowering probability in the same way.

Estimating density-dependent vital rate functions

In order to make predictions about what will happen to vital rates, we compared sequential years of data to create linear and generalized linear mixed models. In order to do this we treated each vital rate as follows: Survival is whether a plant alive at time t is still alive at time $t+1$. This is a Bernoulli distributed value, which can only be 1 (survived) or 0 (died). Growth is the change in log size between t and $t+1$ which is a normally distributed set of values. Flowering probability, much like survival, is whether a plant that flowered at time t also flowered at time $t+1$, and is once again Bernoulli distributed between 1 and 0. Seed production and stem quantity are both counts that are compared at time t to time $t+1$, and distributed as negative binomials, due to being counts from 0 to positive infinity.

Our candidate models predicted each fitness component based on the state of the focal individual, the individual's population, and its neighborhood. We included the current $\log(\text{size})$ as a predictor so we could account for plants of different sizes (often different life stages) differing in performance over its lifecycle. We included focal sex and its interaction with current $\log(\text{size})$ as predictors so that the different sexes could have differing intercepts and slopes for

each vital rate. Since plants do not flower every single year, we used past data if they have flowered to assign them a sex. Our assumption is supported by the observation of consistent sex expression across >15 years of observations from thousands of individual plants (Soule 1981; Petry et al. 2016). We also assume that the sex effect on vital rate was the same regardless of whether the plant was flowering or vegetative. The final fixed predictors of vital rates are the number of neighbors. We treated this predictor in two ways, firstly we lumped it, meaning that the predictor was all neighbors within a certain distance, the second we split it by sex so that we could predict based on values of how many males are in a certain distance, and how many females are within that distance. Within our fixed predictor setups we also included the 2 way and 3 way interactions between these different categories. For vital rates like flowering probability an interaction between size and sex gave the model the ability for the different sexes to have different size thresholds at which they flower, likewise an interaction between size, sex and the number of neighbors allowed the sexes to have different parts of their lifecycle where they may be more or less vulnerable to spill over stem herbivory.

We took advantage of naturally occurring variation in neighbor density and sex composition around our focal individuals. All plants in this census study were marked with a survey grade GPS system (ca. 2cm accuracy). We defined arbitrary neighborhoods of 0.5, 1.0, 1.5 and 2m, then counted the number of conspecific neighbors in total and separately by sex within each radius.

The final part of our models is the group-level predictors (i.e., “random” effects). We used group level predictors to allow for partial pooling among groups in order to avoid overfitting. We grouped by population due to the variation of elevation and climate mentioned earlier. This allowed the model to fit its predictions while accounting for population level differences. We allowed the terms of intercept, main effects of sex and size, and the interaction between them to all vary by population. We also included plant ID nested within population to account for non-independence between observations from the same individual across multiple years

Model fitting

We fit generalized linear mixed models for each vital rate using the rstanarm (v.2.32.1; Goodrich et al., 2024) interface to Stan (v.2.32.6; Stan development team, 2024) in R (v.4.4.1; R Core team, 2024).

Model comparison

We compared the candidate models for each vital rate using Watanabe-Aikake’s Information Criterion (WAIC), which estimates the out of sample prediction error of the model with a penalty on model complexity to avoid overfitting (Watanabe 2010). Lower WAIC scores indicate better predictive skill, and we used an WAIC difference threshold of 2 to determine that a candidate model had better predictive skill than another (following the threshold for AIC of Burnham and Anderson, 2004). In total we had 8 different models for each vital rate, 2 for each

neighborhood distance, 4 of the models including sex differences, and 4 of them lumping all neighbors together. We then compared models within vital rates.

