Demography of the Oregon spotted frog along a hydrologically modified river

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Abstract. Altered flow regimes can contribute to dissociation between life history strategies and environmental conditions, leading to reduced persistence reported for many wildlife populations inhabiting regulated rivers. The Oregon spotted frog (Rana pretiosa) is a threatened species occurring in floodplains, ponds, and wetlands in the Pacific Northwest with a core range in Oregon, USA. All life stages of R. pretiosa are reliant on aquatic habitats, and inundation patterns across the phenological timeline can have implications for population success. We conducted capture–mark–recapture (CMR) sampling of adult and subadult R. pretiosa at three sites along the Deschutes River downstream from two dams that regulate flows. We related the seasonal extent of inundated habitat at each site to monthly survival probabilities using a robust design CMR model. We also developed matrix projection models to simulate population dynamics into the future under current river flows. Monthly survival was strongly associated with the extent and variability of inundated habitat, suggesting some within-season fluctuations at higher water levels could be beneficial. Seasonal survival was lowest in the winter for all three sites, owing to limited water availability and the greater number of months within this season relative to other seasons. Population growth for the two river-connected sites was most strongly linked to adult survival, whereas population growth at the river-disconnected site was most strongly tied to survival in juvenile stages. This research identifies population effects of seasonally limited water and highlights conservation potential of enhancing survival of particularly influential life stages.

Key words: amphibian; capture–mark–recapture; Deschutes River; elasticity; flow; matrix projection model; population survival; water management.

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INTRODUCTION

Human-modified flow regimes shape ecology and biodiversity in many riverine environments (Nilsson et al. 2005). Life history and population demography of lotic and riparian species evolving in floodplain systems are often linked to the timing and extent of inundation (Bunn and Arthington 2002, Lytle and Poff 2004). Adaptations to hydrological fluctuations...
include behavioral avoidance of mortality-causing events, morphological and physiological traits that allow species to withstand drought or flooding, and synchronization of life history events, such as reproduction and somatic growth, with long-term patterns of seasonal water availability (Lytle 1999, Montgomery et al. 1999, Haas et al. 2009). Disruptions to historical flow regimes can have high fitness costs for species that cannot adapt to the altered environment (Waples et al. 2008, Walls et al. 2013). Amphibians, in particular, are susceptible to hydrological changes because of limited dispersal capacity, high rates of population turnover, and a multi-phased life cycle dependent on water (Trenham et al. 2003, Arntzen et al. 2017). Somatic growth, survival, abundance, and diversity of amphibians are commonly tied to water availability (Pechmann et al. 1989, Walls et al. 2013, Lowe et al. 2019).

The Oregon spotted frog (Rana pretiosa) is endemic to northwestern North America where population losses and ongoing threats such as hydrological changes have led to the species’ listing as threatened (USFWS 2014). The species is highly aquatic (overland movements are rarely observed) and typically relies on ponds, lakes, and floodplain marshes that remain at least partially inundated year-round or have surface water connections to permanent waterbodies (Watson et al. 2003, Pearl and Hayes 2004). The R. pretiosa core extant range is located in the Upper Deschutes and Little Deschutes subbasins in central Oregon, USA (Pearl and Hayes 2005). The spring-fed Deschutes River system historically had a relatively stable flow regime, but operation of two large reservoirs, Crane Prairie (constructed 1940) and Wickiup (constructed 1942), produces significant flow variability downstream of Wickiup Dam (Fig. 1). During winter reservoir storage, regulated flows below Wickiup Dam are as low as 0.57 m$^3$/s (approximately 4% of pre-dam winter flows), whereas peak summer irrigation flows can be as high as 50.97 m$^3$/s and average 155% higher than mean pre-dam summer flows (River Design Group 2017, Starcevich et al. 2017). Such large seasonal water level fluctuations have affected channel geomorphology, sedimentation, riparian vegetation, bank erosion, and habitat quality for aquatic species.

Inundation extent and water level fluctuations during critical phenological events (e.g., spring breeding, metamorphosis, summer foraging and somatic growth, and overwintering) can have consequences for amphibian movement, survival, and population persistence (Piha et al. 2007, Lowe et al. 2019). Adult R. pretiosa breed in spring and deposit eggs in sun-exposed shallows (typically <25 cm deep); they have strong site fidelity over years (Pearl and Hayes 2004). Egg masses are typically not attached to structure, making them vulnerable to displacement (i.e., floating into sub-optimal habitat) or desiccation if water levels fluctuate during this time (Bowerman and Pearl 2010). Survival of larvae depends on water persisting through mid-late summer when metamorphosis occurs (Watson et al. 2003). Subadults and adults use deeper water for basking and foraging in summer, and in fall, move to wintering sites that do not freeze (e.g., springs, beaver channels, bank overhangs; Pearl et al. 2018). Aquatic connectivity among breeding, summer foraging, and wintering habitats (i.e., local-scale migration) likely contributes to population persistence in R. pretiosa (Watson et al. 2003, Chelgren et al. 2008).

The effects of managed river flows are not well quantified for ranid frogs like R. pretiosa that inhabit lentic floodplain environments (but see Kupferberg et al. 2012, Yarnell et al. 2012). Rarely do sampling designs allow for survival of amphibians to be estimated across seasons (Muths et al. 2018), and assessments of the relative contribution of life stage vital rates to population growth are lacking (Biek et al. 2002). Moreover, demographic information on R. pretiosa in the Deschutes basin is limited to a study site not directly influenced by reservoir operations (Chelgren et al. 2008). Information on habitat conditions and their effects on seasonal survival and abundance is necessary to improve understanding of R. pretiosa population dynamics in hydrologically modified habitats.

We collected and analyzed four years of capture–mark–recapture (CMR) data for R. pretiosa at three sites along the managed reach of the Deschutes River to evaluate how abundance and survival are related to inundation extent and variability. We then paired our site-specific survival and abundance estimates with vital rate estimates from other studies of R. pretiosa to
Fig. 1. Map of three core (capture-mark-recapture sampling) and six satellite (visual encounter surveys) study sites for *Rana pretiosa* along the Deschutes River, Oregon, 2016–2019. Satellite sites are labeled in italics. Shaded teal areas show U.S. Fish and Wildlife-designated critical habitat (USFWS 2016).
simulate population dynamics, estimate population viability under current flow conditions, and evaluate the elasticity of the population growth rate to R. pretiosa vital rates.

