

RESEARCH ARTICLE

Heat waves decrease fitness and alter maternal provisioning in natural populations of *Mimulus guttatus*

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Abstract

Premise: The increasing frequency and severity of heat waves across the globe is well known. However, few longitudinal studies have tracked demographic change and fitness within natural populations, and fewer still have spanned multiple extreme events. Determining how organisms tolerate, respond, and potentially adapt to extreme events is key for assessing long-term population viability.

Methods: We examined how mortality, fecundity, seed provisioning, and offspring germination differed across 12 populations of annual common monkeyflower (*Mimulus guttatus*) over 5 years.

Results: Two heat waves occurred within the study: a heat wave within the first 10 days of the growing season in 2019 and a heat dome event nearly a month into the growing season in 2021. Mortality was high, and fecundity decreased in a population-specific manner following each heat wave. However, the 2021 heat dome caused declines of 34.5% in seed size and 22.1% in the ability to germinate, while the 2019 heat wave did not significantly affect either. Structural equation models indicated that similar climatic factors—including early-season maximum temperatures and late-season precipitation—are associated with declines in fecundity and slower germination.

Conclusions: These results suggest that the consequences of heat waves will depend on the relative severity and timing of the heat wave in the growing season, and further suggest that this timing may have amplified longer-term impacts because offspring have less provisioning. Specifically, with growing seasons shifting earlier into the spring, later or slower germination could exacerbate population extirpation risk.

KEYWORDS

common yellow monkeyflower, demography, *Erythranthe guttata*, germination, global change biology, longitudinal study, maladaptation, maternal effects, phenology, Phrymaceae, plasticity

As the frequency and severity of heat waves increase across the planet (Meehl and Tebaldi, 2004; Della-Marta et al., 2007; Coumou et al., 2013; Reyes and Kramer, 2023), a key goal for biologists is determining how organisms will respond and whether populations will persist during these extreme events (Harris et al., 2018; Breshears et al., 2021; Calvin et al., 2023). Heat waves have been linked to high mortality (Ruthrof et al., 2018), extirpation of populations (McDonald et al., 2023; Montie and Thomsen, 2023), and the restructuring of communities (Whalen et al., 2023). However,

other organisms or populations seem better able to track environmental extremes (Troth et al., 2018; Rudman et al., 2022). The extensive variation in the demographic and evolutionary consequences of heat waves likely depends on the severity, timing, and duration of the heat waves, the characteristics of the organism, and the extent of historic fluctuations in climate (Orsenigo et al., 2014). Parsing the drivers of these consequences is a challenge because it requires baseline data before the heat wave and similar data collection—potentially at multiple times—after the heat wave.

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Thus, longitudinal data collection within natural populations is a practical and important way to examine the impacts of heat waves or other extreme events (Grant and Grant, 1993; Grant et al., 2017).

The impact that individual heat waves have on a focal population can be approximated by examining declines in survivorship during the heat wave and declines in fecundity relative to more typical growing seasons (Ma et al., 2015). Although relative declines in fitness can be measured through a longitudinal study in a single population, comparisons between nearby populations provide insight into the range of population-specific responses and the broader consequences at a species level (Anstett et al., 2021; Kooyers et al., 2021). For instance, while heat waves are likely to expose all geographically close populations to abnormal heat, the magnitude and severity of those conditions and associated responses will be influenced by heterogeneity in resource availability within the population, presence and abundance of other community members, and the environmental characteristics of the site (Brooker, 2006; He et al., 2013). For instance, a short but extreme heat wave had very different fitness consequences in geographically-close monkeyflower populations along an elevational gradient; populations varied extensively in mortality, and some populations actually had higher fecundity than in “typical” years (McDonald et al., 2023).

Most studies examining the consequences of heat waves have evaluated mortality of impacted populations, and a more limited subset have identified the impacts on fecundity (reviewed by Grant et al., 2017). Impacts of heat waves extend beyond the surviving individuals within a population by altering maternal provisioning in the survivors and transferring epigenetic signals to their offspring (Roach and Wulff, 1987; Mousseau and Fox, 1998; Wolf and Wade, 2009). Indeed, the consequences of such transgenerational effects on offspring can be immense and seem to be common in sessile plant species (Agrawal, 2002; Galloway and Etterson, 2007; Holeski, 2007). For instance, seed size has both heritable and environmental components (Larios et al., 2023) and has consequences for offspring germination and development (Donohue, 2002). Extreme conditions can lead to sterility or decreased maternal provisioning of seeds, resulting in decreased ability to germinate, slower germination, or increased dormancy (Donohue et al., 2008; Singh et al., 2019; Klupczyńska and Pawłowski, 2021). For organisms with short growing seasons, slower germination or germinating in the wrong year may prevent successful reproduction (Donohue et al., 2005). The impacts of decreased survivorship, fecundity, and downstream maternal effects may combine to create compounding or emergent consequences (Walck et al., 2011). For instance, if a heat wave causes decreased fecundity and lowers the ability to germinate in an annual plant, the net number of offspring germinating in the next generation would be lower than with either effect alone. Thus, combining observations of fitness within parent generations with offspring phenotypes is necessary for predicting population resilience.

Organismal responses to heat waves may depend on the timing and magnitude of the heat wave. Heat waves are typically defined relative to the historical mean and maximum temperatures at a given time and location—i.e., three or more consecutive days where the temperature is greater than the historic 90th percentile for a specific location and time of year (Perkins and Alexander, 2013). However, for a given organism, the consequences of a heat wave are likely dependent on when the heat wave occurs within its life cycle (Zhang et al., 2015; Cope et al., 2023). For instance, heat waves directly after germination are likely to cause greater mortality than a heat wave after plants have substantial root structure. Additionally, most studies on extreme events (heat waves or droughts) have focused on longer-term events that last months to multiple growing seasons (Grant and Grant, 1993; Kooyers et al., 2021). While these certainly have a large impact on populations, shorter heat waves provide less time for acclimation than longer events and thus could have equally severe consequences (Grant et al., 2017). Comparisons between successive heat waves on the same populations are useful to understand the predictability of environmental variability on population responses.

In this study, we examined the magnitude and direction of fluctuations in fitness and maternal provisioning in 12 monkeyflower populations across five years that included two heat waves. We used these data to address the following questions. First, how do heat waves impact mortality and fecundity of natural populations? Second, how does fecundity differ between heat-wave years and between heat wave and non-heat-wave years? Third, do heat waves alter seed provisioning and germination characteristics of offspring? If so, do different heat waves have similar effects? Fourth, how do climatic variables influence fluctuations in fecundity, maternal provisioning, and germination? Our results indicate that heat waves generate strong effects on fitness, seed provisioning, and offspring germination phenotypes, and that the extent of these effects differ depending on when the heat wave occurs in the growing season. These results highlight the resilience of—and the threat to—these isolated populations that exist on the edge of their abiotic niche.

