Population models and forecasts using long-term monitoring data

for a recently delisted riparian forb, *Oenothera coloradensis* (Colorado butterfly plant)

# Introduction

A quantitative population viability analysis (PVA) links measured vital rates with environmental covariates to model response functions that can forecast population trends and inform management or regulatory action (Morris and Doak 2002). When data are available, PVA provides one form of “objective, measurable criteria” (ESA) that may guide recovery plans of listed species (Boor 2014). However, others advocate not to use a PVA in isolation as it may limit the scope of recovery or promote overconfidence in modeled extinction thresholds based in part on the analyst’s subjective choices (Wolf et al. 2015). In place of calculating extinction risk, we provide a focused PVA on two aspects of a rare species’ population regulation, including density-dependence and climate covariance, that may inform Post Delisting Monitoring.

Colorado butterfly plant (*Oenothera coloradensis* (Rydberg) W.L. Wagner & Hoch; syn. *Gaura neomexicana* Woot. ssp. *coloradensis* (Rydb.) Raven & Gregory) was listed as Threatened under the Endangered Species Act (USFWS 2000). Its rarity throughout its range has long been recognized (Dorn 1977). It was recently delisted due to the resiliency of populations in rebounding from low numbers and the redundancy/representation reflected in discovery of a large additional population after its listing (USFWS 2019). Long-term viability under climate change was considered in evaluating resiliency, redundancy, and representation. Factors including long-term climate change were interpreted as not a threat (USFWS 2017a, b, 2019). Resilience to environmental stochasticity, and presumably to climate change, comes from prolonged dormancy in the seedbank, the ability of rosettes to delay flowering until favorable years, and ecological amplitude that enables it to respond to varying annual conditions.

Population-wide monitoring on WAFB started in 1986, conducted annually from 1988-2023. We assess the response of population growth to climate by testing which weather variables are important during the multiyear lifecycle of individual plants using this exceptionally long dataset, projecting population growth into the future under scenarios that show how climate may change viability. This dataset was incorporated into delisting decisions and also has relevance in evaluating the Post Delisting Monitoring (PDM) framework. After delisting, the species’ trends are to be monitored for at least five years at a representative subset of populations spanning the species’ distribution, including the FEWAFB population, and compare the range, mean, and median of population counts with historical data to assess the recovery of *O. coloradensis* (USFWS 2019). In the course of conducting monitoring, new environmental stressors are to be noted. In the past, rare flea beetle herbivory outbreaks have impacted populations (Heidel et al. 2011). After trends are assessed from the PDM period, the species will be considered secure once certain standards are met (USFWS 2017).

Population trends are difficult to judge for *O. coloradensis* because it fluctuates annually in flowering plant numbers (Figure 1). This may reflect the variability in environmental cues and associated variability in species’ development including germination from its seedbank, vegetative growth, and flowering stem production (bolting) of it as a semeloparous perennial. The flowering stage is the only life history stage that is readily detected. It has indeterminate flowering, and fruits fall as they ripen. So when we refer to census of flowering plants this corresponds to all reproductive plants of the year. Our PVA will test how many years it may take to detect a significant change in a population based on flowering plant monitoring to inform decisions by the Service after five years.

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Figure 1: Census of flowering plants, by year, of the F. E. Warren Air Force Base population (A) and divided into separate creek subpopulations (B). Lines are the nonlinear fits from generalized additive models (knots = 10) with automatic cross-validation to select the degree of nonlinearity.

# Methods

## Study system

Long-term monitoring of the Colorado butterfly plant population and its three creek subpopulations on F.E. Warren Air Force Base (WAFB) near Cheyenne, Wyoming provides a robust record of population trend. The work was usually conducted in early August by a 2-4 person team, after all flowering plants had bolted and most were in flower. Census of it on WAFB was initiated in 1986, conducted annually starting in 1988. Data storage set up to subdivide the occupied habitat into creek segments of similar habitat conditions starting in 1989, further divided into discrete mapped locations starting in 2002 and recorded as shapefiles of polygons or points. The 36 years of continuous monitoring has been conducted as a census at four spatial scales (Base-wide, creek-wide, by creek segment, and by discrete mapped locations recorded as shapefiles of polygons or points). Our analysis focuses on the population and subpopulations levels, and to a lesser extent on subpopulation segments.

