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Implications of sex and location on California junipers (*Juniperus californica)* at their marginal habitat in the Mojave Desert

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California junipers (*Juniperus californica*) are one of the most drought tolerant species in the genus *Juniperus* and are a dominant species in the piñon-juniper woodlands of the Granite Mountains. Understanding the effects of living at the edge of their local habitat range on California juniper reproductive output and tree health is crucial to discerning how the species and the piñon-juniper plant community will fare in the face of climate change. In this study, we evaluated the differential effects of living in marginal habitat on male and female California junipers' health, growth, and females' reproductive output in the Granite Mountains of the East Mojave Desert. Junipers growing in marginal habitat on the flats had lower yearly growth and were smaller than those growing above the flats on the ridge. Additionally, male junipers had stronger branches and greater yearly growth than female trees. These results support the tendency for females of dioecious trees to show a greater reproductive effort than males under resource stress and for adult junipers to show reduced growth in more water stressed areas. As climate change leads to more variation in precipitation and habitat transformation, understanding the effects of living in marginal habitats on plants and plant communities is vital to inform our understanding of how they will respond.

Keywords: *Juniperus californica*, marginal habitat, Mojave Desert, piñon-juniper woodland

INTRODUCTION

Piñon-juniper woodlands cover about 48 million acres of the western United States (Burns 1983). As they are subject to temperature extremes and limited water availability, small changes to the climate can have drastic consequences for this plant community (Brown et al. 1997). Over time, warming temperatures and decreasing precipitation due to climate change have shifted the range of piñon-juniper woodlands both northward and to areas of higher elevation (Betancourt et al. 1993; Miller and Wigand 1998). However, junipers (*Juniperus* spp.) are generally better able to withstand droughts than their most common associate, the piñon pine (*Pinus monophylla)* (Willson et al. 2008). As a result, junipers often invade drier habitats where conifers are unable to survive, extending their elevational range below that of the piñon pine: 1,370 to 2,290 meters (Willson et al. 2008; Burns 1983). Junipers also have higher recruitment in areas with low shrub and tree cover, and are estimated to become more dominant after periods of drought or insect damage (Redmond and Barger 2013). Despite this, water access is one of the greatest limiting factors in their survival and growth, especially as periods of drought become more frequent and increase in severity (Martin et al. 2020). During periods of drought, competition for water is life-threatening to young junipers, while their older counterparts typically only suffer reduced growth rates (Burns 1983).

California junipers *(Juniperus californica),* one of the most drought tolerant juniper species, are a critical indicator for how other members of the genus *Juniperus* will be affected by climate change: if California junipers' range, survival, growth, fecundity, etc. is being reduced, it could mean more severe consequences for other juniper species (Willson et al. 2008). In the Granite Mountains of the East Mojave Desert, California junipers provide an interesting model for studying the future effects of climate change on the species because their local range extends lower in elevation than the piñon pine. The lower elevation flats, composed of alluvium, have a smaller particle size than the Mesozoic granite of the above ridges, resulting in lower infiltration and retention of water in the flats (Laity et al. 2008; Jennings et al. 2010). Their invasion into lower, drier habitat provides a window into the potential long-term impacts of climate change. This marginal habitat is the boundary between ecological niches—the transition zone between suitable and completely unsuitable habitat (Kawecki 2008). In the Mojave Desert, where climate change is expected to increase drought severity, the drier marginal habitat these junipers inhabit allows us to observe how they may respond to future drier conditions throughout the whole of their range.