RESULTS

As of the summer of 2024 the census has observed 14 transitions (14 time t to time $t+1$). Within the group of studied plants that models predicted on (a group that removed some spatial distance processing errors) there are 1023 female individuals, and 505 males. The range of female densities at 0.5 meters was 0-6, at 1m 0-11, at 1.5m 0-21, and at 2 m it was 0-35. For males it was 0-4 at 0.5m, 0-8 at 1m, 0-12 for 1.5m and 0-18 for 2m. Growth ranged from -0.6931 to 6.3368, stem quantity ranges from 0 to 29, and seed production can range from 0 to 13,395

Table 2. Candidate model WAIC values for vital rates. An asterisk (*) indicates the best model for each fitness component.

Candidate Model	Survival WAIC	Flowering Probability WAIC	Growth WAIC	Stem Quantity WAIC	Seed Production WAIC
Sex 0.5m	7332.187	12988.08	17569.69	42667.93	55576.13
Lumped 0.5m	7335.593	12981.77	17561.91	42660.30*	55578.11
Sex 1m	20556.940	12979.89	17547.07	42662.22	55574.33*
Lumped 1m	7338.377	12978.28	17559.09	42663.59	55580.18
Sex 1.5m	7328.010	12985.24	17505.32	42668.47	55576.41
Lumped 1.5m	7323.601*	12975.58*	17516.68	42667.00	55581.38
Sex 2m	7325.966	12982.00	17474.84*	42666.76	55574.87
Lumped 2m	7326.107	12975.71	17511.92	42662.24	55580.57

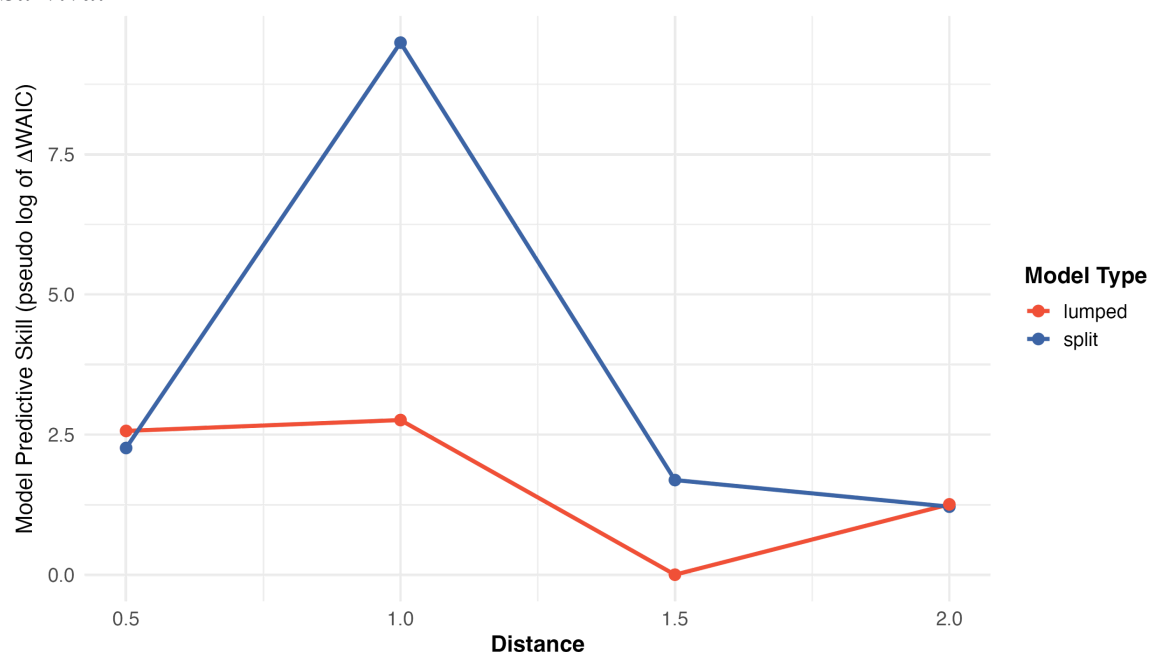
Survival

Figure 1. The lumped 1.5 meter model scored highest predictive skill when predicting survival . Pseudo log used to ease viewing proportional relationships between model WAIC scores. The blue follows the WAIC scores for models that split neighbors by sex, the red follows the WAIC score for lumped neighborhood models

Of the 8 models tested for survival, the model with the best fit was the lumped 1.5 meter model, which had the lowest WAIC score of 7323.601 (Table 2). Including sex or not in the predictions significantly reduced predictive power at medium distances, although including sex did give slightly better predictive power at distances of 0.5 meters.

