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RESEARCH ARTICLE

Population dynamics of the threatened Oregon spotted frog before and after drought mitigation

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Abstract

Amphibians are among the most sensitive taxa to climate change, and species inhabiting arid and semiarid landscapes at the extremes of their range are especially vulnerable to drought. The Jack Creek, Oregon, USA, population of Oregon spotted frogs (*Rana pretiosa*) faces unique challenges because it occupies the highest elevation site in the species' extant range and one that has been transformed by loss of American beavers (*Castor canadensis*), which historically maintained open water. We evaluated the effects of drought mitigation (addition of excavated ponds) on relationships between local and regional water availability, inactive legacy beaver dams, and Oregon spotted frog population dynamics in the Jack Creek system. We conducted egg mass surveys and capture-mark-recapture sampling at a treatment reach with excavated ponds and 3 reference reaches over 13 years; surveys spanned a period before and after pond excavation at the treatment and 1 primary comparison reference reach. We analyzed data using a combination of robust design capture-mark-recapture estimators and generalized linear mixed models to characterize population dynamics. Adult Oregon spotted frog survival was approximately 19.5% higher at the treatment reach than the primary reference reach during the study period. Annual survival was most strongly associated with late summer vegetation greenness, a proxy for water availability, and males had higher survival than females. Among the 4 study reaches, the treatment reach consistently had higher late summer vegetation greenness, and the hydrology functioned more independently of regional precipitation patterns relative to the reference reaches; however, these dynamics were not linked to pond excavation. Breeding was concentrated in 2 legacy beaver ponds that were deepened by excavation during the study compared to an unexcavated beaver pond, 2 excavated ponds without legacy beaver dams, and 9 reference ponds. These results point to the benefit of enhancing existing beaver structures and indicate that management actions aimed at maintaining surface water for breeding in spring and saturated soils and ponded water for adults in late summer would benefit this unique population of Oregon spotted frogs in the face of drought.

KEYWORDS

amphibian, beaver, habitat enhancement, Jack Creek, Oregon, Oregon spotted frog, pond, *Rana pretiosa*, survival, wetland

Climate projections over the next century suggest increased rates of warming and unprecedented shifts in seasonal precipitation and water availability for much of western North America (Mote and Salathé 2010, Musselman et al. 2021). Changes in winter snowpack depth and duration and timing of snowmelt are expected to cause more frequent and severe drought events, particularly in arid and semiarid regions (Halofsky and Peterson 2016, Mote et al. 2018). Information on how ecosystems respond to drought is key to conservation planning under future climate predictions, especially as attention shifts from reactive drought mitigation policies to more risk-based, proactive approaches (Wilhite 2011). In snowmelt-influenced lotic systems and associated waterbodies, many aquatic biota are adapted to periodic disturbance from seasonal water level fluctuations, but they may lack resilience to conditions outside the range of historical variability (VerWey et al. 2018). Isolated populations of dispersal-limited species face higher risk of extirpation than connected populations because they are less capable of range shifts that might afford persistence under changing conditions (Inman et al. 2022).

Increasingly, natural resource managers are being challenged to mitigate for reduced water availability while maintaining habitats that sustain aquatic and semiaquatic species (Moss et al. 2021, Wohner et al. 2022). In dry landscapes, amphibians are disproportionately affected by climate change compared to many other taxonomic groups (Walls et al. 2013, Inman et al. 2022). Pond breeding amphibians require hydroperiods that support egg development through recruitment, and species and populations vary in their capacity to recover from reproductive failure in years with reduced inundation (Crawford et al. 2022). Amphibian habitat restoration for drought mitigation can include the creation of artificial ponds as hydrological refugia or the supplemental deepening or planting in degraded ponds to enhance physical, chemical, or biological function (Kentula 1996). These practices have met short-term amphibian conservation goals in cases where restored ponds promoted aquatic connectivity (Rannap et al. 2009), prolonged inundation during egg laying and development windows (Petranka et al. 2003), or renewed aspects of ecological integrity (e.g., vegetation, water quality, removal of non-natives; Kapust et al. 2012). The long-term efficacy of pond restoration for drought mitigation depends on many factors that can be difficult to achieve, including how well ponds mimic the natural thermal, chemical, and structural conditions required by amphibians (Baumberger et al. 2020). Yet few studies quantify the outcomes of such strategies over sufficient time periods (Heller and Zavaleta 2009) to adequately inform management actions that increase amphibian species' resilience to a changing climate (Shoo et al. 2011, Wilhite 2011).

Climate shifts including summer drying, winter warming, and reduced snowfall are all expected to have negative effects on amphibians in western North America (Miller et al. 2018), such as the federally threatened Oregon spotted frog (*Rana pretiosa*). In a 1995–1996 status assessment, 38% of Oregon spotted frog sites were at risk of drought eliminating suitable habitat, and the most susceptible sites were dependent on surface flows in low precipitation regions (Hayes 1997). The Jack Creek population of Oregon spotted frog in the Klamath Basin of Oregon, USA, faces some of the harshest drought conditions across the historical range between northern California, USA, to southern British Columbia, Canada. It is also the highest elevation (~1,600 m) extant population and one that is relatively isolated from other known populations (Hayes 1997, Blouin et al. 2010). Oregon spotted frogs at Jack Creek are particularly vulnerable to changing climate regimes, as a lack of suitable surrounding habitat limits dispersal opportunities and compounds the effects of low gene flow (Rose et al. 2022).

The Jack Creek watershed has undergone appreciable change in the last 100 years (U.S. Department of Agriculture Forest Service [USDA] Forest Service 2004). Several recent surveys suggest riparian conditions have been affected by channel incision and related lowering of the water table (USDA Forest Service 2004, Gervais 2011). Hydrological function has also been influenced by lodgepole pine (*Pinus contorta*) encroachment, livestock grazing, and loss of North American beavers (*Castor canadensis*), which historically maintained open water and habitat structure. In conjunction with these habitat changes, ongoing monitoring suggests the Oregon spotted frog population has declined considerably since discovery at the site in 1996, when breeding surveys indicated there were over 335 breeding females (Forbes and Peterson 1999). More recent egg mass counts after a series of dry years suggest the same area supported around 17 breeding females (Pearl et al. 2009). Reduced summer stream discharge can directly influence surface water habitat connectivity, which is important for Oregon spotted frog development and seasonal movements (Pearl et al. 2009). The species prefers shallow, warm vegetated benches for breeding, deeper predator-free waters for foraging and growth, and freeze-free protected areas such as springs for overwintering (Pearl et al. 2009). This strong dependence on water makes Oregon spotted frogs vulnerable to periods of drought.

In response to declines in breeding population size, management actions to support the Oregon spotted frog and its wetland habitat have been a priority at Jack Creek. In summer 2014, 4 ponds were excavated in an area along the middle portion of the reach to increase off-channel aquatic habitat for the species. Inactive legacy dams from beavers that inhabited the Middle Jack reach around 20 years ago impounded degraded, infilled ponds, and there was opportunity to enhance existing beaver ponds while also creating new ponds that might be used by Oregon spotted frogs for breeding, foraging, or wintering. In this restoration effort, 2 inactive beaver ponds were deepened by excavation to increase habitat and extend hydroperiods (enhanced beaver ponds), and 2 ponds were excavated nearby where no ponds previously existed (created ponds; collectively, excavated ponds). An additional unexcavated natural inactive beaver pond at Middle Jack and 9 reference ponds distributed across the study area served as comparisons.

We used a before-after-control-impact [BACI] study design to evaluate whether habitat enhancement and creation (i.e., restoration) at Jack Creek benefitted Oregon spotted frogs. Our primary objectives were to determine if 1) Oregon spotted frog egg mass counts and adult survival were higher post-restoration compared to pre-restoration at Middle Jack and relative to reference reaches, (2) Oregon spotted frog egg mass counts and adult survival were linked to water availability, and (3) restoration resulted in greater water availability in support of drought mitigation. At the finer scale, we were also interested in assessing the relative value of reference ponds, natural beaver ponds, enhanced beaver ponds, and created ponds for Oregon spotted frog breeding. We expected to find differences in population responses before and after restoration at Middle Jack and among pond treatments (reference, natural beaver, enhanced beaver, and created) conditional on water availability. We predicted that pond excavation would lead to an increase in egg mass counts and adult survival at Middle Jack, late summer measures of moisture would be positively related to annual survival of adults at all reaches, restoration would increase late summer local water availability at Middle Jack, and among excavated ponds, enhanced beaver ponds would support higher egg mass counts than created ponds.