Methods

Study area

The Deschutes River originates from Little Lava Lake in the eastern slope of the Cascade Mountains and flows south through Crane Prairie and Wickiup Reservoirs before meandering north through Bend, Oregon, and emptying into the Columbia River. Land use in the region is primarily commercial and non-commercial agriculture, livestock grazing, and timber harvest (U.S. Bureau of Reclamation 2003). Climate varies markedly across seasons and is characterized by warm dry summers (historic mean July precipitation of 1.50 cm) and cool wet winters (historic mean December precipitation of 8.97 cm; Western Regional Climate Center 2016). Dominant vegetation is pine forest, juniper, grasses, and shrub rangeland, and soils are porous and volcanic.

Along the 98 river kilometers between Wickiup Reservoir and Bend forming the regulated stretch of the upper Deschutes River, most of the land is managed as forest by federal agencies. This section of the river is used for irrigation supply, recreation, and fish and wildlife conservation. These sometimes-conflicting stakeholder interests are complicated by legal issues related to the conservation of Endangered Species Act (ESA)-listed mid-Columbia steelhead (Oncorhynchus mykiss), bull trout (Salvelinus confluentus), and R. pretiosa, as well as two unlisted salmon species. Measures to mitigate the impacts of flow management on these species are outlined in the Draft Deschutes River Basin Habitat Conservation Plan (USFWS 2019). For R. pretiosa, these proposed actions include increasing (to at least 17 m³/s) and maintaining flows in April during breeding, reducing surface level fluctuations in Crane Prairie Reservoir, and budgeting for higher flows in the fall and winter to support overwintering.

We monitored R. pretiosa at three core study sites that varied in their hydrologic connectivity to the river and are thought to be influenced differently by upstream dam operations (Table 1). Dead Slough is an oxbow 29 river kilometers downstream of Wickiup Dam (Fig. 1) and above significant tributaries that might dampen controlled water releases (USFWS 2017). East Slough Camp and SW Slough Camp are located on either side of the Deschutes River ~45 river kilometers downstream of Dead Slough and three significant tributaries. East Slough Camp is a complex of seasonally connected basins that are strongly influenced by dam operations, whereas the SW Slough Camp hydrology is more strongly linked to groundwater. Additional habitats along the upper Deschutes River are close enough that R. pretiosa movement among sites is possible (Duarte et al. 2020). Thus, we surveyed six other sites (satellite sites; Fig. 1) with potential habitat or earlier observations of R. pretiosa to enhance our odds of detecting inter-site movements. Most (5/6) of our satellite sites were within 3 river km of a core study site, and three satellite sites were <1 river km from a core site. Satellite sites did not receive formal CMR sampling; however, captured individuals were marked. We conducted a total of 51 visual encounter surveys (mean 8.5 per site) at satellite sites in the spring (15 surveys), summer (19 surveys), and fall (17 surveys).

Data collection

At our three core sites, we conducted CMR sampling over three consecutive days (secondary occasions) in each of three seasonal windows (primary occasions) in spring, summer, and fall of 2017–2019, and summer of 2016, for a total of 10 primary occasions and 30 secondary occasions. Spring surveys were conducted after R. pretiosa breeding in mid-to-late May when river flow was relatively low. Summer (mid-July to mid-August) and fall (late-September to mid-October) sampling windows occurred during high and low river flows, respectively.

During each site visit, 2–5 surveyors searched suitable habitat for post-metamorphic stages of R. pretiosa. We captured adult and subadult frogs (>40 mm snout-urostyle length [SUL]) and followed methods in Chelgren et al. (2008) to individually mark frogs with a passive integrated transponder (PTT) tag. 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 assignment in series with ≥2 recaptures); if sex could not be assigned, we did not include the individual in our analyses for this study. We also batch marked frogs <40 mm SUL with a site-specific toe-clip.

We collected data on environmental conditions expected to influence frog activity and detection (Putnam and Bennett 1981, Duarte et al. 2020). We measured air temperature at the start and end of each survey and used the average as a survey covariate in analyses (airTemp). We characterized wind at the start of each survey using a modified Beaufort scale and included as a binary variable reflecting surface disturbance (wind; 0 = calm, 1 = light, moderate, or gusts).

**Characterizing seasonal inundation**

We developed statistical relationships between environmental water availability (i.e., river flow, drought, reservoir storage, and the timing of surface water connection to the river) and surface water inundation using a combination of field observations and remotely sensed data. This approach allowed us to predict the daily extent of inundated habitat (area wet) at each core site across our study period. During opportunistically selected CMR surveys, we used Global Positioning System (GPS) tracks to define the extent of inundated area at our core and satellite sites. We collected tracks by walking the land-water interface with a handheld GPS unit or digital tablet (Samsung Galaxy Tab Active2, Suwon, South Korea) paired to a Garmin GLO Bluetooth GPS receiver (Garmin Ltd., Olathe, Kansas, USA). We aimed to collect at least one track per site × season × year, but logistical constraints prevented this from always being possible, especially at East Slough Camp, a very complex and time-intensive site. We collected 1–9 complete tracks per site over the 4-yr study window. We imported track data into Environmental Systems Research Institute ArcMap software (version 10.7.1, Redlands, California, USA) and overlaid on high-resolution airborne imagery from the National Agriculture Imagery Program (NAIP) to assess locational accuracy and quality of the track data, which varied based on time of year, cloud and canopy cover, and satellite positions. We manually inspected tracks for self-intersecting lines, and we repaired geometries when needed. We calculated the area of each cleaned track polygon and used this as an estimate of the extent of inundated habitat at the time of collection.

