

Stage-Specific Environmental Correlates of Reproductive Success in Boreal Toads (*Anaxyrus boreas boreas*)

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ABSTRACT.—Compensatory recruitment can facilitate the persistence of populations experiencing high adult mortality. Because early life-stages of many taxa, including amphibians, are difficult to mark and recapture, sources of variation in survival at these stages often are unknown, which creates barriers to improving in situ recruitment rates. We leveraged count data and open N-mixture models to examine the environmental factors associated with the hatching of egg clutches, tadpole survival, and probability of metamorphosis in Boreal Toads (*Anaxyrus boreas boreas*) that inhabit pastures leased for cattle grazing in western Wyoming, USA. We conducted weekly surveys and measured a suite of environmental variables at 20 breeding ponds during May–September 2018. The hatching of egg clutches was most strongly related to pond surface area, as clutches often desiccated at smaller ponds. Weekly tadpole survival was lowest in ponds with high abundance of aquatic predators. Predation did not preclude metamorphosis, which was more strongly associated with higher dissolved oxygen and vegetation cover. Cattle grazing reduced vegetation cover in and around breeding ponds, which resulted in lower levels of dissolved oxygen. Grazing-induced habitat changes are therefore likely to negatively influence tadpole metamorphosis both via indirect effects on dissolved oxygen, and direct effects on vegetation cover, which also serves as feeding sites and escape cover from predators. We demonstrate the success of three critical phases in early life-stage development (egg hatching, tadpole survival, metamorphosis) was associated with different environmental factors. The inclusion of stage-specific responses in demographic analyses is therefore critical for a thorough understanding of what limits populations.

Demographic buffering among life-history stages can prevent population declines, such that success in one life-stage compensates for a lack of success in another (Villellas et al., 2015; McDonald et al., 2016). Stage-specific vital rates are commonly shaped by different environmental pressures (Dyballa et al., 2013; Kanno et al., 2015), although most investigations focus on the responses of a single life-stage to a specific stressor (e.g., climate change, infectious disease). Careful study of multiple stressors across several life-stages would provide a more complete understanding of the overall effects on population dynamics and help target conservation actions.

Amphibians are the most threatened vertebrate class worldwide (Catenazzi, 2015), with declines attributed to habitat loss, climate change, exotic introductions, overexploitation, contaminants, and infectious disease (Stuart et al., 2004; Collins, 2010). Given the biphasic life history of most amphibians (aquatic larvae, terrestrial adults), life stages are unlikely to respond uniformly to any given factor. For instance, *Batrachochytrium dendrobatidis* (*Bd*), a fungal pathogen implicated in global amphibian declines (Skerratt et al., 2007; Scheele et al., 2019), disproportionately affects postmetamorphic amphibians compared with larval stages (Rachowicz and Vredenburg, 2004; Scheele et al., 2015). Recruitment of early life-stages into the breeding population compensating for disease-induced adult mortality is, therefore, key to amphibian persistence with *Bd* (Muths et al., 2011; Spitzen-van der Sluijs et al., 2017; West et al., 2020). Sources of variation in the survival of early life-stages often are unknown, which creates barriers to mitigation efforts aimed at improving recruitment rates (Crockett et al., 2020).

Survival during the early life-stages of wild amphibians (e.g., tadpoles) remains understudied, in large part due to difficulties in applying traditional mark-recapture techniques (e.g., small

body size, low recapture rates). Recent advances to closed N-mixture models (Royle, 2004) have relaxed the assumption of closure to allow for the estimation of demographic parameters, such as survival and recruitment, from repeated counts over time, accounting for imperfect detection (Dail and Madsen, 2011; applied by Chandler and King, 2011). Count data are also less intensive to collect than mark-recapture data, permitting coverage of larger spatial scales and life-stages in which tagging is problematic (Bellier et al., 2016). Open population (or dynamic) N-mixture models have been used to model the vital rates of early life-stages in several species, including juvenile Northern Dusky Salamanders (*Desmognathus fuscus*; Zipkin et al., 2014a), yearling Black-Throated Blue Warblers (*Setophaga caerulescens*; Zipkin et al., 2014b), and young of year Brook Trout (*Salvelinus fontinalis*; Kanno et al., 2015). Yet, to date, these models rarely have been applied to early life-stages in anurans (but see Mazerolle et al., 2014; Hossack et al., 2018).

We leveraged count data and open N-mixture models to examine the sources of variation in the survival of early life-stages of Boreal Toads (*Anaxyrus boreas boreas*) in western Wyoming, USA. Infection with *Bd* decreases the survival of adult Boreal Toads (Muths et al., 2003; Pilliod et al., 2010), and high *Bd* prevalence has been documented within populations in western Wyoming (>65% in breeding adults; Murphy et al., 2009). Intervention to improve the survival of early life-stages therefore comprises a potentially effective mitigation action to compensate for disease-induced mortality in adults. Determining the environmental conditions conducive to early life-stage success would inform management efforts and provide an excellent opportunity to develop a more complete understanding of how different extrinsic factors shape survival rates across the life cycle.

Boreal Toads were once widespread and common throughout western North America, but in recent decades have suffered substantial population declines, particularly in the Rocky

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Mountain region (Muths et al., 2003; Scherer et al., 2005). Given recent declines, the distinct Eastern Genetic Clade in the southern Rocky Mountains (e.g., populations in Colorado, Utah, northern New Mexico) had been proposed for listing under the Endangered Species Act (declared not warranted in 2017). In Wyoming, Boreal Toads are listed as a Species of Greatest Conservation Need with the highest conservation priority (Native Species Status 1, Tier 1 in the most recent State Wildlife Action Plan, 2017). The majority of Boreal Toad populations in western Wyoming inhabit landscapes managed by the United States Forest Service, specifically the Bridger-Teton National Forest (BTNF), which is managed for multiple uses such as outdoor recreation, timber harvest, and cattle (*Bos taurus*) grazing. The BTNF is considering implementing grazing habitat standards (e.g., >70% retention of herbaceous vegetation) to protect Boreal Toad populations. However, whereas grazing-induced changes to terrestrial habitats did not scale up to affect the survival of adult Boreal Toads (Barrile et al., 2021a), the influence of cattle grazing on the aquatic environment and survival of early life-stages remains unclear. A better understanding of the effects of cattle grazing on larval stages of Boreal Toads would benefit management.

Our objectives were to: 1) evaluate how cattle grazing alters the aquatic habitat in beaver ponds used as breeding sites by adult Boreal Toads; 2) assess the influence of grazing-induced habitat changes and other environmental conditions on earlier life-stages, including (a) the hatching success of egg clutches, (b) weekly tadpole survival, and (c) the probability of metamorphosis; and (3) determine whether certain ponds provided optimal conditions for all three phases of development (egg hatching, tadpole survival, successful metamorphosis), or if ponds with conditions conducive to the success of one life-stage lacked the conditions necessary for the success of other life-stages.