STUDY AREA

Jack Creek is a tributary of the Williamson River in the Klamath Basin of south-central Oregon. The drainage flows south at a low gradient through a mosaic of public (Fremont-Winema National Forest) and private lands. Precipitation falls mostly as snow between October and April, and snowmelt in late spring drives peak instream flows. Stream flows steadily decline over the summer to their minimum in fall, and when winter precipitation and spring recharge are low, it may take several years for the system to recover (Gervais 2011, Cummings and Eibert 2018). Most of our study reaches of Jack Creek were intermittent during our study, although stretches had perennial flows supported by springs (USDA Forest Service 2004). Instream base flows in the upper reaches of Jack Creek have been estimated at 0.05–0.07 m^3/second (Cummings and Eibert 2018).

Geology of the upper Klamath Basin was transformed by the Holocene eruption of Mount Mazama that formed nearby Crater Lake. Uplands in our study area are primarily lodgepole pine forest with riparian zones supporting willows (*Salix* spp.), bog birch (*Betula pumila*), sedges (*Carex* spp.), and grasses (Poaceae). In addition to Oregon spotted frogs, other threatened, endemic, and rare species occur within the drainage, including the endangered Miller Lake lamprey (*Entosphenus minimus*), Klamath speckled dace (*Rhinichthys osculus klamathensis*), several rare mollusks, and rare plants (USDA Forest Service 1994, Lorion et al. 2000). Unlike many other habitats where Oregon spotted frogs occur, non-native fish and bullfrogs are absent from the Jack Creek Watershed. Beavers were historically active in the upper reaches of Jack Creek through the 1980s but now appear extirpated, with the most recent sighting in 2000 (Markus 2011).

Our 4 study reaches were distributed over approximately 10.5 km of Jack Creek at 1,524–1,617 m elevation: Middle Jack (farthest upstream), Upper Jamison, Lower Jamison, and Davis-Yellow Jacket (farthest downstream). Reaches varied in the amount of riparian land cover in the surrounding floodplain, with the largest seasonally flooded area at Upper Jamison (30.04 ha) followed by Lower Jamison (20.75 ha), Davis-Yellow Jacket (13.26 ha), and Middle Jack (8.45 ha; Figure 1A). These wet meadows receive snowmelt moving through an unconfined pumice aquifer of varying thickness, and Middle Jack and Upper Jamison tend to be more perennial than the downstream reaches because of geomorphology and the distribution of springs and seeps (USDA Forest Service 2004, Weatherford and Cummings 2016). In general, meadow plant communities are similar across study reaches. Our main comparisons for this study were between Middle Jack (treatment reach) and Upper Jamison (reference reach), located about 0.50 km downstream. These 2 reaches historically had beaver dams; however, legacy dams only persist at Middle Jack.

Pond excavation took place at Middle Jack on 26–27 August 2014 by experienced excavator operators. Two excavations were located within the ponded area impounded by 2 legacy beaver dams. The other 2 were located on the floodplain, 10–50 m from the active channel. The ponds were connected to the creek during high winter flows but not during summer low flows, and they frequently dried by the end of summer. Upon construction, excavations ranged from a maximum of 11–23 m long, 5–8 m wide, and 0.5–1 m deep, with an average depth at beaver ponds of 1.04 m and an average depth at created ponds of 0.53 m. We conducted Oregon spotted frog breeding surveys between late March and late May during the wet season, and adult capture-mark-recapture surveys during the comparatively drier summer season between mid-June and late September.

METHODS

Water and vegetation relationships

We explored the ability of multiple regional indicators of drought to explain local water availability within the study reaches. The standardized precipitation evapotranspiration index (SPEI) accounts for precipitation and temperature-related potential evapotranspiration and ranges from −2 (dry conditions) to +2 (wet conditions; Vicente-Serrano et al. 2010).

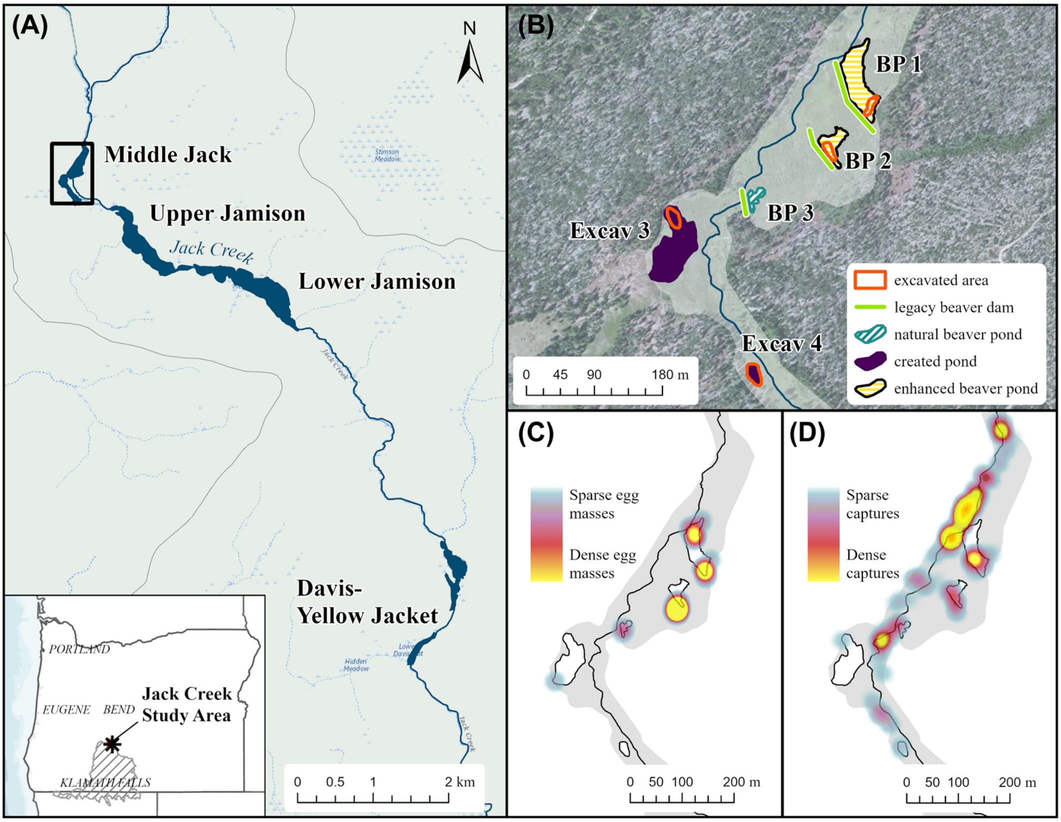

FIGURE 1 A) The 4 study reaches surveyed for Oregon spotted frogs in Jack Creek, Oregon, USA. The black box shows the extent of zoomed-in Middle Jack study area in panels B–D. B) The flooded footprints of Middle Jack breeding ponds in spring, identified by origin (treatment type) with areas that were excavated in orange. C) Heat map showing spatial distribution and relative density of spring egg masses from 2009–2021 at Middle Jack breeding ponds. D) Heat map showing spatial distribution and relative density of summer adult captures at Middle Jack from 2009–2021. Figure was produced in Esri ArcGIS Pro (version 3.1.1).

We derived SPEI at 4-km resolution for our study area at 1-, 2-, 3-, 12-, 24-, and 36-month timescales (cumulative drought state over the previous number of months) for 2005–2021 (latitude = 43.25, longitude = −121.75; https://spei.csic.es/spei_database, accessed 16 Mar 2022). We also calculated SPEI over the wet-season window of November–May. We selected this window because of pre-existing work in similar semi-arid regions suggesting late summer vegetation trends are most strongly influenced by drought conditions in November–May, and because most of the water for the water year enters the system during late fall (rain and snow) through spring (snowmelt) (Albano et al. 2020, Pilliod et al. 2021). To characterize precipitation inputs, we acquired annually accumulated precipitation (cumulative daily precipitation in the form of rain and snow) and snow water equivalent (SWE; the depth of water stored in snowpack) data for 2008–2021 from the nearest available SNOTEL station in Chemult, Oregon, about 16 km west of our study area (Chemult Alternate Station, latitude = 43.23, longitude = −121.81, 1,478 m elevation; https://www.nrcs.usda.gov/wps/portal/wcc/home, accessed 15 Mar 2022).