MATERIALS AND METHODS

The common yellow monkeyflower, *Mimulus guttatus* Fisch. ex DC (Phrymaceae; syn. *Erythranthe guttata* G.L. Nesom; Lowry et al., 2019; Nesom et al., 2019) is a primarily outcrossing herbaceous plant distributed across western North America (Wu et al., 2008). This study focuses on annual inland populations that dominate ephemeral wet, thin-soiled subalpine meadows in the central Oregon Cascade Mountains. Growing seasons within these populations begin with germination after snowmelt in late May to early June and last until soils completely dry out in mid-July (Kooyers et al., 2019). However, the timing and duration of growing seasons is particularly heterogeneous between years and these highly diverse populations have

historically been used as a case study for the maintenance of diverse life-history strategies through fluctuating selection (Hall and Willis, 2006; Hall et al., 2010; Mojica et al., 2012; Puzey et al., 2017; Troth et al., 2018).

Changing climates may also threaten these populations. These populations exhibit an adaptation lag, where populations from elevation-matched populations from the Sierra Nevada, which have earlier growing seasons, have greater fitness than native populations (Kooyers et al., 2019; Scharnagl et al., 2023). Previous observational studies suggest that heat waves and droughts are a particular threat to these populations, exemplified by one population becoming temporarily extirpated for 2 years after a short but extreme heat wave in 2019 (McDonald et al., 2023).

Focal natural populations

This study expands a longitudinal data set of 12 natural populations of *M. guttatus* within a ~25-km² area of the central Oregon Cascades from 2 to 5 years (Figure 1; McDonald et al., 2023). Climate data including daily minimum temperatures, maximum temperatures, and total precipitation were downloaded from NOAA's National Climate Data Center for a nearby NOAA weather station at a similar elevation as the focal populations (Santiam Junction: 44.44, -121.95, 1140 m a.s.l., 16 km from Browder Ridge). We defined a heat wave as three or more consecutive days where maximum temperature was at >1 SD above the historical average maximum temperature during the typical 6-week growing season within these populations (1 June to 14 July). We note that we use >1 SD above the historical average maximum temperature rather than >90th percentile because our data set only goes back to 1980. We also downloaded monthly and annual climate data from ClimateNA (Wang et al., 2016) for each population for each year of the study (2018–2022) and the historical averages (1980–2010; Appendix S1) to use within the piecewise structural equation modeling described below.

Demographic and phenology experiments

We collected data on survival and phenology within 9 of 12 populations in 2019 and 2021. We excluded populations EVS, MTD, and BMP because of time constraints and the logistic difficulty of surveying these populations. We visited each population weekly throughout the growing season (early June to early August) and established two 0.25-m² plots in each population each year. These plots were semi-randomly established to not overlap with each other and to be completely within the main seep area. During each weekly census, we counted the vegetative individuals, the actively flowering individuals, the senesced individuals with fruit, and the senesced individuals without fruit. Thus, each plant was counted only once and placed into one category in each weekly survey. We did not track or tag individuals

because there can be 1000+ within each plot at the beginning of the season. However, we tracked survival across the growing season by dividing the number of plants in the vegetative and actively flowering categories at a given time by the maximum plants alive at any time within the plot (hereafter, “survivorship”). We also created a phenology curve for each plot by dividing the number of plants flowering at a given time by the maximum number of plants alive at any time within the plot. We note that the maximum number of plants alive was typically at the first census, but not always, because some population had additional germinants in subsequent censuses.

Examining the impact of heat waves on survival

To determine the influence of heat waves on survival within each population, we compared survivorship before and after heat-wave events in both 2019 and 2021. We examined deviations in survivorship in heat-wave years relative to more typical conditions using the survivorship data from the 2021 growing season during the Julian dates of the 2019 heat wave as the “typical” year. For the 2021 heat dome, we used the survivorship data from the 2019 growing season during the Julian dates of the 2021 heat wave as the typical year. We note that we could not compare survivorship between heat-wave and non-heat-wave years because we only had weekly surveys for 2019 and 2021.

We quantitatively assessed whether there were differences in survivorship between heat-wave years by determining whether there were differences in rate of change of survivorship during the Julian dates of each heat wave (2019: Day 160–167; 2021: Day 168–180) using a linear mixed model implemented with `lmer()` (Bates et al., 2014) in R version 4.2.2 (R Core Team, 2022). Dates of the heat wave reflect the first and last days that maximum temperature was >1 SD above the historic mean. We calculated rate of change in survivorship by subtracting the proportion of plants surviving after the heat wave from the proportion before the heat wave and then dividing by the number of days between these observations. We ran separate models examining rates of change in survivorship during each of the two time periods (Julian days 160–167, Julian days 168–180). For each model, rate of change in survivorship was the response variable, while year was the fixed factor. Population and plot nested within population were treated as random variables. Statistical significance was examined via ANOVA implemented using the `Anova()` function in the R package `car` (version 3.1-2; Fox et al., 2013).

Determining effects of heat waves on fecundity

To measure fecundity, we visited and collected seed from each focal population every year from 2018 to 2022 following senescence. To make sure we were collecting a random subset of the population, we collected individual