The study area is located on WAFB immediately west of Cheyenne (41° 07’N 104° 52’W) in Laramie County, Wyoming. Oenothera coloradensis occupies riparian habitat along Crow Creek, Diamond Creek, and an unnamed, ephemeral creek (hereafter referred to as Unnamed Creek). The creeks span approximately 5.1 km (3.2 miles) of riparian corridor habitat. Occupied habitat is discontinuous and the cumulative occupied habitat is about 5 ha (12.4 ac). The creeks are all low-gradient but have different hydrological regimes including perennial, seasonal, and ephemeral, flows fed by combinations of groundwater and surface water. They span 1862-1887 m (6110-6190 ft) elevation with a relief of about 5.7 m per km (ca 30 ft per mile). Most occupied habitat is undeveloped and relatively undisturbed.

## Trend detection

We estimated retrospectively when shifts in population growth rate and carrying capacity had occurred across the long-term monitoring data. We used a model comparison algorithm that fits population time-series with all possible breakpoints and selects the most supported shifts in population demographic rates (Bahlai and Zipkin 2020). We ran this algorithm on the full length of monitoring for each creek, and then shortened the dataset systematically to determine how many years of monitoring would have been needed to detect the significant breakpoints in the monitoring trends.

## Population models

We used linear mixed-effects models to estimate annual population growth rates log(*Nt*/*Nt-1*) with the *lme4* package in R 4.0.3 (Bates et al. 2015, R Core Team 2020). Population growth rates were assumed to result from the population-specific intrinsic rate (intercept), density-dependence based on the previous year’s count (fixed effect), environmental conditions (fixed effect of weather covariates), and annual stochasticity shared across segments. The form of density dependent population regulation may either increase or decrease population resiliency under future conditions (Jaatinen et al. 2021). We compared two models and selected Gompertz density-dependence over Ricker density-dependence. We fit models with density-dependence (natural logarithm of previous year’s flower count) and scaled weather covariates identified as important as described below. Each year and population segment varied with random intercepts to account for non-independent observations.

## Environmental covariates

We used monthly temperature, precipitation, and snowfall data from the Cheyenne Municipal Airport weather station (481675) from the Western Region Climate Center (wrcc.dri.edu). We used the monthly Palmer Drought Severity Index (PDSI) from the Lower Platte Climatological division in Wyoming from the NOAA Climate Divisional Database (Vose et al. 2014). Stream discharge data from Crow Creek downstream of the study area was available for 1994-2017 from the USGS site 06755960 (waterdata.usgs.gov/wy/nwis).

Detailed knowledge of the species life history has pointed to the potential impact of temperature, precipitation, and stream discharge on population growth. However, the specific life stages affected may alter the time lags and time windows for when these environmental conditions are important. For example, springtime germination may be a key vital rate affected by weather that would not be until flowering counts in later years. Some conditions may have a cumulative effect of longer than one season, such as prolonged drought. We used the *climwin* R package to search for the optimal model (linear or quadratic) and time windows with a minimum of 3 months duration of up to three years before the August when flower monitoring occurs (Bailey and Pol 2016). The base model for this search included density-dependence and random intercepts for each site as predictors of population growth rates. Model outputs were used to select covariates to use in multiple regression models of population growth rates. Important variables were selected primarily based on model selection (weight based on AICc) and visualizing potential time windows of impact beyond the top model.

## Forecasts

We used the model of population growth rates to project flowering counts in 2021-2040 using the 2020 observed counts as the start. Density-dependence, the selected environmental covariates, site intercepts, and variation from annual intercepts and residual error drawn from Normal distributions determined the annual population growth rate (*r*). The simulated flower count in the following year was drawn from a Poisson distribution with *λ = Nt-1er*. This process was repeated for each of 100 simulations for each scenario.