Cattle activity can influence (positively, negatively, neutrally) larval amphibians and their habitat through many potential pathways (for a review see Howell et al., 2019), including changes to water quality (Schmutzer et al., 2008), aquatic vegetation (Burton et al., 2009), and hydroperiod (Pyke and Marty, 2005). We did not expect grazing to alter aquatic environments during the hatching of egg clutches, as egg laying, development, and hatching in western Wyoming likely occur prior to cattle entering pastures (i.e., May–June). Rather, because reproductive failure in Boreal Toads often results from the desiccation of egg clutches laid in the shallows of pond margins (Carey et al., 2005), we predicted a higher proportion of egg clutches would hatch successfully in deeper ponds with greater surface area and perimeter. We further predicted greater hatching success in ponds with less aquatic vegetation, as greater vegetation cover can increase evapotranspiration rates and consequently expedite the drying of pond margins (Marty, 2005; Pyke and Marty, 2005).

In contrast to egg hatching, the timing of tadpole development and metamorphosis in western Wyoming coincides with the period during which cattle occupy pastures leased for grazing (July–October). We, therefore, expected grazing to alter aquatic environments during tadpole growth and development. For instance, we reasoned that reduced vegetation cover associated with cattle grazing would decrease escape cover and result in higher tadpole mortality from aquatic predators (Heyer et al., 1975; Fig. 1). Several aquatic predators of Boreal Toad tadpoles were present in our study area, including Tiger Salamanders (*Ambystoma mavortium*; Swartz et al., 2014) and

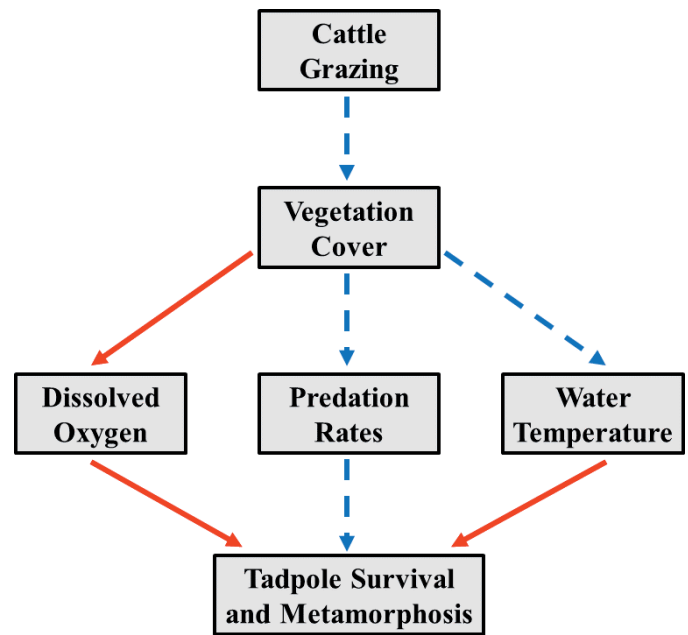


FIG. 1. Conceptual diagram illustrating our hypotheses that the effect of cattle grazing on tadpole survival and metamorphosis is mediated through its effects on the aquatic habitat. Red arrows (solid lines) indicate positive relationships and blue arrows (dashed lines) indicate negative/inverse relationships.

aquatic invertebrates (*Dytiscus* and *Aeshna* spp.; Peterson and Blaustein, 1992; Benard and Fordyce, 2003). We expected low tadpole survival in ponds with a high relative abundance of aquatic predators. We further reasoned that reduced aquatic vegetation would decrease oxygen production in breeding ponds (Fig. 1). Lower dissolved oxygen reduces tadpole activity (Costa, 1967), which can decrease growth (Feder and Moran, 1985) and increase the risk of mortality (Wilbur, 1980; Moore and Townsend Jr., 1998; Schmutzer et al., 2008). Alternatively, reduced vegetation cover from cattle grazing may increase sun exposure, which could help warm water to temperatures preferred by Boreal Toads tadpoles (i.e., 28–32°C; Beiswenger, 1978) and improve survival (Fig. 1). Overall, however, we predicted that the costs of grazing would outweigh its benefits, such that cattle activity would decrease tadpole survival and probability of metamorphosis via alteration of habitat.

Finally, we reasoned that some breeding ponds would possess conditions conducive to the success of all early life-stages in Boreal Toads, such that egg hatching, tadpole survival, and the probability of metamorphosis would be positively correlated. Conversely, density-dependence may exist among early life-stages (Smith, 1983). High hatching success, for example, could increase intraspecific competition among tadpoles and cause density-dependent survival, which would result in a negative correlation between hatching success and weekly tadpole survival.

MATERIALS AND METHODS

Study Area.—We studied the early life-stages of Boreal Toads in 2018 at 20 breeding ponds spanning two mountain ranges in the Bridger-Teton National Forest (BTNF). Sixteen were located in the northern Wyoming Range (42°59'N, 110°24'W), and four in the northern Wind River Range (43°16'N, 109°57'W). Sites in the Wind River Range were at higher elevations (mean = 2,590 m)

than Wyoming Range sites (mean = 2,440 m) and experienced longer winters and lower average temperatures. The landscape was similar between the two mountain ranges; both were composed of mixed-conifer and aspen (*Populus tremuloides*) forest, sagebrush (*Artemisia tridentata*), subalpine meadows, and riparian areas with willow (*Salix* spp.) complexes. Beaver ponds were common in montane stream channels and provided breeding habitat for Boreal Toads and other amphibian species, including Boreal Chorus Frogs (*Pseudacris maculata*), Columbia Spotted Frogs (*Rana luteiventris*), and Tiger Salamanders (*Ambystoma mavortium*). All 20 of our study sites were active or once-active beaver ponds and separated by >100 m. All sites were located within grazing allotments managed by the Forest. Cattle were turned onto pastures (which were nested within allotments) in early July, rotated to a second pasture in mid-August, and removed from the BTNF in early October. Several pastures were rested (no grazing) in a given year.

Hatching Success.—Adult Boreal Toads in western Wyoming congregate at breeding ponds shortly after snowmelt in the spring (~mid-May) and continue spawning through mid-to-late June (prior to cattle arriving on pastures). We surveyed each breeding pond weekly during the spring to record the number of egg clutches present and measure several pond characteristics. Given that no other toad species inhabit our study area, we were confident in our identification of Boreal Toad egg clutches, tadpoles, and metamorphs, as all stages were easily distinguished from the frog and salamander species mentioned above. We recorded percent submergent and emergent vegetation (vegetation piercing the surface of the water) cover (*Vegetation cover*) using quadrat sampling throughout the entire pond surface. We recorded the perimeter (*Perimeter*) of ponds using a handheld GPS from which surface area (*Area*) was calculated. We differentiated between *Perimeter* and *Area* because perimeter may better capture pond complexity, particularly the configuration of shallow edge habitat where most egg clutches were laid. Finally, we measured the maximum water depth (*Depth*) of each pond using a meter stick.

