Contributed Paper

Roles of Patch Characteristics, Drought Frequency, and Restoration in Long-Term Trends of a Widespread Amphibian

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Abstract: *Despite the high profile of amphibian declines and the increasing threat of drought and fragmentation to aquatic ecosystems, few studies have examined long-term rates of change for a single species across a large geographic area. We analyzed growth in annual egg-mass counts of the Columbia spotted frog (Rana luteiventris) across the northwestern United States, an area encompassing 3 genetic clades. On the basis of data collected by multiple partners from 98 water bodies between 1991 and 2011, we used state-space and linear-regression models to measure effects of patch characteristics, frequency of summer drought, and wetland restoration on population growth. Abundance increased in the 2 clades with greatest decline history, but declined where populations are considered most secure. Population growth was negatively associated with temporary hydroperiods and landscape modification (measured by the human footprint index), but was similar in modified and natural water bodies. The effect of drought was mediated by the size of the water body: populations in large water bodies maintained positive growth despite drought, whereas drought magnified declines in small water bodies. Rapid growth in restored wetlands in areas of historical population declines provided strong evidence of successful management. Our results highlight the importance of maintaining large areas of habitat and underscore the greater vulnerability of small areas of habitat to environmental stochasticity. Similar long-term growth rates in modified and natural water bodies and rapid, positive responses to restoration suggest pond construction and other forms of management can effectively increase population growth. These tools are likely to become increasingly important to mitigate effects of increased drought expected from global climate change.*

Keywords: amphibian decline, climate change, constructed ponds, fragmentation, human footprint index, hydroperiod, monitoring, restoration, state-space model

Papeles de las Características del Fragmento, Frecuencia de Sequía y Restauración en las Tendencias a Largo Plazo de un Anfibio Ampliamente Distribuido

Resumen: *A pesar del alto perfil de la declinación de anfibios y la amenaza creciente de sequía y fragmentación que tienen los ecosistemas acuáticos, pocos estudios han examinado las tasas de cambio a largo plazo para una sola especie a través de un área geográfica grande. Analizamos el crecimiento en conteos anuales de cantidad de huevos de la rana moteada (Rana luteiventris) a en el noroeste de los Estados Unidos, un área que incluye 3 clados genéticos. Con base en los datos colectados por múltiples compañeros en 98 cuerpos de agua entre 1991 y 2011, usamos modelos de regresión lineal y estado-espacio para medir los efectos de características, de fragmento, frecuencia de la sequía veraniega y la restauración de humedales sobre el crecimiento poblacional. La abundancia incrementó en los 2 clados con la mayor historia de declinación, pero disminuyó donde las poblaciones se consideraron más seguras. El crecimiento poblacional se asoció negativamente con hidroperíodos temporales y modificación de paisaje (medidos con el índice de huella ecológica humana), pero fue similar en cuerpos de agua naturales y modificados. El efecto de la sequía fue mediado por el tamaño del cuerpo de agua: las poblaciones en cuerpos de agua grandes mantuvieron un crecimiento positivo a pesar de la sequía, mientras que la sequía magnificó las declinaciones en cuerpos de agua pequeños. El crecimiento rápido en humedales restaurados en áreas de declinación poblacional histórica proporcionó evidencias fuertes de un manejo exitoso. Nuestros resultados resaltan la importancia de mantener áreas exensas de hábitat y subrayan la vulnerabilidad mayor de áreas pequeñas de hábitat para la estocasticidad ambiental. Tasas de crecimiento a largo plazo similares en cuerpos de agua modificados y naturales y respuestas rápidas y positivas a la restauración sugieren que la construcción de estanques y otras formas de manejo pueden incrementar efectivamente el crecimiento poblacional. Estas herramientas probablemente se volverán cada vez más importantes para mitigar los efectos de sequía incrementada esperados por el cambio climático global.*

Palabras Clave: Cambio climático, declinación de anfibios, estanques construidos, fragmentación, hidroperíodo, índice de huella ecológica humana, modelo estado-espacio, monitoreo, restauración

Introduction

Monitoring and habitat restoration are often core components of conservation plans and management efforts for declining species (EEC 1992; USFWS 2011). Evaluating population responses to management actions relies on reliable trend estimates from long-term population monitoring, but there is frequently little formal synthesis or evaluation of these efforts (Campbell et al. 2002; Petranka et al. 2007) in part because they may be conducted by several agencies or partners. Collection of data by multiple partners introduces challenges to estimating trends across large regions. However, syntheses of monitoring data are one of the primary mechanisms to evaluate the efficacy of conservation measures and to identify habitat and climate-related factors that affect population growth.