In the Granite Mountains, the closely related Utah juniper *(Juniperus osteosperma)* and California juniper *(Juniperus californica)* co-exist in the piñon-juniper woodlands (Willson et al. 2008). Unlike the Utah juniper, California junipers are largely dioecious (98% of trees) with each individual producing cones of one sex (Adams 2008). Female cones, colloquially known as 'juniper berries,' are blue-brown, spherical and berry-like, as compared to male pollen cones, which are much smaller, yellow-brown conical extensions of their scales. Due to the higher cost of producing female cones, females of dioecious trees often have more demanding habitat requirements, while males are more tolerant of environmental extremes and able to allocate a higher proportion of resources to vegetative growth (Ortiz et al. 2002). This can result in spatial segregation of male and female individuals. Little is known about how this difference in cost of berry and pollen cone production affects how male and female California junipers respond to environmental stress and marginal habitat conditions.

In this study, we evaluated the different effects of living at the edge of their local habitat range on male and female California junipers' health, growth, and females' reproductive output in the Granite Mountains of the East Mojave Desert. We hypothesized that California junipers on the ridge would be healthier, have greater yearly growth, grow larger, and be less water stressed than junipers on the flats, due to decreased water availability in the flats—their marginal habitat. Within each location, we expected males to be healthier, have greater yearly growth, grow larger, and be less water stressed than females due to the higher relative cost of producing juniper berries than male pollen cones. Due to this high relative cost, we predicted that females' reproductive output would be higher on the ridge. Understanding how males and females respond differently to living in marginal habitat is vital to informing how the species will respond to the warming temperatures and decreased precipitation brought about by climate change.

METHODS

2.1 Natural History

We surveyed California junipers in California's East Mojave Desert at the Sweeney Granite Mountains Desert Research Center (SGMDRC), a 9,000-acre reserve in the UC Natural Reserve System located in the Mojave National Preserve. The elevation of the Granite Mountains ranges from 1,128 to 2,071 m. Our survey was focused at around 1200 m—near the local lower elevational limit of California juniper. While piñon-juniper woodlands occur on the granite ridges and nearby flats, the area is dominated by mixed desert and creosote scrub on the flats, bajadas, and washes.

2.2 Research Design

From February 23–28, 2021, we identified California junipers in both marginal habitat and the higher, ridge areas of the SGMDRC. Marginal habitat was defined as the flats below the ridge based on observations of where California junipers were distributed. Juniper's common associate, the piñon pine, did not extend into the flats below the ridge, providing another aid for the visual start of marginal habitat. Junipers shorter than 1m were excluded to mitigate any effects of age on their response to living on the flats versus the ridge.

In order to estimate male-female relative abundance of junipers on both the ridge and flats, we systematically sampled every juniper of the appropriate size in a given area. Each individual was associated with the flats or ridge and determined to either be male or female, based on the presence of male pollen cones or female berries. While we collected data on the monoecious California junipers we came across, they were excluded from our analyses. An index was defined to categorize the size of each individual. This index was derived from tree height and girth categories informed by observed variation. Height was defined as short, medium, or tall. Girth was categorized as small, medium, large, or maximum. From this we defined 7 size categories (Table 1).

To assess individual tree health, we visually estimated the percent of the tree that appeared dead, grouping trees into one of five categories: 0–10% (1), 10–25% (2), 25–50% (3), 50–75% (4), 75–100% (5). We measured the current year's growth in eight distinct places, choosing evenly dispersed locations both vertically and horizontally around each individual tree. The rocky terrain of the ridge limited our ability to sample growth from any point on some junipers, thus growth was taken only at easily accessible points. We then took the average of the eight growth measurements to determine each juniper's average current year's growth.

To measure each female juniper's reproductive output, we utilized both a visual estimate of berry cover (0–25% (1), 25–50% (2), 50–75% (3), 75–100% (4)) and the average mass of one berry, which was calculated by averaging the mass of 40 berries per individual tree. Berries were collected across all accessible areas of the tree. A reproductive index was defined to account for differences in seed predation: (RI = [berry cover (1-4)] * [average mass per cone]).