During each survey, we recorded which egg clutches hatched successfully and which failed due to desiccation. Prior to analysis, we summarized these data into the number of egg clutches that desiccated as a proportion of the total number of clutches laid at each site. To determine whether pond characteristics were associated with the desiccation of egg clutches, we modeled the proportion of egg clutches that failed due to desiccation as a function of each of our four field-derived habitat variables (*Vegetation cover*, *Perimeter*, *Area*, *Depth*). Several of our habitat variables were highly correlated (Pearson's correlation coefficients >|0.65|), so we did not include multiple covariates in a single model, and instead fit four univariate models. We summarized habitat metrics as the average value across weekly surveys at each breeding pond. We centered (by subtracting variable means) and scaled (by dividing centered variables by their standard deviations) covariates to better compare their relative importance to the response (Schielzeth, 2010). We parameterized generalized linear models with a binomial error distribution and logit link function (i.e., logistic regression), with parameters estimated using maximum likelihood in the "stats" package (*glm* function) in Program R (R Core Team, 2020). We used AIC_c (Akaike information criterion corrected for sample size) model selection to compare and rank models and to calculate model weights (Burnham et al., 2011). We considered models with $\Delta AIC_c \leq 2$ to have substantial support from the data (Burnham and Anderson, 2002) and

therefore suitable for inference and to inspect covariate relationships. Finally, we conducted Hosmer–Lemeshow goodness-of-fit tests on supported models, which we performed using the *hoslem.test* function in the "ResourceSelection" package in Program R.

Cattle Grazing and Aquatic Habitat.—We continued weekly surveys at each breeding pond throughout the summer and early fall (June–September) and measured a suite of habitat metrics during each survey. We replicated the methodology used during surveys of egg clutches to assess percent vegetation cover (emergent + submergent vegetation). We deployed a temperature logger (HOBO Pendant MX2201, Onset Computer Corporation, Bourne, Massachusetts, USA) in each pond, which we attached to staked rebar via cable ties to maintain submergence in water. Loggers were placed at a randomly selected egg clutch that hatched successfully and were set to record a temperature reading every minute (*Water temperature*). We averaged water temperature readings between each survey to use as a variable in our statistical models. Lastly, we measured dissolved oxygen (EC500 and DO600, Extech Instruments®, Waltham, Massachusetts, USA; *Dissolved oxygen*) at five random locations within each pond and recorded the average value during each weekly survey.

To develop a metric of cattle activity, we deployed one game camera (Stealth Cam, Model: STC-RX24, Grand Prairie, Texas, USA) at each breeding pond. Cameras were set to capture an image every 10 min. We recorded the number of cattle in and around (i.e., within ~10 m) breeding ponds in each photograph. We then summed the counts over time to obtain an index of cattle activity (*Cattle activity*) between each weekly survey. For example, we calculated *Cattle activity* between survey 2 and survey 3 at a given pond over the interval between the first photograph taken after the completion of survey 2 through the last photograph taken prior to the start of survey 3. Our index of cattle activity therefore corresponded directly to the interval over which water temperature readings were summarized and directly between our measurements of vegetation cover and dissolved oxygen. Because some cattle likely appeared in several consecutive photographs, the index of cattle activity served as composite metric of the number and activity of cattle at a given breeding pond.

To determine the influence of cattle grazing on the aquatic environment, we inserted our metrics of cattle activity, vegetation cover, water temperature, and dissolved oxygen into a path analysis. Path analysis took the form of a structural equation model (SEM) parameterized in the piecewiseSEM package (*psem* function) in Program R (R Core Team, 2020). The SEM represented our hypothesis that the effect of cattle activity on water temperature and dissolved oxygen would be mediated through its effect on vegetation cover. The SEM consisted of three linear mixed-effects models, specifying breeding pond as a random intercept (fit using the *lmer* function in the *lme4* package in R). We standardized model coefficients (placed in units of standard deviations of the mean via the scaling of coefficients by the ratio of the standard deviation of *x* over the standard deviation of *y*) such that the relative strength of predictors could be compared across multiple responses.

Tadpole Survival.—During surveys immediately following the breeding season (late June–early July), we recorded the average Gosner stage of developing embryos (Gosner, 1960). When all Boreal Toads tadpoles at a given site reached Gosner stage 25 (feeding and free-swimming), we began weekly count surveys. Each count survey consisted of two observers. The first observer slowly and systematically walked around the entire pond

perimeter, carefully searching and recording the number of tadpoles from visual encounters using a handheld clicker. After the first survey was complete, the second observer waited 30 min before replicating the methodology of the first observer. Because we observed very few tadpoles swimming through the interior of ponds, we restricted surveys to the edges of ponds. Observers searched for tadpoles from the perimeter of each pond, not directly in the water, which minimized disturbance to tadpoles. Immediately following completion of the second survey, we collected (cupped in hands, nonlethal) and staged 10 tadpoles and recorded average developmental stage. We continued weekly count surveys at all sites until zero tadpoles were recorded by both observers in consecutive weeks.

Adult and larval tiger salamanders (*Ambystoma mavortium*) and aquatic invertebrates (*Dytiscus* and *Aeshna* spp.) consume Boreal Toad tadpoles (Peterson and Blaustein, 1992; Swartz et al., 2014), including at our study sites (G. M. Barrile, pers. obs.). We conducted visual encounter surveys of salamanders and aquatic invertebrates to develop an index of predator abundance. We designated three predator groups: larval salamanders, adult salamanders, and aquatic invertebrates. We separated larval and adult salamanders because adults occurred in most ponds but in low numbers and larvae occurred in few ponds but in high densities. Because we did not conduct replicate count surveys of aquatic predators during each visit to a given pond, we could not account for imperfect detection in the observation process. To accommodate for uncertainty in predator counts, we developed an index by assigning each predator group a 0, 1, or 2 based on the relative abundance observed during each survey: 0 if predator group was absent, 1 if present but less than 10 individuals, and 2 if greater than 10 individuals. We created this numerical distinction because predator groups were either absent from ponds, present in low numbers (i.e., only a few individuals), or highly abundant. We then summed the rankings across all predator groups to obtain an index of predator abundance (*Predation*). For instance, if a site contained zero larval salamanders (0), >10 adult salamanders (2), and <10 aquatic invertebrates (1), the index of predator abundance would equal 3.

We adopted an open population N-mixture model to test our hypothesized relationships between tadpole survival and environmental variation. Models estimated four parameters: initial abundance, survival probability, recruitment rate, and detection probability. Our survey method constituted a robust design in which weekly visits to ponds represented primary periods, and the two surveys during each visit (one by each observer) represented secondary periods within each primary period (Kendall et al., 1997). The tadpole population therefore was considered open to gains and losses between primary periods. However, ponds essentially were closed systems with respect to immigration and emigration (i.e., tadpoles could not disperse to or from the system as ponds were bounded by beaver dams downstream and flowing water upstream). Furthermore, because our count surveys commenced after all tadpoles reached the free-swimming stage (Gosner stage 25; Gosner, 1960), in situ recruitment of tadpoles did not occur between any primary periods. Taken together, there were no additions to the tadpole population, and the only substractions occurred via mortality. We therefore were able to isolate the survival parameter and use our count data to explore sources of variation in tadpole survival, accounting for imperfect detection in the observation process.