We also acquired surface water inundation data from the U.S. Geological Survey Landsat Level-3 Dynamic Surface Water Extent (DSWE) Science Product (Jones 2015, 2019), which was downloaded from Earth Explorer (USGS 2020a). DSWE data are derived from surface reflectance in Landsat 5, 7, and 8 scenes collected every ~8–16 d, since the early 1980s for many U.S. locations, at the spatial grain of 30-m raster pixels. We used the interpreted layer with mask applied

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**Table 1. Hydrological characteristics of core study sites in upper Deschutes River subbasin, Oregon.**

<table>
<thead>
<tr>
<th>Site</th>
<th>Distance below Wickiup Dam†</th>
<th>River connection‡</th>
<th>Estimated area wet (m²)§</th>
<th>Hydrology‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dead Slough</td>
<td>29 river km</td>
<td>High; connected until WICO flow &lt;10.62 m³/s (estimated)</td>
<td>35,513 ± 8287 (14,898–49,325)</td>
<td>Spring supported oxbow; usually connected to river throughout winter even at lowest flows</td>
</tr>
<tr>
<td>East Slough Camp</td>
<td>74 river km</td>
<td>High; connected until WICO flow &lt;18.71 m³/s (estimated)</td>
<td>54,964 ± 32,770 (2581–115,867)</td>
<td>Complex of pools connected at high water; inflow from river</td>
</tr>
<tr>
<td>SW Slough Camp</td>
<td>74 river km</td>
<td>Low; disconnected until WICO flow &gt;42.36 m³/s (estimated)</td>
<td>12,648 ± 7844 (0–28,170)</td>
<td>Variable groundwater support; highest water is in early spring; sits on floodplain terrace</td>
</tr>
</tbody>
</table>

† From USFWS (2017).
‡ River connection and hydrology determined from expert site knowledge. WICO = Oregon Water Resources Department stream gage in the Deschutes River below Wickiup Reservoir.
§ Means ± standard deviation and ranges of area wet were derived from U.S. Geological Survey Dynamic Surface Water Extent data product for Landsat scenes (n = 267) of sites taken 1 April 2010–31 March 2020. See Appendix S1: Table S1 for details.
gages were not strongly related to LAPO (WICO were highly correlated (\(r = 0.972, t = 247.910, df = 3651, P < 0.001\)). Flow data from both of these sites were highly correlated (\(r = 0.953; BENO r = 0.198, t = 12.214, df = 3651, P < 0.001\)).

We only used flow data from the WICO gage in subsequent analyses because it characterized flow moving down the upper Deschutes River well, and it is the control point gage at the outflow of Wickiup Reservoir used for regulatory purposes (USFWS 2017, 2019). We used these flow data and knowledge of each site’s hydrology from 10 yr of field observations to identify flow seasons: ramp up (period in the spring when flows are increasing to supply water for irrigation), ramp down (period in the fall when flows are decreasing to store water in the reservoirs), and disconnected (when the site was not linked to river flows through surface water). We expected the inundated area, particularly when disconnected from the river, to be related to groundwater availability, which we characterized using drought indices and reservoir storage volume. Specifically, we downloaded the 12-, 24-, and 36-month Standardized Precipitation-Evapotranspiration Index (SPEI) Global Drought Monitor for the upper Deschutes River region and used October 1st as the cutoff so that our drought indices matched water years (Vicente-Serrano et al. 2010, data available at http://sac.csic.es/spei). We also used the volume of Wickiup Reservoir at the onset of each water year (i.e., on October 1st) as another proxy for water availability in the system (U.S. Bureau of Reclamation 2020b).

We converted our DSWE estimates of inundated area to proportions of the maximum inundated area indicated by GPS tracks and fit logistic regression models to relate our water metrics to the proportion of the site that is inundated for each day with uncompromised DSWE data from 1 April 2010 to 31 March 2020. We fit separate regressions for each core site and flow season (Appendix S1: Table S1). We posited that when a site was connected to the river its area of inundation would predominately be related to river flows, and although the exact mechanism and potential lags were largely unknown, we suspected different flow metrics would be related to area of inundation during ramp up and ramp down flow seasons. Thus, we used the mean daily flow data at WICO to calculate the mean and maximum flow at one, two, and three weeks prior to each day with uncompromised DSWE data. When a site was connected to the river, we related the proportion of inundated habitat from GPS track data against inundated area from the closest uncompromised DSWE data within 14 d. These two datasets were highly correlated (\(r = 0.951, t = 18.256, df = 35, P < 0.001\)), indicating DSWE was successful in characterizing inundated area across sites.

Next, we established the link between hydrology and DSWE area of inundation estimates to derive a continuous dataset of inundated area for each core site. We downloaded a decade of mean daily flow data (1 April 2010–31 March 2020) from the three Oregon Water Resources Department stream gages in the area (locations in Fig. 1): WICO (Deschutes River below Wickiup Reservoir), BENO (Deschutes River at Benham Falls), and LAPO (Little Deschutes River near La Pine; U.S. Bureau of Reclamation 2020a). Flow data for BENO and WICO were highly correlated (\(r = 0.972, t = 247.910, df = 3651, P < 0.001\)), and flow data from both of these gages were not strongly related to LAPO (WICO

\(r = -0.001, t = -0.058, df = 3651, P = 0.953\).
area to river flow (i.e., mean daily river flow and mean and maximum river flow one, two, and three weeks prior) and the quadratic effect of river flow (except SW Slough Camp because data were too sparse to accommodate quadratic effects of river flow); the drought index the preceding one, two, and three water years; and the reservoir storage at the onset of the water year. When a site was disconnected from the river, we related the proportion of inundated area to the drought index the preceding one, two, and three water years; the reservoir storage at the onset of the water year, and the number of days the site was disconnected from the river. Due to issues of collinearity, we did not fit models with multiple river flow metrics or multiple drought indices simultaneously (i.e., mean river flow one week prior was never in the same model as maximum river flow three weeks prior). Instead, we fit a series of models and conducted multimodel inference using Akaike’s information criterion corrected for small samples (AICc; Burnham and Anderson 2002). We fit every combination of models using the package MuMIn (version 1.43.15; Bartó 2013) in program R (R Development Core Team 2019).