The effects of climate change on aquatic ecosystems have attracted substantial attention and highlighted the importance of long-term data sets for evaluating risks and potential mitigation measures (Lake 2003; Shoo et al. 2011). Increased frequency and severity of drought and continued habitat loss and fragmentation, threaten amphibians and other aquatic and semiaquatic organisms. Not surprisingly, many aquatic and semiaquatic species experience greater population growth or are more likely to occupy permanent water bodies compared with temporary sites (Ruetz et al. 2005; Loman & Andersson 2007; Gould et al. 2012), and the threats of drought and fragmentation can be magnified in small and temporary waters (Lake 2003; Brooks 2009). For example, likelihood of population decline after drought may be related to developmental time (e.g., Daszak et al. 2005). In the arid

Great Basin (U.S.A.), the distribution and decline of the Columbia spotted frog (*Rana luteiventris*) is strongly linked with hydroperiod (Welch & MacMahon 2005; Wente et al. 2005). Despite the dependence of amphibians on water, however, few studies have measured long-term trends relative to drought, especially across multiple populations or large study areas (Walls et al. 2013).

In addition to the potential for long hydroperiods to buffer against drought, a link between hydroperiod and population growth provides opportunities to facilitate recovery (Shoo et al. 2011). In many arid or agricultural areas, most water bodies were created or modified to increase water storage, often to support livestock or game species (Krausman et al. 2006). Amphibians frequently use human-modified water bodies (Hazell et al. 2004; Petranka et al. 2007). However, these water bodies are seldom designed explicitly for conservation and often host more predators and parasites (Adams 2000; Johnson et al. 2002; Pearl et al. 2005) than natural water bodies, and there is a consensus that these sites do not replace the ecological functions of natural water bodies (Pechmann et al. 2001; Shulse et al. 2010). Thus, these seemingly beneficial areas could be ecological traps that reduce rather than augment population growth (e.g., Schlaepfer et al. 2002).

We analyzed trends in abundance of egg mass of the Columbia spotted frog from 98 breeding sites in the northwestern United States. Egg-mass counts of species that lay a single clutch annually, such as the Columbia spotted frog, are often used as a surrogate for size of the female breeding population (Crouch & Paton 2000; Loman & Andersson 2007). Data were collected as part

of long-term monitoring efforts across a large portion of this species' range in the United States and include populations that are candidates for listing under the U.S. Endangered Species Act (USFWS 2011). We used estimated annual exponential growth rate in egg-mass abundance in each breeding site to summarize changes in abundance across the region; evaluated the role of patch characteristics and drought in population growth; and compared growth between restored sites and unrestored sites. Collectively, these results should inform conservation efforts for the Columbia spotted frog and other species that use similar habitats.

Methods

Study Area and Species

The Columbia spotted frog is a highly aquatic species that uses temporary and permanent waters for breeding but requires permanent water for winter hibernation (Werner et al. 2004). Larvae metamorphose within 4 months after egg deposition. This species is widespread in northwestern North America and comprises 3 genetic clades that correspond closely to the distinct population segments used as the basis for listing decisions by the U.S. Fish and Wildlife Service. The northern clade includes most of eastern Oregon and the northern Rocky Mountains and extends north to southeastern Alaska. The Utah clade and a Great Basin clade are composed of isolated populations in Nevada, southwestern Idaho, and southeastern Oregon (Fig. 1) (Funk et al. 2008; USFWS 2011).