Vegetation obstructed our vision when searching for tadpoles, thus we modeled detection probability (using a binomial error distribution) as a function of percent vegetation cover. Additional variables such as weather conditions (e.g., air temperature, cloud cover) could have influenced our detection of tadpoles, though we did not record those data during our surveys. We modeled initial abundance (specifying a Poisson error distribution) as a function of pond area, as a greater proportion of egg clutches hatched in ponds with larger surface area (see Results). Recruitment did not occur (for reasons described above) so we fixed the recruitment parameter to zero in all models. Using these structures for detection, initial abundance, and recruitment, we modeled weekly survival (using a binomial error distribution) as a function of the environmental variables that we hypothesized would influence tadpole success.

We fit four univariate models (models with additive and interactive terms did not converge) that corresponded to our predictions regarding tadpole survival in relation to vegetation cover, dissolved oxygen, water temperature, and our index of predator abundance. Whereas covariate values for vegetation cover, dissolved oxygen, and predation corresponded to measurements obtained during weekly surveys, covariate values for water temperature corresponded to the interval between primary periods. We standardized covariates and ranked models as described in the *Hatching Success* section above. To ensure that losses in the tadpole population were due to mortality and not metamorphosis to the terrestrial morphology, the final primary period in models corresponded to the survey in which late-stage tadpoles (Gosner stages 42–46) were observed or the survey preceding our first observation of metamorphs at a site.

Model parameters were estimated in the “unmarked” package (*pcountOpen* function; Fiske and Chandler, 2011) in Program R (R Core Team, 2020). Given that recruitment was fixed to zero in our models, we specified the dynamics as “constant” to indicate no relationship between survival and recruitment (dynamics also can be set to “autoreg” and “notrend” within the *pcountOpen* function to model recruitment as an autoregressive process or as a function of survival, respectively). Further, we used the default choice as our value of K , or the upper bound for the summation over the random effects in the integrated likelihood (Royle, 2004), which in “unmarked” is the maximum observed count plus 100 (i.e., 845 was our maximum tadpole count, so $K = 945$). We determined the sensitivity of the estimated parameters via increasing the value of K by multiples of 100 (e.g., 1,045, 1,145). Different values of K did not alter the estimates at the level at which we rounded, so we proceeded with the lowest value of K to expedite the analysis (though models still took approximately 6 h to run). Finally, we assessed the goodness-of-fit of supported models using the *Nmix.gof.test* function (specifying 1,000 bootstrap replicates) in the “AICcmodavg” package in Program R.

Probability of Metamorphosis.—We conducted weekly standardized visual encounter surveys at all breeding sites during July–September (period when tadpoles metamorphose). We recorded the presence or absence of metamorphs within a 5-m buffer around the perimeter of each pond (Muths et al., 2014). We considered successful metamorphosis a binary variable (1 = metamorphs present; 0 = metamorphs absent). Given the frequency of our visits to each pond, we contend that we

TABLE 1. Standardized parameter estimates (β) with standard errors (SE) and model selection results including variable name, AIC_c , ΔAIC_c , model weights (w), and number of parameters (K) for three separate procedures to estimate the 1) desiccation probability of egg clutches, 2) weekly tadpole survival, and 3) probability of metamorphosis in Boreal Toads at 20 breeding ponds in the Bridger-Teton National Forest, USA, during May–September 2018.^a

Stage/variable	β	SE	AIC_c	ΔAIC_c	w	K
Desiccation of egg clutches						
<i>Area</i>	−0.68	0.22	70.17	0.00	0.97	2
<i>Vegetation cover</i>	−0.18	0.22	78.83	8.67	0.01	2
<i>Perimeter</i>	−0.05	0.20	79.46	9.29	0.01	2
<i>Depth</i>	0.05	0.22	79.46	9.30	0.01	2
Tadpole survival						
<i>Predation</i>	−0.91	0.08	1973.07	0.00	1	6
<i>Dissolved oxygen</i>	0.45	0.06	2074.48	101.41	0	6
<i>Vegetation cover</i>	0.20	0.05	2120.76	147.69	0	6
<i>Water temperature</i>	−0.02	0.06	2134.01	160.94	0	6
Probability of metamorphosis						
<i>Dissolved oxygen</i>	4.36	2.45	21.34	0.00	0.50	2
<i>Vegetation cover</i>	2.04	0.95	21.74	0.40	0.41	2
<i>Predation</i>	−1.35	0.69	24.74	3.40	0.09	2
<i>Water temperature</i>	−0.54	0.54	29.47	8.13	0.01	2

^a All variables (in italics) were standardized (centered and scaled) in analyses and described in the text. Models can only be compared within, not across, stages (i.e., desiccation of egg clutches, tadpole survival, probability of metamorphosis). Estimates for the desiccation of egg clutches and the probability of metamorphosis were derived from univariate generalized linear models with binomial error distributions. Estimates for tadpole survival were derived from open population N-mixture models. N-mixture models also estimated initial abundance, modeled as a function of *Area*, detection probability, modeled as a function of *Vegetation cover*, and recruitment, which was fixed to zero.

observed the presence or absence of metamorphs with a high detectability.

To determine whether environmental conditions were associated with the probability of metamorphosis, we modeled the presence/absence of metamorphs as a function of our field-derived habitat variables. We summarized covariates over the entire period of tadpole development at each site. We averaged measurements for dissolved oxygen, water temperature, our index of predator abundance, and vegetation cover across all surveys during the tadpole stage. For consistency with the model suites of the other life-stages (egg hatching, tadpole survival) and to facilitate comparisons between the influence of each covariate on weekly tadpole survival versus the probability of metamorphosis, we considered the same model structures as in the *Tadpole Survival* section above (i.e., four univariate models). Variables were standardized, models were ranked, and goodness-of-fit tests were conducted as described in the *Hatching Success* section. We parameterized generalized linear models with a binomial error distribution and logit link function. Model parameters were estimated using maximum likelihood in the “stats” package (*glm* function) in Program R (R Core Team, 2020).

Hatching Success, Tadpole Survival, and Metamorphosis.—To investigate potential correlations between hatching success, weekly tadpole survival, and probability of metamorphosis, we compared values of the three vital rates within each pond. We first obtained estimates of weekly tadpole survival in each pond by fitting an open N-mixture model that included site as a fixed effect. We then calculated the Pearson’s correlation coefficient between the proportion of egg clutches that desiccated and weekly tadpole survival. Finally, we modeled the presence/absence of metamorphs as a function of weekly tadpole survival and the proportion of clutches that desiccated. Model parameters were estimated as described in the *Probability of Metamorphosis* section above.

