

Influence of climate drivers on colonization and extinction dynamics of wetland-dependent species

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Abstract. Freshwater wetlands are particularly vulnerable to climate change. Specifically, changes in temperature, precipitation, and evapotranspiration (i.e., climate drivers) are likely to alter flooding regimes of wetlands and affect the vital rates, abundance, and distributions of wetland-dependent species. Amphibians may be among the most climate-sensitive wetland-dependent groups, as many species rely on shallow or intermittently flooded wetland habitats for breeding. Here, we integrated multiple years of high-resolution gridded climate and amphibian monitoring data from Grand Teton and Yellowstone National Parks to explicitly model how variations in climate drivers and habitat conditions affect the occurrence and breeding dynamics (i.e., annual extinction and colonization rates) of amphibians. Our results showed that models incorporating climate drivers outperformed models of amphibian breeding dynamics that were exclusively habitat based. Moreover, climate-driven variation in extinction rates, but not colonization rates, disproportionately influenced amphibian occupancy in monitored wetlands. Long-term monitoring from national parks coupled with high-resolution climate data sets will be crucial to describing population dynamics and characterizing the sensitivity of amphibians and other wetland-dependent species to climate change. Further, long-term monitoring of wetlands in national parks will help reduce uncertainty surrounding wetland resources and strengthen opportunities to make informed, science-based decisions that have far-reaching benefits.

Key words: amphibian occupancy; breeding dynamics; climate; Grand Teton National Park; NPS Inventory & Monitoring; Special Feature: Science for Our National Parks' Second Century; wetlands; Yellowstone National Park.

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INTRODUCTION

Freshwater wetlands support a disproportionately high diversity of species relative to terrestrial and marine ecosystems (Dudgeon et al. 2006,

Gopal 2009), but these habitats are particularly vulnerable to climate change (Bardecki 1991, Matthews 2010, Lee et al. 2015). Changes in temperature, precipitation, and evapotranspiration (i.e., climate drivers) are likely to alter flooding

regimes of freshwater wetlands and, in particular, accelerate drying of shallow or hydrologically isolated wetland habitats (Burkett and Kusler 2000, Brooks 2004, Erwin 2009). All wetlands are expected to experience some hydrological change, and the cumulative effects of these changes will alter the spatial distribution and connectivity of wetlands (Lee et al. 2015). Combined, wetland drying and changing hydroperiods will likely affect vital rates, influence abundance, restrict distributions, and disrupt synchrony among populations of wetland-dependent species, ultimately threatening the persistence of some species and reducing local and regional biodiversity (Johnson et al. 2010, 2011, Quesnelle et al. 2013, Anderson et al. 2015).

Although many taxa are likely to be affected by climate-induced changes to wetlands, amphibians are among the most climate-sensitive taxonomic groups (Corn 2005, Buckley and Jetz 2007, Eck et al. 2014, Case et al. 2015). Many amphibians breed in shallow or intermittently flooded wetland habitats. While these habitats reduce amphibian susceptibility to fish predation, they are extremely sensitive to the constraints of a warming climate (Brooks 2004, Riordan et al. 2006, Lee et al. 2015). Specifically, increased air temperatures increase evapotranspiration rates, decrease soil moisture levels, shorten hydroperiods, and accelerate wetland drying (Burkett and Kusler 2000, Riordan et al. 2006, McMenamin et al. 2008, Matthews 2010, Matthews et al. 2013). Some species with complex life histories might compensate for changing conditions by accelerating growth or development during embryonic or larval life stages, but often at the expense of reduced size at metamorphosis and lower fitness (Berven 1990, Denver 1997). Furthermore, plasticity in growth and development can vary by life stage and is already near maximum physiological capacities for many species that breed in temporary environments (Newman 1992, Richter-Boix et al. 2011). Longer-lived amphibians may skip breeding in dry years when the risk of mortality is higher and probability of larval survival is low (Church et al. 2007, Cayuela et al. 2014).

Despite these observations, the effects of a warming climate on wetland-associated amphibians are not straightforward, because amphibians also breed in deeper, permanent wetlands. In these deeper habitats, a warming climate could

extend growing seasons and offer fitness benefits to ectotherms (McCaffery and Maxell 2010), especially to amphibians occupying cold regions (Deutsch et al. 2008, McCaffery et al. 2014). Thus, climate effects on shallow wetlands can be distinct from deep wetlands and can have different effects on species with different life histories dependent on the particular wetland types used for breeding. These nonlinear responses to temperature among life stages and habitats, as well as varying demographic sensitivities, make it difficult to predict effects of climate change on populations. Such complexities emphasize the need for studies that assess breeding dynamics across a gradient of wetland types to fully understand the effects of climate on amphibians and other wetland-dependent species (Ryan et al. 2014, Anderson et al. 2015).

A logical place to explore the effects of climate drivers on the dynamics of wetland-associated species is within topographically diverse and climatologically heterogeneous regions. In such regions, spatial and temporal variations in temperature and precipitation act differently on individual wetlands and wetland types and contribute to local patterns of amphibian use (Cayuela et al. 2016). Within the United States, most national parks and wilderness areas occur across topographically complex landscapes and thus offer important baselines for comparing ecological and hydrological responses to more disturbed areas and provide for opportunities to examine climate impacts independent of other anthropogenic stressors (e.g., invasive species and large-scale habitat alterations) that have contributed to declines in biodiversity (Fancy et al. 2009, Lee et al. 2015, Machlis and McNutt 2015). Multiyear amphibian monitoring data sets from U.S. national parks (e.g., Gould et al. 2012, Fellers et al. 2015) are therefore uniquely suited for a focused examination of the impacts of climate variation on distribution, richness, and population dynamics (Ray et al. 2014).

Few researchers have explicitly modeled the effects of annual and spatial variations in precipitation and hydrological regimes on the occurrence and breeding dynamics of amphibians over multiple years (see Cayuela et al. 2012, Walls et al. 2013, Anderson et al. 2015, Cayuela et al. 2016 as exceptions). Here, we integrate multiple years of high-resolution gridded climate and amphibian

monitoring data (see Gould et al. 2012, Ray et al. 2014) from Grand Teton and Yellowstone National Parks to examine the effects of climate drivers and wetland habitat characteristics on amphibian occupancy (i.e., whether the wetland was used for breeding) and on annual breeding dynamics (i.e., local extinction and colonization). Specifically, we examined whether models that included climate drivers strengthened our ability to describe local extinction and colonization dynamics and overall patterns of amphibian occupancy compared with models based on habitat variables alone (Gould et al. 2012). We use the term extinction to refer to the probability that a wetland with amphibian breeding in the previous year was not used for breeding in the following year. Conversely, colonization refers to the probability that a site without breeding in the previous year was used for breeding in the following year. We also explored whether estimates of extinction, colonization, and occupancy varied among wetlands of various depths. By incorporating information on annual variation in climate drivers and specific wetland habitat characteristics, we sought to develop a more mechanistic understanding of the link between climate drivers, wetlands, and amphibian breeding that would facilitate predictions of amphibian occupancy under different climate scenarios.

METHODS

Study area

Grand Teton National Park, John D. Rockefeller Jr. Memorial Parkway, and Yellowstone National Park (combined area ~10,300 km²) are adjacent national park units located primarily in northwest Wyoming (Fig. 1). Hereafter, Grand Teton National Park refers to lands within Grand Teton National Park and the adjacent John D. Rockefeller Jr. Memorial Parkway. Grand Teton and Yellowstone National Parks include some of the most topographically complex and climatologically heterogeneous protected areas in the conterminous United States (Tercek et al. 2012). Elevation ranges from 1600 m in the lowest portion of Yellowstone to >4000 m in the Teton Range (Fig. 1). Vegetation of the two parks includes sagebrush and grasslands at lower elevations, conifer forests at middle and upper elevations, and deciduous trees, willows, grass-sedge, and forbs in moist areas. The

climate is characterized by long, cold winters and brief, cool summers, with considerable spatial heterogeneity in annual precipitation (25 cm to >200 cm; Wright and Gallant 2007). Snow provides the main source of surface water (Pederson et al. 2011a). Wetlands of the study area vary in size, depth, and hydroperiod and are most prominently influenced by local soil permeability (Elliot and Hektner 2000). Isolated, palustrine wetlands are the predominant wetland type and constitute approximately 3% of the area of the two parks (Gould et al. 2012).

There are six native amphibian species within the two parks. Our analysis focused on the three most common species: western tiger salamander (*Ambystoma mavortium*), boreal chorus frog (*Pseudacris maculata*), and Columbia spotted frog (*Rana luteiventris*). Although widespread, western toad (*Anaxyrus boreas*) occurrence was too sparse (<2% of wetlands) to include in the analyses. The other native species are the northern leopard frog (*Lithobates pipiens*), which is apparently extirpated, and the Plains spadefoot toad (*Spea bombifrons*), which was recently documented in Yellowstone National Park (Schneider et al. 2015). All species have complex life histories and require water for breeding and larval habitat before metamorphosing. In brief, the Columbia spotted frog is highly aquatic and typically uses permanent water for breeding. After breeding, spotted frogs may remain at breeding sites or move to other aquatic habitats for foraging or overwintering (Bull and Hayes 2001, Pilliod et al. 2002). Spotted frogs in Yellowstone National Park reach sexual maturity in 4–6 yr (Turner 1960); females of this species likely breed every 2 or 3 yr (Turner 1958). The boreal chorus frog in this region uses a variety of shallow water habitats for breeding (Koch and Peterson 1995) and some individuals of high-elevation populations begin breeding the first or second spring following metamorphosis (Tordoff and Pettus 1977). Although variable across their range, spotted frogs and chorus frogs typically metamorphose within 2–4 months after egg deposition. Western tiger salamanders are long-lived species found mostly in permanent and semipermanent wetlands. In Yellowstone National Park, tiger salamanders reach sexual maturity in 4–5 yr (Spear et al. 2006) and, elsewhere, a closely related species is known to skip