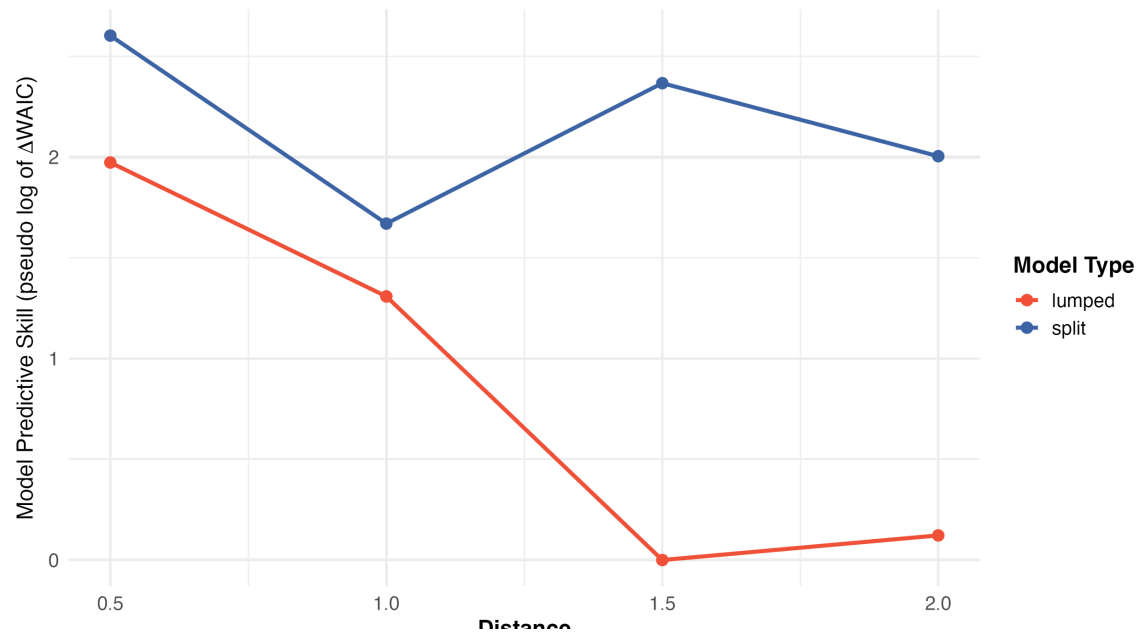
Probability of Flowering

Figure 2. The lumped 1.5 meter model scored highest predictive skill when predicting flowering probability. Pseudo log used to ease viewing proportional relationships between model WAIC scores. The blue follows the WAIC scores for models that split neighbors by sex, the red follows the WAIC score for lumped neighborhood models

Of the 8 models tested for probability of flowering, the model with the best fit was the lumped 1.5 meter model which had the lowest WAIC score of 12975.58 (Table 2). The candidate models that separated neighbor effects by sex did not give the model a stronger predictive power.

