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Hydroperiod and Cattle Use Associated with Lower Recruitment in an r-Selected Amphibian with a Declining Population Trend in the Klamath Mountains, California

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ABSTRACT.—**Recent population declines in amphibians associated with mortality in early life stages highlight the need for a better understanding of the environmental factors related to successful survival to metamorphosis. In our study, we closely examine the relative importance of environmental factors to three stages of recruitment for Cascade frogs (*Rana cascadae*), a declining amphibian, in high-elevation wet meadows. Our results show that local dynamics are strongly associated with breeding site selection, the number of egg masses, and the number of individuals that survive to metamorphosis per egg mass. *Rana cascadae* does not tend to breed in wet meadows where nonnative trout are present. Survival to metamorphosis per egg mass is lower when hydroperiod of pools is shorter, cattle use is higher, and native insect predators are present. Our results suggest that future management efforts to conserve *R. cascadae* should strive to protect and restore wet meadows free from nonnative trout, containing many pools with longer hydroperiods, and subjected to minimal cattle use during sensitive development periods.**

Elevated juvenile mortality in some r-selected amphibian species is leading to population decline, despite the species' evolutionary strategy to produce many offspring with low survival rates during early stages of development. For r-selected species, high juvenile mortality reduces the size of the population and the strength of density-dependent interactions like predation or competition that might otherwise reduce population growth rates (Van Buskirk and Smith, 1991; Werner and McPeek, 1994). Population growth rates for r-selected species are more sensitive to postmetamorphic survival (Biek et al., 2002; Vonesh and De la Cruz, 2002). On the basis of this observation, some have suggested that it is best to invest research effort in the drivers of adult mortality. However, the striking consequences of juvenile mortality for some of the most threatened species indicate a need to identify and quantify the causes and magnitude of early-life-stage mortality. Nonnative species predation, reductions in hydroperiod, and disease have caused juvenile mortality and led to population declines in many western amphibians (Welsh et al., 2006; McMenamin et al., 2008; Longo and Burrowes, 2010). However existing research has failed to determine the relative importance of environmental variables to reproductive success of amphibians in systems where multiple variables act together to influence reproductive outcomes.

The Cascades frog (*Rana cascadae)* is an informative focal species for studies on reproductive success because it is an r-selected amphibian experiencing population decline associated with juvenile mortality (Fellers et al., 2008). *Rana cascadae* breeds in lakes and wet meadows. Each female produces an egg mass annually that contains between 300 and 800 ova (O'Hara, 1981; Nussbaum et al., 1983), and embryos complete their development from egg to metamorphosis over the course of a single summer (May–November). Resurveys of sites formerly inhabited by *R. cascadae* in the southern portion of its range revealed nearly complete absence of *R. cascadae* individuals where populations were once robust (Fellers and Drost, 1993; Fellers et al., 2008). *Rana cascadae* is native to California, Oregon, and Washington State and its International Union for Conservation of Nature Red List status is Near Threatened with a declining population trend. Research focused on determinants of reproductive success may increase the likelihood of conservation of this species.

Wet meadows may play an important role in the reproductive outcomes and population status of *R. cascadae*. Wet meadows are used by many high-elevation amphibians (*R. cascadae*, *Pseudacris regilla*, *Anaxyrus boreas*, *Taricha granulosa*, *Anaxyrus canorus*, etc.) as breeding and rearing habitat. Wet meadows can be highly productive and may provide a valuable source of food for developing larvae and juveniles. Aquatic habitat in wet meadows is complex, and may provide refuge from native and nonnative predators including garter snakes and nonnative trout. Heterogeneity in hydroperiod across permanent lakes and ephemeral or semipermanent wet-meadow pools reduces the variability in frog recruitment and may buffer the population against future environmental stochasticity including climate change (McCaffery et al., 2014). Conditions associated with wet meadows (low canopy density and higher daily average water temperature relative to lakes) are related to lower Bd prevalence and infection intensity (Becker et al., 2012; Hossack et al., 2013). Therefore, wet meadows may play an important role in disease dynamics within amphibian populations. Wet meadows also enhance habitat connectivity and quality of habitat (Berlow et al., 2013), which may also support the persistence of amphibian populations.