To estimate water stress, we measured the kilograms of force required to break a branch from an individual. Branches were taken as a balanced subsample between the four groups: flats males, flats females, ridge males, and ridge females. The first branch noticed of acceptable length (14–20 cm) and circumference (1–3 cm) was chosen, clipped, and labeled with the tree's unique identification number. Its circumference was then measured at the point at which the branch would be broken, which ranged from 1 cm–2.8 cm. This size was chosen because larger branches required more force to break than we were able to apply. To account for differences in time off the tree, branches were broken in the approximate order they were collected 2–3 hours from when they were collected. When breaking, each end of the branch was held down 11 cm apart. A force was then applied perpendicular to the orientation of the branch via a handheld luggage scale at the selected point. The scale was pulled until the branch fractured or snapped. The weight (in kg) it took to break or fracture the branch was recorded.

2.3 Statistical Analyses

Analyses were conducted in RStudio Version 1.4.1103 (R Core Team 2020).

To achieve a balanced design, females from both ridge and flats were randomly subsampled to match sample sizes for the ridge and flats males. An ANOVA was used to examine the effect of size on current year's growth, percent dead vegetation, reproductive output, and force required to break a branch to see if it should be included in the models as a random effect (Table 2). We used a two-way ANOVA and a Tukey post-hoc to test the effect of location, sex, and their interaction on current year's growth (Fig. 1; Supplemental Table 1). To test the effect of location, sex, and their interaction on size, a two-way ANOVA and was used (Fig. 2). To examine the effect of location, sex, and their interaction on percent of tree dead, a two-way ANOVA was utilized.

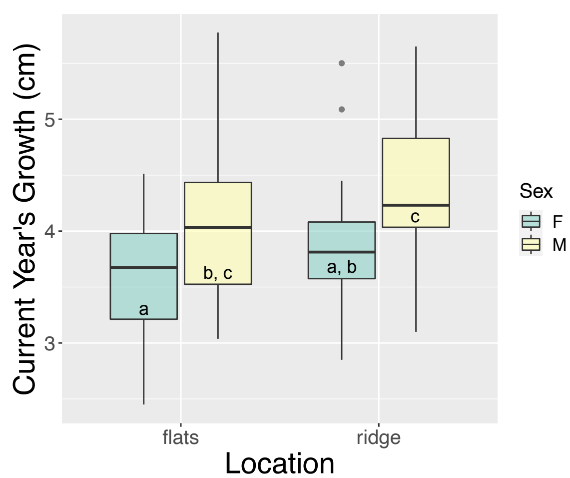

Figure 1. Current Year's Growth. Effects of position and sex on current year's growth (cm) in California junipers *(Juniperus californica)* in the East Mojave Desert. Both sex and position had an effect. Growth was higher in flats males than flats females, ridge males than flats females, and ridge males than ridge females (Table 3). ($N_{Female,\ Flats}$ = 30, $N_{Male,\ Flats}$= 30, $N_{Female,\ Ridge}$ = 28, $N_{Male,\ Ridge}$= 28, F_{Sex} = 20.72, $p_{Sex} < 0.001$, $F_{Position}$ = 6.75, $p_{Position}$ = 0.01, $F_{Interaction}$ = 0.024, $p_{Interaction}$ = 0.876)