RESULTS

Hatching Success.—We observed 116 egg clutches during 80 surveys (4 surveys per site at 20 sites) throughout the breeding

season of 2018. Eighty-three of 116 (71.6%) egg clutches failed to hatch because of desiccation. We did not observe any other form of reproductive failure at the egg stage, though alternate mechanisms were possible (e.g., fungal infection, predation). The best-supported model for the desiccation of egg clutches (model weight, $w = 0.97$) included the effect of pond area (*Area*; Table 1). We did not discover any evidence of lack of fit in the best-supported model (Hosmer–Lemeshow test: $\chi^2 = 8.81$, $df = 8$, $P = 0.36$), thus we proceeded with inference of covariate relationships. Egg clutches were less likely to desiccate in ponds with higher surface area ($\beta = -0.68$ [SE = 0.22], $P = 0.003$; Fig. 2). Water depth, length of perimeter, and vegetation cover in

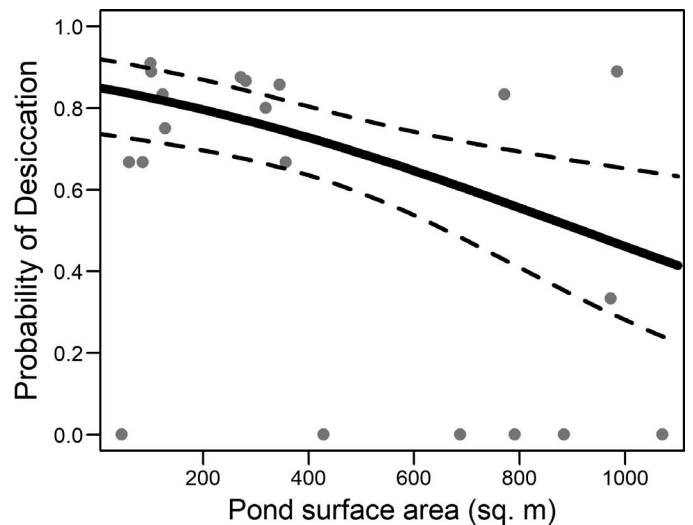


FIG. 2. The proportion of Boreal Toad egg clutches that failed to hatch due to desiccation decreased as the surface area of beaver ponds increased at 20 breeding sites in the Bridger-Teton National Forest, USA, during May–June 2018. Mean predicted values (solid line) and 95% confidence intervals (dashed lines) were derived from the top-performing generalized linear model with binomial error distribution (model weight, $w = 0.97$; Table 1). Grey dots represent raw data (y -values = number of egg clutches that desiccated/total number of egg clutches at a given site).

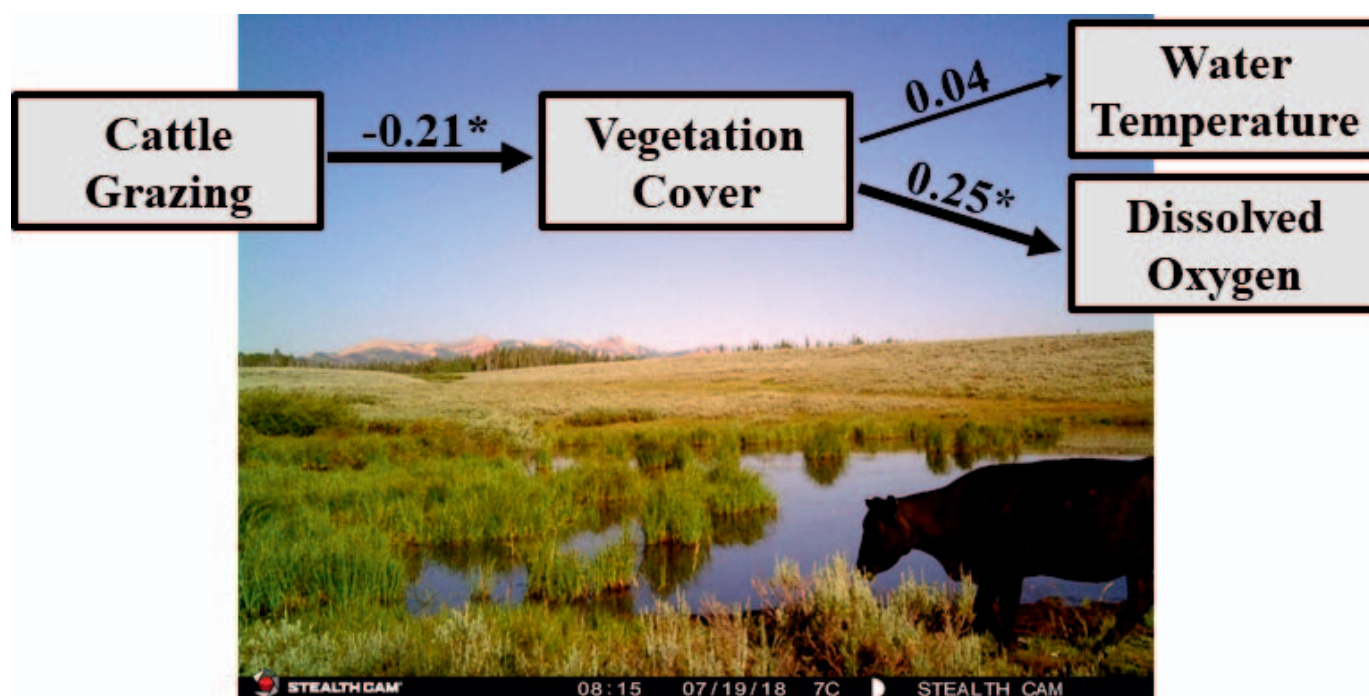


FIG. 3. Structural equation model indicating the relationships between cattle grazing, vegetation cover, water temperature, and dissolved oxygen at 20 beaver ponds used as breeding sites by Boreal Toads in the Bridger-Teton National Forest, USA, during 2018. Numbers above arrows are standardized path coefficients with the relative strength of each indicated by line width. Asterisks denote significance (i.e., $P < 0.05$). The background image of a cow grazing at a breeding pond was captured by one of our game cameras in July 2018.

ponds were not associated with the desiccation of egg clutches (Table 1).

Cattle Grazing and Aquatic Habitat.—We captured spatial and temporal variation in the environmental characteristics measured at each breeding pond (Table S1). Game cameras photographed the presence of cattle at 10 of 20 sites. The effect of cattle grazing on dissolved oxygen was mediated through its effect on vegetation cover; cattle activity decreased vegetation cover in breeding ponds, which resulted in lower levels of dissolved oxygen (Fig. 3; Table S2). By contrast, reduced vegetation cover as the result of grazing did not influence water temperature (Fig. 3; Table S2).

Tadpole Survival.—We conducted 99 surveys of Boreal Toads tadpoles (mean surveys per site = 5; range = 4–7). The best-supported model for tadpole survival (model weight, $w = 1.0$) included the effect of our index of predator abundance (*Predation*; Table 1). We did not discover any evidence of lack of fit or overdispersion in the best-supported model ($\chi^2 = 25.31$, $P = 0.41$, $\hat{c} = 1.27$), thus we proceeded with inference of covariate relationships. Tadpole survival decreased with our index of predator abundance (Fig. 4a). Additionally, our detection of tadpoles decreased with vegetation cover ($\beta = -0.36$ [SE = 0.07], $P < 0.001$; Fig. 4b), suggesting that the inclusion of vegetation cover as a covariate on detection helped correct survival estimates for error in the observation process.