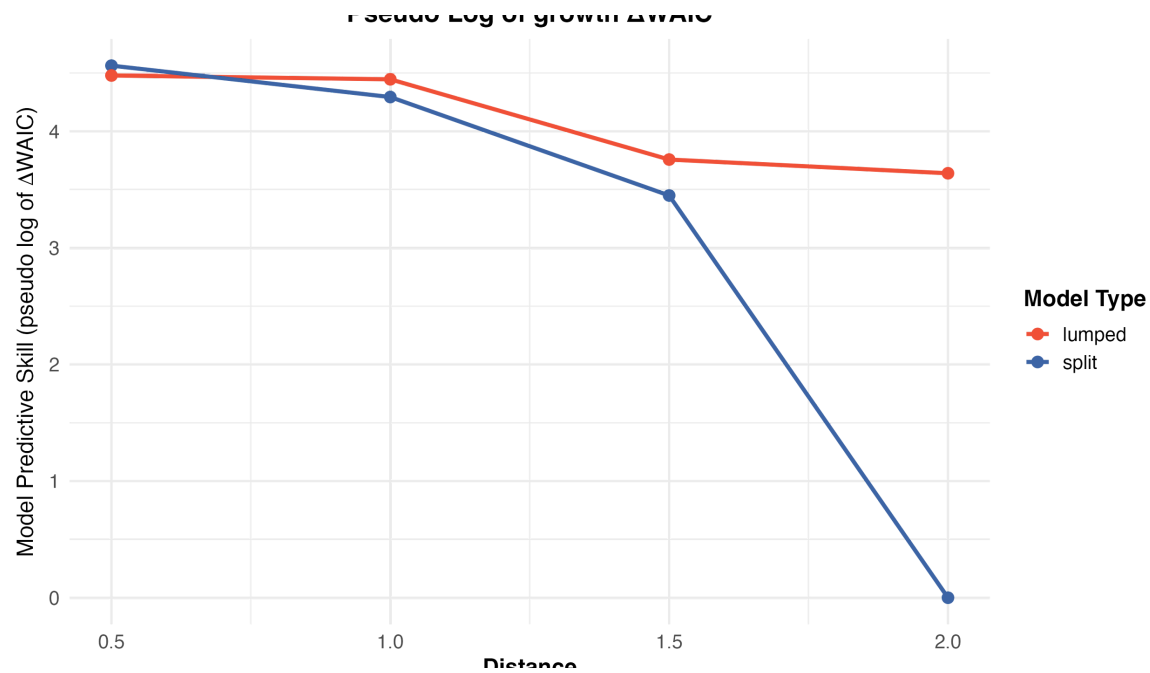
Growth

Figure 1. The split 2 meter model scored highest predictive skill when predicting growth. Pseudo log used to ease viewing proportional relationships between model WAIC scores. The blue follows the WAIC scores for models that split neighbors by sex, the red follows the WAIC score for lumped neighborhood models

Of the 8 models tested for growth, the model with the best fit was the split 2 meter model, which had the lowest WAIC score of 17474.84 (Table 2). Including sex gave better predictive power at all distances except for 0.5 meters.