Despite the importance of wet-meadow habitat, wet meadows also possess a unique set of potential threats to high-elevation amphibians. Future increases in temperature and decreases in precipitation may cause reductions in pool hydroperiod (Cayan et al. 2008) that failed to meet the minimum hydroperiod length required for successful metamorphosis and fitness. In addition, seasonal permits allow ranchers to graze cattle within allotments and cattle require both forage and water resources. Therefore, the habitat requirements of cattle may overlap with amphibian use of wet meadows and the impact of cattle on amphibians is unclear.

The effect of cattle on amphibians may depend heavily on the degree of grazing intensity, the type of habitat where they

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coexist, and movement or habitat requirements of amphibians. Cattle grazing can be negatively associated with amphibian abundance (Fleischner, 1994; Jansen and Healey, 2003; Riedel et al., 2008) and related to increased incidence of ranavirus infection (Hoverman et al., 2012) and parasite abundance (McKenzie, 2007). In other cases, cattle grazing is positively associated with amphibian abundance (Pyke and Marty, 2005) or has no impact on occupancy or reproductive success (McIlroy et al., 2013; Roche et al. 2013). Experimental manipulation and simulation models indicate that, in the face of climate change, cattle grazing maintains hydrologic dynamics in vernal pools that support the endangered California Tiger Salamander (*Ambystoma californiense*) (Pyke and Marty, 2005). In the Sierra Nevada Mountains, Roche et al. (2013) found no significant short-term impacts of cattle grazing on the occupancy of Yosemite Toad (*Anaxyrus canorus*) in high-elevation wet meadows. Few studies have taken into account how responses to the degree of cattle impact may be nonlinear or differ across life stages, making it difficult to assess the existence or degree of cattle-grazing effects or propose quantifiable modifications to grazing practices. Many studies have also failed to incorporate other, potentially significant environmental variables in their analysis and therefore failed to control for the effects of those variables and isolate the effect of cattle grazing on amphibian reproductive success or population dynamics.

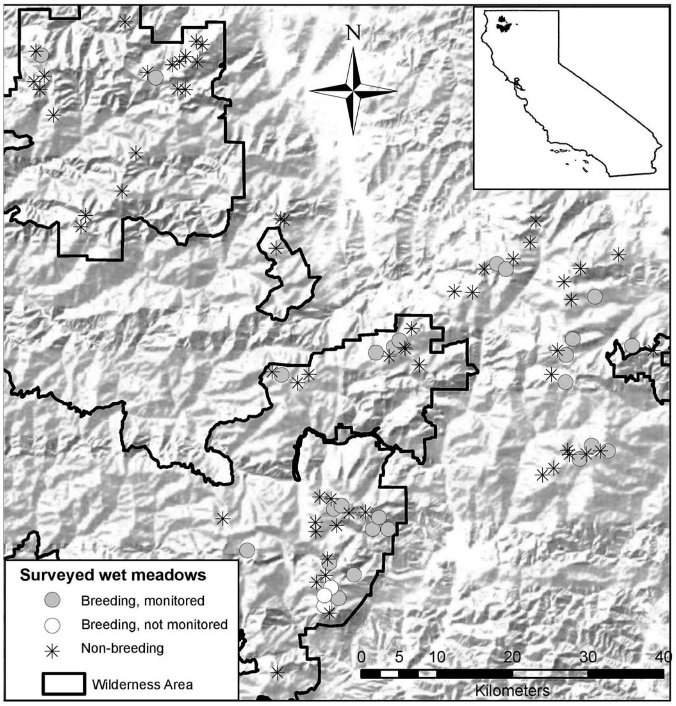

FIG. 1. Map of sampling locations across the Klamath Mountains, California with notation of breeding sites, wilderness area boundaries, and topography.