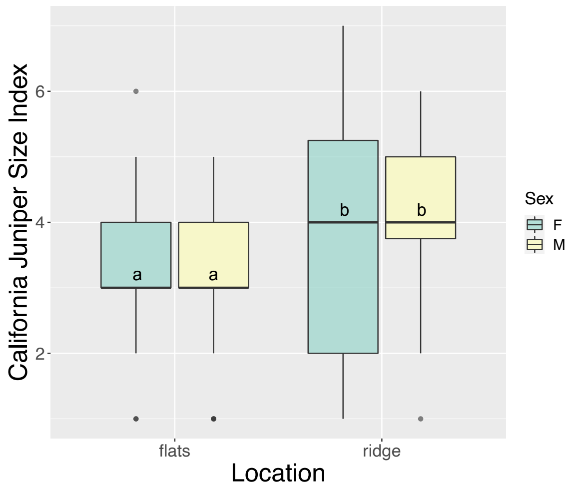

Figure 2. Size Index. Effects of position and sex on size of California junipers *(Juniperus californica)* in the East Mojave Desert. Junipers on the ridge were larger than those on the flats. Sex had no effect. Size Index is detailed in Table 1. ($N_{Female, Flats}$ = 29, $N_{Male, Flats}$ = 29, $N_{Female, Ridge}$ = 28, $N_{Male, Ridge}$= 28; $F_{Position}$ = 6.10, $p_{Position}$ = 0.02, F_{Sex} = 0.079, p_{Sex} = 0.78, $F_{Interaction}$ = 0.312, $p_{Interaction}$ = 0.58)

A chi-squared test was used to examine differences in males and females' relative abundance within our sample. To test the effect of location on the reproductive index (RI), we used an ANOVA. Subsampling was not utilized to assess reproductive output because the ridge female and flats female groups were balanced. To examine the effect of location, sex, and their interaction on force required to break a branch, we defined a linear model between branch circumference and kilograms applied at breaking point. We then used a two-way ANOVA followed by a Tukey Post-Hoc to test the effect of location, sex, and their interaction on the residuals from the linear model (Fig. 3; Supplemental Table 3). For branch breaking, balanced subsampling was conducted in the field.

Table 1. Index used to categorize the size of individual California junipers (*Juniperus californica*) in the East Mojave Desert.

Size Index, 1-7	Height	Girth
1	Shortest	Smallest
2	Short	Small
3	Medium	Small
3	Short	Medium
4	Short	Large
4	Medium	Medium
4	Tall	Small
5	Tall	Medium
5	Medium	Large
5	Short	Maximum
6	Medium	Maximum
6	Tall	Large
7	Tall	Maximum

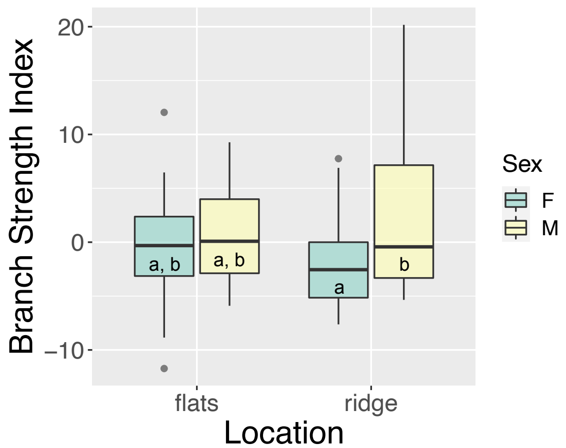

Figure 3. Branch Strength Index. Effects of position and sex on branch strength of California junipers *(Juniperus californica)* in the East Mojave Desert. Male junipers had a higher branch strength index than female junipers. Position had no effect. Branch strength index, here, is defined as the residuals from the ANOVA of kilograms of force applied at breaking point and branch circumference. ($N_{Female,\ Flats}$ = 32, $N_{Male,\ Flats}$ = 24, $N_{Female,\ Ridge}$ = 32, $N_{Male,\ Ridge}$= 23, $_{Sex}$ = 7.31, p_{Sex} = 0.008, $F_{Position}$ = 0.026, $p_{Position}$ = 0.872, $F_{Interaction}$ = 2.97, $p_{Interaction}$ = 0.09)