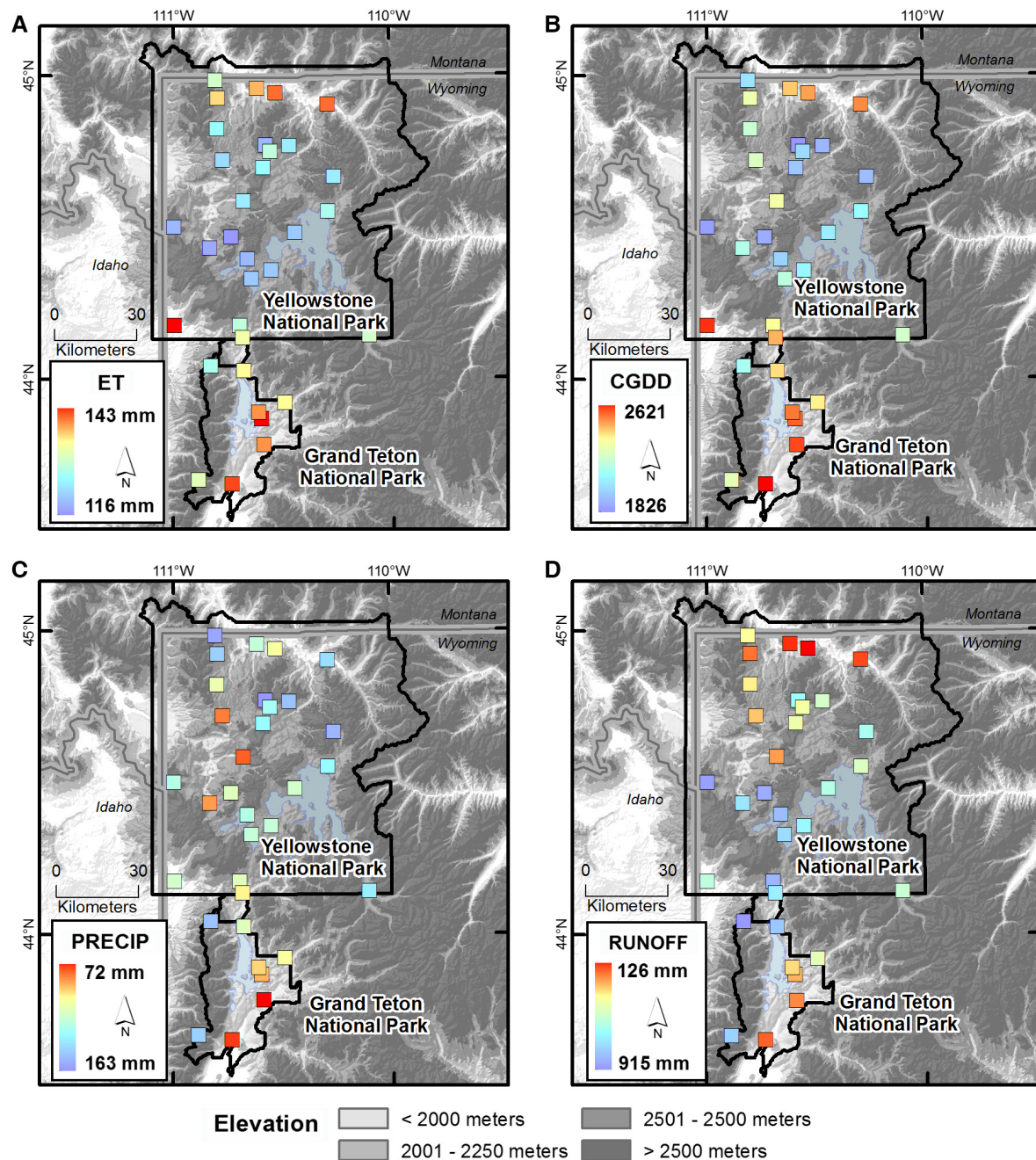


Fig. 1. Study area map showing locations of monitored catchments in Grand Teton and Yellowstone National Parks. Elevation contours are displayed with the lightest areas representing areas <2000 m and darkest areas represent elevations >2500 m. To illustrate the spatial variation in each climate driver (i.e., evapotranspiration, cumulative growing degree-days, precipitation, and runoff) across the region, we show catchment-level means (using all wetlands in each catchment) for year 2007. Panel A shows the mean April to June evapotranspiration estimate (ET; in mm) for all wetlands within each catchment. Panels B, C, and D show the mean estimate of (B) cumulative growing degree-days (CGDD), (C) April to June precipitation (PRECIP; in mm), and (D) annual runoff (RUNOFF; in mm) for all wetlands within a catchment.

breeding in unfavorable years (Church et al. 2007). Additionally, this species is able to use alternative phenotypes to exploit different habitats (Bruzgul et al. 2005). Salamander larvae may complete metamorphosis in the same summer that eggs were laid, or overwinter as larvae for one or more years before completing metamorphosis. Alternatively, in permanent wetlands and ponds, salamanders can reach sexual maturity in their paedomorphic or water-dependent larval form.

Study design and data collection

Our sampling frame and methods are described in detail elsewhere (see Gould et al. 2012, Ray et al. 2014). Briefly, after separating the two parks into 3370 catchments averaging approximately 200 ha in size, we selected a stratified random sample of catchments that contained wetlands with potential amphibian breeding habitat. Catchments were initially stratified based on amount of mapped wetland habitat described on U.S. Fish and Wildlife Service National Wetland Inventory maps (Cowardin et al. 1979). We delineated catchments as (1) high quality, which contained >4 ha of permanent and semipermanent wetlands and >2 ha of seasonally flooded wetlands ($n = 135$ catchments), (2) medium quality, which contained a lesser amount of permanent and semipermanent wetlands (>0 ha and <4 ha) and at least 1 ha of seasonally flooded wetlands ($n = 990$ catchments), (3) and low quality, which were overwhelmingly the most common in both parks ($n = 2245$ catchments) and contained limited amounts of permanent or seasonal wetlands. However, we constrained our analyses based on previous research (Gould et al. 2012) revealing similar occupancy and extinction and colonization rates in high- and medium-quality catchments (>1 ha of seasonally flooded wetland/catchment plus some amount of permanent or semipermanent wetlands). The low-quality habitat stratum (2245 catchments) provided little information and was excluded from our analysis.

Each year, from 2006 to 2012, we surveyed all wetlands within selected catchments that contained water for evidence of breeding and documented the absence of water in dry wetlands. We surveyed wetlands from early June through July (depending on elevation). Surveys were timed to detect evidence of breeding activity

(e.g., presence of eggs, larvae, or metamorphs). Two observers conducted independent dip-net surveys on a single visit that served as replicate surveys for each wetland (Gould et al. 2012). Replicate surveys were separated by at least 15 min with no communication between observers until after survey completion. All wetlands included in the analysis contained water during at least one survey year. If a wetland was dry in a particular year, we recorded all species as undetected for both observers. Elevation of surveyed wetlands ranged from 1947 to 2789 m. When water was present, we recorded information on current size of each wetland (in square meters), extent of emergent vegetation (percent cover), and maximum depth (<0.5, 0.5–1, 1–2, >2 m).

For our analyses, we selected wetland elevation, emergent vegetation cover, maximum depth, and estimated wetland area as covariates because they are commonly associated with occurrence, abundance, and colonization and extinction of wetland-dependent amphibians in this region (Gould et al. 2012, Hossack et al. 2015). We also used the average distance from a site to all other wetlands in a catchment as a measure of isolation. We expected isolation would be inversely related to occupancy and colonization, because close proximity of other populations could provide colonists and prevent local extinction (*sensu* Brown and Kodric-Brown 1977).

Climate drivers/covariates

We used high-resolution spatially interpolated Daymet gridded climate data sets (Thornton et al. 2014) to summarize daily estimates of air temperature and precipitation for all monitored wetlands within the study area. We combined gridded (1 × 1 km grid cells) estimates of daily meteorological parameters with a modified Thornthwaite water balance model (Gleick 1986, Thoma et al. 2015) to estimate evapotranspiration (in mm) and runoff (in mm) at the same scale. In brief, the water balance model approach incorporates gridded meteorological summaries in monthly time steps to quantify the consequences of monthly and annual variations in precipitation and temperature (Gleick 1986). Importantly, the water balance approach has been shown to reliably estimate runoff (i.e., surplus waters that fill wetlands) for locations in the mountainous

western United States (Gray and McCabe 2010) and provides estimates of climate drivers at a finer resolution than alternative approaches (e.g., Palmer Drought Index). Gridded data sets like Daymet have been described as critical to characterizing fine-scale climate variation in topographically complex regions that contain steep climate gradients (Hijmans et al. 2005).

We used a Thornthwaite-type single soil layer water balance model that characterizes the dominant input, storage, and abstraction processes at a monthly time step (Lutz et al. 2010). We used this model to estimate monthly runoff and monthly actual evapotranspiration for each wetland following Appendix S1 in Lutz et al. (2010). We calculated the water balance for each year and carried December soil moisture and snow-pack water content over to the following January, which allows for accumulation of water from the preceding calendar year. Although soil water capacity varies considerably in this region, we maintained a constant water-holding capacity at 100 mm (Dingman 2002) for all wetlands to help isolate the signal generated from annual and spatial variation in climate drivers. On an annual basis, we assumed there is no appreciable change in soil moisture storage.

In its simplest form, the water balance equation is,

$$P = Ro + AET$$

where P is annual precipitation (in mm), Ro is runoff (in mm), and AET is actual evapotranspiration (in mm). Precipitation (P) is the sum of daily Daymet grid cell precipitation. Runoff (Ro) is surplus water input after soil water-holding capacity is satisfied, and in this model, includes downward infiltration plus lateral interflow and surface runoff. Actual evapotranspiration (AET) is water that returns to the atmosphere via transpiration and evaporation.

We hypothesized that snow melt runoff serves as the primary source of moisture filling high-elevation wetlands (Corn 2005). Because snow may persist in higher elevation regions for longer periods, we estimated runoff annually for each site. In addition to the above, we also hypothesized that precipitation and actual evapotranspiration rates from April to June were most likely to affect wetland persistence during amphibian breeding, oviposition, and larval development

(Murphy et al. 2010). Accordingly, we estimated precipitation and evapotranspiration totals using data from April to June each year.

Finally, we recognized that air temperature effects on wetlands and amphibians are complex but that growing season lengths are critically important to amphibians of this region (Murphy et al. 2010). At lower elevations, increased temperatures are likely to increase evapotranspiration rates and lead to wetland desiccation (McMenamin et al. 2008). Alternatively, increased temperatures could extend growing seasons, warm standing surface waters, and facilitate larval development at high-elevation wetlands (McCaffery and Maxell 2010). To capture variation in temperature across years and sites located within a climatologically heterogeneous landscape, we estimated annual cumulative growing degree-days (CGDD) for each site. Because amphibians in this region are physiologically active at temperatures above 0°C, we used this as our base temperature for estimating annual CGDD estimates.