High-elevation wet meadows in the Klamath Mountains of Northern California provide the opportunity to evaluate the relative importance of environmental variables to reproductive stages in a declining amphibian species. On a local level, cattle use, nonnative trout presence, native predator presence, hydroperiod, and the number of pools vary across wet meadows in the Klamath Mountains. Humans introduced cattle and trout to the Klamath Mountains over 70 yr ago. There is evidence of cattle grazing as early as 1911within the Trinity Alps Mountains. Although the number of grazing allotments and cattle density was drastically reduced by the 1970s, cattle are still granted access to over half of the region (G. Laurie, pers. com.). The California Department of Fish and Wildlife stocked trout (Salmonidae) in the Klamath Mountains in 1930s and the practice continues today. Although the agency no longer stocks most lakes, self-sustaining fish populations have established and trout populations persist in most of the large lakes and streams throughout the region (Welsh et al., 2006). Native predators, including garter snakes (*Thamnophis sirtalis*, *T. attratus*, and *T. elegans*) and predatory insects (Belastomatidae, Aeshnidae, and Cordulidae), also are widely distributed across the region and prey on larval stages of native amphibians (Pope et al. 2008; Joseph et al., 2011). The hydrology of high-elevation wet meadows is highly dynamic, with hydroperiods affected by local precipitation, groundwater inputs, and temperature (Driver 2010). At a landscape level, the configuration and composition of aquatic habitat, vegetation, and frog populations varies across basins within the Klamath Mountains. Previous studies have shown that landscape dynamics, including the distance between habitat patches, the degree of vegetative cover, and occupancy of neighboring wetlands amphibian populations, can influence amphibian populations (Heyer, 1967; Riedel et al., 2008; Scherer et al., 2012).

The objective of our study was to determine which local and landscape variables drive reproductive success in an r-selected species experiencing a decreasing population trend in a complex landscape that includes lakes, ponds, and high-elevation wet meadows. Our particular focus was on discerning the attributes of recruitment success in the wet meadows. To better understand the effects of environmental variables in these meadows, we examined their relationship with three stages of reproduction leading to successful survival through metamorphosis: 1) selection of breeding sites, 2) the number of egg masses laid at each site, and 3) the reproductive success (defined here as number of metamorphs/egg mass) of *R. cascadae* in high-elevation wet meadows. We hypothesized that features at the landscape level would determine the selection of breeding sites, whereas local dynamics would be more strongly associated with reproductive output (number of egg masses) and reproductive success (number of metamorphs/egg mass) of *R. cascadae* in high-elevation wet meadows. With rapid environmental changes documented in alpine meadow complexes and an uncertain climatic future, we need a better understanding of the role of wet meadows for high-elevation amphibian populations, and the factors within a meadow and the surrounding landscape that are associated with reproductive success.

MATERIALS AND METHODS

Study System.—Our study focused on high-elevation (>1,600 m) basins in the Klamath Mountains of northwestern California, with sample sites located in the Marble Mountain, Russian, and Trinity Alps Wilderness areas (Fig. 1). The climate is Mediterranean, consisting of warm, dry summers, and moderately cold winters with heavy snowfall (peak average annual snow depth 1–4 m; California Department of Water Resources, 2014). The proximity of the Klamath Mountains to the Pacific Ocean produces strong west-to-east moisture and temperature gradients across the range (Skinner et al., 2006). Sample sites are generally snow covered from late October through mid-May. The Klamath Mountains are composed of a heterogeneous network of habitat patches of coniferous forest, dry meadows, wet meadows, fens, boulder or talus fields, and lakes and ponds. The geology of the region is diverse, including significant areas of metamorphic, ultramafic, and granitic rock types.

Monitoring Site Selection.—We surveyed 90 wet meadows, spanning elevations of 1,602–2,396 m, three times over the course of 2 yr (once between 22 June and 10 September 2010 and twice between 29 June and 16 September 2011). We defined wet meadows as areas greater than 1,000 m^2 in which the vegetation consists of a mixture of rushes, sedges, grasses, and perennial herbs. Most meadows also contain snowmelt- or spring-fed, ephemeral, and perennial pools up to 2 m in depth and 1,200 m^2 in area. We considered water bodies larger in area or depth to be components of lake ecosystems and not included in the analysis. To increase statistical independence of sites, we selected only one meadow from each basin. We defined basins as single drainages into major streams isolated from other such basins by well-defined ridgelines. We initially selected potential sites using remote-sensing images (U.S. Forest Service, 2009) and we made a final selection after field inspection to ensure that meadows met our predetermined criteria. We documented breeding at 29 of the 90 meadows and we randomly reduce from 29 to 25 breeding sites for focused monitoring in 2012 (Fig. 1).