RESULTS

Current year's growth was higher in male junipers and on the ridge (NFemale, Flats = 30, NMale, Flats = 30, NFemale, Ridge= 28, NMale, Ridge = 28, FSex= 20.72, pSex< 0.001, FLocation = 6.75, pLocation = 0.01; Fig. 1; Supplemental Table 1). The effect of location on growth did not depend on sex (NFemale, Flats = 30, NMale, Flats= 30, NFemale, Ridge = 28, NMale, Ridge= 2, FInteraction = 0.024, pInteraction= 0.876). Junipers on the ridge were larger than those on the flats, but sex had no impact on size (NFemale, Flats = 29, NMale, Flats = 29, NFemale, Ridge = 28, NMale, Ridge = 28; FLocation = 6.10, pLocation = 0.02, FSex= 0.079, pSex = 0.78, Fig. 2). The effect of location on size did not depend on sex (NFemale, Flats = 29, NMale, Flats = 29, NFemale, Ridge = 28, NMale, Ridge = 28, FInteraction = 0.312, pInteraction = 0.58). There was no effect of location, flats versus ridge, or sex on percent dead (NFemale, Flats = 30, NMale, Flats = 30, NFemale, Ridge = 28, NMale, Ridge = 28, FLocation = 0.20, pLocation = 0.65, FSex= 1.50, pSex = 0.22). The effect of location on percent dead did not depend on sex (NFemale, Flats = 30, NMale, Flats = 30, NFemale, Ridge = 28, NMale, Ridge = 28, FInteraction = 2.99, pInteraction = 0.087). We found more females on the landscape than males (NFemale = 96, NMale = 58, χ2 = 9.38, p = 0.002). Location had no effect on reproductive output (NFemale, Ridge= 49, NFemale, Flats = 47, F = 1.55, p = 0.27). Size only had an effect on reproductive output, thus it was included as a random variable in only this model (Table 2). Males had a higher branch strength index than females (NFemale, Flats = 32, NMale, Flats = 24, NFemale, Ridge = 32, NMale, Ridge = 23, FSex= 7.31, pSex = 0.008, FLocation = 0.026, pLocation = 0.872; Figure 3; Supplemental Table 3). The effect of sex on branch strength did not depend on location (NFemale, Flats = 32, NMale, Flats = 24, NFemale, Ridge = 32, NMale, Ridge = 23; FInteraction = 2.97, pInteraction = 0.09). Out of 157 individuals, only four (2.5% of our sample) were monoecious.

Table 2. ANOVA results, which examine the effect of California juniper (Juniperus californica) size on current year's growth, percent dead, reproductive index, and branch strength index.

Response	N Female, Flats	N Male, Flats	N Female, Ridge	N Male, Ridge	F	p
Current Year's Growth	30	30	28	28	3.69	0.06
Branch Strength Index	29	29	28	28	2.66	0.11
Reproductive Index	47	n/a	49	n/a	13.17	<0.001
Percent Dead	30	30	28	28	2.03	0.16

DISCUSSION

Our results fell in line with many, but not all, of our initial predictions. With regards to location on the landscape—ridge versus flats—our results agreed with our predictions that current year's growth and size would be higher on the ridge, indicating better health. We posit that this is because California junipers in the flats have lower water availability, resulting in more water stress on the flats as compared to the ridge (Mahaffey et al. 2020). The Mesozoic granite of the ridges in the East Granite Mountains has a larger particle size than the alluvium of the flats, allowing for greater infiltration and retention of water (Laity et al. 2008; Jennings et al. 2010). Lower infiltration and retention in the flats result in water stress, which reduces growth rates for adult junipers (Burns 1983). This may result in smaller tree size in areas of higher water stress, supporting our finding of larger tree size on the ridge when compared to flats.

We found no difference in the percentage of dead vegetation on junipers between the ridge and flats. From previous research, we would expect junipers to follow the segmentation hypothesis, in which junipers improve overall water balance by sacrificing distal branches (Hacke and Sperry 2001; Zimmermann 1983). From this, we would expect the percentage of dead vegetation to be higher in the flats than the ridge in order for junipers in the water stressed flats to be able to better allocate resources. However this was not observed in our results. Perhaps surveying a larger distance from their marginal habitat would result in a larger difference in observable water stress, and thus may find a difference in percentage of dead vegetation between ridge and flats. Additionally, future studies may consider it more reliable to measure canopy coverage or proportion of dead branches over percent of dead vegetation, following a previous study in the Sonoran Desert that found decreased canopy coverage as elevation increased (Mahaffey et al. 2020).