Cumulative growing degree-days were calculated following McMaster and Wilhelm (1997) as

$$CGDD = \sum_{(January\ 1)}^{(December\ 31)} \left[\frac{T_{max} + T_{min}}{2} \right] - T_{base},$$

where T_{max} is the daily maximum air temperature (°C), T_{min} is daily minimum air temperature (°C), and $T_{base} = 0^{\circ}\text{C}$ is the temperature below which biological activity ceases.

Analysis

Because our primary goal was to determine whether incorporating climate-related drivers of wetland hydrology improved our ability to describe breeding dynamics compared with habitat-only models, we developed a small set of *a priori* models based upon habitat associations for each species as identified in recent analyses (Gould et al. 2012, Hossack et al. 2015). We modeled changes in breeding occupancy using the multi-season explicit dynamics model in program MARK (White and Burnham 1999). Occupancy in 1 yr (initial occupancy) is the estimated probability that breeding is present. Annual estimates of extinction (ϵ_t) and colonization (γ_t) in subsequent years describe the mechanistic processes that

drive changes in system state (MacKenzie et al. 2006). Extinction is the probability that a site occupied (i.e., used for breeding) in 1 yr is unoccupied (i.e., not used for breeding) the next year, whereas colonization is the probability that an unoccupied site in 1 yr is occupied the next year. Annual occupancy estimates ($\hat{\psi}_i$) are derived from the extinction and colonization probabilities. Assumptions of this model include no changes in occupancy between surveys within years, proper identification of species, and no unmodeled heterogeneity in detection probabilities among sites. We have confidence in the first two assumptions and have attempted to reduce violations of the third using covariates most pertinent to detection and presence of these species.

We first used a multistage modeling process in which we identified appropriate model structure for detection probability, followed by initial occupancy before focusing on hypothesized drivers of colonization and extinction (Gould et al. 2012, Hossack et al. 2015). We modeled detection rates by iteratively fitting different combinations of habitat covariates and time structures (i.e., detection varied annually or was constant) while the dynamic parameters were held as time specific. Once the most supported detection parameterization was determined for each species, we fit models to estimate initial occupancy for each species based on previously identified habitat associations. A small number of habitat covariates for initial occupancy were specified a priori for each species, and we then fit different a priori combinations of the habitat covariates and climate variables to find the most parsimonious fit.

After determining the most supported model for describing detection and initial occupancy, we focused on how the four climate drivers (precipitation, runoff, evapotranspiration, and cumulative growing degree-days) and their interactions with habitat affected the probability that a particular wetland was colonized or went extinct in a particular year. We developed 52 models that were functions of individual variables, combinations of climate variables, or combinations of habitat, and climate variables. Collinearity was screened using cross-correlation in which variables with $r > 0.60$ were not included together in the same model (Dormann et al. 2013). In some cases, we emphasized interactions between the climate drivers and wetland area and depth

because we expected these wetland characteristics would be most responsive to annual variation in weather. In general, we consider these to represent two groups of models: one based on water yield (precipitation, runoff) and one based on water losses (evapotranspiration, CGDD).

For each model that contained an interactive effect of a climate driver and wetland depth or area, there was a similar model based only on additive effects (e.g., [runoff + depth + runoff $\times$ wetland depth] and [runoff + wetland depth]). To demonstrate the effects of multiple covariates, we estimated occupancy and dynamic parameters based on three different wetland depths representing shallow (0.25 m), intermediate (0.75 m), and deep wetlands (2 m) within our sample frame. Approximately 70% of wetlands over the years were considered either shallow or intermediate in depth. Finally, we fit a model that considered completely random (non-Markovian) changes in breeding occupancy and a model that assumed wetland occupancy was static over seasons ($\epsilon_i = \gamma_i = 0$). All models were compared within an information theoretic framework (Burnham and Anderson 2002) using Akaike's information criterion (Akaike 1973) adjusted for small sample size.

RESULTS

Variations in climate drivers

Between 2006 and 2012, we conducted 2368 surveys of 528 wetlands. Across all monitored wetlands, annual estimates of April to June precipitation varied greatly. For example, median precipitation was three times higher in 2011 than in 2007 (Fig. 2). Similarly, estimated runoff across the region was two times higher in 2011 than in 2007. Across all sites, April to June evapotranspiration estimates were lowest in 2011 and highest in 2006. In addition to yearly changes in climate drivers, within-year variation (exemplified by 2007 estimates displayed in Fig. 1) among wetlands differed greatly for some drivers (e.g., 2010 April to June evapotranspiration; Fig. 2).

Western tiger salamanders

For tiger salamanders, the best fitting model of detection rates was a time-varying model; detection probability ranged from 0.19 (SE = 0.06) in 2010 to 0.84 (SE = 0.07) in 2006. Initial occupancy

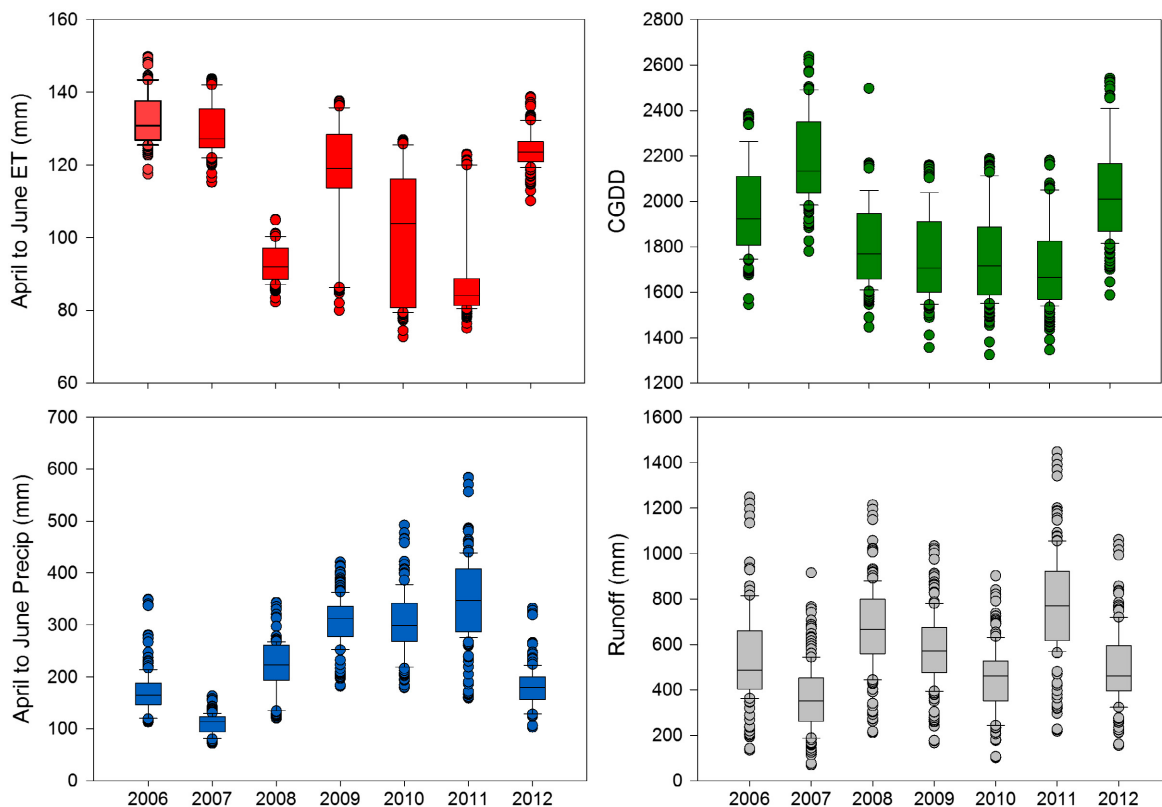


Fig. 2. Annual variation in climate drivers for all monitored wetlands within the study area. Summaries were generated from high-resolution spatially interpolated Daymet gridded climate data sets. Gridded (1×1 km grid cells) estimates of daily meteorological parameters (e.g., precipitation and temperature) were combined with a water balance model to estimate evapotranspiration (ET; mm) and runoff (mm) at the same scale. Variation in temperature across years and sites was expressed as annual cumulative growing degree-days (CGDD) for each site using 0°C as the base temperature.

for tiger salamanders was higher for deeper sites (2 m) and at higher elevations, but was also negatively associated with April to June precipitation. Precipitation was exchanged for runoff in the second-ranked model, but three of the four models with any weight favored precipitation (Table 1).

The top-ranked models for the dynamic parameters of salamanders all included depth and runoff as additive effects (Table 1) except for the third-ranked model, which included an interaction of depth and runoff. Because the interaction term explained little additional variability, we considered it to be an uninformative parameter (Arnold 2010) and based our inferences on the top-ranked model. There was a negative association between extinction probability and depth, but only a weak positive association between

depth and colonization. Counter to our expectations for salamanders, there was a notable positive association of extinction with runoff in all years across the region (Fig. 3). There was no association of colonization with runoff. Estimates of extinction probability varied greatly across years (e.g., 2006 to 2007 $\hat{\epsilon} = 0.224$, $\text{SE} = 0.073$ vs. 2010 to 2011 $\hat{\epsilon} = 0.747$, $\text{SE} = 0.141$). In contrast, colonization probabilities were low and varied little across years (e.g., 2006 to 2007 $\hat{\gamma} = 0.016$, $\text{SE} = 0.005$ vs. 2010 to 2011 $\hat{\gamma} = 0.026$, $\text{SE} = 0.006$).

Using mean values of covariates, occupancy estimates for salamanders were low ($\hat{\psi}$ range: $\hat{\psi} = 0.002$, $\text{SE} = 0.002$ in 2006 to $\hat{\psi} = 0.046$, $\text{SE} = 0.009$ in 2010; Fig. 4) and varied annually. Occupancy trends differed based on depth. In deep wetlands, average occupancy increased fourfold

Table 1. Top-ranked models used to estimate initial occupancy (Ψ), extinction (ϵ) and colonization (γ), and detection (p) for the western tiger salamander (*Ambystoma mavortium*), boreal chorus frog (*Pseudacris maculata*), and Columbia spotted frog (*Rana luteiventris*) in Grand Teton and Yellowstone National Parks.