Declines have been documented in all 3 clades, although populations in the northern clade are considered most secure (USFWS 2011). Greater declines in the Utah and Great Basin clades have been linked to population isolation and limited water in these arid regions (Welch & MacMahon 2005; Wente et al. 2005; USFWS 2011). The Great Basin populations are candidates for listing under the U.S. Endangered Species Act; they warrant legal protection but are precluded by higher priority species or distinct population segments (USFWS 2011). Utah populations were removed from consideration as a candidate species in 2002 after the state implemented a formal conservation agreement that included long-term monitoring and habitat restoration (Bailey et al. 2006).

We monitored egg-mass abundance at a variety of types of water bodies that we refer to collectively as sites. Monitored sites in Utah were in the Wasatch Front and the West Desert regions. Most of these sites were associated with natural, permanent spring complexes, including some large water bodies (Bailey et al. 2006) (Table 1). All monitored sites in the Great Basin clade were in the Owyhee Mountains of southwest Idaho. These isolated populations were associated with small springs and slow-flowing streams. Most of these sites were human-modified and permanent (Lohr 2011). The

northern clade is the largest and included sites in diverse settings (Table 1). Many eastern Oregon sites were impoundments associated with small mining operations or were surrounded by pasture (Bull & Hayes 2000; Adams et al. 2009). Other sites in the northern clade were primarily in forest, including wilderness and national parks. We based selection of most sites on presence of historical data and extant populations or because they represented the largest remaining populations. Three sites in each of the Utah and Great Basin clades received targeted habitat restoration (i.e., management actions were taken expressly to improve habitat for frogs or other native species). These actions included creating ponds specifically to increase breeding habitat for Columbia spotted frogs, reintroducing beaver (*Castor canadensis*), and restoring natural hydrological regimes (Bailey et al. 2006; Lohr 2011).

Data Collection

We obtained time series of egg-mass counts from long-term monitoring or research programs conducted by natural resource agencies and university cooperators. Columbia spotted frogs produce 1 egg mass during a discrete breeding season that typically lasts <2 months (Licht 1975). Egg-mass counts of anurans are often used as a surrogate for size of the female breeding population because they provide a feasible method to track reproductive effort across several sites (Loman & Andersson 2007; Petranka et al. 2007). Also, females of many anuran species are reclusive and unavailable for capture during the breeding season, which limited our ability to estimate their abundance or vital rates (Muths et al. 2010). The correlation between abundance of female Columbia spotted frogs and egg masses is unknown, but in the closely related wood frog (*Lithobates sylvaticus*), egg-mass counts are highly correlated ($r = 0.97$) with number of females at 8 ponds (Crouch & Paton 2000). We refer to changes in egg-mass counts as population growth, but acknowledge that the counts may be an imperfect surrogate.

Counts were conducted by repeated searches of breeding sites within years. Counts started as early as 1991; most continued through 2010 or 2011. Most sites were surveyed annually, with occasional data gaps that resulted from inability to access sites or uncertainty that counts reflected complete breeding effort. To reduce error, we worked with those who collected or managed the data to identify and eliminate potentially unreliable data.

Statistical Analyses

GROWTH ESTIMATES

We used the exponential-growth state-space (EGSS) model from Humbert et al. (2009) to estimate the mean instantaneous growth rate (μ) on the basis of time series of