Nine scenarios were projected with climate covariates. To simply incorporate the temporal correlation between years in weather, we used the observed weather in previous decades to project population counts forward. These scenarios used every combination of the 1990-1999, 2000-2009, and 2010-2019 decadal weather for nine 20-year forecasts. The 2000s were a decade with a seven-year period of drought, and we expected the 20-year scenario with the 2000s repeated twice would have the most pessimistic outcome. This is a conservative extrapolation of current conditions consistent with the National Climate Change Viewer (USGS 2021). It projects relatively stable annual and seasonal precipitation levels through 2050 in the Crow Creek watershed, but these projected conditions are accompanied by projected net increases of temperatures in all seasons, reduction in snow water equivalent in both winter and spring, and reduction in soil water storage in all seasons as key factors consistent with drought.

We forecasted populations at the segment level, but aggregated results to the three creek populations and total WAFB population for the results. We compare the median and range of observed counts over 32 years to those of the forecasted scenarios. To simplify the results, we present three of the nine scenarios that span the range of outcomes: 1990s, 2000s, and 2010s weather repeated for 2021-2040.

# Results and discussion

Our PVA tested how many years it may take to detect a significant change in a population from flowering plant census to inform decisions by the Service after five years. Trend detection breakpoints in the 36-year dataset indicate that an average of ?? years census data would have been necessary to detect change in the WAFB population, or ??-?? years if the Base had only one of the three subpopulations. Results were tempered by environmental covariates and forecasted growth rates that varied over time.

## Trend detection

Detecting trends within a five-year monitoring window, as proposed, is unlikely as indicated by past trends. Automatic detection of changes in the monitoring time-series did not detect the significant breakpoint in the population trend until 4-8 years after the change had occurred.

The selected breakpoint years in the population trends change depending on the scale of population (total on WAFB, creek population, or smaller segment subdivisions). If summing the entire WAFB population together, no decline during the 2000-2006 drought would be detected (Figure 12) as evidence for the subpopulations buffering overall population trend. If each of the three creek were separate populations, significant decline would be detected on Crow Creek. We see how the decline on Crow Creek was masked by the relative stability on Diamond and Unnamed Creeks.

The Crow Creek population has approximately halved twice during the 32-year monitoring period. Across these two trend breakpoints, carrying capacity was estimated at 1,585 in 1988-1997, 841 in 1998-2001, and 346 in 2002-2019 (Figure 12). The decline in carrying capacity would be a key goal for post-delisting monitoring to detect. The breakpoint detection algorithm was carried out with shorter time-series from 1988 to varying endpoints from 1995-2020 to see when changes were detected. The changes on Crow Creek were not detected until after 2005, at a lag of either 4 or 8 years depending on whether the breakpoint in 1997 or 2001 is the basis. Either 1997 or 2001 were considered as the best single breakpoint as the time-series length grew until the final identification of two distinct breakpoints in 1998 and 2001 solidified in 2016.

For an example of the algorithm performance with an increasing population, the Unnamed Creek carrying capacity increased from 1731 in 1988-1994 to 2503 in 1995-2019. The algorithm was carried out with time-series from 1988 to varying endpoints from 1995-2020 to see when changes were detected. Including a breakpoint for 1994 was not considered in the best models until after 2003. It was consistently included for all longer time-series. For a couple years of analysis, an additional breakpoint in 2012 was estimated as the start of another increase in carrying capacity but was no longer supported with more data. We also determined the breakpoints for each segment showing differences with stream determinations in the number of break points, differences of break point timing, and different break point trends. This breakpoint detection for the population simulations with climate models would give greater insight into how frequently trend detection algorithms would give accurate results.

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Figure 12: Breakpoints were estimated for the monitoring time-series, and the modeled carrying capacity for each distinct era is plotted as dashed lines. If lines are missing, the algorithm gave unrealistic results that we exclude here. Data points are flower counts observed during monitoring.

## Environmental covariates

The best time window and time lag for covariates and the form of the relationship (linear or quadratic) varied. We interpreted the results of the top models in light of the lifecycle, but the associations in the best-fit models are unlikely to be the sole time window in which the environment affects population growth rates.

Stream discharge for Crow Creek, assumed to correlate with conditions across all segments, has the most supported time window (weight 11%) 23-7 months before the August census (red region in Figure 2A). The quadratic model suggests that both low and high flow in the two years prior to flowering counts decreases the annual population growth rates, while growth rates are maximized at intermediate flow (Figure 2B).