Vegetation greenness in water-limited areas can indicate vegetation productivity related to subsurface water availability (Aguilar et al. 2012). The normalized differential vegetation index (NDVI) is the ratio of near infrared to red light reflected by vegetation that is measured by satellites and is used as a proxy for vegetation chlorophyll capacity (greenness). We obtained Landsat NDVI data at 30-m^2 resolution derived from 16-day composite images from 9 May to 30 September of each year between 2008 and 2021 from the Robinson application (Robinson et al. 2017) or Climate Engine (Huntington et al. 2017). For better resolution of data within small and irregularly shaped reaches, we resampled 30-m grid cells to 10 m. For Davis-Yellow Jacket, we used NDVI values from the upstream Davis Flat portion of the site because 92% of Oregon spotted frogs were in this reach and shadows from upland forest interfered with NDVI estimates in the small downstream portion. We calculated the spatial mean and the spatial median of all cloud-free 10-m pixels within each reach from late summer 16-day composite windows of 29 August–13 September and 14–30 September for each year. We then averaged the values in the 2 windows to derive an estimate of late summer NDVI for each year and reach. A small band of resampled 10-m grid cells within the Lower Jamison contained null NDVI values in the 2014 window starting 14 September because the original imagery was affected by cloud cover. However, 95.5% of the total reach area (2,865 out of 3,000 pixels) contained viable data; thus, we included this composite in calculations of mean and median late summer NDVI.

We used Pearson correlations to determine the strength of the relationship between late summer NDVI and precipitation metrics. We were interested in differences in inter-reach sensitivity to precipitation inputs and whether pond excavation at Middle Jack resulted in this reach being more or less sensitive to these inputs. By considering water metrics at the regional annual scale (SPEI and precipitation) and local scale (NDVI), we were able to assess the relative importance of inter-annual versus inter-reach differences in water for Oregon spotted frog breeding and survival.

Capture-mark-recapture data

We conducted capture-mark-recapture sampling over 3 consecutive days (secondary occasions) in summer across multiple years (primary occasions). We sampled our core comparison sites, Middle Jack (13 primary occasions 2009–2021) and Upper Jamison (11 primary occasions 2009–2019), over the greatest number of occasions. We sampled Oregon spotted frogs during 5 primary occasions (2017–2021) at Davis-Yellow Jacket and 2 primary occasions (2018–2019) at Lower Jamison. During each secondary occasion, 1–3 surveyors searched suitable habitat for post-metamorphic stages of Oregon spotted frogs. We captured and marked adult and subadult frogs with ≥40 mm snout-urostyle length (SUL) with a passive integrated transponder (PIT) tag inserted under the skin of the dorsum. We recorded SUL, mass, and sex for all newly tagged individuals, and for previously tagged frogs during the first capture of each primary occasion. We classified sex based on the presence of thumb nuptial pads in mature males; if early sex designations conflicted with later designations, we used the most recent assignment (which was also always the most common designation in series with ≥2 recaptures). We collected data on environmental conditions expected to influence frog activity, including air temperature and wind at the start and end of each secondary occasion (Duarte et al. 2020, Rowe et al. 2021).

We fit robust design models (Kendall and Nichols 1995, Kendall et al. 1995) with a conditional likelihood abundance estimator (Huggins 1989) to our capture-mark-recapture data to estimate apparent survival probability (ϕ), temporary emigration (γ''), and capture probability (p). This model assumes population closure at a site within a primary occasion. Apparent survival is the probability an individual survives and does not permanently emigrate from a site. Temporary emigration is the probability an individual is unavailable for capture during a primary occasion. We then estimated abundance (N) as a derived parameter.

We related each of these probabilities to covariates we *a priori* hypothesized would influence these parameters. Many of the water metrics we considered were correlated (e.g., accumulated precipitation was correlated with SPEI at multiple lagged time frames, and median and mean NDVI were correlated), so we retained select metrics where Pearson's $|r| \leq 0.6$. We modeled survival as a function of sex (female = 0, male = 1), mean size across captures (SUL), the interaction of sex and mean size, median NDVI within the reach during late summer, median NDVI within the reach during late summer the previous year, cumulative SPEI for the wet season, cumulative SPEI for the wet season the previous year, and whether habitat restoration had occurred (Middle Jack site only; Table 1).

TABLE 1 Summary of covariates included in the Oregon spotted frog capture-mark-recapture analysis (survival [ϕ], temporary emigration [γ''], and capture probability [p]) and the egg mass count analysis for surveys in Jack Creek, Oregon, USA, 2009–2021.

Covariate	Analysis and parameters	Varied by	Mean	SD	Range or frequency
SUL: snout-to-urostyle length of individual frog, taken as the mean across all captures.	capture-mark-recapture (ϕ, γ'', p)	individual	58.17 mm	7.74 mm	42.00–82.00 mm
Sex: sex of individual frog.	capture-mark-recapture (ϕ, p)	individual			female (n = 178); male (n = 182)
Median NDVI: local metric of water availability; median normalized differential vegetation index (NDVI) value of all cloud-free Landsat 10 m pixels within the reach from 29 Aug–30 Sep of the survey year.	capture-mark-recapture (ϕ, γ'')	reach × year	0.54	0.07	0.39–0.68
Median NDVI lag: local metric of water availability; median NDVI value of all cloud-free Landsat 10 m pixels within the reach from 29 Aug–30 Sep of the previous survey year.	capture-mark-recapture (ϕ, γ'')	reach × year	0.54	0.07	0.43–0.68
SPEIwet: annual metric of water availability; cumulative standardized precipitation evapotranspiration index (SPEI) for the wet season (Nov–May) of the water year corresponding to the survey.	capture-mark-recapture (ϕ, γ'')	year	−0.17	0.93	−1.36–1.48
SPEIwet lag: annual metric of water availability; cumulative SPEI for the wet season (Nov–May) of the previous water year.	capture-mark-recapture (ϕ, γ'')	year	0.03	1.00	−1.36–1.48
Restoration: whether pond excavation occurred. Excavation did not take place at reference reaches or at Middle Jack 2009–2014.	capture-mark-recapture (ϕ), egg mass	reach × year			no excavation (n = 41); excavation (n = 7)

(Continues)

TABLE 1 (Continued)

Covariate	Analysis and parameters	Varied by	Mean	SD	Range or frequency
Day: day of calendar year starting from 1 Jan.	capture-mark-recapture (*p*)	reach × survey × year	day 229	day 29	day 166–273
Temperature: air temperature at the start of the survey.	capture-mark-recapture (*p*)	reach × survey × year	20.11°C	4.99°C	10.50–34.00°C
Wind: wind at the start of each survey using a modified Beaufort scale.	capture-mark-recapture (*p*)	reach × survey × year			calm (*n* = 44); light breeze, moderate breeze, windy (*n* = 49)
Observers: number of observers conducting the survey.	capture-mark-recapture (*p*)	reach × survey × year			1 observer (*n* = 5); 2 observers (*n* = 67); > 2 observers (*n* = 21)
Person minutes: number of observers multiplied by time spent surveying.	capture-mark-recapture (*p*)	reach × survey × year	353.58 min	114.19 min	114.00–565.00 min
Excavation: whether breeding pond was excavated.	egg mass	breeding pond × year			unexcavated breeding pond (*n* = 108); excavated breeding pond (*n* = 28)
Beaver: whether breeding pond was created by a beaver dam impoundment (beaver pond).	egg mass	breeding pond			not beaver pond (*n* = 11); beaver pond (*n* = 3)
CI: whether breeding pond was ever excavated; scored 1 for pre-excavation if later would become an excavation (control-impact).	egg mass	breeding pond			pond never excavated (*n* = 10); pond eventually excavated (*n* = 4)
BA: whether year is pre- or post-restoration (before-after).	egg mass	breeding pond			0 prior to 2015, 1 2015 and later
Years since excavation: years since 2014 habitat restoration occurred.	egg mass	breeding pond	2.40 yr	2.44 yr	1–7 yr; 0 prior to 2015

TABLE 1 (Continued)

Covariate	Analysis and parameters	Varied by	Mean	SD	Range or frequency
Mean NDVI lag: local metric of water availability; mean NDVI value of all cloud-free Landsat 10 m pixels within the reach from 29 Aug to 30 Sep from the previous survey year.	egg mass	reach × year	0.55	0.06	0.41–0.68
Annual SPEI: annual metric of water availability; annual SPEI for the month leading up to the final date of breeding surveys.	egg mass	year	−0.14	0.99	−1.87–1.27
Precipitation: annual metric of water availability; cumulative daily precipitation in the form of both rain and snow for the water year leading up to the final date of breeding surveys.	egg mass	year	549.30 mm	153.20 mm	363.00–871.00 mm

We assumed random temporary emigration (i.e., $\gamma 0 = \gamma''$) and related temporary emigration to mean size across captures, median NDVI within the reach during late summer, median NDVI within the reach during late summer the previous year, cumulative SPEI for the wet season, and cumulative SPEI for the wet season the previous year. We assumed capture and recapture probabilities were equal and modeled capture probability as a function of sex, mean size across captures, day of year, temperature at the start of the survey, wind at the start of each survey using a modified Beaufort scale (0 = calm, 1 = light breeze, moderate breeze, windy, or gusts), the number of observers (0 = 2 observers, 1 = 1 observer, 2 = > 2 observers), person minutes during surveys, and whether habitat restoration had occurred (Middle Jack site only).