Model	AICc	Δ AIC	AICc weight	Model likelihood	No. parameters
Western tiger salamander					
$\hat{\Psi}$ (depth + precip + elev) $\hat{\epsilon}$ (ro + depth) $\hat{\gamma}$ (ro + depth)p(t)	964.45	0.00	0.596	1.000	17
$\hat{\Psi}$ (depth + ro + elev) $\hat{\epsilon}$ (ro + depth) $\hat{\gamma}$ (ro + depth)p(t)	966.66	2.21	0.198	0.332	17
$\hat{\Psi}$ (depth + precip + elev) $\hat{\epsilon}$ (ro + depth + ro $\times$ depth) $\hat{\gamma}$ (ro + depth + ro $\times$ depth)p(t)	967.81	3.35	0.111	0.187	19
$\hat{\Psi}$ (depth + precip + elev) $\hat{\epsilon}$ (precip + depth) $\hat{\gamma}$ (precip + depth)p(t)	969.08	4.62	0.059	0.099	17
Boreal chorus frog					
$\hat{\Psi}$ (depth + veg + evap) $\hat{\epsilon}$ (evap + depth + veg) $\hat{\gamma}$ (evap + depth + veg)p(t + veg)	2642.20	0.00	0.83795	1.0000	20
$\hat{\Psi}$ (depth + veg + evap) $\hat{\epsilon}$ (veg + evap + depth + evap $\times$ depth) $\hat{\gamma}$ (veg + evap + depth + evap $\times$ depth)p(t + veg)	2645.48	3.29	0.16199	0.1933	22
Columbia spotted frog					
$\hat{\Psi}$ (depth + cgdd + isol) $\hat{\epsilon}$ (ro + depth + ro $\times$ depth) $\hat{\gamma}$ (ro + depth + ro $\times$ depth)p(t + veg)	1813.88	0.00	0.997	1.0000	20

Notes: Only models Δ AICc < 7 are shown. Abbreviations in models are as follows: precipitation (precip), elevation (elev), runoff (ro), time (t), emergent vegetation cover (veg), evapotranspiration (evap), cgdd (cumulative growing degree-days), and average distance from a site to all other wetlands in a catchment (isol).

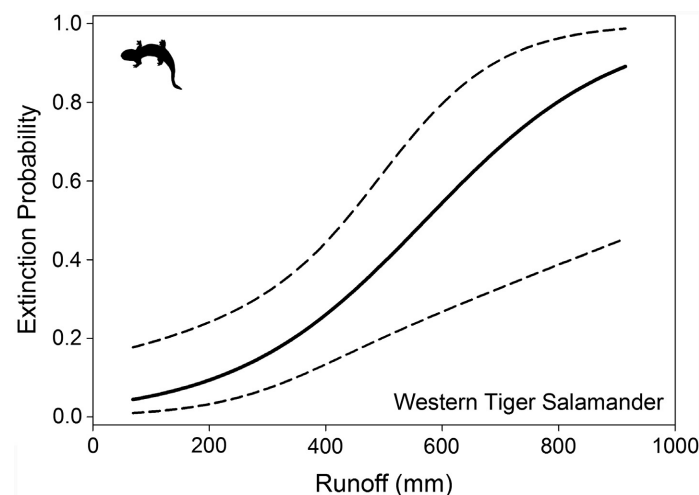


Fig. 3. Western tiger salamander (*Ambystoma mavortium*) extinction rate summarized as a function of runoff in 2007. Solid line summarizes estimated extinction and dashed lines indicate 95% confidence interval.

from 2006 ($\hat{\Psi} = 0.049$, SE = 0.043) to 2012 ($\hat{\Psi} = 0.214$, SE = 0.073; Fig. 5). In contrast, occupancy was relatively constant for shallow (0.25 m)- and intermediate (0.75 m)-depth wetlands over 7 yr (Fig. 5). Because the majority of monitored wetlands are <2 m deep, the net result was only a

slight increase in overall occupancy for salamanders between 2006 and 2012.

Boreal chorus frogs

The top-ranked model indicated that detection varied annually and increased with the extent of

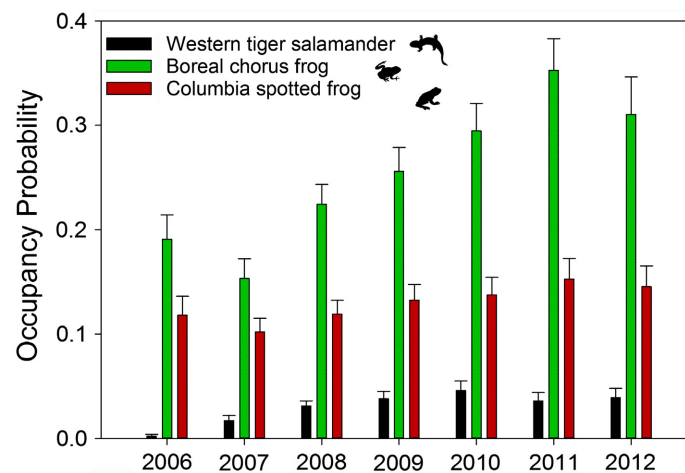


Fig. 4. Annual breeding occupancy ($\pm$ SE) estimates for all three amphibian species monitored in Grand Teton and Yellowstone National Parks. Estimates are derived from the top-ranked model for each species (see Table 1). Western tiger salamander (*Ambystoma mavortium*) occupancy is shown in black, boreal chorus frog (*Pseudacris maculata*) in green, and Columbia spotted frog (*Rana luteiventris*) in red.

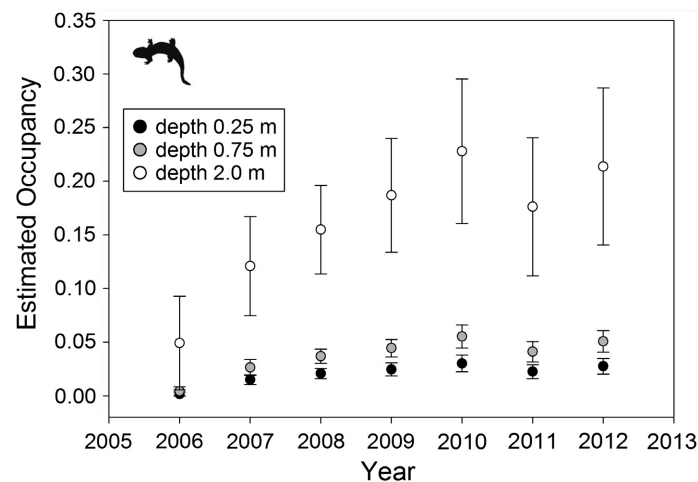


Fig. 5. Estimated annual breeding occupancy ($\pm$ SE) for the western tiger salamander (*Ambystoma mavortium*) summarized for three (0.25, 0.75, and 2.0 m) wetland depths.

wetland vegetation. Detection probability for chorus frogs ranged from 0.60 (SE = 0.04) in 2010 to 0.92 (SE = 0.03) in 2006, based on average vegetation cover of all monitored wetlands. Estimated initial occupancy was higher for deeper sites with more vegetation cover and was negatively related to evapotranspiration (Table 1).

The top-ranked models for the dynamic parameters included depth, vegetation cover, and evapotranspiration (Table 1). The interaction

between depth and evapotranspiration in the second-ranked model explained little additional variance and was therefore considered to be uninformative (Arnold 2010) and resulted in inferences from the top-ranked model with additive effects. There was a strong negative association of extinction probability and depth in dry (e.g., 2007) and wet (e.g., 2011) years (Fig. 6A, B) and a positive association of depth with colonization in most years. Chorus frog extinction

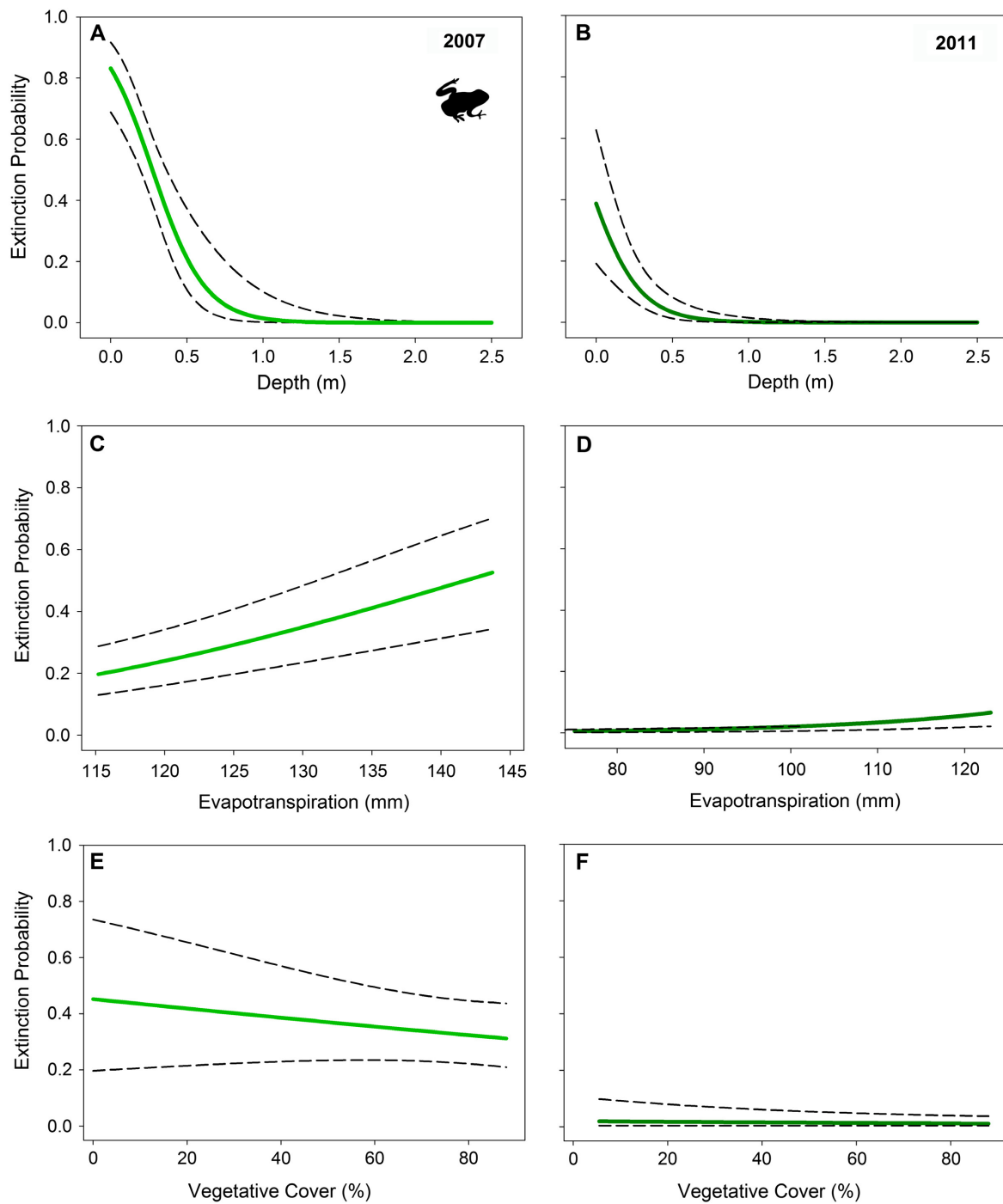


Fig. 6. Estimated extinction probability for boreal chorus frog (*Pseudacris maculata*) in years 2007 (hot, dry year) and 2011 (cool, wet year) as a function of wetland depth (A and B), actual evapotranspiration (C and D), and estimated vegetation cover (E and F).