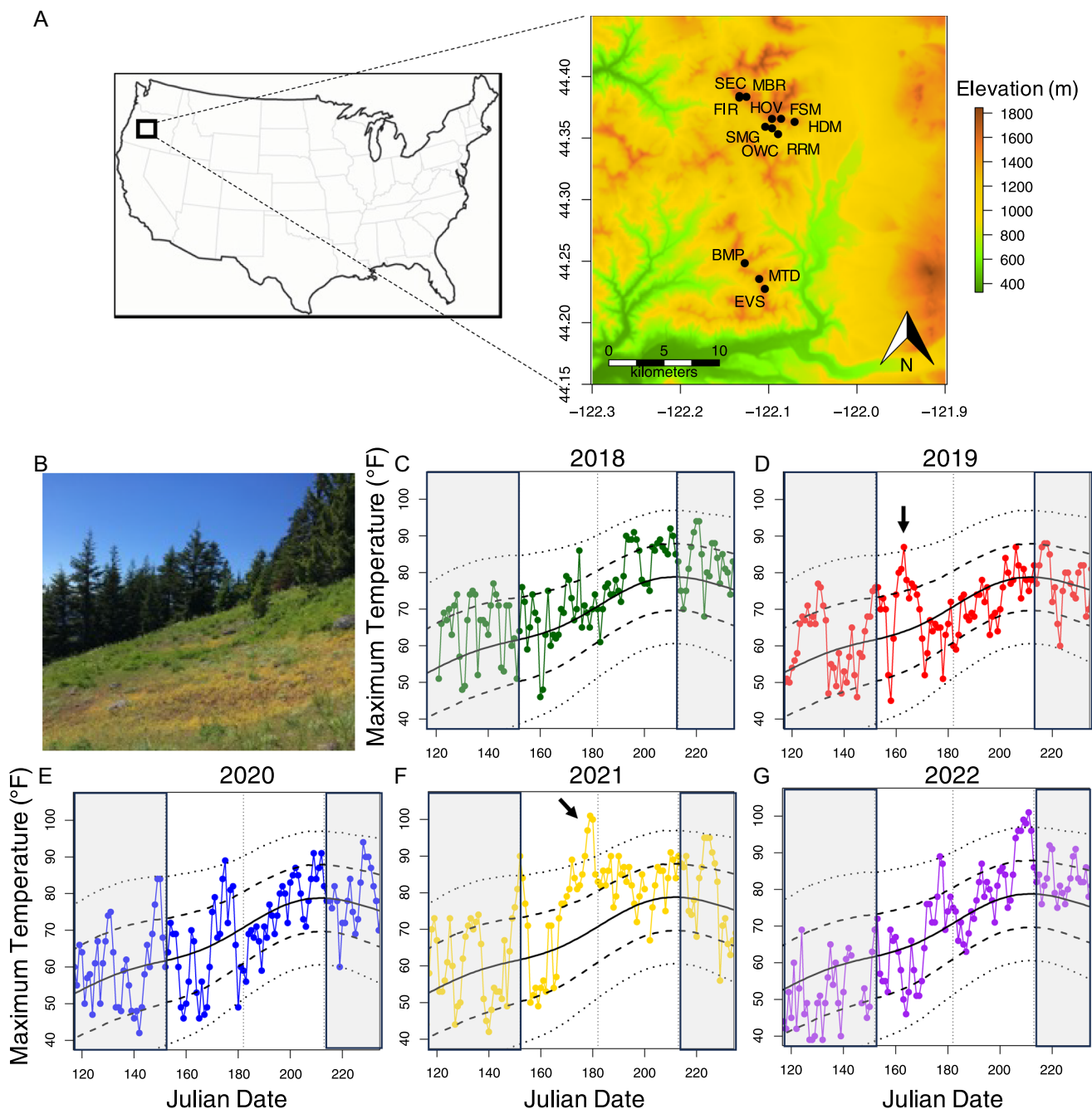


FIGURE 1 Focal study region and variation in maximum temperature across monkeyflower growing seasons from 2018 to 2022. (A) Map of central Oregon Cascades study region and focal populations. The raster legend in the insert depicts elevation in meters across the study region. (B) Example annual *Mimulus guttatus* seep population in the central Oregon Cascades (BMP). (C–G) Maximum daily temperature extracted from nearby NOAA site (Santiam Junction, OR) across the typical annual *M. guttatus* growing season from 2018 to 2022. Solid black trend lines represent the average maximum temperature, dashed lines are 1 SD above or below the average; and dotted lines are 2 SD above or below the average. Arrows represent heat waves in 2019 and 2021. The additional heat wave at the end of the 2022 growing season had limited impact on focal populations as all plants were already senesced.

plants along two 7.5-m transect lines spanning each population. We collected the nearest plant to the transect line every 15 cm along the transect (50 plants per transect; 100 per population per year). After 2020, we began collecting plants every 30 cm along the transect because some populations exhibited declines in response to recent climate fluctuations and we wanted to reduce our impact on the

populations. For populations with extensive declines and/or poor recruitment in certain years (Populations: OWC, HDM), we counted all seeds in the field, kept a limited number of seeds per individual, and distributed the majority of seeds back into the population.

We evaluated how fecundity varied across populations and years using general linear models (LMs) implemented

using the function `lm()` in R version 4.2.2. Univariate LMs were conducted for number of flowers and number of seeds. Each model had population, year, and the population-by-year interaction included as factors. Number of flowers and number of seeds were log-transformed before analysis and models used an identity link function and assumed a Gaussian distribution of residuals. Model distributions and link functions were chosen to best match model assumptions. To directly evaluate whether there were differences in fecundity between heat-wave and non-heat-wave years, we used univariate linear mixed models (LMM) implemented via the `lmer()` function in the R package `lme4` for each fecundity metric, with heat-wave year (yes/no) as a fixed effect and population crossed with year as random effects (i.e., $1 | \text{Population:Year}$). We also report percentage declines between non-heat-wave and heat-wave years as: $100 \times (\text{Mean}_{\text{non-heat-wave years}} - \text{Mean}_{\text{heat-wave years}}) / \text{Mean}_{\text{non-heat-wave years}}$. To test whether there were differences among heat-wave years, we subset our data to just heat-wave years (2019, 2021) and conducted an LMM with year as a fixed effect and population as a random effect. In all cases, significance was assessed via ANOVA as above with type III sum of squares. We also note that an assisted gene flow experiment was started in a subset of these populations in 2021. Inclusion of this treatment as a random factor did not impact any of our below conclusions.

Identifying impacts of heat waves on maternal provisioning and germination

We counted the seeds from every plant, and weighed out ~20–30 seeds from 12 randomly selected lines per population per year. Average seed mass was calculated by dividing the total mass of the seeds by the number of seeds weighed (termed “seed mass” below). We tested seed germination after collection each year (~2 months after collection on the same timeline as the natural populations). We planted eight seeds per pot from each maternal line with the exception of some lines in threatened populations that had fewer than eight seeds (HDM). Pots were randomized into 25.4×50.8 -cm flats with humidity domes and cold-stratified for 7 days at 4°C. Flats were then moved to growth shelving with four growth lights (1.22-m 8-bulb T5 fluorescent fixture) with timers set for 16 h day/8 h night cycles at 23°C. After 7 days, flats were moved to greenhouse kept at 22°C with supplemental lighting (16 h day/8 h night) and the humidity domes were removed. We counted and marked new germinants for the first time after 24 h on growth shelving (termed day 1 below). Germination was monitored daily for at least 7 days and surveyed again later in the experiment, typically 20+ days later, but the date differed among gardens. Two different metrics of germination success were used. We calculated the proportion of germinated seeds at day 5 by dividing the number of germinants that had germinated by day 5 by the total number of germinants surveyed in the first 10 days in the same pot (termed “germination speed” below). This metric addresses the speed of germination because 5 days to germination represents a relatively standard germination time for

these *M. guttatus* populations grown under control conditions. Second, we examined whether any seeds had germinated in each pot across the entire time surveyed (Y/N; termed “ability to germinate” or “germination ability” below). This metric examines absolute ability to germinate as often seeds that did not have substantial provisioning, exhibit extreme dormancy cues, or were aborted would not germinate under our conditions.

We evaluated potential differences in seed mass and germination among years, differences between heat-wave and non-heat-wave years, and differences among heat waves using similar GLMs, LMMs, and GLMMs as used for fecundity metrics. The only difference was the response variable: Univariate GLMs were conducted with average seed mass, ability to germinate, and germination speed as response variables. Seed mass and germination speed models had a Gaussian distribution with identity link functions, while ability to germinate models had a binomial distribution with a logit link function. Log transformation (seed mass) or $\sqrt[3]{(1-x)}$ transformation (germination speed) produced poorer model fits. Significance was assessed as above.

Determining climatic drivers via structural equation modeling

We examined relationships between climate, seed traits, and germination traits with piecewise structural equation models (PSEM). We first compared four hypothesis-driven models (Appendix S2). Climate variables were exogenous and included mean and maximum temperature, precipitation, and climate moisture deficits (all measured in both June and July), the beginning of the frost-free period, and the percentage of precipitation occurring as snowfall. Seed traits included number of seeds and seed mass. Germination traits included germination speed and germination ability. Our full model (Appendix S2A) allows climate variables to predict both seed and germination traits and allows seed traits to predict germination traits. We did not draw any paths between climate variables because they are all exogenous. We treated paths within seed and germination traits as correlated errors because these traits may arise from the same underlying process and the direction of causality is unclear. Because it includes all paths, the full model did not have a *P*-value; instead, it was a useful starting point against which to compare the AICc scores of the nested models. The three other models were nested within this full model. The first nested model (Appendix S2B) assumes that climate does not directly affect germination traits; rather, climate affects germination only through effects on seed traits. The second nested model (Appendix S2C) assumes that climate affects seed and germination traits, but seed traits do not affect germination traits. The third nested model (Appendix S2D) assumes that climate and seed traits affect germination traits, but climate does not affect seed traits. Each nested model is a simplification of the full model that may be preferable if the removed paths lack predictive power.