Evaluation of Anuran Life Stages and Environmental Variables.—In addition to evaluating breeding site choice, we also evaluated egg production and survival to metamorphosis in *R. cascadae* to assess which factors were most strongly associated with each reproductive stage contributing to successful recruitment. This approach allowed us to capture factors that may play an important role in reproductive success but have a targeted effect at one stage of reproduction. We determined the number of egg masses laid at each meadow using visual surveys. Once larvae began to metamorphose, we completed three visual encounter surveys (VES) (Crump and Scott, 1994) within 20 d to estimate the number of embryos per egg mass that survived to metamorphosis. Abundance estimates were lower during our first count because some, but not all, individuals completed development to metamorphosis. The second count captured peak abundance, whereas the third count had lower abundance potentially related to movement of juveniles away from natal pools or heightened predation pressure caused by new exposure to terrestrial predators. We estimated recruitment success by using the number of metamorphs we detected at each site during peak abundance during the second census divided by the number of egg masses previously detected at that site, a value we define as the number of surviving metamorphs per egg mass. We recognize that this likely underestimates true recruitment success.

To evaluate local environmental variables, we visited the 25 focal wet meadows every 15 d from 2 June 2012 to 12 October 2012. At each meadow sample site we collected data on local habitat conditions that other studies have suggested may influence amphibian populations, including elevation, number of pools, cattle use (measured as the number of cattle fecal pats/m^2), nonnative trout presence, abundance of predatory snakes (calculated as detections/h), presence of predaceous insects, and hydroperiod (Fleischner, 1994; Cushman, 2006; Welsh et al., 2006; Cole and North, 2014). We averaged the abundance of predatory snakes over multiple surveys completed at each wet-meadow site over the course of the season. We averaged hydroperiods across pools at each wet-meadow site.

Using VES, we recorded developmental stage of *R. cascadae*, abundance of metamorphosed individuals, presence of aquatic predaceous insects, presence of nonnative trout, and abundance of predatory garter snakes (Crump and Scott, 1994). We completed VES surveys during peak amphibian activity, between the hours of 1000 h and 1800 h. We identified amphibians and reptiles to species and aquatic insects to family from orders Coleoptera, Diptera, Ephemeroptera, Hemiptera, Megaloptera, Odonota, and Tricoptera. If we were unable to identify aquatic insects to family visually using a hand lens in the field, we preserved one individual specimen for identification and verification with voucher specimens. We also estimated the number of pools by counting distinct lentic water bodies present at snowmelt. Pool hydroperiod was determined on the basis of the number of days from snowmelt to absence of standing water. We estimated cattle use on site using fecal density rather than permitted number of cattle/acre. Cattle use of grazing allotments can vary substantially with slope, season, and proximity to water sources (Tate et al., 2003), and fecal density may be a more direct measure of local use. Because of slow decomposition rates in high-elevation systems, fecal density in mountain meadows represents an aggregate assessment of the impact of cattle over the last 5–10 yr (Roche et al., 2013). We determined the number of lakes and wet meadows within each basin that contained breeding populations of *R. cascadae* and the distance to the nearest lake with a breeding population of *R. cascadae* (California Department of Fish and Wildlife, unpublished data).