As expected, our modeling procedure often resulted in competing models based on AICc. Thus, we used the top models (i.e., ΔAICc < 2) for each site × flow season combination to develop model-averaged predictions for the proportion of the site inundated. These proportions were then multiplied by the total extent of each site to estimate the total area of inundation at a site for each day throughout our study period. For each interval between our primary sampling occasions, we summarized the mean of the monthly minimum, mean, maximum, coefficient of variation, and range of area wet at each site. Several of these were strongly correlated; thus, we retained values of mean of the monthly mean area wet (mnWet) and mean of the monthly coefficient of variation in area wet (cvWet) for covariates in our CMR analysis.

**Capture–mark–recapture analysis**

We used a robust design model (Kendall and Nichols 1995, Kendall et al. 1995) with a conditional likelihood abundance estimator (Huggins 1989) to analyze our CMR data (Rowe et al. 2020). This model assumes population closure across secondary sampling occasions, but individuals can enter or leave between primary sampling occasions. We fit this model to our CMR data to estimate survival probabilities (ϕ) while accounting for temporary emigration (γ) and capture probability (P), with abundance (N) estimated as a derived parameter. The model does not discriminate between survival and permanent emigration, so our survival parameter should be interpreted as apparent survival: the probability an individual survives and does not permanently emigrate from a site. We accounted for the unequal time intervals (i.e., spring to summer and summer to fall are two months, while fall to spring is eight months) by rescaling the time intervals between primary occasions such that the estimated survival parameter corresponded to a monthly survival probability. We examined the influence of sex, body size at first capture (size; 0 = small frogs ≤58.5 mm SUL mean across all captures, 1 = large frogs >58.5 mm SUL), site, mnWet, cvWet, and the interaction between mnWet and cvWet on monthly survival probability (Table 2). We also estimated temporary emigration, defined as the probability an individual is unavailable for capture during a primary occasion even though it is still alive and has not permanently emigrated from the site. Although we were able to statistically account for the unequal time intervals between primary occasions for the survival parameter, the temporary emigration parameter cannot be corrected in the same way. Thus, this parameter should be carefully interpreted with respect to time interval lengths and we only considered simpler models for this parameter. In particular, we modeled temporary emigration as random such that the probability of temporary emigration at time t + 1 for unobservable and observable frogs at time t was set equal: γ = γ". We considered models of temporary emigration that were constant or varied by seasonal transition (seasTrans) of spring to summer (sp2su), summer to fall (su2fa), or fall to spring (fa2sp). Finally, we assumed capture and recapture probabilities were equal and modeled capture probability as a function of sex, body size, site, air temperature, wind, season (spring, summer, or fall), and year. When fitting models, capture probability was fixed at zero in fall 2016 because no surveys took place that primary occasion.
We used a sequential-by-submodel strategy to develop and select the most supported models based on AICc. Specifically, we fit all combinations of capture probability models while holding the other two parameters constant. We then carried all capture probability submodels that had a $\Delta$AICc < 5 to the next step, where we modeled all combinations of temporary emigration probability. We then carried all capture probability and temporary emigration submodels that had $\Delta$AICc < 5 to the next step, where we modeled all combinations of survival probability. Our final model set was restricted to the submodels that had a $\Delta$AICc < 5 in each step of this process (Appendix S2: Table S1). Notably, this strategy has been shown to be an efficient alternative to fitting every combination of covariates on all model parameters simultaneously and does a decent job of recovering the true model space (Morin et al. 2020). This strategy resulted in competing models (i.e., multiple models with $\Delta$AICc < 2). Thus, we report model-averaged survival, temporary emigration, and capture probabilities and abundance estimates. Before calculating model-averaged estimates, we discarded any competing models with uninformative parameters (Arnold 2010). These analyses were carried out using program MARK (version 9.0; White and Burnham 1999) called from program R (R Development Core Team 2019) using the package RMark (version 2.2.7; Laake 2013).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Summary</th>
<th>Param</th>
<th>Level</th>
</tr>
</thead>
</table>
| Mean of mean monthly area wet (mnWet) | Range: 5817–84,332 m²  
Mean (SD): 32,076 (23,635) m²  
*Dead Slough:*  
Range: 21,506–41,959 m²  
Mean (SD): 33,093 (7802) m²  
*East Slough Camp:*  
Range: 12,418–84,332 m²  
Mean (SD): 53,232 (26,195) m²  
*SW Slough Camp:*  
Range: 5817–14,832 m²  
Mean (SD): 9903 (2875) m² | $\phi$ | Site × Season |
| Mean of monthly coefficient of variation in area wet (cvWet) | Range: 0.03–0.36  
Mean (SD): 0.12 (0.09)  
*Dead Slough:*  
Range: 0.03–0.13  
Mean (SD): 0.07 (0.03)  
*East Slough Camp:*  
Range: 0.04–0.25  
Mean (SD): 0.15 (0.06)  
*SW Slough Camp:*  
Range: 0.04–0.36  
Mean (SD): 0.15 (0.12) | $\phi$ | Site × Season |
| Seasonal transition (seasTrans) | Spring to summer (sp2su): 9  
Summer to fall (su2fa): 12  
Fall to spring (fa2sp): 9 | $\gamma''$ | Season |
| Season | Spring: 27  
Summer: 36  
Fall: 36 | $P$ | Season |
| Wind | Calm: 29  
Windy: 61 | $P$ | Site × Survey |
| Air temperature (airTemp) | Range: 6.3–31.8°C  
Mean (SD): 18.7 (5.9)°C | $P$ | Site × Survey |
| Day of year (doy) | Range: 134–291  
Mean (SD): 210.8 (53.0) | $P$ | Site × Survey |
| Sex | Female: 282  
Male: 202 | $\phi, P$ | Individual |
| Body size (size) | Small (≤58.5 mm SUL): 256  
Large (>58.5 mm SUL): 228 | $\phi, P$ | Individual |

Notes: SD, standard deviation; SUL, snout-urostyle length.
**Matrix projection model**