PSEMs were run using R package piecewiseSEM (version 2.3.0; Lefcheck, 2016). Response variables were transformed as needed to meet model assumptions. Germination speed and ability to germinate were left-skewed but were normalized by taking the square root of 1 minus the original value: $(1 - x)^{1/2}$. Number of seeds was right-skewed and normalized with a natural-log plus one transformation: $\ln(x + 1)$. Within the PSEMs, all models were generalized additive models [function `gam()` in R package `mgcv`; Wood, 2011] to allow for potentially nonlinear relationships. We included year and population as random effects [using the `bs = "re"` argument in function `gam()`].

Of the full model and three nested models, we chose the best model based on two criteria. First, we used modelwide *P*-values, which quantify the chance that important paths have been omitted. Second, we used bias-corrected Akaike information criterion (AICc) (Akaike, 1973; Sugiura, 1978), which is designed to balance a model's predictive power with its complexity and should preclude unnecessarily complicated models. We first excluded PSEMs with modelwide *P*-values above 0.05, and then used AICc to select the best model of the remaining PSEMs. Finally, we refined the causal structure of the best model by removing non-significant paths from highest to lowest *P*-value, again using AICc as a guide for whether the removal increased model quality. The random effects were retained or removed using this same process. Beginning with hypothesis-driven models, refining models in this way is a recommended practice in structural equation modeling (Grace et al., 2012).

RESULTS

Temperatures during the growing season varied dramatically across years, with two heat waves impacting the focal populations (Figure 1). We previously reported a heat wave over 8 days during the first 2 weeks of the growing season in 2019 (Days 160–167; McDonald et al., 2023). As measured at a nearby NOAA weather station, temperatures during this heat wave peaked at 30.6°C, 12.7°C above average and the second-hottest maximum temperature for this day over the last 40 years. A second heat wave occurred in 2021, caused by a heat dome event across the Pacific Northwest (White et al., 2023). This heat dome resulted in 26 days of above-average temperatures and a 4-day stretch of maximum temperatures in the top 0.1% of maximum temperatures for that day in the last century. The 2021 heat dome occurred ~3–4 weeks into the growing season for our surveyed populations. The 2019 heat wave was both less intense and shorter than the 2021 heat dome.

Heat waves strongly decreased survivorship across nearly all populations. During the 2019 heat wave, 15 of 18 plots had declining abundance during the beginning of the growing season when many of these populations normally have additional germination and establishment (Figure 2A–C). Indeed, the rate of change in survivorship during dates of the 2019 heat wave was more negative in the 2019 growing

season than in the 2021 growing season ($F_{1,17} = 23.2$, $P = 0.0002$); abundance declined by 2.56%/day in 2019 but increased by 1.28%/day in 2021. However, all populations but one (HDM) had some individuals survive in 2019. The 2021 heat wave was equally impactful; all 18 plots had declining numbers of individuals, and 9 plots experienced complete mortality following the peak of the heat wave (Figure 2D). By this point in the growing season, the number of individuals typically starts to decline in these populations because early-flowering individuals are beginning to senesce; however, declines were more severe during the 2021 growing season than the 2019 growing season during these Julian dates ($F_{1,17} = 56.8$, $P < 0.0001$). During the 2021 heat wave, plots declined by 4.66%/day, whereas during the same dates in 2019, plots only declined by 0.98% per day. We note that the rate of decline for 2019 plants during the 2021 heat wave period is potentially biased because the 2019 plants had already survived an early-season heat wave.

Fecundity in terms of number of flowers and number of seeds fluctuated dramatically between populations and across years and was strongly influenced by heat waves. There was a strong effect of year on both fecundity measures (number of flowers, year: $F_{4,3854} = 10.3$, $P < 0.0001$; number of seeds, year: $F_{4,3810} = 20.4$, $P < 0.0001$; Appendices S3–S5). Years with heat waves (2019, 2021) had 35% and 59% drops in number of flower and seeds, respectively, compared to non-heat-wave years (number of flowers: $\chi^2 = 28.6$, $P < 0.0001$, number of seeds: $\chi^2 = 30.0$, $P < 0.0001$; Figures 2E, 2F, 3A, 3B; Appendix S6). There were also slight differences in fecundity metrics between the two heat-wave years, but these differences were minor in effect size and not consistent between fecundity metrics (Figure 2E, F; Appendix S7).

While heat waves strongly influenced fecundity, there were also population-specific effects. Some populations had greater than double the flowers and six times the seeds as other populations (number of flowers: population: $F_{11,3854} = 27.1$, $P < 0.0001$; number of seeds: population: $F_{4,3810} = 19.6$, $P < 0.0001$). Notably, there were also population-specific differences in how fecundity fluctuated across years (number of flowers, population:year: $F_{42,3854} = 6.04$, $P < 0.0001$; number of seeds, population:year: $F_{42,3810} = 8.2$, $P < 0.0001$). For instance, the majority of populations have drops in fecundity during heat-wave years (2019 and 2021) and increases in 2022, but populations RRM, FIR, and SEC had relatively slight fluctuations between years, and population SMG had no decrease in fecundity in 2021. One population (HDM) completely died without producing any seeds in 2019, and new seedlings did not establish again until 2021.

Variation in maternal provisioning and consequences between populations and years

Seed mass, germination speed, and germination ability all varied substantially across populations and years (Figure 3;