Statistical Analyses.—We constructed general linear models to evaluate the relationship between local and landscape variables and the occurrence of *R. cascadae* breeding, the number of egg masses, and the estimated number of young that survived to metamorphosis per egg mass. We completed model selection on the basis of Akaike's information criterion corrected in R using the packages "glmulti" and "MuMIn" (Wood, 2011; Calcagno, 2012; R Development Core Team, 2012). We evaluated 42 models testing the relationship between *R. cascadae* breeding in 90 wet meadows and presence of nonnative trout, elevation, number of pools, and cattle use, number of sites where *R. cascadae* is present in the basin, and distance to nearest lake where *R. cascadae* breeds. Within 25 wet-meadow sites where breeding occurred, we tested 84 models examining the relationship between the number of eggs masses laid and elevation, number of pools, cattle use, garter snake abundance, presence of predatory aquatic insect families, hydroperiod of breeding pools, number of sites where *R. cascadae* is present in the basin, and distance to nearest lake where *R. cascadae* breeds. Finally, we evaluated 20 different models that tested the relationship between breeding success (metamorph CPUE/egg mass) and elevation, cattle use, trout presence, snake abundance, predatory insect presence, and hydroperiod. None of the predictor variables in any of the models varied collinearly on the basis of Pearson correlation coefficients. We log transformed cattle use, the number of embryos that survived to metamorphosis per egg mass, and the number of egg masses. All other variables were normally distributed. We did not test any interaction terms to minimize the number of parameters in the model.

To prevent overfitting, we restricted the number of predictor variables to six for the model predicting the occurrence of breeding across the 90 wet meadows and three predictors for the models evaluating the number of egg masses and successful metamorphosis within 25 wet meadows where breeding occurred. We evaluated the relative importance of predictor variables in the top 10 models by considering the number of

TABLE 1. Top 10 models for response variables of three stages of *R. cascadae* reproduction used to select best descriptive model. AICc, corrected Akaike information criterion.

Rank	Predictor variables	ΔAICc	Weight
Response variable: breeding presence			
1	trout + pools + frogsinbasin + cattle	0	0.384
2	trout + pools + frogsinbasin + elevation + cattle	2.2	0.127
3	trout + pools + frogsinbasin + nearlake+ cattle	2.3	0.122
4	trout + pools + frogsinbasin	2.7	0.1
5	trout + pools + cattle	3.2	0.078
6	trout + pools + nearlake + cattle	3.9	0.053
7	trout + pools + frogsinbasin + elevation + nearlake + cattle	4.6	0.039
8	trout + pools + frogsinbasin + nearlake	4.9	0.034
9	trout + pools + frogsinbasin + elevation	4.9	0.033
10	trout + pools + elevation + cattle	5.2	0.029
Response variable: number of egg masses			
1	insects + elevation + frogsinbasin	0	0.732
2	insects + pools + frogsinbasin	4.1	0.093
3	insects + elevation + cattle	6.1	0.034
4	insects + frogsinbasin + cattle	6.7	0.025
5	insect + elevation + nearlake	7.1	0.021
6	pools + elevation + frogsinbasin	7.1	0.021
7	pools + trout + frogsinbasin	7.2	0.020
8	insects + trout + frogsinbasin	7.2	0.020
9	insects + nearlake + frogsinbasin	7.4	0.018
10	insects + frogsinbasin + snakes	7.2	0.017
Response variable: breeding success			
1	insects + hydroperiod + cattle	0.0	0.427
2	insects + hydroperiod + snakes	2.3	0.135
3	hydroperiod + trout + snakes	2.5	0.125
4	hydroperiod + cattle + trout	3.0	0.095
5	hydroperiod + elevation + snakes	3.5	0.074
6	hydroperiod + trout + insects	3.8	0.065
7	insects + hydroperiod + elevation	4.3	0.049
8	hydroperiod + cattle + elevation	6.6	0.016
9	hydroperiod + trout + cattle	8.0	0.008
10	hydroperiod + trout + elevation	8.1	0.007

models in which the predictor variable occurs and the weights of those models (Anderson, 2008).

We tested model fit using the area under the receiver-operating characteristic curve (AUC), which measures model fit in presence–absence models. Values closer to one indicate better model fit; values closer to 0.5 are equivalent to the null model (Jiménez-Valverde 2012). We evaluated relative variable importance quantitatively by including the occurrence of predictor variable in the top 10 models and model weights.

RESULTS

Across the basins in our study, there was an average (±SD) of 1.82 (±1.73) wet meadows. Over the three sampling periods, *R. cascadae* adults were present at least once in 74 of 90 wet meadows sampled across the Klamath Mountains and reproduced in 29 of the 90 wet meadows.