We fit models using Program MARK (version 9.0; White and Burnham 1999) called from R (R Core Team 2021) using the package RMark (version 2.2.7; Laake 2013). We standardized continuous covariates to have mean of 0 and a standard deviation of 1 prior to fitting models. Furthermore, we fixed capture probability at 0 when surveys did not take place at a site during a given secondary occasion. We implemented an exploratory model selection approach and used Akaike's Information Criterion corrected for small sample size (AIC_c) for model comparisons (Burnham and Anderson 2002). We fit all combinations of capture probability models while modeling survival and temporary emigration as constants. We then examined all capture probability submodels that had a $\Delta AIC_c \leq 2$ and omitted models that contained uninformative parameters (Arnold 2010). We carried forward the remaining competing models to the next step, where we modeled all combinations of temporary emigration. We then carried all capture probability and temporary emigration submodels that had $\Delta AIC_c \leq 2$ and no uninformative parameters to the next step, where we modeled all combinations of survival probability. Our final model set was restricted to the submodels that had a $\Delta AIC_c \leq 2$ and no uninformative parameters in each step of this process. We considered models in our final model set to have similar support if the ΔAIC_c was ≤2. We described model parameters by their mean, standard error, and 95% confidence interval. We also interpreted our logistic regression results using predicted probabilities on the real scale and odds ratios calculated from model coefficients (Hosmer and Lemeshow 2000).

Egg mass data

Oregon spotted frogs are explosive breeders, often completing oviposition in 1–2 weeks, and egg mass counts provide an index of breeding population size because breeding females produce 1 egg mass per year (Licht 1971). We conducted egg mass count surveys at each of 4 study reaches: Davis-Yellow Jacket (surveyed during 1–3 visits annually 2014–2021), Middle Jack (surveyed during 1–4 visits annually 2009–2021), Lower Jamison (surveyed during 1–3 visits in 2018–2020), and Upper Jamison (surveyed on 1–4 visits annually 2009–2020). We conducted surveys roughly weekly during peak breeding season (late Mar–late May). We targeted mid-breeding season in single-visit years. Teams of 1–3 surveyors systematically searched all areas with standing water, and when an Oregon spotted frog egg mass was detected, they recorded oviposition location, microhabitat characteristics (water column depth, dominant vegetation), and embryo development data. Surveyors used flagging, global positioning system (GPS) coordinates, and hand-drawn maps to track egg mass locations for reference on subsequent visits, and they did not count previously detected egg masses in cumulative totals. We attempted to conduct a complete census of egg masses during annual surveys by using repeat visits with multiple observers. Oregon spotted frog egg masses are usually conspicuous (i.e., they are large and often found floating near the water surface) and there are no other species in our study area with similar-looking egg masses, so we have high confidence in our counts. Other studies have reported amphibian egg mass detection probabilities near 1 and linkages to adult population size (Crouch and Paton 2000, Campbell Grant et al. 2005).

Breeding Oregon spotted frogs tend to deposit eggs communally in the same locations across years, so interannual differences in counts within regularly used breeding habitats could indicate changes in microhabitat quality. We identified areas within each reach that were used for breeding by Oregon spotted frogs for ≥2 years and considered these discrete features to be breeding ponds (Table S1, available online in Supporting Information; Figure 1B–D). We overlaid egg mass GPS coordinates on high-resolution orthoimagery (https://evwhs.digitalglobe.com, accessed 7 Jun 2022) in ArcMap software (version 10.8.1; Esri, Redlands, CA, USA) relative to maximum wetted extent of identified breeding ponds. We determined breeding pond footprints using a combination of orthoimagery, expert site knowledge, and 0.3 m topographic contours extracted from LiDAR elevation data (bare earth digital elevation model; https://gis.dogami.oregon.gov/maps/lidarviewer, accessed 3 Jun 2022). Given GPS error, we considered any egg masses within 6 m of the delineated breeding pond to be in the pond. We scored breeding ponds based on whether they were excavated as part of the 2014 restoration and whether they were impounded by a remnant beaver dam. The 14 ponds in our breeding analysis varied in size from 0.004–0.342 ha and were 0.5–1.5 m deep when full (Table S1; Figure 1B).

We selected a set of candidate generalized linear mixed models (GLMMs) to evaluate hypotheses about the effects of beaver and pond excavation on egg mass counts. We also incorporated water metrics we suspected *a priori* could have lagged and unlagged effects on breeding: mean NDVI in late summer the previous year, annual SPEI in the month leading up to the latest date of breeding surveys, and accumulated precipitation for the water year up to the final date of breeding surveys. To test whether the combined effect of legacy beaver ponds and excavations on egg mass counts was stronger than their singular effects relative to reference ponds and the natural beaver pond, we fit models including the interaction between beaver ponds and excavations with or without the additive effect of previous year NDVI in late summer, annual SPEI, or accumulated precipitation. To investigate the prediction that excavated ponds have higher annual egg mass counts in years after excavation (i.e., a BACI comparison; Popescu et al. 2012), we fit models testing the interaction between a pond that was ever excavated and the period pre- or post-restoration (CI × BA), with and without water metrics. We also fit a variation of this interaction with a time-dependent excavation effect (CI × years since excavation). We fit other models for comparison with the following fixed effects: excavation × water metric, beaver × water metric, excavation + water metric, beaver + water metric, excavation, beaver, and water metric (Table 1). In all models, we included the random effect of year to account for additional variation; there was no support for including reach and breeding pond as random effects based on likelihood ratio tests.

We tested for overdispersion using the variance inflation factor $\hat{c}$ (residual deviance/degrees of freedom) and the observed/simulated standard deviation of the data using the DHARMa package in program R (R Core Team 2021). Count data were overdispersed and highly right-skewed, so we compared goodness of fit among zero-inflated and non-zero-inflated GLMMs fit to Poisson, quasi-Poisson, and negative binomial error distributions using the glmmTMB package (Brooks et al. 2017). We compared models using AIC_c (Burnham and Anderson 2002).

Population trends

We quantified the interannual trends in egg mass counts for the main comparison reaches of Middle Jack and Upper Jamison by calculating the finite rate of increase (λ), or counts in year t + 1 relative to counts in year t. We fit a linear regression model with log-transformed counts as the response variable and time as the predictor to determine whether egg mass counts were declining or growing over our study period. We also fit a regression model with the treatment-time interaction (CI × BA) to test for a restoration effect beyond background spatiotemporal differences in the study years shared by both Middle Jack and Upper Jamison, 2009–2020.

We investigated the link between spring egg mass counts in year t and abundance of adult females in year t using Pearson correlations. We considered 2 measures of adult female abundance: the abundance estimates derived from the capture-mark-recapture model that include individuals that were temporarily unavailable for capture (unadjusted abundance) and the abundance estimates derived from the capture-mark-recapture analysis scaled by the annual estimated proportion of frogs unavailable for capture (adjusted abundance).

RESULTS

Frog survival

We captured 390 individual adult and subadult frogs across all reaches and years (Rowe et al. 2023). Of those unique individuals, 41% were captured more than once across years, with some frogs detected up to 7 years after their first capture (Table 2). We had multiple competing capture-mark-recapture model models ($\Delta AIC_c \leq 2$) in our final set, but parameter estimates varied little across models so we based our inferences on the top model (Table 3).