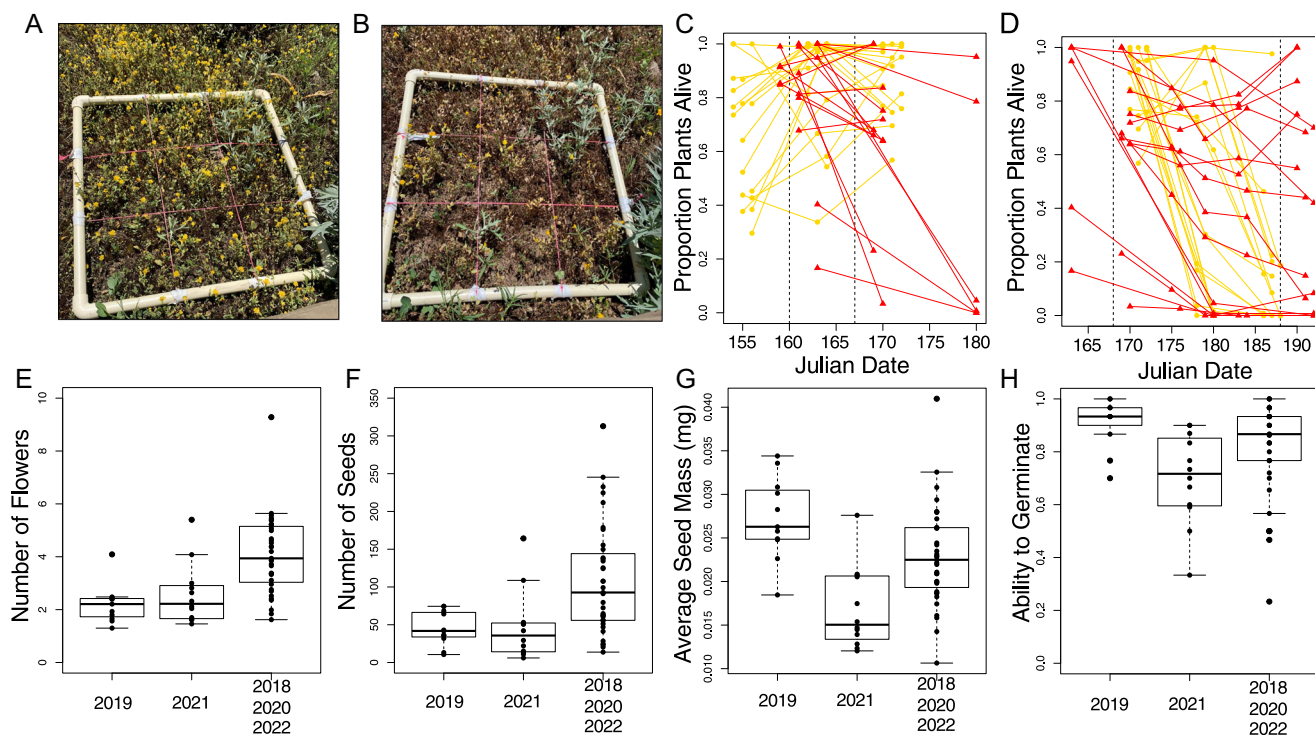


FIGURE 2 Comparison of fitness and maternal effects within heat wave vs. more normal years. (A, B) Comparison of 0.25-m² plots at the HOV population before (29 June 2021) and after (7 July 2021) the peak of the 2021 heat dome. (C, D) Survivorship across early and late portions of the growing season compared between the 2019 (red) and 2021 (yellow) growing seasons. Dotted lines represent heat-wave dates from the initial date crossing >1 SD above average maximum temperature to next date falling below >1 SD historic average maximum temperature. The period within the dotted lines in panel C are the Julian dates of the 2019 heat wave, the period within the dotted lines of panel D are the Julian dates of the 2021 heat wave. Each line represents change across a single population. (E–H) Boxplots depicting number of flowers, number of seeds, seed mass, and germination ability between heat-wave (2019, 2021) and non-heat-wave years (2018, 2020, 2022). Each point is a population average.

Appendices S3, S4), but did not uniformly differ between heat-wave and non-heat-wave years (Figure 2; Appendix S7). Across populations, seed mass was generally highest in 2018 and 2019 and dropped in subsequent years with lowest levels in 2021, coincident with the heat dome event. Specifically, seed mass was 30.4% lower on average in 2021 than in 2018–2020 and significantly differed between heat-wave years ($\chi^2 = 62.0$, $P < 0.0001$; Appendix S7). Greater seed mass was weakly associated with germination ability and speed (Appendix S8). Like seed mass, germination ability declined 22.1% in 2021 relative to 2018–2020 and significantly differed between heat-wave years ($\chi^2 = 36.3$, $P < 0.0001$; Appendix S7). Although some populations recovered their pre-2021 germination rate in 2022, others did not (Figure 3D). Germination speed had a different pattern seemingly unrelated to heat waves—germination speed declined by 55% in 2022 compared to other years. Like fecundity metrics, there was substantial variation among populations in seed mass and germination metrics (Appendix S4). For instance, populations RRM and MBR did not have any seed mass declines in 2021, and population BMP had a decline in 2020 rather than 2021. Together, these results suggest that the 2021 heat wave, but not the 2019 heat wave, strongly impacted maternal provisioning and ability to germinate.

One population stands out as highly variable for each of these measures: HDM had complete mortality and no reproduction during the 2019 heat wave, no establishment in 2020, and very low number of seedlings in 2021 and 2022. Interestingly, seed mass from HDM was nearly double the average seed mass in 2022, but these seeds had substantial germination issues following re-establishment. Germination speed of HDM was the slowest of any populations. This effect in HDM could be due to biased collections in 2021 and 2022 because we counted seeds in the field and kept only a subset of seeds for downstream common garden experiments. The rest of the seeds were thrown back into the population to limit our impact on a recovering population. However, we would have expected that this bias of keeping larger seeds would also lead to faster germination and greater ability to germinate. We observed the opposite of this prediction, where the extremely large seeds of HDM in 2022 had the lowest germination ability of any population.

Similar climatic predictors underlie differences in fitness and germination related traits

Piecewise structural equation models revealed a complex network of connections between climatic variables, fecundity,