We developed a stochastic, stage-based post-breeding census matrix projection model (Caswell 2001) to evaluate the viability of *R. pretiosa* populations at each of our core sites under the current river flow management regime. The model focused on the female segment of the population and operated at a one-year time interval, where each matrix element is made of one or more vital rates (Morris and Doak 2002). We included four stages or age classes: young-of-year (age 0), juveniles (age 1), subadults (age 2), and adults (age 3). Similar to other models that have been developed for *R. pretiosa* (Kissel et al. 2014, Duarte et al. 2017), we assumed 27% and 100% of subadult and adult females, respectively, deposit egg masses each year and that the sex ratio for young-of-year frogs was 1:1. We used site-specific annual adult survival probability estimates that were calculated based on the seasonal survival probability estimates (shown in Fig. 2). The other vital rates we used to simulate *R. pretiosa* population dynamics included published empirical estimates and expert knowledge based on field observations (Table 3). The model initialized by randomly sampling an adult female abundance using a lognormal distribution based on the most recent female abundance estimates (shown in Fig. 3). We assumed a stable age distribution for estimating the number of individuals in each of the other stages in year one of the simulation. In each iteration, we randomly sample stage-specific survival parameters and the number of eggs per female using a beta and triangle distribution, respectively. We constrained the annual survival probability of younger age classes to be less than or equal to the survival probability of the next older age class in each iteration to account for the positive relationship between age-related body size and survival in anurans. Similarly, we constrained clutch size for subadults (first reproductive age class) to be less than or equal to clutch size for adults in each iteration. We simulated population dynamics forward for each of our core sites for 12 yr (approximately three *R. pretiosa* generations) and each simulation was run for 10,000 iterations. The number of adult females in each year was summarized using the median, 0.025th percentile, and 0.975th percentile across all iterations. We report the proportion of simulations in which adult female abundance fell below 20 individuals each year, which we considered a quasi-extinction threshold. Finally, we calculated the population growth rate (\(\lambda\)) and elasticity values (\(\varepsilon\)) in each iteration to quantify the proportional change in \(\lambda\) at each site that is expected with a proportional change in each vital rate (Heppell et al. 2000). An important property of age-based matrices is that survival probabilities of non-reproductive age classes are multiplied such that values of \(\varepsilon\) for young-of-year and juveniles are identical and equal to the sum of adult fecundity elasticities (Heppell 1998, Heppell et al. 2000). These simulations were carried out in program R (R Development Core Team 2019) using the package popbio (Stubben and Milligan 2007).

**RESULTS**

Using WICO flow data between 1 April 2010 and 31 March 2020, we identified the mean transition date between ramp up and ramp down flow seasons at day 189 of the year, roughly 8 July. We generated a total of 267 DSWE estimates of area wet for our core sites during this same time period for use in logistic regression models relating water metrics to the proportion of the site that is inundated. We used 91 remotely sensed values for the ramp down flow season (Dead Slough \(n = 49\), East Slough Camp \(n = 27\), and SW Slough Camp \(n = 15\)), 72 values for the ramp up flow season (Dead Slough \(n = 42\), East Slough Camp \(n = 23\), and SW Slough Camp \(n = 7\)), and 104 values for the disconnected flow season (Dead Slough \(n = 10\), East Slough Camp \(n = 17\), and SW Slough Camp \(n = 77\); Table 1). The hydrological predictors included in top models describing DSWE proportion of area wet varied by site and flow season (Appendix S1: Table S1).

We captured a total of 263 unique adult and subadult frogs at Dead Slough, 243 frogs at East Slough Camp, and 90 frogs at SW Slough Camp. Of these individuals, a total of 484 were of known sex and thus included in the analysis. Across the 10 primary occasions, 24.5% (\(n = 51\)), 32.7% (\(n = 65\)), and 15.6% (\(n = 12\)) of frogs were captured more than once at Dead Slough, East Slough Camp, and SW Slough Camp, respectively (see Appendix S3: Table S1 for recaptures by season and year). Females (\(n = 282\)) had
Fig. 2. Predicted monthly survival probabilities (a) and average seasonal survival probabilities (b) (mean ± 95% confidence interval) for *Rana pretiosa* at Dead Slough (black dots), East Slough Camp (white dots), and SW Slough Camp (gray dots) based on model-averaged predictions from the top capture–recapture models. Also shown are daily predicted area wet for each site across our study period (c) and mean daily flow at the WICO stream gage on the Deschutes River below Wickiup Reservoir (d). Seasons are as follows: Spring, interval between capture–mark–recapture (CMR) sampling in May and July (~2 months); Summer, interval between CMR sampling in July and September (~2 months); Winter, interval between CMR sampling in September and the following May (~8 months).
mean SUL of 61.4 (standard deviation [SD] = 9.6) mm at first capture, while males (n = 202) had mean SUL of 54.5 (SD = 6.0) mm at first capture. We marked 140 young-of-year frogs across core sites and recaptured 5 (3.6%). We captured *R. pretiosa* at only one satellite site (eight frogs at S Oxbow). Out of 1065 total adult, subadult, and young-of-year capture events across core and satellite sites, we observed a single instance of inter-site movement by a marked frog: An adult female (75 mm SUL at first capture) captured at SW Slough Camp in summer
2018 was recaptured across the river at East Slough Camp in spring 2019 (279 d and 274 m straight line distance between captures).

Monthly adult and subadult survival probability was positively related to mean monthly area wet and mean monthly coefficient of variation in area wet between primary occasions (Appendix S2: Table S1, Table 4). East Slough Camp had the highest mean monthly area wet and SW Slough Camp had the highest mean monthly coefficient of variation in area wet, but these values varied across the study window (Table 2, Fig. 2). Probability of monthly survival was ca. 1.82 times higher at the highest mean monthly area wet value of 84,332 m^2 than at the lowest value of 5817 m^2. Monthly survival probability was highest for *R. pretiosa* at East Slough Camp followed by Dead Slough and oscillated predictably along with area wet and WICO flows between a winter minimum and a similar spring and summer maximum (range of WICO flows for study period: 2.73–48.71 m^3/s; Fig. 2). There was a less consistent pattern in monthly survival probability across seasons and years at SW Slough Camp; monthly survival probability was near 1 during spring months and lowest survival probabilities were either in winter months or summer months across years. Model-averaged seasonal (spring = spring to summer, summer = summer to fall, and winter = fall to following spring) survival probabilities across all sites were $\phi_{spring} = 0.975$ (confidence interval [CI] 0.958–0.985), $\phi_{summer} = 0.874$ (CI 0.850–0.911), and $\phi_{winter} = 0.492$ (CI 0.434–0.550). Seasonal survival probability at East Slough Camp and Dead Slough, respectively, was, on average, 1.46–1.41 times higher in summer and 2.54–1.96 times higher in winter compared with SW Slough Camp.