Adult survival was strongly related to sex and body size. For every 1 standard deviation (8.23 mm) increase in SUL, the odds of survival were 1.85 times higher. Males had higher annual survival probability than females (Figure 2A). Annual survival of males at reference reaches and Middle Jack pre-restoration averaged 0.81 (95%CI = 0.55–0.94), while mean female survival probability was 0.69 (95%CI = 0.48–0.65). After restoration, male survival probability in Middle Jack increased to 0.92 (95%CI = 0.49 – 0.99) and female survival increased to 0.84 (95%CI = 0.48 – 0.97), but the 95% confidence interval for the restoration coefficient estimate overlapped 0. Local water availability metrics for late summer were the strongest environmental predictors of adult Oregon spotted frog survival. The odds of surviving were 1.85 times higher with a 1 standard deviation (0.07) increase in late summer NDVI (Figure 2B). In contrast, there was a negative relationship between previous year late summer NDVI and survival probability. For every 1 standard deviation (0.07) increase in late summer NDVI for the previous year, the odds of survival were 2.53 times lower. Regional water metrics of wet season SPEI were also included in the top model but had little explanatory effect.

TABLE 2 Summary of adult Oregon spotted frog capture events across primary occasions at each reach in the Jack Creek, Oregon, USA, study area, 2009–2021. Mean snout-urostyle length (SUL) was calculated as the cross-capture mean for individuals averaged for each sex category of female, male, or unknown. Some recaptured frogs are counted both as sexed adults and unsexed subadults, and 2 frogs moved between reaches, hence totals of *n* by sex do not necessarily align with the number of uniquely tagged individuals.

Reach	Primary occasions	Total captures	Annual mean captures	SD of annual captures	Individuals	Sex	SUL (mm) *n*	SUL (mm) Mean	SUL (mm) SD
Davis-Yellow Jacket	5	62	12.4	7.2	37	Female	22	67.7	8.1
						Male	10	61.0	3.5
						Unknown	6	44.5	3.1
Lower Jamison	2	55	27.5	11.34	53	Female	29	67.4	5.1
						Male	22	57.9	3.1
						Unknown	2	40.0	0.0
Middle Jack	13	318	24.5	10.0	173	Female	61	59.1	6.1
						Male	97	51.0	3.5
						Unknown	31	45.4	3.3
Upper Jamison	12	238	19.8	11.4	129	Female	66	62.9	7.1
						Male	53	54.9	3.9
						Unknown	19	44.7	3.9

TABLE 3 Top Oregon spotted frog capture-mark-recapture model for surveys in Jack Creek, Oregon, USA, 2009–2021. Mean estimate with standard error (SE) and 95% confidence intervals are shown for each parameter of survival (ϕ), temporary emigration (γ''), and capture probability (p).

Parameter[a]	Mean	SE	95% CI
ϕ			
Intercept	0.78	0.31	0.19, 1.38
Sex: male	0.69	0.34	0.02, 1.35
SUL	0.62	0.21	0.20, 1.03
Median NDVI	0.62	0.30	0.02, 1.21
SPEIwet	0.50	0.34	−0.16, 1.17
SPEIwet lag	0.34	0.37	−0.39, 1.07
Median NDVI lag	−0.93	0.47	−1.85, −0.00
Restoration	0.91	0.60	−0.27, 2.08
γ''			
Intercept	−0.66	0.28	−1.21, −0.12
SUL	−0.67	0.25	−1.15, −0.18
SPEIwet	0.42	0.18	0.08, 0.77
SPEIwet lag	0.61	0.20	0.23, 0.99
p			
Intercept	−0.75	0.10	−0.95, −0.55
Sex: male	−0.52	0.15	−0.81, −0.23
Temperature	−0.10	0.06	−0.21, 0.01
Observer 1	0.72	0.28	0.16, 1.27
Observer 3	−0.15	0.16	−0.46, 0.17
Person minutes	0.37	0.06	0.25, 0.49

[a] Parameters include snout-urostyle length (SUL), median normalized differential vegetation index (NDVI) within the reach from 29 Aug–30 Sep of the survey year (median NDVI), median NDVI value within the reach from 29 Aug–30 Sep of the previous survey year (median NDVI lag), cumulative standardized precipitation evapotranspiration index (SPEI) for Nov–May of the survey water year (SPEIwet), cumulative SPEI for Nov–May of the previous water year (SPEIwet lag), whether pond excavation occurred (restoration), air temperature at the start of the survey (temperature), whether there was 1 observer (observer 1) or 3 observers (observer 3) conducting the survey, and number of observers multiplied by time spent surveying (person minutes).

Egg mass counts

Egg mass counts varied by reach and across years (Figure 3). Using data from all 4 reaches, the top model describing egg mass counts included the interaction between excavation and beaver pond (38% cumulative model weight; Table 4). The 3 models with the excavation-beaver pond interaction plus a water metric were also competitive (all $\Delta AIC_c < 2$, cumulative model weights 16–31%), but none of the water metrics were strongly supported (all 95% CI for the coefficients crossed 0).

Based on our top model for egg mass counts (Table 4), created ponds, on average, were expected to have 2.55 fewer egg masses than reference ponds. Enhanced beaver ponds were predicted to have 3.68 more egg masses than reference ponds. Egg mass count models were not strongly influenced by the addition of late summer NDVI

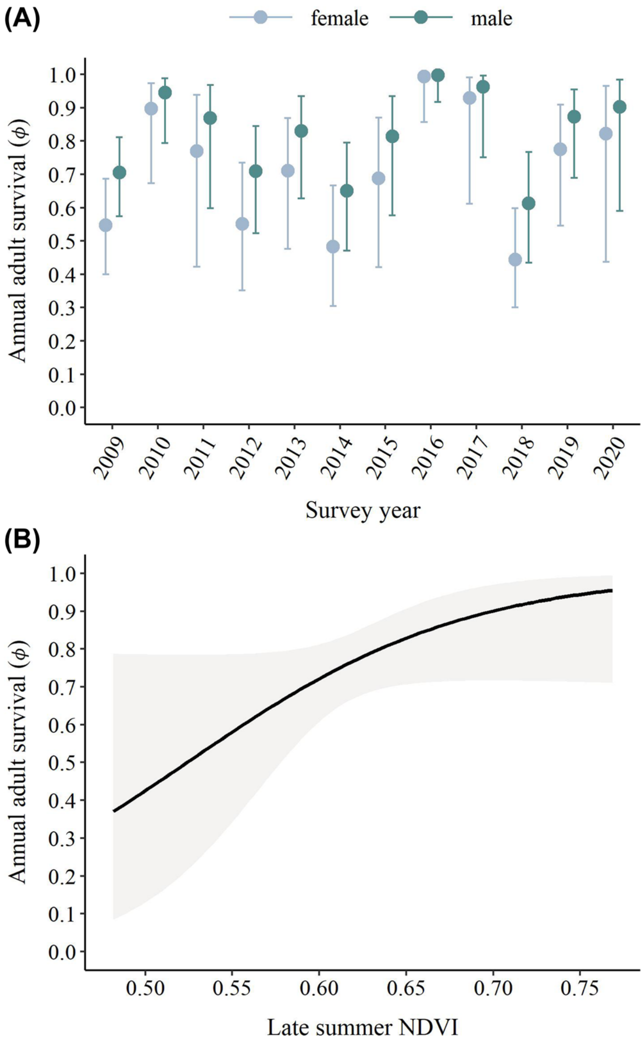

FIGURE 2 Estimates of annual adult Oregon spotted frog survival probability from time t to t + 1 predicted from the top capture-mark-recapture model using data from 2009–2021 sampling at Jack Creek, Oregon, USA. Panels represent adult survival (with 95% CI) as a function of A) sex and B) late summer normalized differential vegetation index (NDVI; spatial median) in time t + 1.

(reach-level spatial mean), SPEI the month prior to the latest month of breeding surveys, or water year precipitation accumulated through the last month of surveys (Table 4)·

Water availability metrics and vegetation indices

Late summer NDVI (spatial median) was higher at Middle Jack compared to all other reaches ($F_{3,66}$ = 16.60, P < 0.001, Tukey's honestly significant difference [HSD] test of pairwise differences all P < 0.050; Figure 4A). However, the data did not indicate a difference in late summer NDVI pre- and post-pond excavation (Wilcoxon rank sum test; W = 23, P = 0.836), suggesting higher moisture retention at this reach can be attributed to other features, such as beaver dams, vegetation composition, or geomorphology.