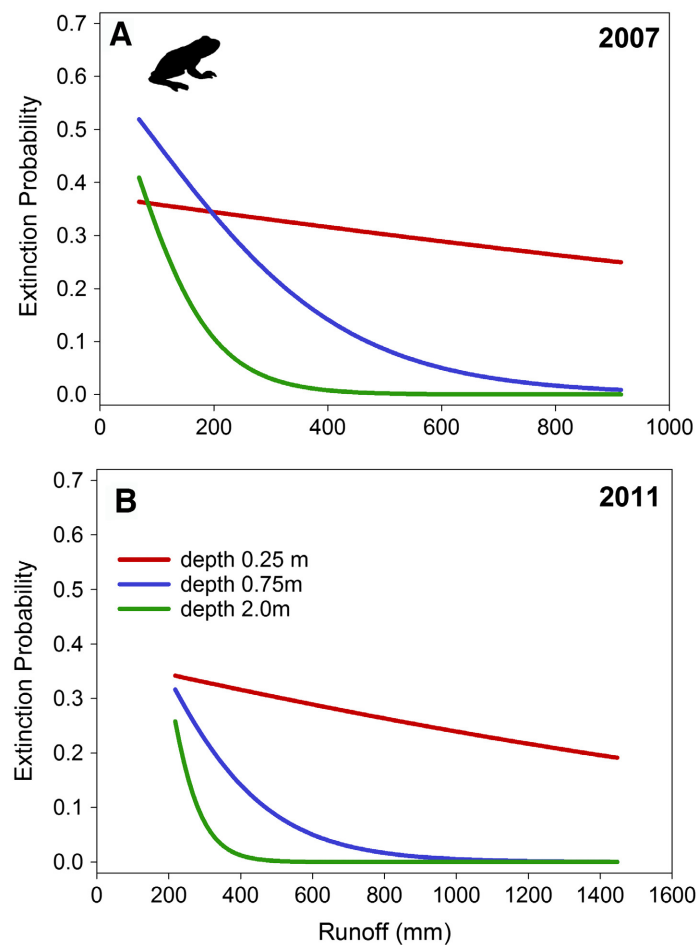


Fig. 7. Estimated extinction probability for Columbia spotted frog (*Rana luteiventris*) as a function of runoff in 2007 (hot, dry year; A) and 2011 (cool, wet year; B) and summarized for three (0.25, 0.75, and 2.0 m) wetland depths.

increased with evapotranspiration in some years (e.g., 2007, Fig. 6C); this relationship was weak in 2011—the year with the lowest region-wide average evapotranspiration in our 7-yr record. Finally, extinction was lower in wetlands with extensive vegetation cover in dry years (Fig. 6E), but no association with vegetation in wet years (Fig. 6F). Overall, there was a positive association of colonization with vegetation cover.

Based on our top-ranked model (Table 1), estimates of dynamic parameters for chorus frogs varied dramatically across years. Estimated extinction probabilities between dry years were as much as 25 times higher (2006 to 2007 $\hat{\epsilon} = 0.349$, SE = 0.065) than the transition from a dry to wet year (e.g., 2007 to 2008 $\hat{\epsilon} = 0.014$, SE = 0.009 and 2010 to 2011 $\hat{\epsilon} = 0.013$, SE = 0.008). Colonization

rates were less responsive than extinction to changes in climate drivers (2006 to 2007 $\hat{\gamma} = 0.036$, SE = 0.008 vs. 2007 to 2008 $\hat{\gamma} = 0.088$, SE = 0.012).

Annual occupancy estimates for chorus frogs were much higher than the other wetland breeding species and ranged from $\hat{\psi} = 0.153$ (SE = 0.019) in 2007 to $\hat{\psi} = 0.353$ (SE = 0.030; Fig. 4) in 2011, but responded annually to variable extinction and colonization rates. Colonization likely contributed disproportionately to annual occupancy in 2008 and 2011, when April to June evapotranspiration rates were low. The reverse was true in 2007 and 2012, when estimated evapotranspiration rates were high. Annual occupancy estimates also varied markedly by wetland depth. Occupancy increased from 2006 to 2012 for intermediate ($\hat{\psi} = 0.268$, SE = 0.029 in 2006 to $\hat{\psi} = 0.479$,

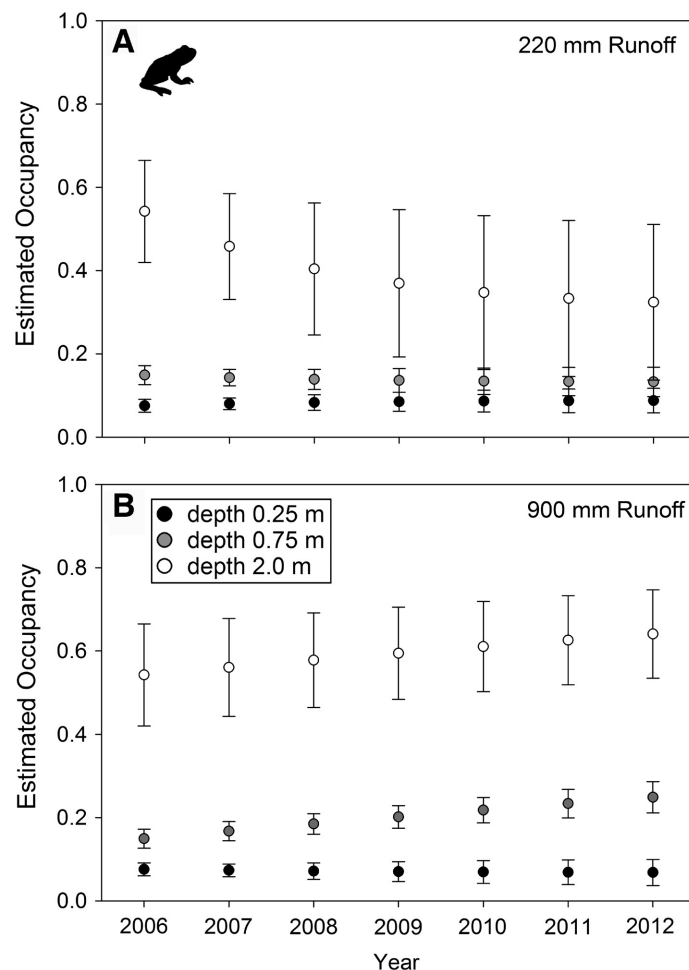


Fig. 8. Estimated occupancy rates for Columbia spotted frog (*R. luteiventris*) showing the interaction between wetland depth and runoff. Occupancy is summarized for three (0.25, 0.75, and 2.0 m) wetland depths. When runoff is held to (A) low levels (220 mm; 5th percentile of runoff levels of all site–year combinations) for 7 yr, occupancy estimates vary considerably by wetland depth and show declining or stable trends for deep and intermediate-depth wetlands. In contrast, occupancy estimates associated with (B) high runoff (900 mm; 95th percentile of runoff levels) suggest increasing trends in deep and intermediate-depth wetlands.

SE = 0.040 in 2012) and deep ($\hat{\psi} = 0.705$, SE = 0.087 in 2006 to $\hat{\psi} = 0.926$, SE = 0.034 in 2012) wetlands, but was variable and lacked a detectable occupancy trend for shallow wetlands (total $\hat{\psi}$ range: $\hat{\psi} = 0.077$, SE = 0.013 in 2007 to $\hat{\psi} = 0.167$, SE = 0.023 in 2011).

Columbia spotted frogs

The top-ranked detection model for the Columbia spotted frogs showed detection probability varied annually and increased with extent of wetland vegetation. Based on average vegetative cover, estimated detection probability ranged

from 0.49 (SE = 0.05) in 2010 to 0.82 (SE = 0.04) in 2006. Estimated initial occupancy was higher for deeper sites with higher CGDD and negatively related to wetland isolation. On average, wetlands that were isolated by ≥ 1.8 km had a less than 5% probability of being occupied by breeding spotted frogs.

The top-ranked model for the dynamic parameters included depth, runoff, and their interaction (Table 1). There was a strong negative association of extinction probability with runoff and depth and a positive association of runoff and depth with colonization. As examples, in a dry year

(2007) and wet year (2011), extinction declined with increased runoff (Fig. 7A, B). However, increased runoff did not eliminate extinction risk in shallow wetlands (0.25 m depth) in 2007 or 2011. In contrast, the probability of extinction approached zero in both intermediate and deep sites when runoff approached 800 and 400 mm, respectively.

Across all wetlands, net occupancy for spotted frogs increased modestly between 2006 and 2012 (Fig. 4). However, because of the variable extinction rates across wetland depths, spotted frog occupancy estimates also varied by wetland depth. In shallow wetlands, occupancy estimates declined from 2006 to 2012. Occupancy estimates for intermediate and deep wetlands increased modestly from 2006. The highest occupancy estimates occurred in deep sites and ranged from $\hat{\psi}=0.520$, $SE=0.111$ in 2006 to $\hat{\psi}=0.672$, $SE=0.084$ in 2012. To further examine the interaction between depth and runoff on spotted frog breeding occupancy, we estimated annual breeding occupancy by wetland depth for two different runoff levels (220 and 900 mm) that approximate 5th and 95th percentiles of runoff levels of all site-year combinations. At a runoff of 220 mm, estimated occupancy was relatively low and remained constant in shallow- and intermediate-depth wetlands but was reduced by approximately half in deep wetlands (Fig. 8A). When annual occupancy was modeled using a runoff of 900 mm, estimated occupancy increased in intermediate and deep wetlands, but was low and remained constant in shallow wetlands (Fig. 8B).