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Figure 2: The timing of stream discharge associated with models of annual population growth rates has its best fits in the red region (A) and shows maximum growth rates with intermediate discharge within the time window (B). Data points show the growth rates of each segment and year, with the blue color lightening as years are more recent.

A negative linear model of temperature’s effect was supported over a quadratic model (Figure 3B). The best model (69% weight) included fall-winter of two years before census (23-19 months ago)(Figure 3A). The small region of yellow in the lower left region showed that temperature in the months immediately preceding the August census also impacted the estimates of population growth rates, with higher temperatures lowering the growth rate (not shown).

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Figure 3: The timing of temperature associated with models of annual population growth rates has its best fits in the red region (A) and shows decreasing growth rates with higher temperatures within the time window (B). Data points show the growth rates of each segment and year, with the blue color lightening as years are more recent.

For precipitation, there was strong support (69% weight) for a longer window starting two years before (24-2 months ago) (Figure 4A). The quadratic model was strongly supported over linear (ΔAICc = 31.0) with higher population growth rates at intermediate values (Figure 4B).

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Figure 4: The timing of precipitation associated with models of annual population growth rates has its best fits in the red region (A) and shows higher growth rates at intermediate values within the time window (B). Data points show the growth rates of each segment and year, with the blue color lightening as years are more recent.

Snowfall had a surprisingly narrow window with the highest impact. The best models started 4-6 months before census (Feb-April) and ended within 1-3 months of the census (Figure 5A). Since the endpoint was during the summer with very little snow, the takeaway could be that late season snow has a larger impact that early winter snow. This is new snowfall, and an analysis of accumulated snowfall and how long it persists in the spring could be important as well. The quadratic model is strongly supported over linear (ΔAICc = 31.7) with higher population growth rates at intermediate values (Figure 5B).

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Figure 5: The timing of snowfall associated with models of annual population growth rates has its best fits in the red region (A) and shows higher growth rates at intermediate values within the time window (B). Data points show the growth rates of each segment and year, with the blue color lightening as years are more recent.

Water availability (PDSI) had no clear top model (best weight 10%) and the top linear models performed slightly better than top quadratic models (ΔAICc = -5.02). The linear model had the strongest support in the lower left corner (Figure 6A, 7-4 month before census) which suggests greater water availability in the spring has a slight positive affect on population growth rates (Figure 6B). Regions of support in the upper left and upper right of figure 6A suggest that cumulative water availability over the last three years is important, as is water availability two years previous.

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Figure 6: The timing of water availability (PDSI) associated with models of annual population growth rates has its best fits in the red region (A) and shows increasing growth rates with higher water availability within the time window (B). Data points show the growth rates of each segment and year, with the blue color lightening as years are more recent.

After the best time windows were selected for environmental covariates, we tested for correlations between them. Water availability (PDSI) (7-4 months prior) and stream discharge (23-7 months prior) were strongly correlated (Pearsons’s *r* = 0.72), so discharge was removed as it had years of missing data. Using all years for the other variables, paired correlation coefficients were all less than or equal to 0.31.

## Population models

Annual population growth rates showed strong negative density-dependence, with lower growth following years with high counts. All environmental covariates identified in the above analysis and their quadratic terms (if selected) were added to the density-dependence population model (Table 1). Variables were removed if not significant (p > 0.05). The quadratic effect of snow and the linear effect of PDSI were not significant in multiple regression and were removed for the simulations. Even though these variables may improve model fit when tested in isolation in the time window analysis above, when included with other variables they did not improve the model fit. The final model, used for population simulations, included temperature, precipitation (linear and quadratic effects), and snowfall as important drivers of population growth rates.