Another previous study on a different dioecious species, the common juniper (*Juniperus communis*), across two locations in their upper elevational zone—ridge and wash—observed that the reproductive output of both male and female trees decreased with proximity to marginal habitat (Ortiz et al. 2002). It would seem then that female junipers are healthier and thus more capable of sustaining cone production further from their marginal habitat. We found no difference in the reproductive output of female trees between the ridge and flats, but a larger distance from marginal habitat might capture greater variation in environmental stress, resulting in a similar pattern of decreasing reproductive output in marginal habitat. Interestingly, there were more females than males on the landscape. Previous work on the common juniper across an elevational gradient found that sex ratios did not vary greatly at lower elevation, but that above 2600 m, male trees dominated populations (Ortiz et al. 2002).

Our results agreed with our predictions that both current year's growth and branch strength would be higher in male junipers. These results support the tendency for females of dioecious trees to show a greater reproductive effort than males even under resource stress despite being more likely to suffer environmental stress (Rabska et al. 2020; Zhang et al. 2018). Branches from female trees may break more easily because they allocate more resources, mainly water, to cone production over general growth (Peng et al. 2016).

While our study provides a snapshot of how California junipers in the East Mojave Desert are responding to living in marginal habitat under current conditions, a longer-term study, as well as a broader study area, could better inform our understanding of California junipers' response to change in temperatures and water availability over time. Future studies could also look more closely at the plasticity in morphology across elevational and habitat gradients by introducing more relevant variables: the oneseed juniper (*Juniperus monosperma*), has been observed to have higher soil moisture and canopy coverage on north-facing slopes (Westerdand et al. 2015). These studies could provide valuable insight into the potential for differences in male and female junipers responses to habitat and climate change to result in spatial segregation or other barriers to reproduction.

Understanding the implications of spatial segregation could be further informed by future study on monoecious California junipers (2% of the population) (Adams 2008). Studies over a broader area could look at ratios of monoecy to dioecy at varying distances from marginal habitat to see if moving towards monoecy could be a potential response to spatial segregation of the sexes in the species. It would also be interesting to look at differences in growth on the male and female sections of the tree. Comparisons on the same plant provide a unique perspective on how growth varies within a plant across the male and female portions, which have access to the same nutrient and water resources. Understanding how male and female California junipers respond differently to living at the drier, lower elevational portions of their range is vital to informing how the species and other drought-tolerant dioecious species will respond to the warming temperatures and decreased precipitation brought about by modern-day climate change.

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APPENDIX

Supplemental Table 1. Results of a Tukey post-hoc used to test differences in the effects of position and size on growth among California juniper (Juniperus californica) ridge males, ridge females, flats males, and flats females in the East Mojave Desert.

Relationship	Difference	p
Ridge Females - Flats Females	0.29	0.31
Flats Males - Flats Females	0.48	0.01
Ridge Males - Flats Females	0.78	< 0.001
Flats Males - Ridge Females	0.21	0.51
Ridge Males - Ridge Females	0.52	0.008
Ridge Males - Flats Males	0.30	0.21

Supplemental Table 2. Results of a Tukey post-hoc used to test differences in effects of position and sex on branch strength between California juniper *(Juniperus californica)* ridge males, ridge females, flats males, and flats females in the East Mojave Desert.

Relationship	Difference	p
Ridge Females - Flats Females	-1.60	0.61
Flats Males - Flats Females	1.01	0.89
Ridge Males - Flats Females	2.87	0.19
Flats Males - Ridge Females	2.61	0.26
Ridge Males - Ridge Females	4.47	0.01
Ridge Males - Flats Males	1.87	0.61