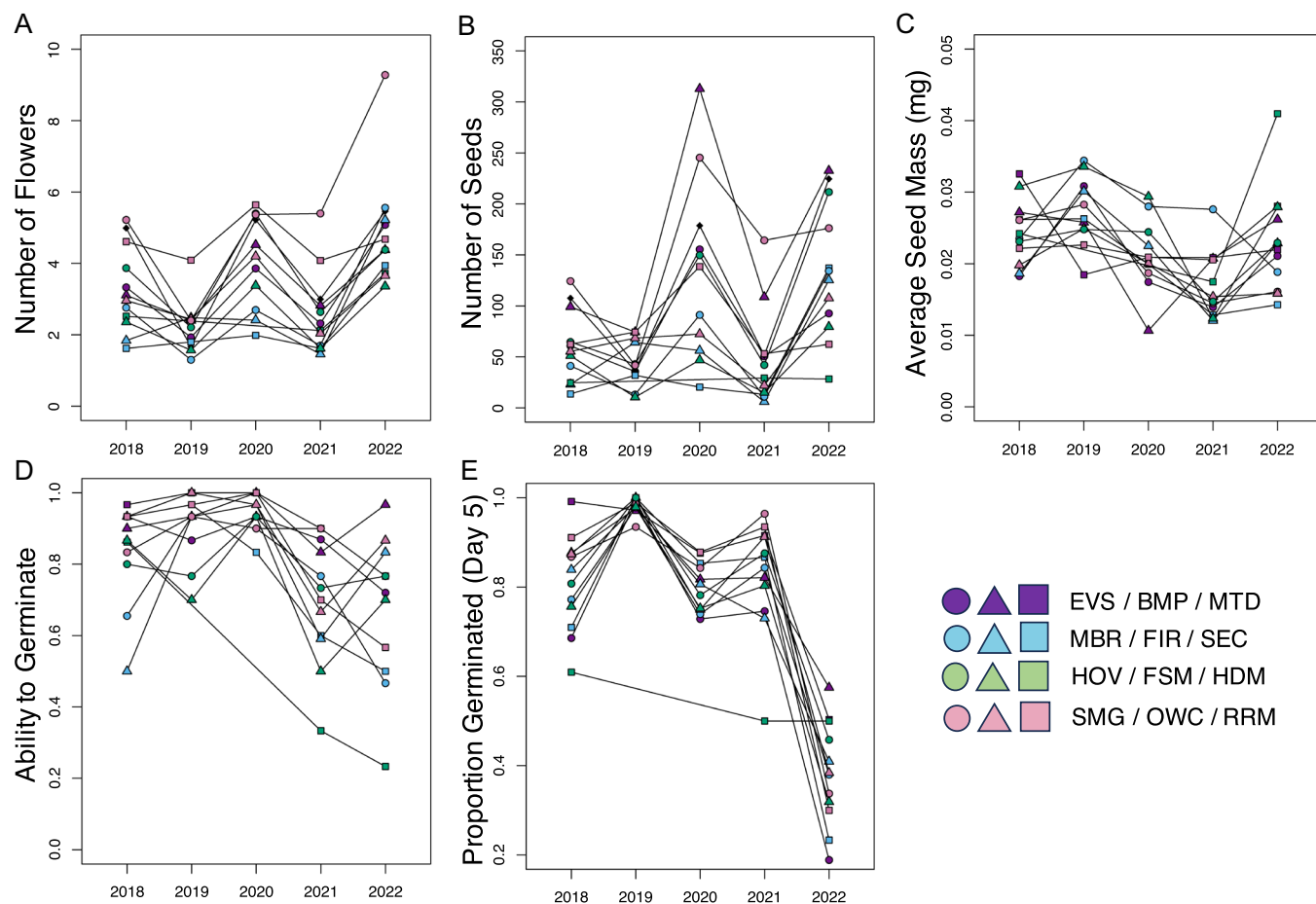


FIGURE 3 Key fitness parameters fluctuate across years and populations. Line graphs depict variation in number of flowers (A), number of seeds (B), average seed mass (C), germination ability (D) and germination speed (E). The shape and color of points indicates different populations; points of the same color are geographically closer and similar in elevation to one another. We emphasize that this figure depicts the same data as in Figure 2, just displayed in a different way. Letters correspond to populations names; locations can be found in Appendix S1.

seed mass, and germination. The full model could not be fully evaluated because its inclusion of all paths makes it impossible to calculate a model-wide P -value. Instead, it was used as an AICc starting point against which the nested models could be evaluated. The first two nested models were rejected ($P < 0.05$, Table 1) because climate and seed traits both had strong effects on germination traits. The third nested model was also rejected ($P < 0.05$), and further, its AICc score suggested it was overly complex for its explanatory power relative to the full model. Because none of the nested models were promising, we chose to refine the full model by removing nonsignificant paths from highest to lowest P -value and confirmed the choice by checking whether AICc decreased after each removal. The refined model, which was well supported by both its AICc and P -value (Table 1), revealed several interesting patterns that were too nuanced for our nested models to fully capture (Figure 4). Number of seeds and germination speed responded to many climate variables, but average seed mass and ability to germinate responded to few. Climatic variables largely have similar effects on both fecundity and germination speed—an unexpected pattern that has implications for

TABLE 1 AICc and P -values for the five tested PSEMs. The full model does not have a P -value because calculating P requires some potential paths to be omitted, which was not the case for the full model. The asterisk indicates the only model with $P > 0.05$, which indicates greater confidence that important paths have not been omitted.

Model	P	AICc
Full Model	NA	−324.46
Nested Model 1	<0.001	−355.73
Nested Model 2	0.008	−326.93
Nested Model 3	<0.001	−89.71
Refined Model	0.579 *	−416.22

how selection and maternal effects may interact. Percentage of precipitation as snowfall affected germination traits, but not number of seeds or seed mass. Finally, seed traits often predicted germination speed and success, even after the direct effects of climatic variables were considered.

Because we used GAMs in our PSEMs, all relationships (other than the random effects) had the chance to take on

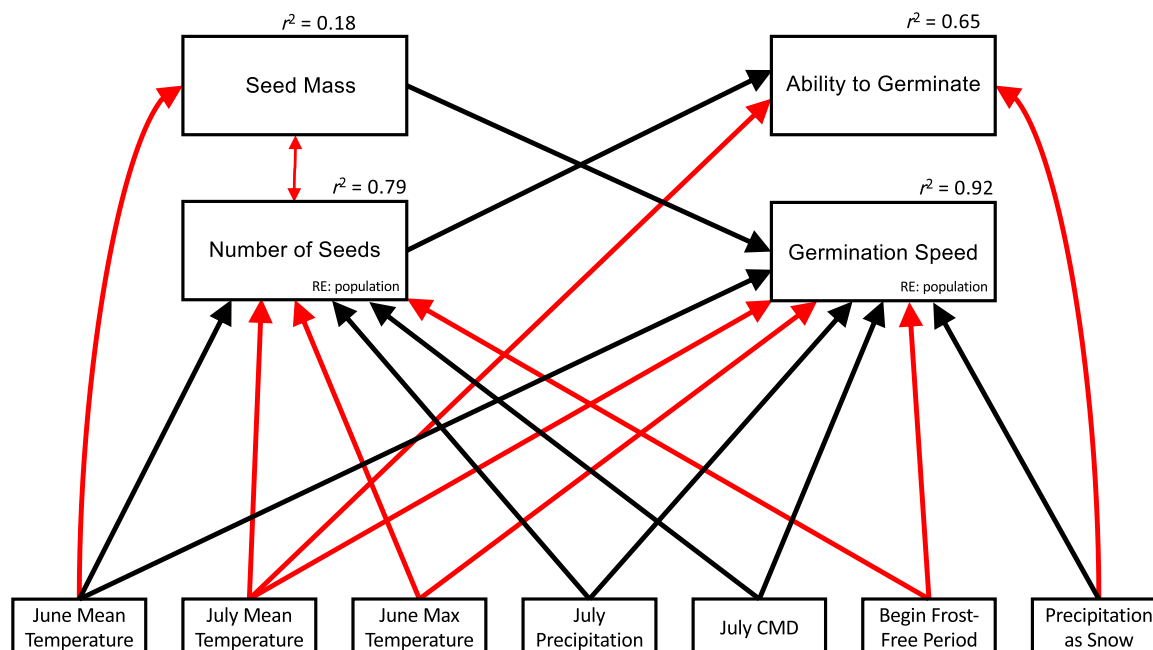


FIGURE 4 Refined piecewise structural equation model. Black lines represent positive associations; red lines represent negative associations. Boxes with RE: population had best models that include a population smooth, indicating there was some variation among populations. Line width does not represent interaction strength; generalize additive models do not provide effect sizes but do allow for non-linear interactions. CMD: Hargreave's climatic moisture deficit.

nonlinear forms. Slight nonlinearity, in the form of saturating or accelerating relationships, was common, but nearly every relationship was monotonic, allowing us to represent the relationship as positive or negative in Figure 4. These nonlinear relationships allowed us to explain some nonintuitive pathways. For instance, number of seeds increased with increasing June mean temperatures, but decreased with increasing June maximum temperatures. The GAMs suggest that the negative effect of June maximum temperatures arises when maximum temperatures are exceedingly high (i.e., the 2021 heat dome), but higher temperatures during the growing season typically led to higher fecundity. Likewise, precipitation as snow only increases germination speed at exceedingly high levels of snowfall—a scenario when there is likely selection for rapid life cycling as growing seasons begin later. Finally, seed mass does not increase germination speed until seeds are quite large.