Table 1: Two mixed-effects models of annual population growth rates with density-dependence only or including the selected climate covariates.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **Density-dependence** | | | **\_+ climate covariates** | | |
| *Predictors* | *Estimates* | *CI* | *p* | *Estimates* | *CI* | *p* |
| (Intercept) | 1.99 | 1.38 – 2.59 | **<0.001** | 1.35 | 0.67 – 2.04 | **<0.001** |
| Log(Nt-1) | -0.40 | -0.48 – -0.32 | **<0.001** | -0.40 | -0.47 – -0.32 | **<0.001** |
| Scaled temperature  (23-19 months prior) |  |  |  | -0.27 | -0.42 – -0.12 | **<0.001** |
| Scaled precipitation  (24-2 months prior) |  |  |  | -0.00 | -0.16 – 0.15 | 0.964 |
| Scaled precipitation2 |  |  |  | -7.05 | -10.00 – -4.10 | **<0.001** |
| Scaled snowfall  (4-1 months prior) |  |  |  | 0.74 | 0.28 – 1.21 | **0.002** |
| **Random Effects** | | | | | | |
| σ2 | 0.52 | | | 0.52 | | |
| Std Dev | 0.36 year | | | 0.13 year | | |
|  | 0.54 segment | | | 0.52 segment | | |
| N | 13 segment | | | 13 segment | | |
|  | 31 year | | | 31 year | | |
| Observations | 403 | | | 403 | | |
| Marginal R2 / Conditional R2 | 0.304 / 0.744 | | | 0.425 / 0.745 | | |

## Forecasts

When density-dependence is strong as in our population models, annual population growth rates increase at lower counts and generally prevent the population from declining to extinction. We compare the range and median of forecasted counts to emulate the assessments to be performed under the post-delisting monitoring plan (USFWS 2017). Previous PVA of *O. coloradensis* where demographic plots were ranked by extinction probability (Floyd 1995, Floyd and Ranker 1998, Stears 2022) and trials were run for all of WAFB (Wepprich xx).

Under a density-dependent model without environmental covariates, the WAFB creek subpopulations and total population are expected to increase from the 2023 numbers and fluctuate around the static carrying capacity estimated in this model. Simulations vary based on annual stochasticity and sampling, so the 25th-75th percentile of counts vary substantially, with expectations of the total WAFB count between about 4,000 and 11,000 flowers counted each year (Figure 7).

With climate scenarios, population simulations diverge depending on the weather experienced. Scenarios including the 1990s weather had higher average population level 2-3 times that of those with 2000s or 2010s weather (Figure 8). Annual variation was more correlated across the 100 simulations and the median value fluctuating more widely than in the model without climate included. The simulations demonstrate the quick population growth that can occur with multiple years of positive effects of weather with the example of the 1990s scenario that nearly doubles within 3 years in 2028-2030 and 2038-2040, corresponding to the observed weather in 1997-1999 (Figure 8). One surprise is that simulations with weather drawn from the 2010s did not have the population grow from its current size, even though observed populations rebounded under this weather regime from the major drought in the 2000s. These scenarios show that population size, while fluctuating between years, will average lower with weather similar to that of the last two decades compared to the higher growth years in the 1990s.

We show the simulated values in three scenarios to the whole time-series of observed counts since 1988 (Figure 9). Crow Creek is unlikely to rebound to its higher population levels unless weather is extremely favorable. Diamond Creek and Unnamed Creek populations may average lower than the observations in 2010 with weather similar to either the 2000s or the 2010s. The ranges of the observed counts (1988-2020) and the simulated counts overlap considerably, which may lead to lower statistical power to detect population trends, if they should occur (Figures 10 and 11). The median value of the simulations was generally lower than the median of the observed counts. Approximately, in the event of two decades of weather similar to the 1990s the population size may double. However, the forecasted median is lower than the long-term monitoring median for either the 2000s (60% of observed) or 2010s (85% of observed) weather scenarios.

Climate change that increases temperature and decreases snowfall would likely lower population growth rates further. The impact of precipitation, as a quadratic relationship, would predict decreased population growth rates at either extreme. Density-dependence is a key factor that increases population buffering after years of low growth and would need to be investigated further to know if its impact will change with climate.