Stems

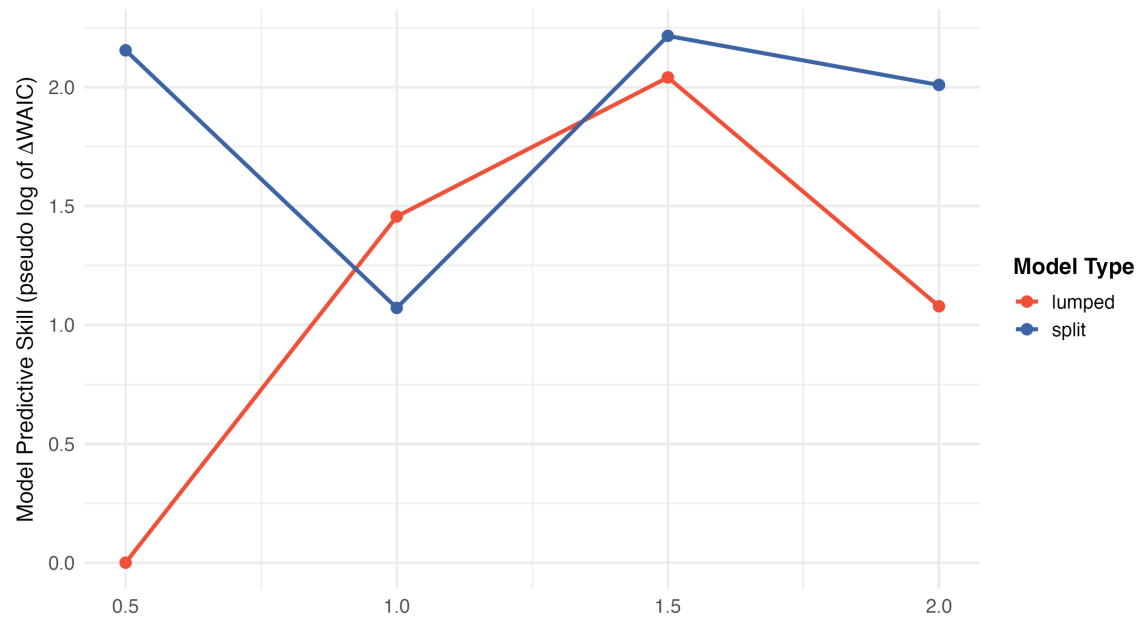


Figure 2. The lumped 0.5 meter model scored highest predictive skill when predicting stem quantity. Pseudo log used to ease viewing proportional relationships between model WAIC scores. The blue follows the WAIC scores for models that split neighbors by sex, the red follows the WAIC score for lumped neighborhood models

Of the 8 models tested for stem quantity, the model with the best fit was the lumped 0.5 meter model which had the lowest WAIC score of 42660.30 (Table 2). The candidate models that separated neighbor effects by sex did not give the model a stronger predictive power, except for distances of 1 meter.

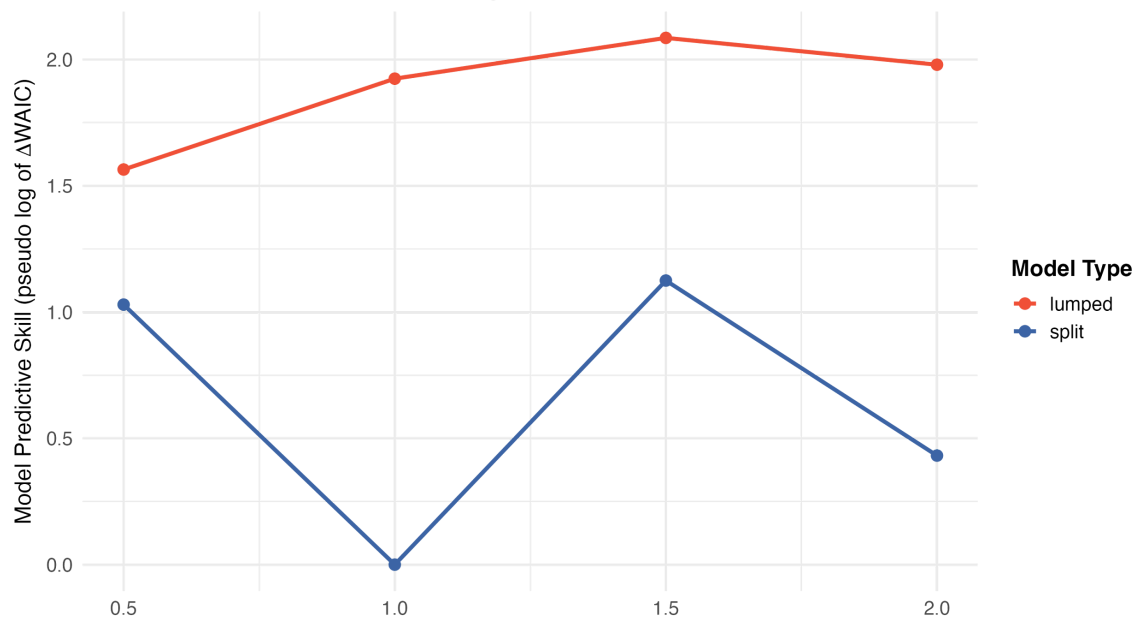
Seeds

Figure 2. The lumped split 1 meter model scored highest predictive skill when predicting seed production. Pseudo log used to ease viewing proportional relationships between model WAIC scores. The blue follows the WAIC scores for models that split neighbors by sex, the red follows the WAIC score for lumped neighborhood models

Of the 8 models tested for seed production, the model with the best fit was the split 1 meter model which had the lowest WAIC score of 55574.33 (Table 2). Every model that included the sex of neighbors in its prediction of seed production had better predictive power than its lumped counterpart.