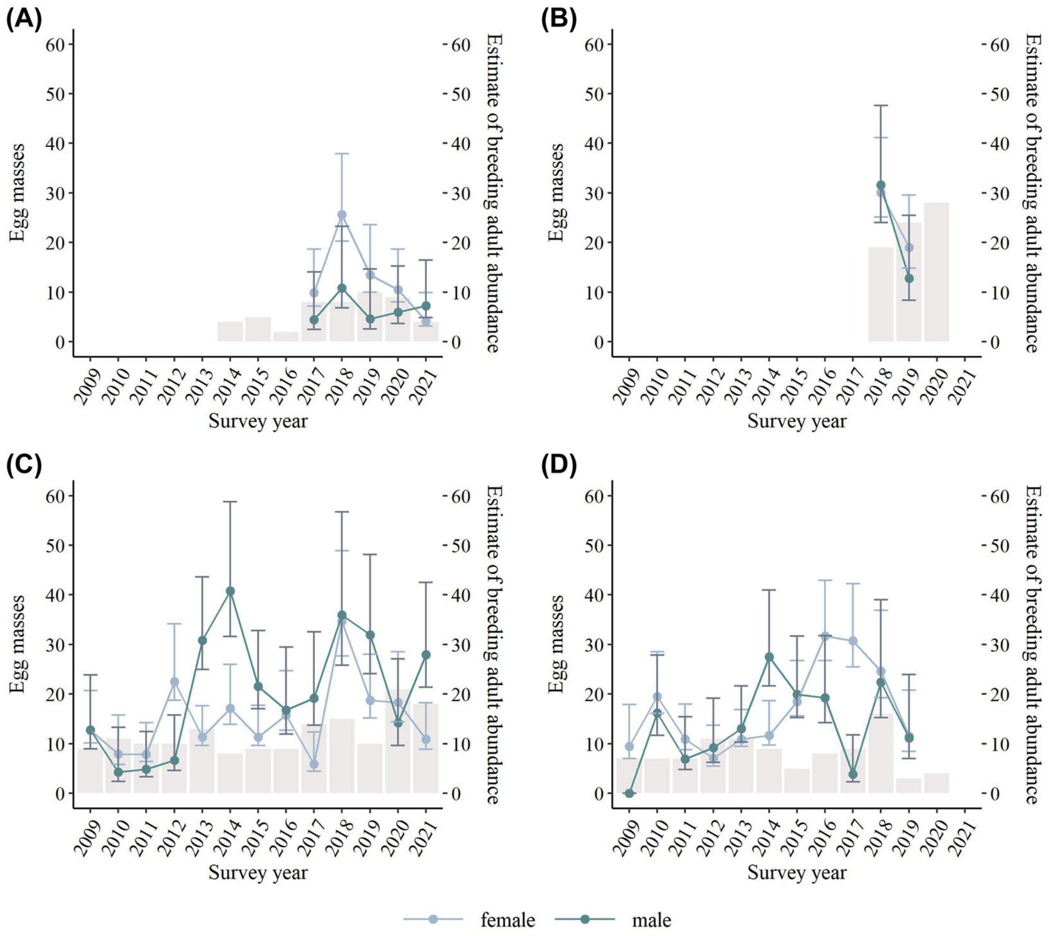

FIGURE 3 Oregon spotted frog annual 2009–2021 spring egg mass counts (light grey bars) and summer adult abundance (*N*; light blue lines = female, dark blue lines = male) estimated from the top capture-mark-recapture model, with 95% confidence intervals. Panels represent data collected during Jack Creek, Oregon, USA, sampling in 2009–2021 at A) Davis-Yellow Jacket, B) Lower Jamison, C) Middle Jack, and D) Upper Jamison.

Among water years during our study (2009–2021), precipitation accumulation was highest in 2017 at 922 mm and lowest in 2018 (419 mm) and 2021 (434 mm; Figure S2, available in Supporting Information). Monthly SPEI ranged from −2.33 (corresponding to the driest month of Jun 2021) to 2.58 (corresponding to the wettest month of Sep 2017; $\bar{x}$ = −0.22 ± 1.02[SD]). Water years 2015, 2018, 2020, and 2021 experienced moderate drought conditions (SPEI −1.5– −1.0; Figure 4B) and 2018 stood out as an especially dry year with low accumulated precipitation and minimal snowpack that was completely gone by April (Figure S1A–B). In 2015, accumulated precipitation was moderate; however, annual SWE was among the lowest on record.

Late summer NDVI (reach-level spatial median) was progressively lower moving south from Middle Jack ($\bar{x}$ = 0.59 ± 0.05) to Davis-Yellow Jacket ($\bar{x}$ = 0.48 ± 0.05). There were inter-reach differences in the regional water metrics that were related to local late summer NDVI during our study period. At non-restored (reference) sites of Upper Jamison, Lower Jamison, and Davis-Yellow Jacket, late summer NDVI was most strongly correlated with SPEI from the previous 12 months (all $r = 0.70 – 0.82$, $n = 13$, $P < 0.001 – 0.005$), SPEI from the previous wet-season (Nov–May; all $r = 0.63 – 0.74$, $P = 0.002 – 0.016$), and accumulated precipitation (all $r = 0.43 – 0.69$, $P = 0.006 – 0.125$). Late summer NDVI at Middle Jack in years prior to (2009–2014) and after (2015–2021) pond excavation was unrelated

TABLE 4 Top Oregon spotted frog egg mass count models based on differences in Akaike's Information Criterion corrected for small sample size ($\Delta AIC_c < 2$) with model weights (w_i). We provide the mean coefficient estimate with 95% confidence intervals for each parameter included in the model.

Parameter[a]	Model 1 ($\Delta AIC_c = 0.0$, $w_i = 0.38$)	Model 2 ($\Delta AIC_c = 0.4$, $w_i = 0.31$)	Model 3 ($\Delta AIC_c = 1.7$, $w_i = 0.16$)	Model 4 ($\Delta AIC_c = 1.8$, $w_i = 0.16$)
Intercept	0.88 (0.58 to 1.18)	0.82 (0.50 to 1.14)	0.80 (0.59 to 1.20)	0.88 (0.58 to 1.18)
Excavation	−2.55 (−4.53 to −0.57)	−2.41 (−4.40 to −0.42)	−2.62 (−4.60 to −0.63)	−2.55 (−4.53 to −0.57)
Beaver	0.05 (−0.50 to 0.60)	0.19 (−0.40 to 0.78)	0.04 (−0.52 to 0.59)	0.05 (−0.5 to 0.6)
Excavation × beaver	3.68 (1.60 to 5.75)	3.53 (1.44 to 5.61)	3.68 (1.61 to 5.76)	3.68 (1.60 to 5.75)
Mean NDVI lag		−0.15 (0.38 to 0.07)		
Annual SPEI			−0.08 (−0.29 to 0.14)	
Precipitation				−0.07 (−0.28 to 0.13)

[a] Parameters include whether breeding pond was excavated (excavation), whether breeding pond was created by a beaver dam impoundment (beaver), mean normalized differential vegetation index value within the reach from 29 Aug–30 Sep of the previous survey year (mean NDVI lag), annual standardized precipitation evapotranspiration index for the month leading up to the final date of breeding surveys (annual SPEI), and cumulative daily precipitation for the water year leading up to the final date of breeding surveys (precipitation).

to other water metrics, suggesting vegetation in this reach may be less sensitive to precipitation inputs and that excavations had no influence on this relationship (Figure 4C).

Population trends

Mean egg mass counts were higher at the treatment reach than the reference reach over the 13-year study period ($t_{23} = 3.86$, $P < 0.001$). Estimated population growth fluctuated between increasing and declining during our study period (Figure 5A); however, based on the slope of regression fit lines, there was an overall trend of growth at Middle Jack (Figure 5B). Egg mass counts were predicted to increase by 1.05 ($F_{1,11} = 7.59$, $P = 0.019$) per year at Middle Jack. The data did not support a trend in egg mass counts at Upper Jamison ($F_{1,10} = 0.90$, $P = 0.370$). Middle Jack supported more egg masses post- compared to pre-restoration and compared to Upper Jamison, but the BACI effect was not strong (treatment-time interaction $P = 0.127$). In pre-restoration years (2009–2014) and post-restoration years (2015–2020), Middle Jack on average had 1.5 and 5.5 more egg masses, respectively, than Upper Jamison.

Across all reaches, the data did not support correlations between log-transformed egg mass counts and estimates of log-transformed adult female abundance unadjusted for temporary emigration ($r = 0.27$, $n = 31$, $P = 0.138$) or estimates adjusted for temporary emigration ($r = 0.24$, $n = 29$, $P = 0.202$).