DISCUSSION

We found that heat waves strongly influence monkeyflower populations by causing fluctuations in fecundity, maternal provisioning, and germination speed across years. While there were some general similarities in terms of fitness consequences, there were clearly differences between heat-wave events and between geographically proximate populations. Both heat waves caused mortality and decreased fecundity in the majority of populations. However, the 2021 heat-dome event caused substantial declines in seed

provisioning and germination ability, while the 2019 heat wave did not. The divergent consequences of these heat waves likely reflect differences in severity and timing of the heat waves—the 2019 heat wave occurred early in the growing season and caused variable mortality across populations, while the 2021 heat dome occurred during reproduction causing universal mortality and impacted seed development. More broadly, the climate factors driving variation in fecundity also seem to influence germination characteristics including the ability to germinate and germination speed. Below, we discuss these results in the context of organismal responses to changing climate.

Consequences of heat waves depend on severity and timing of heat waves

Few studies have examined the fitness consequences of multiple heat waves (or other extreme events) on the same populations (but see Grant et al., 2017), which leads to a basic question: Do similar heat waves have similar consequences? A striking result of our work is the differences in fitness responses between heat waves. Although our observational study cannot directly test the causal mechanisms underlying the divergent consequences between heat waves, we hypothesize that the differences were likely due to the strength, duration, and relative timing of the heat waves within the growing season. The 2019 heat wave occurred earlier in the growing season, but was less severe and shorter than in the 2021 growing season. Because the 2019

heat waves occurred within 2 weeks of snowmelt for most surveyed populations, plants within these populations were mostly small non-reproductive rosettes with only a few pairs of true leaves. These small plants experienced more mortality during the heat wave (McDonald et al., 2023); however, all populations besides HDM had at least some individuals that survived the 2019 heat wave. With relatively benign conditions for the rest of the growing season (Figure 1), four populations (OWC, RRM, FIR, SEC) actually increased in fecundity relative to the previous year. Notably, these represent four of the five lowest-elevation populations and typically have growing seasons that begin earlier (i.e., early to mid-May). Thus, plants in these population were likely larger when the 2019 heat wave began than in the other populations.

The peak of the 2021 heat dome occurred 16 days later than the peak of the 2019 heat wave—a substantial difference for rapid-cycling annual populations. Mortality was much higher in the 2021 heat wave than in the 2019 heat wave, with half of the survey plots having complete mortality by the beginning of July and the rest following by the time that temperatures dropped to historical averages in the next 10 days. However, unlike the 2019 heat wave, half of the populations had individuals that were flowering before the start of the 2021 heat wave, and all had flowers by the peak of the heat wave. Thus, unlike in 2019, all populations produced flowers and seeds. As in the 2019 heat wave, low-elevation populations (e.g., SMG, RRM) had relatively lower declines in fecundity, and there was higher variation in fitness production among populations. These populations were further into their life cycle and likely less impacted by the stress. These results suggest that if we had measured only mortality, phenology, and fecundity, the heat dome of 2021 would appear to have less detrimental consequences on population viability.

However, extreme conditions during reproduction and seed development can also have negative consequences that can translate into reduced maternal provisioning and downstream maternal effects. For instance, studies in natural populations and in controlled conditions suggest that higher temperatures during seed development can delay or prevent seed germination (Singh et al., 2019; Klupczyńska and Pawłowski, 2021). A central difference between the 2019 and 2021 heat waves was the drop in seed mass and ability to germinate associated with the 2021 heat dome (Figures 2, 3). Differences in germination ability and speed in 2021 and 2022 could be caused by mechanisms with different long-term consequences. Lack of germination or slowed germination could be simply due to less maternal investment into seeds (i.e., lower maternal provisioning) (Roach and Wulff, 1987). Differential maternal provisioning of seeds depending on environmental conditions is common across plants species with many-fold variation in seed mass (Moles et al., 2007). Smaller seed sizes may be expected to be associated with less ability to germinate and slower germination speeds (Venable and Brown, 1988; Rees, 1994, but see Norden et al., 2009) as also shown by our data (Figure 4;

Appendix S3). However, lack of germination or slowed germination could also be due to selection imposed by heat waves for individuals that have different germination or dormancy cues that allow seeds to germinate later in the growing season or wait until conditions are better. We suggest that both mechanisms are likely in our system. If only maternal provisioning underlies the observed differences in germination ability, we would have expected recovery of germination ability the next year (2022), which was relatively wet. Instead, we observed only partial recovery of germination ability in 2022, suggesting some role for selection of dormancy or reduced germination.

A paradoxical result is the decrease in germination speed across nearly all populations in 2022. Climatic conditions across the growing season in 2022 strongly resembled the moderate conditions in 2018 and 2020. If germination speed is related to climate, we would have expected 2018, 2020, and 2022 to have similar germination speeds. While the lack of correlation between years suggests that germination speed is not tightly linked to abiotic conditions, both our a priori pSEM models and post hoc model refining suggest associations with climate are indeed important and predictive (Figure 4). Two possibilities exist. First, the drop in germination speed is real and due to a delayed response (i.e., a lag; Branch et al., 2024). For instance, the 2022 populations may include fewer germinants from 2021 parents, and the remaining germinants were biased toward seeds from the seed bank with greater dormancy. Second, the decline in germination speed could be due to unmeasured experimental conditions. Germination trials were run with identical conditions as in previous years, but something as simple as a different lot of soil could be associated with germination speed differences. Germination speed results from subsequent generations of the 2022 offspring will be needed to parse these hypotheses.

Selection and population-level responses to heat waves

The differences in mortality and fecundity among heat waves have evolutionary implications. Theoretical models suggest that extreme events cause strong selection pressures for survival, acclimation or tolerance that will lead to improved fitness during future extreme events—i.e., the silver lining hypothesis (Coleman and Wernberg, 2020). Our results suggest that the likelihood of a silver lining will be low because phenotypes under selection would likely differ between heat waves. Selection in the 2019 heat wave is likely to favor acclimation and/or tolerance to high heat and/or low water because there was differential mortality at the seedling stage before reproduction with a substantial proportion of each population surviving. Stronger acclimation and stress tolerance phenotypes often trade off with rapid growth, flowering, and reproduction (Geber and Dawson, 1990; McKay et al., 2003), and thus, the 2019 heat wave may favor slower time to flowering. Alternatively, since reproduction

already occurred before the 2021 heat wave and the heat wave ended the growing season, selection would likely favor plants that reproduced early and hardened their seeds quickly. That is, there were no individuals that survived through the heat wave and reproduced later in the year and likely no selection for dehydration avoidance or tolerance responses (Kooyers, 2015). Studies of constitutive and induced drought-related phenotypes in *Mimulus guttatus* suggest that phenotypes associated with drought escape and dehydration avoidance are heritable (FitzPatrick et al., 2023). Thus, we would predict that the two heat waves have a limited silver lining and instead generate selection gradients in the *opposite* direction for flowering time. It is even possible that selection from the 2019 heat wave could have increased mortality during the 2021 heat wave. That is, selection for later flowering caused by the 2019 heat wave may have led to fewer individuals reproducing during the 2021 heat wave. Additionally experimental work in common gardens is necessary to parse potential interactions between heat waves.