Probability of Metamorphosis.—We conducted 71 surveys for metamorphosis (mean surveys per site = 4; range = 3–6). Thirteen out of 20 (65%) ponds supported successful metamorphosis (Table S1). The best-supported models for the probability of metamorphosis included the effect of dissolved oxygen and vegetation cover (model weights, $w = 0.50$ and 0.41 , respectively; Table 1). We did not discover any evidence of lack of fit in the best-supported models (Hosmer–Lemeshow test: $\chi^2 = 11.41$, $df = 8$, $P = 0.18$ and $\chi^2 = 6.64$, $df = 8$, $P = 0.58$, respectively), thus we

proceeded with inference of covariate relationships. The probability of metamorphosis increased in ponds with higher levels of both dissolved oxygen (Fig. 5a) and vegetation cover (Fig. 5b).

Hatching Success, Tadpole Survival, and Metamorphosis.—Weekly tadpole survival was unrelated to the proportion of egg clutches that failed to hatch because of desiccation (Pearson's correlation coefficient = 0.17). Whereas the probability of metamorphosis also was unrelated to the proportion of clutches that desiccated ($\beta = 1.27$ [SE = 1.25], $P = 0.31$; Fig. 6a), metamorphosis increased in ponds with higher weekly tadpole survival ($\beta = 15.06$ [SE = 7.00], $P = 0.03$; Fig. 6b).

DISCUSSION

Compensatory recruitment can facilitate the persistence of amphibian populations challenged with *Bd* (Muths et al., 2011; Scheele et al., 2015). Determining the habitat requirements of early life-stages is therefore critical for mitigation efforts aimed at improving recruitment rates. We examined the environmental factors associated with the hatching of egg clutches, tadpole survival, and probability of metamorphosis in Boreal Toads, a species which suffers adult mortality due to *Bd* (Pilliod et al., 2010). Hatching success was most strongly related to pond surface area, as clutches often desiccated at smaller ponds. Weekly tadpole survival was lowest in ponds with a high abundance of aquatic predators. Predation did not preclude metamorphosis, however, which was more strongly associated with dissolved oxygen and vegetation cover. Taken together, the success of three critical phases in early life-stage development (egg hatching, tadpole survival, and metamorphosis) was associated with different environmental factors. These results highlight the importance of considering stage-specific responses in demographic analyses.

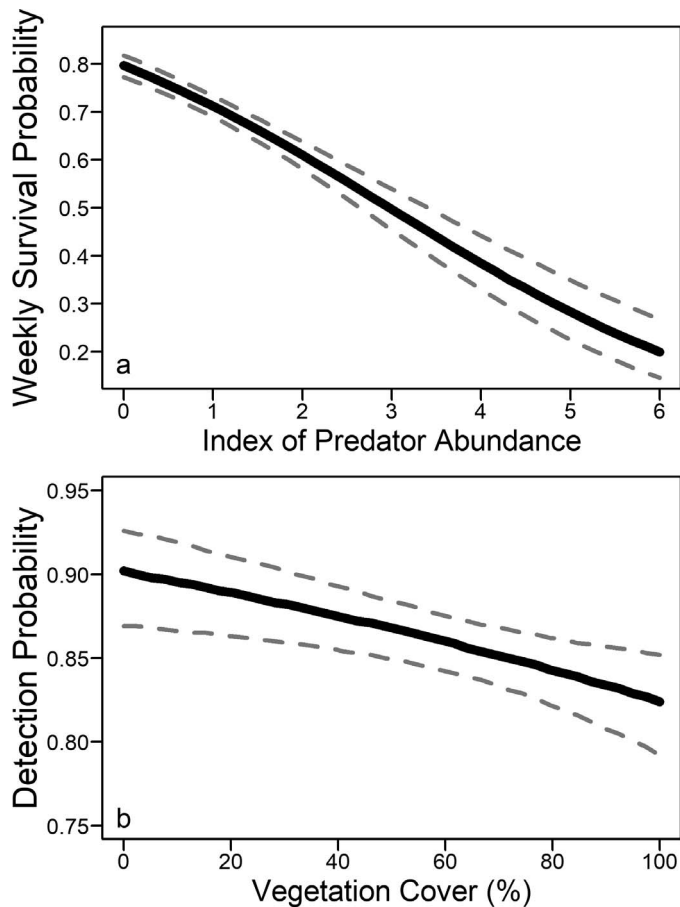


FIG. 4. Weekly survival probability of Boreal Toad tadpoles decreased as (a) predation pressure from tiger salamanders and aquatic invertebrates increased at 20 breeding ponds in the Bridger-Teton National Forest, USA, during June–August 2018. Observer detection probability of tadpoles was lower in (b) ponds with higher amounts of vegetation cover (emergent + submergent vegetation). Mean predicted values (solid lines) and 95% confidence intervals (dashed lines) were derived from the top-performing open population N-mixture model (model weight, $w = 1.0$; Table 1). Models also included initial abundance, which was modeled as a function of pond surface area ($\beta = -0.15$ [SE = 0.04], $P < 0.001$), and recruitment, which was fixed to zero.

Cattle grazing reduced vegetation cover in and around breeding ponds during the period of tadpole development. Contrary to our prediction, reduced vegetation cover did not increase water temperature. Consistent with our prediction, however, reduced vegetation cover decreased dissolved oxygen levels. Low levels of dissolved oxygen were associated with a low probability of metamorphosis, suggesting that grazing-induced changes to vegetation cover likely had a negative effect on tadpole metamorphosis. The probability of metamorphosis was low in ponds with low vegetation cover, such that reductions in vegetation cover also may have influenced the success of early life-stages more directly. For instance, low vegetation cover may limit food availability and/or feeding sites for herbivorous tadpoles. Given the probable adverse effects of grazing-induced reductions in vegetation cover to the metamorphosis of Boreal Toad tadpoles, managers could work with ranchers to alter the timing, duration, and density of cattle in and around breeding ponds during the period of tadpole development (July–August). Cattle could be excluded entirely from grazing at breeding ponds during this period, for example, or moved away from ponds when vegetation cover reaches a certain threshold.

Cattle also can introduce nitrogenous compounds into the water that elevate ammonia, nitrite, and nitrate levels, all of which have been linked to decreased survival in amphibian larvae (Jofre and Karasov, 1999; Marco et al., 1999). We originally planned to incorporate nitrogen into our analyses; however, nitrate was undetectable (i.e., 0 ppm) at all sites except one during the study period (using a LaMotte test kit and colorimeter [0.0–15.0 ppm]; LaMotte Company, Chestertown, Maryland, USA). Low nitrate concentrations suggested that the levels of grazing intensity permitted within the Bridger-Teton National Forest at the time of study did not reach those required for adverse effects to water quality via nitrogen inputs. By contrast, farm ponds on land used for agriculture and runoff from feedlots used for animal production likely have a larger effect on aquatic environments than cattle grazing on multiuse land such as national forests (NRC, 1992; Schmutzer et al., 2008). Increases in the level of grazing intensity permitted on public lands such as the Bridger-Teton National Forest, however, could result in further negative impacts to aquatic amphibian habitat (Pfennig et al., 1991), in addition to reductions in vegetation cover.