DISCUSSION

We show that occupancy dynamics of widely distributed amphibians are complex and vary with annual fluctuations and spatial variation in climate drivers (i.e., precipitation, runoff, and evapotranspiration). High-resolution climate data have been used to explain the complexity of climate–species interactions at local and regional scales (see Lutz et al. 2010); however, this work represents one of few attempts to blend local climate drivers with habitat data to model occupancy dynamics of wetland-dependent species through space and time. For all three species examined, models incorporating local climate drivers outperformed models of amphibian

breeding dynamics that were exclusively habitat based. Moreover, our multiyear monitoring data revealed that annual variation in climate drivers contributed most to variation in extinction rates, but little to colonization rates, and disproportionately influenced amphibian occupancy of wetlands. Interestingly, both the strength and direction of relationships between dynamic occupancy parameters and climate drivers varied among species.

Over our time series, tiger salamander occupancy was highest and extinction rates were lowest in deep wetlands. In Grand Teton and Yellowstone National Parks, deep, permanent wetlands support both metamorphic and paedomorphic individuals, and larvae in these wetlands reach larger sizes than larvae in ephemeral wetlands (McMenamin and Hadly 2010). Given the potential fitness costs associated with salamander use of ephemeral sites and that premature drying increases variability in larval survival (Church et al. 2007), higher occupancy and reduced extinction levels in deeper wetlands were not unexpected. More surprising was our finding that salamander extinction rates were consistently high, but positively associated with runoff across years. We suspect the positive relationship between extinction and runoff may reflect a predictable relationship of increased runoff at high elevations (positive in all years). In montane environments, high-runoff years are typically associated with large snowpacks, abbreviated growing seasons, cold summer water temperatures, and delayed breeding. Over a 20-yr study, a high-elevation (elevation 3500 m) population of Arizona tiger salamanders (*A. tigrinum nebulosum*) exhibited large interannual population fluctuations. Importantly, these high-elevation populations periodically experienced large winter mortality events (both paedomorphic and overwintering larvae) after prolonged winters with large snowpacks (Whiteman and Wissinger 2005). The 2007/2008 and 2010/2011 winters in Grand Teton and Yellowstone National Parks that produced the greatest runoff in our time series also had the largest April 1 snowpacks; these same years corresponded with years with the highest estimates of extinction for salamanders. We suspect some combination of factors (e.g., winter mortality combined with reduced number of breeding females) described

above could have contributed to the higher extinction rates documented during years with large snowpacks and high runoff.

For Columbia spotted frogs, a widely distributed species that has declined significantly over parts of its range (Hossack et al. 2013), the effects of runoff on extinction included an interaction with wetland depth. This interaction demonstrated high extinction rates in shallow wetlands at all runoff levels, but that high runoff can reduce or even eliminate extinction in intermediate and deep wetlands. In the western United States, the hydroperiods of larger and deeper wetlands are less sensitive to annual variations in meteorological conditions and are able to withstand extended periods of drought better than shallower wetlands (Hossack et al. 2013, Lee et al. 2015). Within Yellowstone National Park, loss of wetlands has been well documented over the last several decades. Despite these losses, deeper groundwater- or surface water-connected wetlands with relatively stable water levels have persisted (Schook and Cooper 2014). Our multi-year results from Grand Teton and Yellowstone National Parks show that spotted frog occupancy in deep and intermediate wetlands was 7.5 and 2.5 times higher than shallow wetlands. Given the extended development window for this species (time to metamorphosis is approximately three months), it is not uncommon in dry years for shallower ponds to dry prior to metamorphosis (Turner 1958, 1960). Spotted frogs exhibit strong fidelity to breeding sites (Pilliod et al. 2002), so multiple years of pond drying can severely depress local and regional recruitment levels (Turner 1960). Here, we show that spotted frog occupancy in deep ponds increased over our time series. Hossack et al. (2013) showed that across the species' range, annual growth rates for spotted frogs were higher for large water bodies than for small water bodies. Similarly, Arkle and Pilliod (2015) showed that spotted frog occupancy was positively associated with waterbody depth in the Great Basin. Interestingly, when we imposed 7 yr of low runoff on spotted frog breeding occupancy, 40% declines in spotted frog occupancy were projected even within deep wetlands. This magnitude of decline has been documented elsewhere within the species range (Pilliod and Scherer 2015) and confirms that multiyear drought cuts across wetland differences in

depth and contributes to increases in extinction rates even within protected areas.

Higher evapotranspiration rates and shallower depths corresponded with lower initial occupancy, higher extinction, and lower colonization rates for boreal chorus frogs. In this region, chorus frogs (more than the other native species) rely on shallow or ephemeral wetland habitats for breeding (Koch and Peterson 1995). Therefore, higher evapotranspiration rates would disproportionately affect chorus frogs occupying ephemeral compared with permanent wetlands. Amburgey et al. (2012) showed that chorus frog tadpoles from permanent ponds metamorphosed faster than those in ephemeral ponds. These counterintuitive results show that ecological responses to multiple and potentially interacting factors such as desiccation risk, predators, and food resources are complex (e.g., Newman 1992). Notably, the highest extinction estimates and the lowest estimate of chorus frog breeding occupancy in our time series occurred in 2007, when more than 40% of surveyed wetlands were dry. In Grand Teton and Yellowstone National Parks, 2007 was the driest year between 2000 and 2012 and April to June evapotranspiration exceeded precipitation totals. Regional April to June evapotranspiration estimates in 2012 were similar to 2007; however, the precipitation totals were higher and, interestingly, extinction rates were below that documented in 2007.

Although not formally evaluated here, antecedent weather conditions contribute to regional soil moisture levels (Gleick 1986) and may influence current year wetland condition (Lee et al. 2015) and amphibian breeding dynamics (Church et al. 2007, Hossack et al. 2013). Wetland conditions and breeding dynamics in 2012 followed a cool wet year in 2011, whereas 2007 followed an equally hot 2006. Moreover, all years between 2000 and 2005 had relatively high April to June evapotranspiration levels (median evapotranspiration ~ 120.0 mm) that most likely contributed to a severe water deficit (*sensu* Brooks 2004) and manifested in the dry conditions observed in 2007. A string of dry years, like those experienced between 2000 and 2005, may have large cumulative impacts on species like chorus frogs that rely upon consistent recruitment for maintaining stable population growth. This hypothesis might shed new light on amphibian declines reported in Yellowstone's

northern range. For example, our results show that colonization and extinction rates for chorus frogs—the species that likely matures the earliest and has the shortest life span—were more responsive to annual and spatial variations in climate drivers than western tiger salamanders or Columbia spotted frogs. These results suggest that prolonged drought created by consecutive hot, dry years may have contributed to high extinction rates over multiple years and, ultimately, the decline of chorus frogs reported by McMenamin et al. (2008) in Yellowstone's Lamar Valley.

All three widespread amphibian species of Grand Teton and Yellowstone National Parks had lower extinction rates, higher occupancy rates, and more positive occupancy trends in deep wetlands. These findings are consistent with work of others (Loman and Andersson 2007, Karraker and Gibbs 2009, Hossack et al. 2013, Anderson et al. 2015, Arkle and Pilliod 2015) and confirm that deep, fishless permanent wetlands provide habitat for the largest range of amphibian species and life histories (Ryan et al. 2014). These findings, however, must also be considered along with projections of increased climate variability (Easterling 2000). In multispecies assemblages, climate-driven variation to wetlands may be more beneficial to some amphibian species than others as the mosaic of available habitats shifts from highly connected deep wetlands to a preponderance of isolated, ephemeral habitats (Funk et al. 2005, Werner et al. 2009). Other multiyear amphibian data sets demonstrate that shallow and intermediate ponds may not support the highest occupancy estimates overall, but play a vital role in stabilizing amphibian populations under certain meteorological conditions (Maret et al. 2006, Skidts et al. 2007, Werner et al. 2009, McCaffery et al. 2014). In fact, in a complex of montane wetlands, population growth rates for Columbia spotted frogs were highest in intermediate-depth, semipermanent wetlands (McCaffery et al. 2014). Similarly, Cayuela et al. (2012) showed that reproduction was high and constant in wetlands with an intermediate hydroperiod relative to permanent wetlands or shallow, ephemeral wetlands. Taken together, a portfolio of wetland depths and types embedded within a heterogeneous, protected landscape will be necessary to conserve amphibian populations in a changing climate.

Across much of the western United States, increasing temperatures and declining snowpacks have resulted in increased evapotranspiration rates and declines in runoff (Mote 2006, Hamlet et al. 2007, Pederson et al. 2011b). These changes could eliminate many shallow wetlands, produce fewer permanent wetlands, and further limit the distribution of amphibians and other wetland-dependent species (Ryan et al. 2014, Lee et al. 2015). Periods of elevated temperatures and reduced precipitation can negatively influence breeding probability and survival of amphibians (Church et al. 2007, Cayuela et al. 2014). Multiyear droughts also strongly influenced occupancy levels and local extinction dynamics (Walls et al. 2013, Anderson et al. 2015) and reportedly contributed to genetic bottlenecks in salamander populations (Spear et al. 2006). In addition, variations in climate drivers have been used to explain annual dynamics in breeding probability, recruitment, and survival within (Cayuela et al. 2016) and among amphibian species (Werner et al. 2009).

Anticipated future change in temperature, evapotranspiration, snowpack, and runoff suggest drought in the western United States will become increasingly common and potentially more severe (Ault et al. 2014). These predictions portend difficult times for amphibians and other wetland-dependent species. The cumulative impacts of sustained drought are predicted to be experienced disproportionately by species that depend on ephemeral wetlands and on species with short life spans (i.e., annual plants, insects, and some amphibians [e.g., boreal chorus frogs in our region]). Species with short life spans likely rely upon consistent recruitment for maintaining stable population growth (Morris et al. 2008). In contrast, longer-lived species that can better persist through hard times (i.e., perennial plants, birds, long-lived amphibians [e.g., Columbia spotted frogs and western tiger salamanders in our region]) may be able to avoid breeding and other costly behavior when drought or other unfavorable conditions are present (Church et al. 2007, Cayuela et al. 2014). Lastly, drought conditions can also disproportionately affect larval survival and juvenile survival (Cayuela et al. 2016). Our findings clearly link amphibian breeding extinction and colonization rates to variability in climate drivers and offer valuable insight into how wetland species with

differing life histories may respond to future climate change (*sensu* Morris et al. 2008).