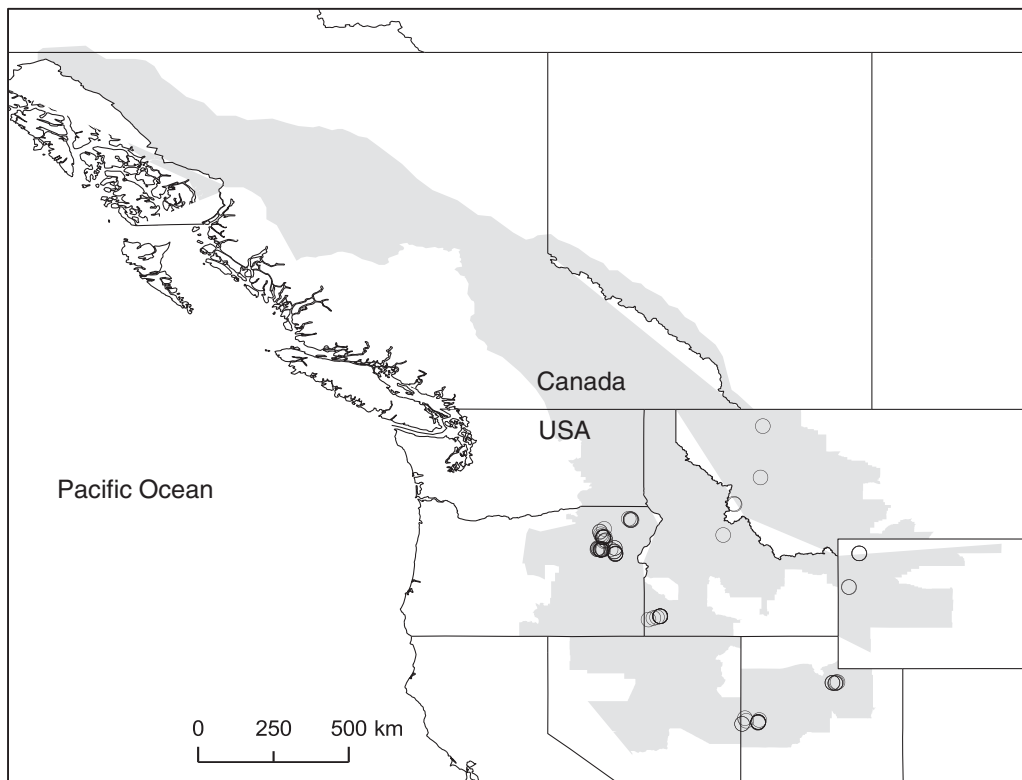*Figure 1. Location of 98 water bodies (circles), where we conducted annual counts of Columbia spotted frog (Rana luteiventris) egg masses between 1991 and 2011 (gray, species' range) (IUCN 2012).*

Table 1. Mean (range) characteristics of 98 Columbia spotted frog (*Rana luteiventris*) breeding sites in 3 genetic clades in the northwestern United States.

	Clade		
Variable[a]	*northern* (n = 65)	*Great Basin* (n = 11)	*Utah* (n = 22)
No. years	11.15 (5–21)	9.91 (5–12)	10.95 (4–16)
Water body size (ha)	0.64 (0.01–12.60)	0.06 (0.01–0.32)	13.12 (0.20–110.24)
Human footprint index	3.56 (1.49–9.99)	2.26 (1.76–2.94)	3.77 (2.23–7.16)
Modified sites	0.69	0.82	0.05
Permanent hydroperiod	0.68	0.82	0.91
Summer drought	0.70 (0.25–1.00)	0.24 (0.00–0.33)	0.51 (0.20–0.70)

[a]*Number of years refers to the mean length of time series that egg-mass counts were conducted. The human footprint index ranges from 1 to 10 and increases with anthropogenic effects such as roads, agriculture, and fragmentation and was measured in the 1-km surrounding each breeding site. Modified sites were human created or altered. Drought frequency, modified sites, and hydroperiod are proportions. Drought was summarized as the proportion of summers in moderate or severe drought according to the Palmer hydrological drought index (PHDI ≤ −2).*

egg-mass counts at each site (R Development Core Team 2011). The EGSS model allows separate estimation of process variance (σ^2), which governs stochastic growth of the unobserved population, and sampling variance (τ^2), which affects observed abundance values (Humbert et al. 2009; Mills 2013). These growth estimates are robust to variation in the length of the time series and missing observations, although precision increases with number of observations (Humbert et al. 2009). After we estimated growth rate in each clade, we used the equation for exponential growth to project mean changes over time ($N_0 e^{rT}$) (Mills 2013).

EXTRINSIC FACTORS IN UNRESTORED SITES

We used the EGSS estimate of growth for each site as the response variable in linear-regression models to identify factors linked to population growth. We weighted each estimate by the inverse of its variance so that longer time series and more precise estimates of growth contributed more information. We used this 2-stage modeling approach because even small amounts of observation error can produce biased growth and covariate estimates, especially if error and environmental variation are correlated (Lindén & Knape 2009).