Boreal Toads persist in our study area despite high *Bd* prevalence in adults (Barrile et al., 2021b), in contrast to populations in other portions of the species' range. Severe declines in Boreal Toad populations in the southern Rocky Mountains (southeast Wyoming, Colorado, northern New Mexico), for example, have been attributed to chytridiomycosis (Muths et al., 2003; Scherer et al., 2005). As few effective strategies exist for increasing the survival rates of adults, conservation efforts have focused on earlier life-stages, in particular, the reintroduction of hatchery-raised tadpoles to their native range. Capture-mark-recapture studies have produced important insights on the survival and probability of metamorphosis in reintroduced tadpoles (Muths et al., 2014; Crockett et al., 2020); however, the intensive field methods used in such work restricted the number of sites visited, and therefore, the amount of environmental variation captured. Our study suggests that count surveys may provide a complementary approach to capture additional variation in potentially important drivers of tadpole survival, which could help develop appropriate criteria for site selection in reintroduction efforts.

Repeated count surveys, moreover, when paired with open N-mixture models, emerged as an appealing approach to assess the survival of larval amphibians (Mazerolle et al., 2014; Hossack et al., 2018). However, researchers should proceed with caution when using N-mixture models to estimate vital rates. Depending on system dynamics and the sensibility of assumptions, N-mixture models can provide accurate estimates of demographic parameters (Ficetola et al., 2018), accurate estimates for some parameters but not others (Zipkin et al., 2014b), or insert considerable bias in estimates, particularly when detection probability is low and count data contains unmodeled heterogeneity (Duarte et al., 2018). Further, despite high detection probability in our system (Fig. 4b), we encountered limitations when fitting N-mixture models. For example, models with additive and interactive terms failed to converge. We therefore were unable to test whether reduced vegetation cover as a result of cattle grazing exposed tadpoles to increased predation risk (i.e., vegetation cover \times predation interaction term).

Univariate models converged, however, and our index of predator abundance was the most important predictor of

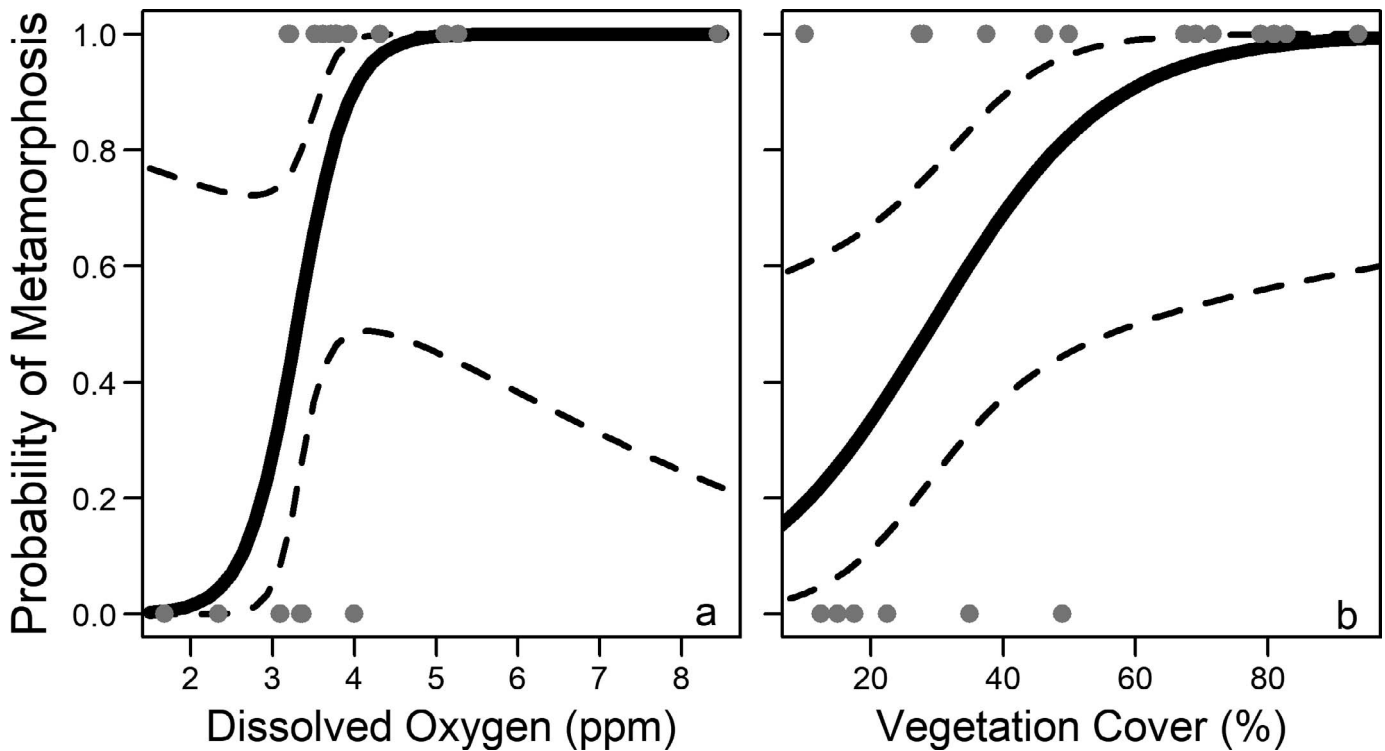


FIG. 5. The probability of metamorphosis in Boreal Toad tadpoles increased at beaver ponds with higher levels of (a) dissolved oxygen and (b) vegetation cover at 20 breeding sites in the Bridger-Teton National Forest, USA, during July–September 2018. Mean predicted values (solid lines) and 95% confidence intervals (dashed lines) were derived from the two top-performing generalized linear models with binomial error distributions (Table 1). Grey dots represent raw data (y -values = presence [1] or absence [0] of metamorphs at a given site).