DISCUSSION

The success of pond creation as a habitat restoration and drought mitigation tool for amphibians varies and is influenced by many factors, including features of the ponds (e.g., hydroperiod, surface area, vegetation) and location within the landscape (e.g., near other breeding populations; Pearl et al. 2009). In our study, habitat restoration had minimal positive effect on adult survival for frogs at Middle Jack, and excavations did not increase overall late

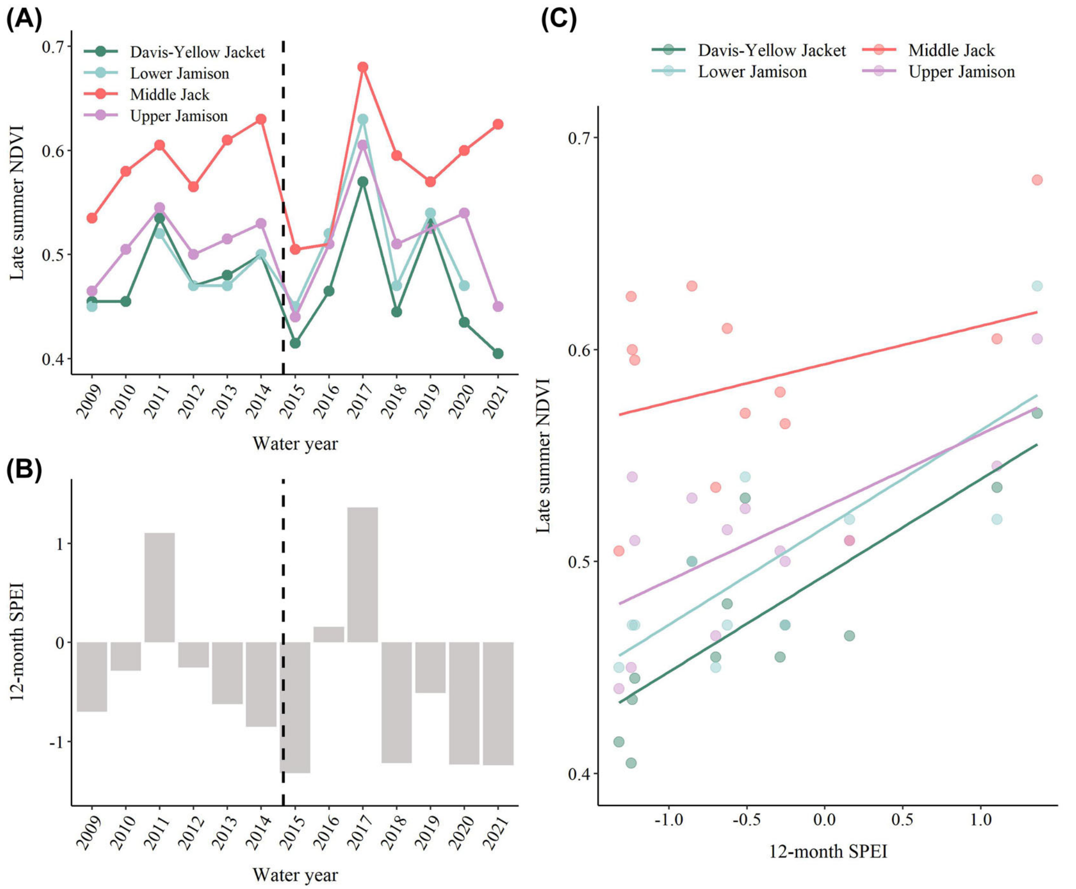

FIGURE 4 Plots of A) annual reach-level mean normalized differential vegetation index (NDVI) for the late summer dry season (29 Aug–30 Sep), B) 12-month standardized precipitation evapotranspiration index (SPEI), and C) reach-level relationships between NDVI and SPEI for each water year of the 2009–2021 study period at Jack Creek, Oregon, USA. Vertical dashed line shows time of pond excavation.

summer moisture at the reach scale. Enhanced beaver ponds were disproportionately used for breeding likely because the ponds already served as structurally favored habitat, and this emphasizes the importance of considering location and long-term water retention when constructing ponds. In the right context, excavations can have value, as evidenced by the reach-level increase in egg mass counts post-restoration at Middle Jack relative to the Upper Jamison reference reach.

Importance of late summer moisture for adult survival

Late summer local water availability was a stronger predictor of annual adult Oregon spotted frog survival than habitat restoration. A different relationship was observed in a study of adult Columbia spotted frog (*R. luteiventris*) survival at a drought mitigation site in the Toiyabe Mountains of Nevada, USA; although excavated ponds were associated with a significant increase in late summer (dry season) NDVI, the effect of the excavations on survival was stronger than the effect of increased moisture (Pilliod et al. 2021). Pilliod et al. (2021) concluded that the presence of deep ponded surface water was especially important in the dry period. In our system, excavated ponds

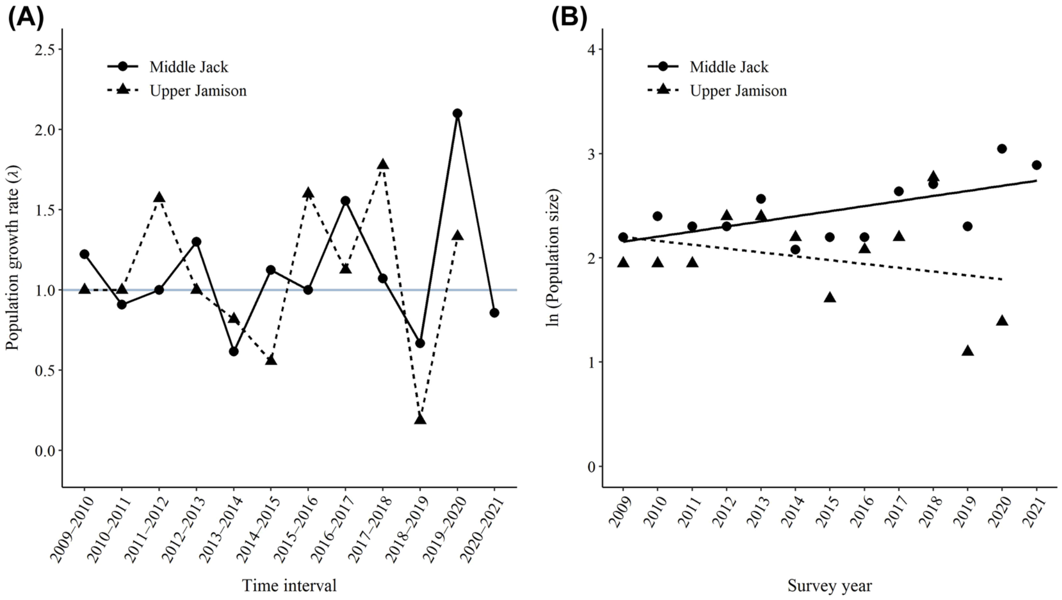

FIGURE 5 Figure of Oregon spotted frog egg mass count trends at Middle Jack (sampled 2009–2021) and Upper Jamison (sampled 2009–2020) reaches of Jack Creek, Oregon, USA. A) Egg mass population growth rate (λ) for annual time intervals calculated as the proportion of counts in time $t + 1$ relative to time t; $\lambda > 1$ indicates an increasing population and $\lambda < 1$ indicates a decreasing population. Horizontal grey line is $\lambda = 1$ where the population is neither increasing nor decreasing. B) Linear relationship between year and log-transformed egg mass counts.

were usually dry by late summer, but the unique pumice aquifer hydrology can lead to prolonged near-surface water retention supporting fens and wetlands (Weatherford and Cummings 2016). Thus, we suspect greater vegetation greenness reflects higher saturation of the pumice layer, and that groundwater is intermittently exposed in shallow depressions or unconsolidated wet soils used by Oregon spotted frogs. This points to the value of constructing ponds with a variety of hydroperiods to support various states of seasonal phenology and development. Other studies have highlighted the importance of hydrologic refugia in mediating negative effects of drought on occupancy or persistence of amphibians (Keppel et al. 2012; Zylstra et al. 2015, 2019). Ponds can increase overall connectivity and provide other resources like prey or predator refugia and wintering habitat (Hossack et al. 2013, Cartwright et al. 2022). In other riparian meadows with incised channels, restoration whereby segments of a stream channel are filled with sediment and others are left as ponds has been particularly effective in raising the floodplain water table and restoring hydrological processes (pond and plug restoration; Hammersmark et al. 2008, Hunt et al. 2018).