Breeding Site Selection.—The top model for breeding site selection indicated that breeding was negatively associated with nonnative trout presence, and positively associated with numbers of pools, total sites occupied by *R. cascadae* in the basin, and cattle use. The model had an R^2 of 0.27 and AUC of 0.824 (Table 2). Relative variable importance supports a conclusion that number of pools (1.0), nonnative trout presence (1.0), number of *R. cascadae* populations in the basin (0.84), and cattle use (0.83) are among the most important variables associated with breeding site selection (Table 3).

Egg Masses Laid.—The number of egg masses was positively associated with predatory insect presence, elevation, and the total sites occupied by *R. cascadae* in the basin (Table 2). The model had an R^2 of 0.56. On the basis of the top 10 ranked models, predacious aquatic insects (0.96), the number of populations of *R. cascadae* in the basin (0.94), and elevation (0.81) were the variables of the greatest relative importance (Table 3).

Survival of Embryos to Metamorphosis.—The top general linear model indicated that recruitment was positively associated with breeding pool hydroperiod and negatively associated with the presence of predatory insects, and cattle use in wet meadows (Table 2). The model had an R^2 of 0.73. Relative variable importance indicates that the breeding pool hydroperiod (1.00) is the most important variable, followed by presence of predatory insects (0.68) and cattle use (0.55) (Table 3).

Isolating the effect of hydroperiod on breeding success (number of metamorphs/egg mass) using partial residuals of our averaged model (Fig. 2) shows that the relationship between hydroperiod and recruitment is not linear. There is a threshold response of recruitment to hydroperiod. If the hydroperiod is shorter than 120 d, the average number of individuals that survives to metamorphosis per egg mass is 0.9, whereas if the breeding pool hydroperiod is longer than 120 d, the average number of individuals that survive to metamorphosis per egg mass is 9.1.

DISCUSSION

Our study divides the process of *R. cascadae* recruitment in wet meadows into three stages and shows that from breeding site selection to egg mass production and survival to metamorphosis, the environmental drivers and their relative importance shift over time. Presence of nonnative trout and the number of pools were the most important variables associated with breeding site selection. Number of egg masses in wet meadows was most closely associated with presence of predacious aquatic insects and the number of sites occupied by *R. cascadae* in the basin. Survival of embryos to metamorphosis was most strongly associated with hydroperiod. These findings illustrate the complexity of the mechanisms driving successful recruitment in highly dynamic aquatic systems and may explain why previous literature has failed to arrive at a consensus about the effects of some environmental variables on amphibian recruitment in wet meadows. Our results also support the large amount of evidence indicating the importance of nonnative species and hydroperiod to frog recruitment.

The impact of nonnative trout and number of pools on breeding site selection is consistent with previous studies that show *R. cascadae*'s negative association with nonnative trout (Welsh et al., 2006; Pope, 2008) and positive association with the number of pools found within meadows (Cole and North, in

TABLE 2. Top general linear models indicating important environmental variables associated with *Rana cascadae* breeding, number of *R. cascadae* egg masses, and number of metamorphosed *R. cascadae* per egg mass in wet meadows. Top models shown, on the basis of corrected Akaike information criterion selection criteria.

			Confidence interval	
Terms	Coefficient (SE)	Odds ratio	2.5%	96.5%
Breeding presence				
Intercept	−2.49 (0.610)	0.085	0.022	0.248
Trout	−1.74 (0.706)	0.176	0.038	0.628
Pools	0.075 (0.022)	1.08	1.04	1.13
Frogsinbasin	0.379 (1.69)	1.46	1.06	2.08
Cattle	33.4 (15.9)	3.35×10^{14}	47.6	2.33
Number of egg masses				
Intercept	−6.286 (2.502)		−11.190	−1.383
Predacious aquatic insects	1.387 (0.374)		0.654	2.121
Elevation	0.004 (0.001)		0.001	0.006
Frogsinbasin	0.292 (0.092)		0.111	0.474
Number of metamorphs/egg mass				
Intercept	−0.576 (0.569)		−1.692	0.540
Hydroperiod	0.022 (0.004)		0.014	0.031
Predacious aquatic insects	−0.775 (0.274)		−1.311	−0.238
Cattle	−13.193 (6.654)		−26.234	−0.151

press). In addition to direct predation, nonnative trout can compete with native species for aquatic food resources (Epanchin et al., 2010; Joseph et al., 2011) and inflate native predation pressure by garter snakes (Pope et al., 2008).