Seasonal transition was an important predictor of temporary emigration in two of the three top models (Table 4). Although the estimated temporary emigration values are complicated by the different time intervals between primary occasions, model-averaged temporary emigration probability was highest during the summer-to-fall transition ($\gamma^* = 0.685$, CI 0.47–0.84), lowest during the spring-to-summer transition ($\gamma^* = 0.436$, CI 0.16–0.75), and moderate during fall-to-spring transition ($\gamma^* = 0.546$, CI 0.36–0.72). Model-averaged capture probabilities ranged from 0.039 to 0.180 (mean = 0.082, CI 0.053–0.127) and were higher for females than males.

### Table 4. Top capture–mark–recapture submodels ($\Delta$AIC_c < 2) used for model-averaged predictions, with model weights ($w_i$).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Model 1 ($w_i = 0.478$)</th>
<th>Model 2 ($w_i = 0.277$)</th>
<th>Model 3 ($w_i = 0.246$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\beta$</td>
<td>SE</td>
<td>CI</td>
</tr>
<tr>
<td>$\phi$ Intercept</td>
<td>3.99</td>
<td>0.54</td>
<td>2.94–5.05</td>
</tr>
<tr>
<td>mnWet</td>
<td>1.96</td>
<td>0.67</td>
<td>0.64–3.27</td>
</tr>
<tr>
<td>cvWet</td>
<td>0.80</td>
<td>0.28</td>
<td>0.25–1.35</td>
</tr>
<tr>
<td>$\gamma$ Intercept</td>
<td>0.99</td>
<td>0.35</td>
<td>0.31–1.67</td>
</tr>
<tr>
<td>seasTrans: fa2sp</td>
<td>−0.83</td>
<td>0.49</td>
<td>−1.80 to 0.13</td>
</tr>
<tr>
<td>seasTrans: sp2su</td>
<td>−1.47</td>
<td>0.79</td>
<td>−3.01 to 0.07</td>
</tr>
<tr>
<td>$p$ Intercept</td>
<td>−1.80</td>
<td>0.31</td>
<td>−2.40 to −1.19</td>
</tr>
<tr>
<td>Sex: male</td>
<td>−1.12</td>
<td>0.20</td>
<td>−1.51 to −0.74</td>
</tr>
<tr>
<td>Size: large</td>
<td>−0.54</td>
<td>0.18</td>
<td>−0.89 to −0.19</td>
</tr>
<tr>
<td>Wind: yes</td>
<td>0.45</td>
<td>0.14</td>
<td>0.18–0.72</td>
</tr>
<tr>
<td>Season: summer</td>
<td>−0.79</td>
<td>0.39</td>
<td>−1.56 to −0.02</td>
</tr>
<tr>
<td>Season: spring</td>
<td>0.43</td>
<td>0.30</td>
<td>−0.16 to 1.03</td>
</tr>
<tr>
<td>airTemp</td>
<td>0.16</td>
<td>0.09</td>
<td>−0.01 to 0.32</td>
</tr>
</tbody>
</table>

**Notes:** Coefficient estimates ($\beta$) with standard error (SE) and 95% confidence intervals (CI) are shown for each parameter (row) and model (column). See Appendix S2: Table S1 for the additional models that were in the final model set based on our model selection strategy but not included in model-averaged predictions. AICc, Akaike’s information criterion corrected for small samples.
males. We were 1.57–1.63 times more likely to capture a small individual than a large individual. Probability of capture increased with air temperature in two of the three best-supported models. Capture probability was also generally more likely under windier survey conditions (i.e., values other than calm) and was highest in spring.

Estimated abundances of adult and subadult male and female *R. pretiosa* across the study window were highest at Dead Slough and lowest at SW Slough Camp (Fig. 3). Abundance was highest for all three sites in the summer of 2018, although there was very high uncertainty in these estimates. No other consistent patterns were observed across sites and seasons.

Simulations indicated the SW Slough Camp population faced the greatest risk of local extinction, with 100% of the iterations falling below 20 adult females in six years (Fig. 4). East Slough Camp and Dead Slough simulations resulted in ~10% and ~30% of the iterations having the population go extinct in 13 yr. Simulated median abundance over 13 yr decreased from 99.72 (CI 58.92–172.06) to 40.88 (CI 0.28–3029.94) at Dead Slough (\(\lambda = 0.94, \text{CI} = 0.61–1.32\)), increased from 64.59 (CI 34.55–117.34) to 264.84 (CI 2.87–16,773.62) at East Slough Camp (\(\lambda = 1.14, \text{CI} = 0.78–1.58\)), and decreased from 29.30 (CI 13.38–63.19) to 0.00 (CI 0.00–0.79) at SW Slough Camp (\(\lambda = 0.48, \text{CI} = 0.27–0.74\)), with CIs growing exponentially larger with greater uncertainty into the future. Mean elasticity was highest for the adult survival parameter at East Slough Camp and Dead Slough, followed by young-of-year and juvenile survival at all sites (Fig. 5). SW Slough Camp was the only site where elasticity of adult survival was lower than elasticity of subadult, juvenile, and young-of-year survival. Subadult fecundity was the parameter with the lowest elasticity in all three sites.