DISCUSSION

Findings in this study suggest that for *V. edulis* every distance tested (0.5, 1.0, 1.5, 2.0) strongly influences the plant for a different vital rate. For two vital rates, growth and seed production, there is better predictive power when you include the sex of neighbors in the predictions. It is interesting that we see a mix of sex mattering for some vital rates, and other vital rates being ambivalent to the sexual composition of their neighborhoods.

Fitness components had similar neighborhood sizes

Distances bring significant variation in predictive power. For each vital rate predicted, we saw a different distance with the most predictive power. This implies that individual *V. edulis* experience many different neighborhoods. We can best predict how an individual of *V. edulis* will respond to neighbors around them, when we look at a neighborhood that matters for that vital rate, rather than just choosing one neighborhood that “defines” all outcomes for an individual's

fitness. Some studies have looked into worlds of interaction which work on much smaller scales, such as 0-40cm (adler et al. 2010) and a study which found that water acquisitions from 10cm away rather than central to the plant can limit growth (Hook and Lauenroth 1994) , but it proves difficult to find papers showing long range interaction within herbaceous species. There have been studies that look into longer distances (Tyler and D'antonio, 1995) but the study organisms have been larger shrubs whose increased distance of interaction can be explained through their larger sizes. At least based on biological intuitions the large zones of interactions for survival, flowering probability and growth in *V. edulis* cannot be explained through morphological characteristics alone.

When does sex matter?

Based on the distances and candidate models, using sex significantly altered 2 models' ability to predict changes in vital rates at any neighborhood distances. These were growth and seed production models. Because seed production relies so strongly on the movement of gametes, it is not surprising that the sex of an individual's neighbors has more influence over seed production than just the number of all neighbors. It is interesting though that sex matters for growth at such a far distance. This could imply that resources use and acquisition differs between males and females, or that other organisms that are being attracted by *V. edulis* that infringe upon growth (mainly herbivores and pathogens) are more likely to go to groups of one sex or another, although further analysis and experimentation is needed to confirm either of these hypotheses. Putting our findings into context with studies like Miller and Compagnoni (2022) it is surprising that in a dioecious species we do not find evidence of sex influencing all interactions between individuals. If there were strong sex-specific interactions that influenced the species, we would find evidence of strong aggregation or repulsion of the sexes within different populations. If they existed, these repulsions and aggregations would have been reflected in the predictive strength of all our models. Based on the candidate models' relative strengths, they imply that *V. edulis* does not strongly differ on the basis of sex within its interactions, except for growth and seed production.

Based on the small differences between predictive powers of inclusive sex and lumped sex, sex had less predictive power for survival, flowering probability and stem quantity over all. In some plant species, sexes can compete most strongly for different resources (Conn and Blum 1981, Harris and Pannell 2008). In that case we would expect models to have more power when using sex, because of relative ease or hindrance to resource acquisition. Because we don't see this, it could imply that the sexes of *V. edulis* are not so different from each other in their ecology within a given population, except for having flowers of a different sex.

It seems that an individual plant's survival rate (Fig. 1) is better predicted by the amount of neighbors around them (how many ways are the resources being split), rather than the kinds of neighbors around them (who pulls resources in what way). Flowering probability and stem quantity are slightly more complicated. There are differences in when sexes of dioecious plants flower and the resources needed to create different sexes of flower (Forrest, 2014, Richardson et

al. 2023), meaning that growing by more males as a male would result in increased competition for a limited group of resources, which one would expect could lead to a decrease in the probability of flowering. This is not what the models are showing (Fig. 2), which could imply that *V. edulis* does not experience much of a difference in the nutrients it invests into different types of flowers.