It is more challenging to include the differential effects of heat waves on seed mass and germination ability in evolutionary and ecological predictions. Lower ability to germinate in the next generation could result in slower germination in the field or increased dormancy in the seed bank. Slower germination would be nearly universally detrimental to population growth within the context of these rapidly cycling populations (Hall and Willis, 2006). Germinating even days later can severely compromise reproductive output; however, these individuals may survive some years because variation in growing season length causes directional selection in different directions in different years (Mojica et al., 2012; Troth et al., 2018; Kelly, 2022). Greater dormancy could also have a positive effect in less-predictable environments by generating a larger seed bank. The HDM population that had zero reproductive output in 2019 likely re-emerged through a seed bank (McDonald et al., 2023). However, slower germination or increased dormancy is often associated with slower times to flowering in other systems (Donohue, 2002). Thus, the prediction of earlier flowering evolving after the heat dome event may not necessarily be consistent with the maternal effects observed here (i.e., limited seed provisioning and slower germination). That is, selection and transgenerational effects may be occurring in different directions on key life-history phenotypes. Resurrection or common garden experiments designed to parse maternal effects from heritable phenotypic effects are necessary to determine patterns of selection caused by the 2021 heat dome. More generally, dormancy and seed bank lifespan are largely untested with *M. guttatus* (but see Vickery, 1999), and deserve to be highlighted as critical information for understanding herbaceous species responses to changing climates.

While we are unable to assess whether patterns of selection fall in the same directions as maternal effects, we can evaluate how fitness, maternal provisioning, and germination characteristics are interrelated and associated with key climatic predictors. The interactive network of effects between climate, fitness, seed size, and germination are

complex, and piecewise structural equation modeling helped us visualize and explore these relationships. The direct negative link between fecundity and seed mass suggests that there are clear trade-offs (e.g., genetic, physiological, or resource allocation) governing this relationship. Positive associations between seed mass and germination speed as well as number of seeds and germination ability may reflect positive maternal body condition, where successful mothers have high fitness and produce well-provisioned seeds. While these associations have been observed in other systems, the most interesting result from our pSEM is that similar climatic variables drive both fecundity and germination speed of offspring. Notably, earlier growing seasons, higher average June temperatures, lower July average temperatures, and greater July precipitation are linked to greater seed production and earlier germination (Figure 4). Higher maximum June temperatures (as observed in heat-wave years) are linked directly to lower seed production and slower germination, and indirectly to lower germination ability. These associations with climate could lead to higher probabilities of extirpation of individual populations. That is, early-season heat waves lead to decreased fecundity and offspring that are less primed for success in an environment with truncated growing seasons.

Should these population be considered threatened?

Key questions for climate change scientists are determining whether populations should be considered threatened and, if so, whether management actions should be taken. Though it is clear that *M. guttatus* is common and abundant through its range in western North America, the degree to which the focal *M. guttatus* populations are threatened is more debatable. Some evidence points to significant threats. These populations are on the edge of their niche in terms of growing season length, and there are few *M. guttatus* populations that exist at similar or higher elevations (1250–1700 m a.s.l.) either south or north of these populations. Instead, a closely related relative, *Mimulus alsinoides* occupies a similar niche on exposed thin-soiled meadows and rock walls (N. Kooyers, personal observations). Further, one population did not have any reproductive output during 2019 (HDM; McDonald et al., 2023) and only re-emerged from the seed bank with low establishment in 2021. This population has low germination ability and generally low fecundity compared to other populations, exhibiting patterns associated with a strong bottleneck. Other populations have very limited emergence and fecundity in certain years (OWC), but have very successful establishment during years with longer growing seasons (i.e., 2022).

However, several other factors point to a relatively low probability of extinction within these populations. First, all of these populations exist in a relatively small geographic

region and have extensive gene flow leading to near panmixia (Colicchio et al., 2021). These high levels of gene flow suggest that these populations may behave more like a metapopulation with the ability for both seed transfer and genetic rescue through pollination. Second, surviving individuals produce large numbers of seeds even in relatively extreme years. While these raw numbers suggest that there should be high population growth rates, high early-life mortality is likely in this species, and it is difficult to accurately measure seed germination and early mortality rates. Annual *M. guttatus* occupies only thin-soiled meadows that are saturated for an extended period after snowmelt, and thus, seeds must be “lucky” enough to land in the right environment (i.e., sweepstakes reproductive success; Hedgecock, 1994). Existing demographic models infer high seed germination and have limited information on mortality of early germinants—still in a drought year in California, population growth rates fall below replacement (DeMarche et al., 2016). Additional experiments measuring seed germination, early survival transitions, and size-driven variation in reproductive output and survival are necessary to create more predictive structured demographic models.

CONCLUSIONS

Spring heat waves across the Pacific Northwest have more than doubled in frequency and/or severity since the mid-1990s with substantial consequences for subalpine communities (Reyes and Kramer, 2023). Our work suggests that the impact of heat waves depend on the timing and severity of the heat wave relative to the life cycle of the organism in question. Small changes in timing impact the degree of mortality, maternal provisioning of offspring and even the traits impacted by selection, potentially causing impacts that may not be adaptive in the next generation or for the next extreme event. Notably, our results demonstrate the importance of measuring offspring phenotypes because not all seeds are created equal. Synthesizing the consequences of extreme events such as heat waves on organismal fitness components across generations is a necessary practice for generating accurate estimates of extinction probability.

AUTHOR CONTRIBUTIONS

N.J.K. conceived and designed the experiments. N.J.K., S.G.I., A.T., D.M.H., B.J.L., C.M.P. collected data and performed the experiments. N.J.K. and M.A.G. analyzed the data. N.J.K. and M.A.G. wrote the original draft of the manuscript, and all authors reviewed and edited the manuscript. All authors approved of the final submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no competing interests that may have influenced this manuscript.

DATA AVAILABILITY STATEMENT

The survivorship data set, the longitudinal data set, and the germination data set from this manuscript have been uploaded to Dryad (<https://doi.org/10.5061/dryad.g1jwstr44>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Historic climate summary for focal populations.

Appendix S2. Schematics representing different alternative models for piecewise structural equation models.

Appendix S3. Fitness, seed mass, and seed germination means across populations.

Appendix S4. ANOVA model summary statistics for fecundity, seed mass, and germination phenotypes.

Appendix S5. ANOVA model summary statistics for fecundity, seed mass, and germination phenotypes with alternate model structures.

Appendix S6. ANOVA summaries for models examining differences in fecundity, seed mass, and germination phenotypes between heat-wave and non-heat-wave years.

Appendix S7. ANOVA summaries for models examining differences in fecundity, seed mass, and germination phenotypes between the 2019 and 2021 heat-wave years.

Appendix S8. Associations between seed mass and germination characteristics.

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