Fig. 4. Simulated *Rana pretiosa* adult female abundance (median ± 95% confidence intervals) (top row) and the proportion of simulations that fell below 20 adult females (bottom row) for Dead Slough (a), East Slough Camp (b), and SW Slough Camp (c) based on the matrix projection models. Note the different ranges on the y-axes for abundance. To facilitate interpretation, plots are zoomed below upper limit of 95% confidence intervals; see text for complete intervals.
DISCUSSION

We found that adult and subadult monthly survival probability was lowest when water was most limiting, that is, over the winter (fall to spring) at Dead Slough and East Slough Camp when river flows were lowest and in late summer in most years at SW Slough Camp when groundwater recharge from precipitation is minimal (Gannett et al. 2001). Despite lower survival in the winter, frogs at the two river-connected sites (Dead Slough and East Slough Camp) had monthly survival probabilities near 1 across all seasons, perhaps indicating adaptive resiliency to human-modified flow regimes. However, the comparatively low survival at the river-disconnected site (SW Slough Camp) warrants further investigation. SW Slough Camp mean monthly areas wet were consistently low (<2.9 ha) and similar to winter minimums at the other two sites, suggesting water is limiting to survival across all seasons. This site is also vulnerable to complete drying in drought years based on remotely sensed DSWE data and field observations.

Our finding of low seasonal and monthly survival in the winter and increasing monthly survival with greater surface water is consistent with studies of other anurans in water-limited environments (e.g., *Rana yavapaiensis*; Zylstra et al. 2015, 2019, and *R. luteiventris*; McCaffery and Maxell 2010). However, it contrasts with findings from the nearby river-disconnected Dilman Meadow population, in which *R. pretiosa* of both sexes had higher two-week survival probabilities in the winter and the lowest two-week survival probabilities in the early spring breeding window (Chelgren et al. 2008). Physiological stress experienced by *R. pretiosa* over the phenological timeline can contribute to differing mortality rates across seasons dependent on sex, body condition, and site characteristics (Licht 1974, Muths et al. 2003). Our lowest seasonal wintering survival probability was at SW Slough Camp, where a radio-telemetry study found most *R. pretiosa* winter in beaver tunnels and willow thickets near the river (Pearl et al. 2018). Monthly and seasonal winter survival was higher at East Slough Camp, where frogs use interstitial spaces of lava rock piles. We lack data on thermal and moisture attributes of wintering locations at these sites, but it is possible frogs at SW Slough Camp are more vulnerable to predators or unfavorable environmental conditions in wintering refugia than frogs at East Slough Camp. Both sublethal and lethal effects of wintering on subadult and adult frogs could reduce their contributions to breeding the following spring (Tattersall and Ultsch 2008).

Monthly adult and subadult survival probability was positively related to mean monthly coefficient of variation in inundated area. A study of a Plethodontid stream salamander demonstrated post-metamorphic life stages were relatively resistant to hydrologic fluctuations (Lowe et al. 2019), but it is less clear how to interpret this finding in our system. Most likely, this pattern is driven by dynamics at the river-connected sites, where high variability in inundated area corresponds to the period of highest inundation extent during spring and summer. Because these two sites never completely dried, a certain amount of within-season variability may be beneficial to wetland productivity and community structure (e.g., by promoting vegetation growth and diversity or influencing abundance of macroinvertebrate
prey), perhaps translating to increased survival for adult and subadult *R. pretiosa* (Neckles et al. 1990, Casanova and Brock 2000).

Capture probability was lowest in the summer and temporary emigration was highest during the transition between summer and fall. Redistribution from summer to wintering habitats during this time (Chelgren et al. 2008) could lead to fewer frogs being detectable at a site. Individuals may also cue to dropping water levels and move to other nearby sites. Maintenance of aquatic corridors could promote migration between seasonal habitats (Watson et al. 2003, Pearl et al. 2018) as well as inter-site dispersal (Duarte et al. 2020). Supplementing populations and supporting persistence through recolonization after local extinction (Marsh and Trenham 2001). Despite our core and satellite sites being within presumed movement distances, only one adult female was detected moving between sites. Movement between sites is difficult to observe, and even rare dispersal events can have important implications for populations and metapopulation persistence (Muths et al. 2018). In many amphibians, young-of-year and juveniles are primary dispersers to new sites (Semlitsch 2008), and we had very low recaptures of young-toed clipped individuals. More intensive movement studies are needed to understand population connectivity in this system.

We identified annual and seasonal fluctuations in adult and subadult abundance. The especially high abundance in summer 2018 aligned with the comparatively high captures across all sites in the same year (Appendix S3: Table S1). Given survey effort remained roughly consistent across sampling occasions and year was not supported as a covariate on capture probability, we believe the peak in 2018 abundances reflect a true population pattern. Winter (November–March) WICO flows were higher in the 2018 water year (\(\bar{x} = 5.84\, \text{m}^3/\text{s}\), range = 3.43–16.68 \(\text{m}^3/\text{s}\)) than in the winters of 2016 (\(\bar{x} = 1.02\, \text{m}^3/\text{s}\), range = 0.57–15.72 \(\text{m}^3/\text{s}\)), 2017 (\(\bar{x} = 3.20\, \text{m}^3/\text{s}\), range = 2.76–11.10 \(\text{m}^3/\text{s}\)), or 2019 (\(\bar{x} = 3.07\, \text{m}^3/\text{s}\), range = 2.73–11.41 \(\text{m}^3/\text{s}\)) water years, translating to higher area wet and higher monthly survival probabilities for frogs during the winter at the river-connected sites. September 2017 (total precipitation 1.96 cm) was the only summer month in our study period to experience above average precipitation based on 1981–2010 normals, which may have contributed to the relatively high summer monthly survival of frogs at SW Slough Camp in that year and higher abundances the following year (Arguez et al. 2010). Amphibian populations are vulnerable to deterministic and stochastic events leading to local extinctions (Semlitsch et al. 1996, Marsh 2001). Accordingly, short-term population fluctuations are common (Pechmann et al. 1991, Salvidio 2009), and sporadic years of high recruitment can be enough to sustain populations (Daszak et al. 2005).