Conservation implications for the National Park Service

The overriding effects of climate change on wetlands and wetland-dependent species are beginning to attract the attention of scientists and policymakers (Erwin 2009). Long-term data sets from the National Park Service and other federal partners will be crucial to evaluate the risk of loss and to contemplate future mitigation measures (Hossack et al. 2013, Anderson et al. 2015). In Grand Teton and Yellowstone National Parks, climate trends are contributing to an earlier onset of spring, increasing temperatures (Sepulveda et al. 2015), and decreases in the number of frost days (Pederson et al. 2011a). These changes have already altered the timing and magnitude of wetland-filling flooding events (e.g., snowmelt and runoff) and contributed to altered hydrological regimes, including the complete drying of shallow wetlands (McMenamin et al. 2008, Schook and Cooper 2014). Shortened hydroperiods can produce wetlands that are unable to support larval development and metamorphosis and contribute to declines of amphibians and other wetland-dependent species (Daszak et al. 2005, Walls et al. 2013, Ryan et al. 2014).

Species-specific responses to climate change should be anticipated. For example, tiger salamanders in Grand Teton and Yellowstone National Parks may shift toward increased rates of metamorphic vs. paedomorphic individuals (Semlitsch 1987, Bruzgul et al. 2005). Spotted frogs and chorus frogs may exhibit a greater dependence on permanent water bodies. All three species may breed earlier (Corn 2005) and use previously snow-covered breeding sites at higher elevations (Ryan et al. 2014). There is observational support for this latter strategy as many of these widespread species already occupy wetlands at higher elevations in the southern parts of their range (Hossack et al. 2015). Unfortunately, upslope migration may be limited by reduced available area of shallow, high-productivity habitats or small lakes that are free of fish predators (Ryan et al. 2014). High-elevation sites in this region may also become increasingly susceptible to "false springs" (Augsburger 2013). Over the last 50 yr, late winter and early spring periods in this region have experienced the

greatest warming (Sepulveda et al. 2015). With the earlier onset of spring, amphibian breeding commences earlier, and resulting egg masses have a higher risk of freezing (Corn 2005).

At lower elevations, larvae of some amphibian species might adjust to or compensate for changing hydroperiods by accelerating growth or development, but this could come at the expense of reduced size at metamorphosis, heightened susceptibility to diseases, and lower fitness (Denver 1997, Gervasi and Foufopoulos 2008, McMenamin and Hadly 2010). Furthermore, adjusting to shortened hydroperiods through plastic growth and development may not be possible for all species that breed in shallow, temporary wetlands; some species are already at or near maximum physiological capacities (McMenamin and Hadly 2010, Richter-Boix et al. 2011, Amburgey et al. 2012). Species-specific abilities to respond to changes in the onset of ice-off or changes in hydroperiod make it more difficult to predict which populations or species will be able to respond to future climate change.

Wetland and amphibian monitoring programs are underway in national parks across the country. To date, the National Park Service has reported >225 amphibian species on 286 park units (NPS 2015). In addition, seven of 32 NPS Inventory and Monitoring programs actively monitor amphibians as part of their vital sign monitoring campaigns. Collectively, these long-term monitoring programs can address landscape-scale dynamics and climate influences that are rarely studied (Jones 2011). Through the next century, robust, long-term monitoring data sets will provide critical information on the status and trends of amphibians and other wetland-dependent species on NPS lands. Long-term monitoring programs will be necessary to inform managers of documented change and to describe the efficacy of restoration activities such as reconnecting wetlands, removing non-native species, or the landscape-level effects of climate and emerging disease.

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and R. Daley assembled amphibian breeding and climate data. W. Gould completed statistical analyses and A. Ray, W. Gould, and R. Daley created figures and tables. A. Ray, W. Gould, B. Hossack, A. Sepulveda, D. Thoma, D. Patla, and R. Al-Chokhachy wrote the manuscript. We acknowledge the efforts of current and past field crews that collectively produced the data available for this analysis. We recognize our debt to P.S. Corn for his leadership in conceiving and establishing this and other amphibian monitoring programs in national parks and to C.R. Peterson for his contributions to our understanding of amphibian natural history and for his efforts to implement monitoring in the Greater Yellowstone Area. We thank B. Halstead for comments on an earlier version of this manuscript. Northern Rockies Conservation Cooperative has been an important partner for the monitoring work discussed. Funding for this effort was provided by the National Park Service's Greater Yellowstone Network and the U.S. Geological Survey's Amphibian Research and Monitoring Initiative (ARMI). Any use of trade, product, or firm names is descriptive and does not imply endorsement by the U.S. Government. This manuscript is ARMI product no. 550.

LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and B. F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Amburgey, S., W. C. Funk, M. Murphy, and E. Muths. 2012. Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in boreal chorus frog tadpoles (*Pseudacris maculata*). *Herpetologica* 68:456–467.
- Anderson, T. L., B. H. Ousterhout, W. E. Peterman, D. L. Drake, and R. D. Semlitsch. 2015. Life history differences influence the impacts of drought on two pond-breeding salamanders. *Ecological Applications* 25:1896–1910.
- Arkle, R. S., and D. S. Pilliod. 2015. Persistence at distributional edges: Columbia spotted frog habitat in the arid Great Basin, USA. *Ecology and Evolution* 5:3979–3994.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175–1178.
- Augspurger, C. K. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* 94:41–50.
- Ault, T. R., J. E. Cole, J. T. Overpeck, G. T. Pederson, and D. M. Meko. 2014. Assessing the risk of persistent drought using climate model simulations and paleoclimate data. *Journal of Climate* 27:7529–7549.
- Bardecki, M. J. 1991. Wetlands and climate change: a speculative review. *Canadian Water Resources Journal* 16:9–22.
- Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71:1599–1608.
- Brooks, R. T. 2004. Weather-related effects on woodland vernal pool hydrology and hydroperiod. *Wetlands* 24:104–114.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates of insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449.
- Bruzgul, J. E., W. Long, and E. A. Hadly. 2005. Temporal response of the tiger salamander (*Ambystoma tigrinum*) to 3,000 years of climatic variation. *BMC Ecology* 5:7.
- Buckley, L. B., and W. Jetz. 2007. Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B* 274:1167–1173.
- Bull, E. L., and M. P. Hayes. 2001. Post-breeding season movements of Columbia spotted frogs (*Rana luteiventris*) in northeastern Oregon. *Western North American Naturalist* 61:119–123.
- Burkett, V., and J. Kusler. 2000. Climate change: potential impacts and interactions in wetlands of the United States. *Journal of the American Water Resources Association* 36:313–320.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Case, M. J., J. J. Lawler, and J. A. Tomasevic. 2015. Relative sensitivity to climate change of species in northwestern North America. *Biological Conservation* 187:127–133.
- Cayuela, H., A. Besnard, A. Béchet, V. Devictor, and A. Olivier. 2012. Reproductive dynamics of three amphibian species in Mediterranean wetlands: the role of local precipitation and hydrological regimes. *Freshwater Biology* 57:2629–2640.
- Cayuela, H., A. Besnard, E. Bonnaire, H. Perret, J. Rivoalen, C. Miaud, and P. Joly. 2014. To breed or not to breed: past reproductive status and environmental cues drive current breeding decisions in a long-lived amphibian. *Oecologia* 176:107–116.
- Cayuela, H., D. Arsovski, J. M. Thirion, E. Bonnaire, J. Pichenot, S. Boitard, C. Miaud, P. Joly, and A. Besnard. 2016. Demographic responses to weather fluctuations are context dependent in a long-lived amphibian. *Global Change Biology* 22:2676–2687.

- Church, D. R., L. L. Bailey, H. M. Wilbur, W. L. Kendall, and J. E. Hines. 2007. Iteroparity in the variable environment of the salamander *Ambystoma tigrinum*. *Ecology* 88:891–903.
- Corn, P. S. 2005. Climate change and amphibians. *Animal Biodiversity and Conservation* 28:59–67.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Office of Biological Services, U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Daszak, P., D. E. Scott, A. M. Kilpatrick, C. Faggioni, J. W. Gibbons, and D. Porter. 2005. Amphibian population declines at Savannah River site are linked to climate, not Chytridiomycosis. *Ecology* 86:3232–3237.
- Denver, R. J. 1997. Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. *American Zoologist* 37:172–184.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA* 105:6668–6672.
- Dingman, S. L. 2002. *Physical hydrology*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Dormann, C. F., et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46.
- Dudgeon, D., et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81:163–182.
- Easterling, D. R. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.
- Eck, B., A. Byrne, V. D. Popescu, E. B. Harper, and D. A. Patrick. 2014. Effects of water temperature on larval amphibian predator-prey dynamics. *Herpetological Conservation and Biology* 9:302–308.
- Elliot, C. R., and M. M. Hektner. 2000. Wetland resources of Yellowstone National Park. Yellowstone National Park, Wyoming, USA.
- Erwin, K. L. 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetlands Ecology and Management* 17:71–84.
- Fancy, S. G., J. E. Gross, and S. L. Carter. 2009. Monitoring the condition of natural resources in US national parks. *Environmental Monitoring and Assessment* 151:161–174.
- Fellers, G. M., P. M. Kleeman, and D. A. W. Miller. 2015. Wetland occupancy of pond-breeding amphibians in Yosemite National Park, USA. *Journal of North American Herpetology* 2015:22–33.
- Funk, W. C., M. S. Blouin, P. S. Corn, B. A. Maxell, D. S. Pilliod, S. Amish, and F. W. Allendorf. 2005. Population structure of Columbia spotted frogs (*Rana luteiventris*) is strongly affected by the landscape. *Molecular Ecology* 14:483–496.
- Gervasi, S. S., and J. Foufopoulos. 2008. Costs of plasticity: responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. *Functional Ecology* 22:100–108.
- Gleick, P. H. 1986. Methods for evaluating the regional hydrologic impacts of global climatic changes. *Journal of Hydrology* 88:97–116.
- Gopal, B. 2009. Biodiversity in wetlands. Pages 65–95 in E. B. Maltby, editor. *The wetlands handbook*. Blackwell Publishing, Chichester, UK.
- Gould, W. R., D. A. Patla, R. Daley, P. S. Corn, B. R. Hossack, R. Bennetts, and C. R. Peterson. 2012. Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the Greater Yellowstone Ecosystem. *Wetlands* 32:379–389.
- Gray, S. T., and G. J. McCabe. 2010. A combined water balance and tree ring approach to understanding the potential hydrologic effects of climate change in the central Rocky Mountain region. *Water Resources Research* 46:W05513.
- Hamlet, A. F., P. W. Mote, M. P. Clark, and D. P. Lettenmaier. 2007. Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. *Journal of Climate* 20:1468–1486.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatolgy* 25:1965–1978.
- Hossack, B. R., et al. 2013. Roles of patch characteristics, drought frequency, and restoration in long-term trends of a widespread amphibian. *Conservation Biology* 27:1410–1420.
- Hossack, B. R., W. R. Gould, D. A. Patla, E. Muths, R. Daley, K. Legg, and P. S. Corn. 2015. Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. *Biological Conservation* 187:260–269.
- Johnson, W. P., M. B. Rice, D. A. Haukos, and P. P. Thorpe. 2011. Factors influencing the occurrence of inundated playa wetlands during winter on the Texas High Plains. *Wetlands* 31:1287–1296.
- Johnson, W. C., B. Werner, G. R. Guntenspergen, R. A. Voldseth, B. Millett, D. E. Naugle, M. Tulbure, R. W. H. Carroll, J. Tracy, and C. Olawsky. 2010. Prairie wetland complexes as landscape functional units in a changing climate. *BioScience* 60:128–140.
- Jones, J. P. G. 2011. Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* 48:9–13.
- Karraker, N. E., and J. P. Gibbs. 2009. Amphibian production in forested landscapes in relation to wetland hydroperiod: a case study of vernal pools and