Interestingly, general linear models did not identify the presence of nonnative trout as an important environmental variable to later stages of recruitment. Several mechanisms of coexistence might explain this result. Because of the disconnected nature of aquatic habitat in wet meadows, trout may exist in streams or pools that are isolated from those where breeding occurs. Trout tend to inhabit pools or streams that are hydrologically connected to lakes stocked by California Department of Fish and Wildlife. In wet meadows, local habitat heterogeneity in water depth and vegetative cover can reduce predation pressure on aquatic environments (Sredl and Collins, 1992; Porej and Hetherington, 2005). In addition, the co-occurrence of unpalatable amphibian species, similar in morphology to *R. cascadae*, may deter trout predation (Hartman et al., 2014). Wet meadows may provide important refuges for frogs breeding in landscapes currently stocked with trout.

The number of *R. cascadae* populations in the basin and presence of predacious insects were among the most important variables associated with number of eggs laid in wet meadows. Metapopulation dynamics can play a very important role in population dynamics (Marsh and Trenham, 2001). Wet meadow occupancy by Yosemite Toad (*A. canorus*) in the Sierra Nevada was strongly associated with network connectivity among habitat patches (Berlow et al., 2013). *Rana cascadae* frogs can travel long distances (up to 1 km) across rough and dry terrain and exhibit high breeding-site fidelity while showing low natal-site fidelity (Garwood, 2009). Therefore, wet-meadow sites located within 1 km of natal sites are more likely to contain breeding populations of *R. cascadae*. The positive relationship between presence of predatory aquatic insects and number of egg masses in wet meadows may seem harder to explain because predatory aquatic insects prey on *R. cascadae* larvae. However, although aquatic insects may select for the same habitat types as reproducing frogs, they also provide a food resource for reproducing adults (Joseph et al., 2011).

The number of embryos that survived to metamorphosis from each egg mass was most strongly associated with hydroperiod. Hydroperiod strongly influences community structure and population dynamics of many other amphibian species (Semlitsch, 1987; Semlitsch et al., 1996; Van Buskirk, 2005). We observed high levels of egg and larval mortality because of desiccation of meadow pools over the course of this study (Cole, pers. obs.). The rate of pool drawdown differs significantly among years so the effect of hydroperiod may not be as strong during years of high precipitation or low temperatures. We expected to observe high survivorship because the year that we sampled, 2012, had an above-average snowpack and below-average temperatures, on the basis of annual means in the region from 2003 to 2013 (California Department of Water Resources, 2014). The low success we observed during relatively favorable conditions, however, suggests that quality of wet-meadow habitats for *R. cascadae* may be threatened by climate change. Climate change may continue to shorten the hydroperiod of breeding pools (Cayan et al., 2008). This will reduce the amount of available breeding habitat and could place the species at risk (McMenamin et al., 2008). The importance of the threat posed by climate change relative to other causes of population decline is yet to be determined.

Cattle grazing on public lands has been a controversial management activity because of its potential for negative effects on native plants and wildlife (Fleischner, 1994). The effect of cattle grazing on amphibians is unclear. Studies conducted in different habitats at different grazing intensity have failed to produce consistent results (Jansen and Healey, 2003; Pyke and Marty, 2005; McKenzie, 2007; Riedel et al., 2008; Hoverman et al., 2012; McIlroy et al., 2013; Roche et al., 2013). Our results suggest that one potential cause of these inconsistencies may be that cattle grazing had different effects on the different life stages leading to recruitment.

Cattle grazing was positively associated with breeding in wet meadows and negatively associated with survival to metamor-

TABLE 3. Relative predictor variable importance by response variable (*Rana cascadae* breeding, number of *R. cascadae* egg masses, and number of metamorphosed *R. cascadae* per egg mass) on the basis of top 10 models.