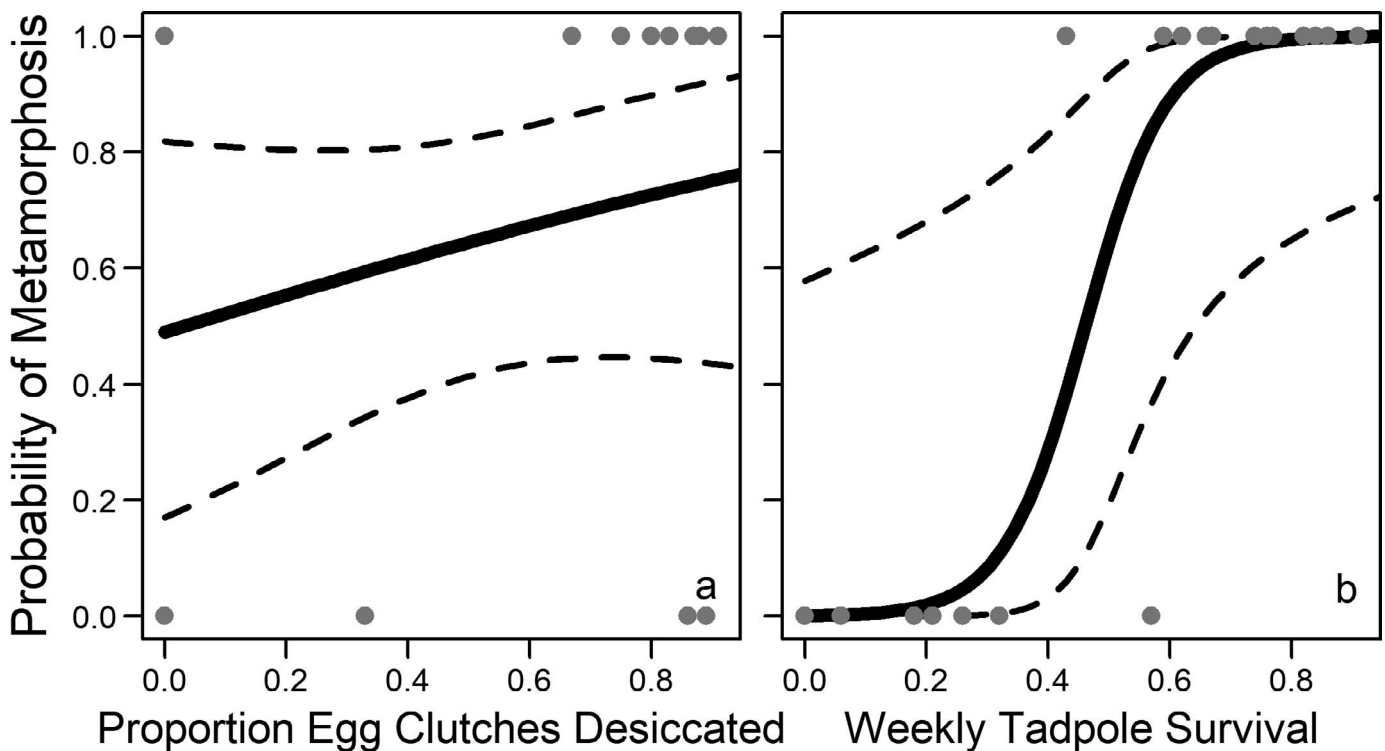


FIG. 6. The probability of metamorphosis in Boreal Toad tadpoles was unrelated to (a) the proportion of egg clutches that failed to hatch because of desiccation and increased in beaver ponds with (b) higher weekly tadpole survival at 20 breeding sites in the Bridger-Teton National Forest, USA, during 2018. Mean predicted values (solid lines) and 95% confidence intervals (dashed lines) were derived from generalized linear models with binomial error distributions. Grey dots represent raw data (y -values = presence [1] or absence [0] of metamorphs at a given site).

tadpole survival in our system. We suspect that salamanders and invertebrates were the primary aquatic predators, as fish, including trout, did not negatively affect tadpole survival in other Boreal Toad systems (Crockett et al., 2020). We did not quantify the effects of terrestrial predators, such as birds, though very few photographs from game cameras included potential avian predators (e.g., herons). Despite overwhelming support for a negative effect of aquatic predators on tadpole survival, we acknowledge that our index of predator abundance may have been biased to some degree. For instance, we did not account for imperfect detection during our surveys of salamanders and aquatic invertebrates, which could have biased negatively our index of predator abundance. We also did not account for potential temporary emigration in adult salamanders, such that an adult counted during a survey may not have contributed to previous tadpole mortality (e.g., if that individual recently arrived at the site). We did not observe any temporal variation in our index of predator abundance (standard deviation = 0; Table S1), however, suggesting that sites largely were closed with respect to predator movement to or from each study pond. Further, tadpoles experienced low weekly survival in ponds with a high index of predator abundance (Table S1). Taken together, although our index of predator abundance may have contained some biases, we ultimately were confident that aquatic predators comprised a high source of mortality in Boreal Toad tadpoles.

Notably, low tadpole survival due to predation may not decrease recruitment rates, if, for example, metamorph survival is density-dependent (Vonesh and De la Cruz, 2002). In such cases, lower densities of emergent metamorphs can result in increased recruitment as each individual may be in better condition (e.g., larger body size) with a greater chance of transitioning to juvenile and adult stages (Smith, 1987; Harper and Semlitsch, 2007; Cabrera-Guzmán et al., 2013). Targeted study of metamorph survival is needed to determine how tadpole density ultimately scales up to effect recruitment of early life-stages into the breeding population. Further, the probability of metamorphosis in our system was more strongly influenced by dissolved oxygen and vegetation cover than predation pressure (though predation may have had a stronger influence on the number that metamorphosed). Both dissolved oxygen and vegetation cover can influence predator-prey dynamics; low oxygen conditions can increase tadpole susceptibility to predation (e.g., Moore and Townsend Jr., 1998; McIntyre and McCollum, 2000) whereas high vegetation cover may offer refuge from predators. Future work should consider the interplay of these variables when evaluating the conditions conducive to the success of early life-stages.

Improving the survival of larval amphibians comprises a potentially effective mitigation action to compensate for disease-induced losses in the adult stage (Scheele et al., 2015; West et al., 2020). With respect to Boreal Toads, our results suggest the prioritization of ponds with high surface area for egg hatching, suitable refugia from predators for tadpole survival, and high dissolved oxygen and vegetation cover for successful metamorphosis. Weekly tadpole survival and the probability of metamorphosis were highly correlated, moreover, indicating that ponds with high tadpole survival also tended to support successful metamorphosis. By contrast, hatching success was unrelated to both tadpole survival and metamorphosis, suggesting that no single pond provided optimal conditions for all three phases of development. Larger ponds with lower rates of egg desiccation may contain more predators. Therefore, rather

than protecting ponds with specific characteristics, managers instead could facilitate natural beaver activity to create a mosaic of aquatic patches in shifting successional states (Naiman et al., 1988; Johnston and Naiman, 1990). Heterogeneity in pond conditions may offer a variety of breeding sites suitable for early life-stage survival, which ultimately may reduce variability in recruitment (McCaffery et al., 2014). Efforts to maintain beaver populations therefore could be critical for the long-term reproduction and persistence of Boreal Toads and other organisms that rely on beaver-modified habitats (Hossack et al., 2015).

Recruitment is key to the persistence of populations that are challenged with disease, particularly for species in which disease primarily affects the adult life-stage (Tobler et al., 2012; Scheele et al., 2015). Conservation efforts to improve recruitment rates hinge on a solid understanding of the environmental conditions that promote survival of early life-stages (Crockett et al., 2020). Our results suggest that reproductive success can depend on stage-specific responses to different forms of environmental variation, which underscores the importance of determining habitat requirements for each life-stage. Further, whereas traditional mark-recapture techniques often limit spatial inference (Bellier et al., 2016), we demonstrate the utility of count data across multiple sites when evaluating sources of variation in the vital rates of early life-stages (Zipkin et al., 2014a). Our study, therefore, provides a framework to better understand demographic processes of life-stages that are difficult to study in natural settings, ultimately informing mitigation efforts for declining populations.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.1670/21-023.S1>