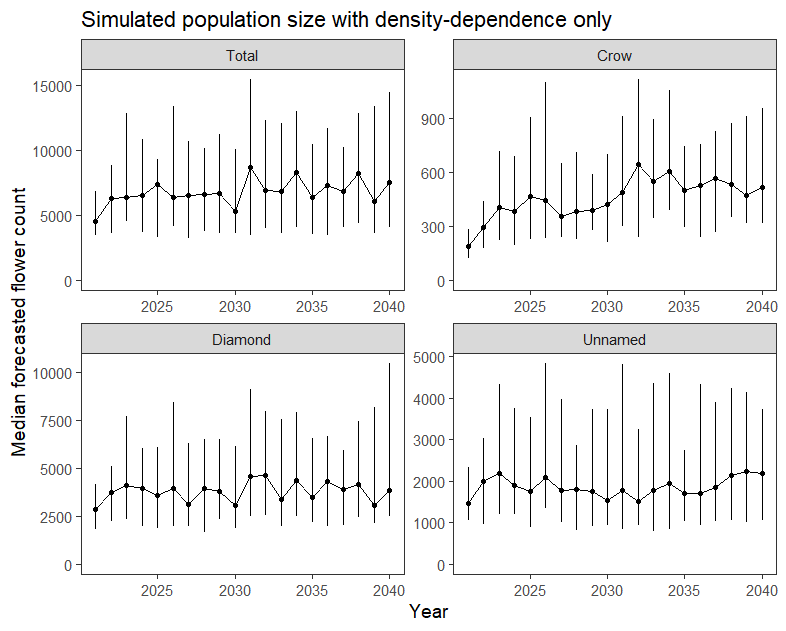


Figure 7: Simulated variation in counts under a model with density-dependence and annual stochasticity, but without weather covariates (Table 1, left model). Data points show the median simulated value with 25th-75th percentile error bars.

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Figure 8: Simulated variation in counts under a model with density-dependence, annual stochasticity, and weather covariates (Table 1, right model). Data points show the median simulated value with 25th-75th percentile error bars. Scenarios included weather covariates from the listed decade, repeated twice over 20 years in order.

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Figure 9: Simulated variation in counts under a model with density-dependence, annual stochasticity, and weather covariates (Table 1, right model). Data points show the median simulated value, with observed monitoring counts from 1988-2023. Scenarios included weather covariates from the listed decade, repeated twice over 20 years in order.

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Figure 10: Comparison of median and range of observed (1988-2020) versus simulated (2021-2040) counts under a model with density-dependence, annual stochasticity, and weather covariates (Table 1, right model). Data points show the median simulated value, thick lines the 25th-75th percentiles, and thin lines the 5th-95th percentile. Scenarios included weather covariates from the listed decade, repeated twice over 20 years in order.



Figure 11: Comparison of median and range of observed (1988-2020) versus simulated (2021-2040) counts under a model with density-dependence, annual stochasticity, and weather covariates (Table 1, right model). Data points show the median simulated value, thick lines the 25th-75th percentiles, and thin lines the 5th-95th percentile. Scenarios included weather covariates from the listed decade, repeated twice over 20 years in order.

Figure 13: Breakpoints were estimated for the monitoring time-series, and the modeled carrying capacity for each distinct era is plotted as dashed lines. If lines are missing, the algorithm gave unrealistic results that we exclude here. Data points are flower counts observed during monitoring.

There is some basis for hypothesizing longer droughts. Declines in winter snowfall have been demonstrated in historic meteorological data recorded in Cheyenne, WY (Shumann 2010) and further snowfall declines are projected in future decades (2049-2074) for Crow Creek watershed in particular (USGS 2021). Snowfall is linked to trends in soil moisture storage capacity as needed for *O. coloradensis* seed germination early in the growing season, and to evaporation deficit in the summer as needed for *O. coloradensis* seedling establishment and growth of vegetative plants later in the growing season.

The distribution of occupied habitat spans over 5 km and we note that other populations are in much shorter segments of intact habitat. The contrasts in breakpoints between segments illustrates that there is important habitat sorting even on low-gradient stream segments, and that they are not interchangeable.

Conclusion points that might be developed

Population trends are buffered by contrasts within and between subpopulations. The whole is greater than the sum of its parts.

Five years of PDM monitoring DOES/DOES NOT suffice on WAFB, particularly if only one of the three subpopulations constituted the only population.

Negative density-dependence is adaptive for changeable climate conditions and habitat heterogeneity

Positive relation between ppt two years prior with census numbers contrasts with negative relation between stream flow (and presumably water table levels) two years prior as consistent with negative density-dependence and fluctuating numbers

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