	Predictor variables								
Response variable	Elevation	Pools	Cattle	Trout	Garter snakes	Predacious aquatic insects	Hydroperiod	*R. cascadae* populations in basin	Distance to nearest lake
Breeding presence	0.23	1.00	0.83	1.00	-	-	-	0.84	0.25
Egg masses	0.81	0.13	0.06	0.04	0.02	0.96	0	0.94	0.04
Metamorphosed frogs/egg mass	0.15	-	0.55	0.20	0.43	0.68	1.00	-	-

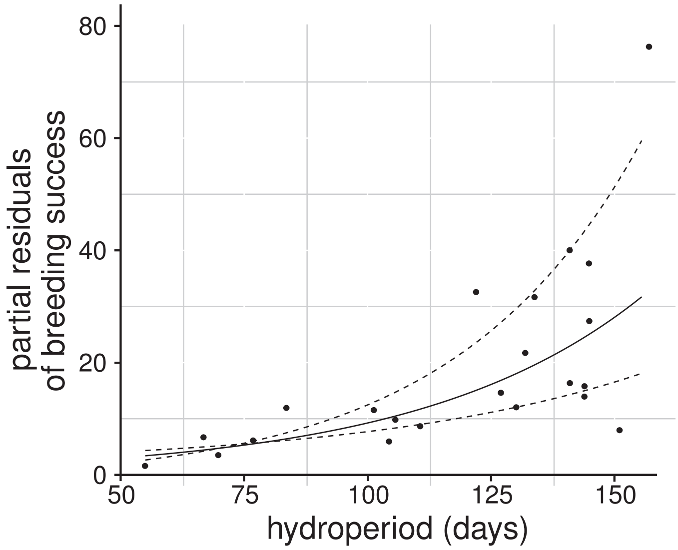

FIG. 2. Relationship between breeding-pool hydroperiod and the partial residual of the number of *R. cascadae* individuals that survived to metamorphosis (detections/h) per egg mass, on the basis of the top general linear model.

phosis. Past studies found a positive association between cattle and native species in ecosystems where cattle can perform a substitute function to large ungulates that have gone extinct (Bengtsson et al., 2000). Roosevelt Elk (*Cervus canadensis roosevelti)* are native to the Klamath Mountains and still use wet meadows in the region, but there is no evidence to suggest that the impact of cattle on wet meadows in the Klamath Mountains is analogous to the impact of this large, native ungulate. A more likely explanation for the positive relationship between *R. cascadae* breeding and cattle use of wet meadows is shared habitat preferences. Cattle require access to water and herbaceous vegetation. Therefore, ranchers place cattle in wet meadows and the cattle themselves move within grazing allotments to locate suitable conditions for forage and water. Higher sensitivity and vulnerability of early life stages may be responsible for the negative association between cattle use of wet meadows and survival to metamorphosis. Egg and larval life stages are less mobile and sensitive to changes in local habitat and localized water quality associated with cattle grazing (Jansen and Healy 2003; Schmutzer et al. 2008). In contrast to mobile juveniles and adults, results of this study suggest that early life stages (egg and larval) may be more susceptible to mortality associated with cattle use. Cattle occur in wet meadows where *R. cascadae* breeds, and once there, cattle are likely exerting a degree of impact that is having a negative effect on the number of individuals per egg mass surviving to metamorphosis in some wet meadows.

Overall, our study presents a detailed examination of *R. cascadae* reproduction and describes hitherto unknown dynamics in wet meadows. Our study suggests that management strategies seeking to encourage *R. cascadae* reproduction in wet meadows should focus on nonnative trout eradication, reduction of cattle use during egg and larval stages of development, and protection or artificial creation of pools of sufficient hydroperiod. Highest survival of embryos to metamorphosis occurred where pool hydroperiods exceeded 116 d, cattle use was minimal or nonexistent, and predatory aquatic insects were largely absent. In-depth hydrologic models may provide the necessary information to assess the risk of future loss of aquatic habitat because of climate change. Dynamics within wet meadows are complex, unique, and are one component of a large network of habitat patches that should be considered when designing targeted, cost-efficient management for the conservation of *R. cascadae* in California.

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