Towards finer resolution of neighborhood size

Within this study we defined 4 arbitrary zones of interaction, which we used to explore how neighborhood size influences predictive power. As is often the case in ecology, setting arbitrary zones can lead to pitfalls when the zones don't account for all the biological realities of the individuals. There is one morphological trait of *V. edulis* that could be hindering our models predictive abilities: in rosette growing species individuals with larger rosettes will have less individuals in a fixed neighborhood around them, due to the simple fact that the large individual takes up a greater proportion of that space (Stoll and Weiner, 2000). This leads to an issue where individuals may be large because they have few neighbors, but could also have few neighbors because they are larger. To get a fuller picture of how this could have impacted modeling efforts, an approach needs to be taken that bases those fixed neighborhood sizes on the size of the individual. We can also take a more nuanced view of plant neighborhoods, using a dynamical approach that could account for not only the amount of plants within a neighborhood, but the spatial distribution of the plants within that neighborhood (Law and Dieckmann, 2000). Combining fine-scale spatial distributions along with the axes that individuals vary upon, size, sex, genetic heritage, etc., we can begin to move towards modeling efforts that faithfully capture natural realities of what neighborhood composition really means for individuals involved.

Towards mechanistic understanding of neighborhood size

We can infer many different impacts and relationships between different intermediaries and the *V. edulis* that interact with them, but in order to test hypotheses and predictions that come out of this study, we would need to use more mechanistic approaches. In terms of survival, outcomes of this fitness component are often mediated by plants searching for nutrients (McCown, 1978), and being stores of nutrients for other species, i.e herbivores (Warner and Cushman, 2002). Mariah Slaughter (2022) demonstrated that deer presence can have powerful reductions on the viability of entire plant species in the eastern forests. Based on field observations, deer browse a substantial portion of inflorescences across all populations that we studied. A study could be done to compare deer browsing rates across and within populations, and to look for correlation between increased deer browsing and death rate. If a correlation was found it would imply that the nutrient investment into flowers is substantial enough to influence a plants ability to survive into the next year. A similar approach could be used to study the impacts of the powdery mildew found within some populations. These two intermediaries could also be what's influencing growth, so it could be important to look not just at how they kill *V. edulis*, but also how they slow down rosette expansion.

Ability to flower is primarily mediated by nutrients access, energy, and biomass. In dioecious species, sexes can experience different thresholds of what quantity of nutrients (mainly nitrogen) and what biomass is required to flower (Antos and Allen 1990). To better understand the lack of neighbor sex effect on flowering probability and stem quantity in *V. edulis*, one could do chemical analyses of the flowers themselves, to understand how much nitrogen, carbon, phosphorus, and other common plant nutrients are used to make the flowers. If there's very little difference that could support the lack of effect seen in the sex models. If there was a substantial difference, it could point to problems in the way that we're trying to predict these vital rates. It may also be important to conduct a study of the approximated biomass of individuals and how it relates to flowering. A similar mechanistic exploration could be done for growth, but to instead explore if the sexes are indeed differing in what nutrients they take out of the soil.

Ecology has long conceptualized intraspecific interactions in plants as occurring between homogeneous individuals at very localized spatial scales. We have demonstrated that these small scale neighborhoods may obscure a fuller picture. Based on our findings of maximum predictive power existing at 4 different distances for one species,, we should explicitly test for interactions at many spatial scales, which don't need to be explained solely by belowground resource competition. It is also clear that plant researchers must understand that different axes of individual variation (size, sex, genotype, etc) are going to matter, or not, for different kinds of interactions. We must use our knowledge that plants interact at many spatial scales, with many different kinds of conspecific members, to better study and support plant species generally. We need to increase our understanding of which members of populations interact with each other, and how individual variation influences the outcomes of these interactions for different types of individuals within one species.

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