Later life stages of amphibians tend to have a greater proportional effect on long-term population dynamics than early life stages (Biek et al. 2002, Kissel et al. 2014), consistent with our finding of high elasticity in the adult survival parameter at Dead Slough and East Slough Camp. In contrast, elasticity was highest for young-of-year and juvenile frogs at SW Slough Camp, suggesting population-level benefits may result from improving conditions for all life stages. Low adult survival at this site implies juveniles and young-of-year represent a greater proportion of the total lifespan, and because survival elasticity is related to this proportion, high survival elasticities in younger life stages could be a symptom of high population instability (Heppell 1998). However, survival of younger life stages was not explicitly estimated in this study, and results are built on the assumption that vital rates for juveniles are comparable to other published studies (Chelgren et al. 2008, Duarte et al. 2017). Our understanding of Deschutes *R. pretiosa* population demographics would be improved with data on early life stage survival through post-metamorphosis, as well as timing of metamorphosis relative to river flows.

At all three of our sites, modeled areas wet were moderately high during spring breeding season; however, instead of the increasing inundation pattern seen at the river-connected sites, SW Slough Camp area wet dropped precipitously during the mid-summer larval rearing period. In fact, we observed the complete drying of the site and its spring source in July of 2020 while *R. pretiosa* at nearby sites were metamorphosing (B. McCready, unpublished data). Under current management, SW Slough Camp is connected to the river only during high flows.
The potential for reproductive failure at this site, especially during drought years, suggests it may be possible to enhance population growth by managing the number and timing of high flows to supplement water levels or stave subsurface draining in the summer. Achieving this requires careful assessment of alternative dam operation strategies so flows are sufficient at the onset of irrigation season to inundate emergent vegetation for breeding at Dead Slough (WICO flows ~25.49 m$^3$/s) and East Slough Camp (BENO flows ~42.48 m$^3$/s) and they remain stable enough to minimize risk of egg or larval stranding and desiccation (USFWS 2017). There may also be opportunities in situ to maintain complex vegetation and depth gradients providing microhabitat refuges as water levels change (Wassens et al. 2010, McGinness et al. 2014).

Our annual survival estimates for adult and subadult $R.\ pretiosa$ at East Slough Camp ($\phi = 0.68$, SD = 0.06) and Dead Slough ($\phi = 0.49$, SD = 0.04) were comparable to estimates from Dilman Meadow (0.55–0.70 survival probability for large adult frogs; Chelgren et al. 2008) and Klamath Basin Crane Creek populations (0.56 survival probability for adult frogs; Duarte et al. 2017). The relatively high annual survival probabilities for adult and subadult $R.\ pretiosa$ at East Slough Camp and Dead Slough likely contribute to population persistence over time. Estimated annual survival at SW Slough Camp was much lower ($\phi = 0.18$, SD = 0.04), and our simulations suggest frogs there face relatively high local extinction probability based on the quasi-extinction threshold of 20 breeding females in a year. Our abundance estimates indicate this population was near this threshold during our study, and simulated adult survival may be insufficient to sustain the population above this threshold in the long term. The other two sites were also shown to drop below our quasi-extinction threshold in a portion of the iterations after only simulating three generations (or 12 yr) into the future. The matrix projection model analysis represents a simple, robust approach to evaluate the importance of vital rates on population growth rates and provides some context for how populations might fare into the future. Although the analysis provides baseline information informed by recent abundance and survival estimates in these at-risk populations, it does not account for certain processes occurring in real systems, including catastrophic events, demographic stochasticity, or density dependence. Furthermore, our approach captures emigration from a site through the apparent survival parameter but does not consider individuals immigrating into the populations over time (Cooch et al. 2001, Duarte et al. 2016). Thus, these results represent a worst-case scenario where connectivity among sites is treated as nonexistent, apparent survival probabilities are treated as true survival, and riverine flows are not augmented to better meet the needs of $R.\ pretiosa$. Future modeling efforts in the Upper Deschutes subbasin would benefit from considering connectivity among sites and directly evaluating interplay between flow management scenarios and $R.\ pretiosa$ population dynamics using a decision analytic approach (DeWeber and Peterson 2020).

Complex and spatially variable relationships exist between the water level of floodplain wetlands and the Deschutes River channel. The timing and magnitude of filling of off-channel features vary geographically and seasonally depending on instream flows, proximity to the main channel, geomorphology of the wetland, and local and regional groundwater characteristics (Gannett et al. 2001). We examined the utility of the U.S. Geological Survey DSWE data product in estimating the area of inundation at sites along the Deschutes River, which, to our knowledge, represents the first time these data have been used to evaluate ecological hypotheses in this way. With the exception of persistent cloud cover, our Deschutes study area exhibits all the challenges to optical remote sensing for long-term monitoring of wetland dynamics (Jones 2011). The low spectral contrast between target (variably sized, vegetated wetlands) and background (vegetated upland, including non-deciduous forest), dark soil substrates, as well as relatively rugged terrain, all make separation of water with submerged and emergent vegetation from surrounding upland particularly difficult. However, we found a strong link between DSWE surface water estimates and our field data. Thus, we are cautiously optimistic that DSWE, which provides a multi-decade and growing record of U.S. surface water dynamics without need for extensive processing by the user (USGS 2019), offers a cost-
effective approach to monitor water availability across large spatial and temporal scales. In this case, additional data processing (e.g., polygonizing DSWE data and clipping to the maximum inundation extent) was required, and further validation of this tool is needed before wide use for small wetland monitoring can be suggested. For especially small wetland sites, other methods requiring relatively intensive, scene-specific processing (Sall et al. 2020) may be necessary.

The results from this study provide baseline information to inform ongoing population monitoring and modeling how storage and release strategies relate to abundance and persistence of Deschutes River populations of \textit{R. pretiosa}. Our finding of reduced monthly survival related to lower water availability suggests strategies to increase winter inundation at river-connected sites and summer inundation at disconnected sites could be especially important for population growth and persistence. Effective conservation of \textit{R. pretiosa} and other floodplain species hinges on the ability to forecast how populations will respond to proposed flow management scenarios in the face of environmental uncertainty.

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**LITERATURE CITED**


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