Adult survival in our study decreased with higher NDVI the previous summer, a finding consistent with Columbian spotted frogs in Nevada (Pilliod et al. 2021). This pattern might exist if there are latent costs to more robust vegetation growth or higher water when frogs are migrating to wintering habitats. We did not see a similar negative association between previous summer water availability and following spring egg mass counts; thus, non-breeding subadults may mostly drive the trend. Although modeling indicated an effect of previous year wet season SPEI on survival, we concluded that the parameter was uninformative. This highlights the incongruence between the broad-scale drought index and the localized NDVI index and the need for finer scale information on water availability at Oregon spotted frog sites, especially those in complex volcanic systems. Our use of NDVI provided a spatially explicit representation of hydrological conditions at each of our 4 study reaches. The 30-m resolution was an appropriate scale for the riparian meadows in our study system, and limiting NDVI to late summer meant comparisons were less likely to be confounded by presence of surface water, which could skew values low. We did not differentiate vegetation types within NDVI pixels, so some amount of unaccounted variation exists, but all dominant functional groups in our study area are expected to respond similarly to increased moisture. In the absence of on-the-ground stream gage or water level data, NDVI can be a good proxy for the extent of area with robust groundwater-supported vegetation at a timeframe that is ecologically relevant for Oregon spotted frogs; however, expanding the network of groundwater monitoring stations would likely provide more accurate baseline data on water availability.

Stream systems that are largely groundwater supported are generally more resilient to drought compared to systems dependent on surface flows. Our Middle Jack study reach tended to maintain higher NDVI across years regardless of precipitation patterns, suggesting it may be less sensitive to periods of drought than the 3 downstream study reaches. Based on the link between late summer moisture and adult survival, survival of frogs at Middle Jack was approximately 19.5% higher than survival of frogs at Upper Jamison during the study period. Geomorphological features of the Middle Jack reach may support water retention, such as its position higher in the watershed and the presence of spring-fed seeps (USDA Forest Service 2004). Historical beaver activity and shrub vegetation is more evident in our Middle Jack study reach compared to our other reaches, and legacy dams also likely contribute to greater water retention. For example, at a beaver reintroduction site along the Skykomish River in Washington, USA, the local water table rose by 30 cm within a single year (Dittbrenner et al. 2022). Regardless of the mechanism driving greater late summer moisture at Middle Jack, Oregon spotted frogs in this reach are more likely to persist under drought conditions compared to frogs in our other study reaches.

Importance of existing beaver features at Middle Jack

Excavated ponds were used less for breeding than reference ponds unless the excavation was within a beaver pond. Given our limited pond treatment replicates and lack of fine-grain microhabitat information, this result warrants further investigation. Enhanced beaver ponds held 97% (152/157) of egg mass counts at Middle Jack, indicating these ponds provide favorable habitat conditions for Oregon spotted frog breeding (Figure 1C). Similarly, northern leopard frogs (*Lithobates pipiens*) in an arid region of Wyoming, USA, preferentially bred in beaver ponds over ponds without beavers, especially in an early-snowmelt year, and active beaver ponds held more water and were used more than inactive or relict beaver ponds (Zero and Murphy 2016). We observed only 4 egg masses in the natural beaver pond, and at the enhanced beaver ponds, egg mass counts were either higher (BP2, 30 pre- vs. 62 post-excavation) or stayed approximately the same (BP1, 31 pre- vs. 29 post-excavation) after ponds were excavated. Deepening legacy beaver ponds may have helped restore aspects of historical structure and function, such as edge complexity (Knutson et al. 1999) and water table attenuation (Lowry 1993), to increase their value as breeding ponds (Stevens et al. 2007). Adult captures at Middle Jack were concentrated in the active channel and the excavated beaver ponds, providing further evidence that frogs make use of these habitats during multiple seasons (Figure 1D). Oregon spotted frog persistence at sites in Oregon is tied to the presence of beaver dams (Duarte et al. 2020), and it appears managers can capitalize on these legacy beaver features to enhance breeding habitat and support greater water retention into the summer for conservation on the landscape scale.

Population trends

Fluctuations in population growth based on egg mass counts could generally be explained by patterns of water availability. For example, egg mass counts declined by 81% at Upper Jamison but only 33% at Middle Jack between 2018 and 2019, a period of moderate drought (2018 SPEI = −1.24). In 2020 (late summer NDVI = 0.60) and 2021 (late summer NDVI = 0.63), Middle Jack egg mass counts increased to the highest in the series. Survival of adult males and females was highest in 2016–2018 during years of high groundwater recharge in the upper Jack Creek catchment. Data from a nearby piezometer station monitored in 2010 to 2017 indicated recharge was the highest in water years 2011 (84 cm) and 2016 (83 cm), and the greatest 1 June pumice saturation levels were in 2011 (79%) and 2017 (76%; Cummings and Eibert 2018). Abundant groundwater in spring could have increased the amount of suitable breeding habitat, and the heavily saturated soils in spring likely translated to greater moisture retention through summer. Continued monitoring of Oregon spotted frogs and their habitat could benefit from high-resolution groundwater and surface water measurements in Jack Creek.

The comparison of breeding and capture datasets can elucidate demographic parameters such as sex ratios and effective versus total population size, and data can validate the use of egg mass counts as a proxy for adult breeding population size (Phillipsen et al. 2010, Fellers et al. 2017). The relative strength of the relationship between egg mass counts and adult female abundance could reflect consistency in the proportion of females in breeding condition within the population, levels of recruitment, and skipped breeding opportunities (Muths et al. 2010, Phillipsen et al. 2010). At Middle Jack over our 13-year study, the mean ratio of egg masses (in spring) to adult female abundance (in summer) was 0.995, suggesting that on average females breed once per year. In contrast, at Upper Jamison our data indicate egg masses accounted for only 60% of the adult female population, suggesting skipped breeding events, lower survival of adults in early summer before our sampling, or both. In both reaches, the lack of annual correlation between egg mass counts and abundance reveals individuals may be more likely to be temporarily unavailable for capture after breeding. This effort is an important first step toward a more robust integrated population model, which uses a single joint estimator to allow for data sharing between the breeding and capture-mark-recapture datasets in life stage-specific demographic estimates (Duarte et al. 2017, Rose et al. 2021).

Our estimates of higher male than female survival is rare among true frogs (Wood et al. 1998, Howell et al. 2020). In Oregon spotted frogs at lower elevations, survival was either higher in females (site elevation = 1,300 m; Chelgren et al. 2008, Rowe et al. 2021) or there was no difference in survival between the sexes (site elevation = 1,270 m; Duarte et al. 2017). In 90% of the 589 amphibian species included in Shine (1979), females were larger than males, potentially indicative of greater selection pressure for larger-bodied females with fast growth rates. Males in our study were on average 8 mm smaller than females and size was positively related to survival, suggesting higher male survival is related to dimorphism in a different trait, perhaps cryptic coloration or behavior. Reduced capture of males supports the hypothesis that males may be more wary of or less conspicuous to predators. As representatives of an extreme within the Oregon spotted frog range, frogs at Jack Creek could have unique physiological tolerances, so it is not surprising some aspects of demography stray from patterns found in westerly lower elevation populations.

MANAGEMENT IMPLICATIONS

Pond excavation at Jack Creek could provide the greatest benefit to Oregon spotted frogs if situated to take advantage of legacy beaver dams. Survival of adults was linked to local proxies of water availability. Our results suggest Oregon spotted frog recovery is supported by habitat enhancement efforts focused on increasing moisture retention into the late summer by raising the overall water table (e.g., using the pond and plug method, earthen dams, or beaver dam analogs), and by mimicking the activities of the ecosystem engineer that historically influenced Jack Creek hydrology. Excavation of legacy beaver ponds is not necessarily a surrogate for beaver activity, which could alter habitat at the broader scale by managing woody vegetation encroachment, creating channels, accumulating organic particulates, and increasing overall habitat complexity and availability. Given the link between regional precipitation and gene flow in Oregon spotted frogs, high habitat permeability through connected surface waters and saturated soils may be especially important for this relatively isolated Jack Creek population in a future of climate uncertainty.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Animals were handled in accordance with animal welfare guidelines set by the Institutional Animal Care and Use Committee of the USGS Forest and Rangeland Ecosystem Science Center. Field surveys were authorized under scientific collecting permits from the Oregon Department of Fish and Wildlife (096-09, 094-10, 050-11, 054-12, 047-13, 024-14, 034-15, 018-16, 033-17, 018-18, 054-19, 075-20, 049-21) and recovery permits from the United States Fish and Wildlife Service (TE-49790B-0, TE-49790B-2, TE-49790B-3).

DATA AVAILABILITY STATEMENT

Data from this study are available to download from the U.S. Geological Service ScienceBase Catalog at https://doi.org/10.5066/P9IMAFNN.

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SUPPORTING INFORMATION

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