- beaver ponds. *Biological Conservation* 142:2293–2302.
- Koch, E. D., and C. R. Peterson. 1995. *Amphibians & reptiles of Yellowstone and Grand Teton National Parks*. University of Utah Press, Salt Lake City, Utah, USA.
- Lee, S. Y., M. E. Ryan, A. F. Hamlet, W. J. Palen, J. J. Lawler, and M. Halabisky. 2015. Projecting the hydrologic impacts of climate change on montane wetlands. *PLoS ONE* 10:e0136385.
- Loman, J., and G. Andersson. 2007. Monitoring brown frogs *Rana arvalis* and *Rana temporaria* in 120 south Swedish ponds 1989–2005. Mixed trends in different habitats. *Biological Conservation* 135:46–56.
- Lutz, J. A., J. W. van Wagtenonk, and J. F. Franklin. 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. *Journal of Biogeography* 37:936–950.
- Machlis, G., and M. McNutt. 2015. Parks for science. *Science* 348:1291.
- MacKenzie, D., J. Nichols, J. Royle, K. Pollock, L. L. Bailey, and J. Hines. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, San Francisco, California, USA.
- Maret, T. J., J. D. Snyder, and J. P. Collins. 2006. Altered drying regime controls distribution of endangered salamanders and introduced predators. *Biological Conservation* 127:129–138.
- Matthews, J. 2010. Anthropogenic climate change impacts on ponds: a thermal mass perspective. *Biodiversity and Ecosystem Risk Assessment* 5:193–209.
- Matthews, J. H., W. C. Funk, and C. K. Ghalambor. 2013. Demographic approaches to assessing climate change impact: an application to pond-breeding frogs and shifting hydroperiods. Pages 58–85 in J. F. P. Brodie and D. Doak, editors. *Wildlife conservation in a changing climate*. University of Chicago Press, Chicago, Illinois, USA.
- McCaffery, R. M., and B. A. Maxell. 2010. Decreased winter severity increases viability of a montane frog population. *Proceedings of the National Academy of Sciences USA* 107:8644–8649.
- McCaffery, R. M., L. A. Eby, B. A. Maxell, and P. S. Corn. 2014. Breeding site heterogeneity reduces variability in frog recruitment and population dynamics. *Biological Conservation* 170:169–176.
- McMaster, G. S., and W. W. Wilhelm. 1997. Growing degree-days: one equation, two interpretations. *Agricultural and Forest Meteorology* 87:291–300.
- McMenamin, S. K., and E. A. Hadly. 2010. Developmental dynamics of *Ambystoma tigrinum* in a changing landscape. *BMC Ecology* 10:10.
- McMenamin, S. K., E. A. Hadly, and C. K. Wright. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy of Sciences USA* 105:16988–16993.
- Morris, W. F., et al. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89:19–25.
- Mote, P. W. 2006. Climate-driven variability and trends in mountain snowpack in western North America. *Journal of Climate* 19:6209–6220.
- Murphy, M. A., J. S. Evans, and A. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91:252–261.
- Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. *BioScience* 42:671–678.
- NPS. 2015. NPSpecies—the National Park Service biodiversity database. National Park Service, Fort Collins, Colorado, USA. <https://irma.nps.gov/npspecies/>
- Pederson, G. T., S. T. Gray, T. Ault, W. Marsh, D. B. Fagre, A. G. Bunn, C. A. Woodhouse, and L. J. Graumlich. 2011a. Climatic controls on the snow-melt hydrology of the northern Rocky Mountains. *Journal of Climate* 24:1666–1687.
- Pederson, G. T., S. T. Gray, C. A. Woodhouse, J. L. Betancourt, D. B. Fagre, J. S. Littell, E. Watson, B. H. Luckman, and L. J. Graumlich. 2011b. The unusual nature of recent snowpack declines in the North American Cordillera. *Science* 333:332–335.
- Pilliod, D. S., and R. D. Scherer. 2015. Managing habitat to slow or reverse population declines of the Columbia spotted frog in the Northern Great Basin. *Journal of Wildlife Management* 79:579–590.
- Pilliod, D. S., C. R. Peterson, and P. I. Ritson. 2002. Seasonal migration of Columbia spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. *Canadian Journal of Zoology* 80:1849–1862.
- Quesnelle, P. E., L. Fahrig, and K. E. Lindsay. 2013. Effects of habitat loss, habitat configuration and matrix composition on declining wetland species. *Biological Conservation* 160:200–208.
- Ray, A., A. Sepulveda, B. Hossack, D. Patla, and K. Legg. 2014. Using monitoring data to map amphibian breeding hotspots and describe wetland vulnerability in Yellowstone and Grand Teton National Parks. *Park Science* 31:112–119.
- Richter-Boix, A., M. Tejedo, and E. L. Rezende. 2011. Evolution and plasticity of anuran larval development in response to desiccation. A comparative analysis. *Ecology and Evolution* 1:15–25.
- Riordan, B., D. Verbyla, and A. D. McGuire. 2006. Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research: Biogeosciences* 111:G04002.

- Ryan, M. E., W. J. Palen, M. J. Adams, and R. M. Rochefort. 2014. Amphibians in the climate vise: loss and restoration of resilience of montane wetland ecosystems in the western US. *Frontiers in Ecology and the Environment* 12:232–240.
- Schneider, D., J. J. Treanor, J. Richards, J. Wood, E. Lee, and A. Waag. 2015. Plains spadefoot, *Spea bombifrons*, confirmed in Yellowstone National Park. *Northwestern Naturalist* 96:227–229.
- Schook, D. M., and D. J. Cooper. 2014. Climatic and hydrologic processes leading to wetland losses in Yellowstone National Park, USA. *Journal of Hydrology* 510:340–352.
- Semlitsch, R. D. 1987. Paedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. *Ecology* 68:994–1002.
- Sepulveda, A. J., M. T. Tercek, R. Al-Chokhachy, A. Ray, D. Thoma, B. Hossack, G. Pederson, A. Rodman, and T. Olliff. 2015. The shifting climate portfolio of the Greater Yellowstone Area. *PLoS ONE* 10:e0145060.
- Skidds, D. E., F. C. Golet, P. W. C. Paton, and J. C. Mitchell. 2007. Habitat correlates of reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed. *Journal of Herpetology* 41:439–450.
- Spear, S. F., C. R. Peterson, M. D. Matocq, and A. Storfer. 2006. Molecular evidence for historical and recent population size reductions of tiger salamanders (*Ambystoma tigrinum*) in Yellowstone National Park. *Conservation Genetics* 7:605–611.
- Tercek, M. T., S. T. Gray, and C. M. Nicholson. 2012. Climate zone delineation: evaluating approaches for use in natural resource management. *Environmental Management* 49:1076–1091.
- Thoma, D., A. Rodman, and M. Tercek. 2015. Water in the balance: interpreting climate change impacts using a water balance model. *Yellowstone Science* 23:29–35.
- Thornton, P. E., M. M. Thornton, B. W. Mayer, N. Wilhelm, Y. Wei, R. Devarakonda, and R. B. Cook. 2014. Daymet: daily surface weather data on a 1-km grid for North America, Version 2 Active Archive Center, Oak Ridge, Tennessee. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Tordoff, W., and D. Pettus. 1977. Temporal stability of phenotypic frequencies in *Pseudacris triseriata* (Amphibia, Anura, Hylidae). *Journal of Herpetology* 11:161–168.
- Turner, F. B. 1958. Life-history of the western spotted frog in Yellowstone National Park. *Herpetologica* 14:96–100.
- Turner, F. B. 1960. Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird & Girard, in Yellowstone Park, Wyoming. *Ecological Monographs* 30:251–278.
- Walls, S. C., W. J. Barichivich, M. E. Brown, D. E. Scott, and B. R. Hossack. 2013. Influence of drought on salamander occupancy of isolated wetlands on the Southeastern Coastal Plain of the United States. *Wetlands* 33:345–354.
- Werner, E. E., R. A. Relyea, K. L. Yurewicz, D. K. Skelly, and C. J. Davis. 2009. Comparative landscape dynamics of two anuran species: climate-driven interaction of local and regional processes. *Ecological Monographs* 79:503–521.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Whiteman, H. H., and S. A. Wissinger. 2005. Amphibian population cycles and long-term data sets. Pages 177–184 in M. J. Lannoo, editor. *Amphibian declines: the conservation status of United States species*. University of California Press, Ltd., Berkeley, California, USA.
- Wright, C., and A. Gallant. 2007. Improved wetland remote sensing in Yellowstone National Park using classification trees to combine TM imagery and ancillary environmental data. *Remote Sensing of Environment* 107:582–605.