To identify extrinsic factors linked to growth in the 92 unrestored sites, we fit a set of models we based on patch characteristics and climatic relations we hypothesized would affect populations. To limit the model set, we included size (log$_e$ transformed) and hydroperiod (permanent or temporary) of each water body and the mean human footprint index value from a 1-km area around sites in all models. Although few studies explicitly link trends with water body size or hydroperiod, these characteristics are often strong predictors of distribution or abundance of amphibians (Karraker & Gibbs 2009; Gould et al. 2012). The human footprint index ranges from 1 to 10 and increases with anthropogenic effects, such as roads, agriculture, and fragmentation (Leu et al. 2008; USGS 2013). We also included the clade of each population in all models. We used this basic model ($\mu \sim$ clade $+ \log_e$[site size] $+$ hydroperiod $+$ footprint) as the starting point for evaluating hypotheses about how drought, site origin, and interactions among predictor variables affected growth. Although most sites we monitored lacked exotic predators such as American bullfrogs (*L. catesbeianus*) and introduced fishes, we did not have consistent information among data sources and thus excluded this factor from analyses.

After fitting the basic habitat model, we evaluated models with site size × hydroperiod and the footprint × hydroperiod interactions. The first model described the hypothesis that population growth increases with site size and permanence. The second model represented the hypothesis that populations in permanent sites surrounded by intact landscapes grow more than populations in temporary sites in highly modified landscapes. A drying water body can force individuals to emigrate terrestrially, an action that can increase probability of mortality. We expected these risks would be elevated in highly modified landscapes and ultimately reduce population growth.

We also fit models with additive and interactive effects of site origin and drought. Site origin described whether a water body had been created or physically altered by humans for reasons other than restoration. We hypothesized that populations in modified sites would have lower growth rates than populations in unmodified sites. The model with site origin × drought described the hypothesis that persistent drought affects population growth differently in natural and modified water bodies. The models with the site size × drought and hydroperiod × drought interactions describe our hypothesis that populations in small or temporary water bodies are particularly vulnerable to drought.

Drought was represented by the frequency of summers with moderate or more severe drought on the basis of mean July and August Palmer hydrological drought index (PHDI values ≤ -2) (NOAA 2013). The PHDI is a common measure of relative drought that reflects groundwater recharge and reservoir storage. Although Columbia spotted frogs breed in the spring, often while there is still extensive snow cover, we used values from only July and August because Palmer (and other) indexes do a poor job of quantifying moisture held in snowpack, the dominant form of precipitation for much of our study area (Dai et al. 2004).Also, amphibians in our region metamorphose during summer and often must disperse to suitable water bodies for foraging and winter hibernation. Lacking a strong a priori reason to select a particular time lag, we evaluated 1-, 2-, and 3-year lagged drought indexes. We used drought data with a 1-year lag (i.e., the summer before egg deposition) because it was the most strongly correlated with growth estimates.

We used differences in the Akaike information criterion (ΔAIC$_c$) and Akaike weights to measure support for competing models. Akaike weights represent the probability that a particular model is the best for a given set of models and data (Burnham & Anderson 2002). Among predictor variables, only site size and origin were even moderately correlated ($r = -0.51$). For all other variable pairs, $|r| \leq 0.27$. These correlations are well below the typical threshold of $|r| \leq 0.70$ used for screening redundant variables in regression analyses (Dormann et al. 2013). Before fitting models, we used Morans' *I* to test for spatial autocorrelation in growth estimates that we based on distance among breeding sites. Although many sites were <1 km apart, we did not find evidence of significant correlation ($I = 0.077$, $p = 0.446$) and concluded that a nonspatial model was adequate (Moran 1950).

EFFICACY OF SITE RESTORATION

On the basis of the best model from the set described in the previous section, we added the 6 restored sites to the data set of 92 unrestored sites and compared mean population growth. We did not include restored sites in the initial analyses because population trajectories after restoration actions may not be governed by the same habitat or climatic relations as other populations (Zedler & Callaway 1999). Time series from restored sites covered 5–12 years in the Great Basin clade and 15–16 years in the Utah clade.

Results

Growth Estimates

Across all 3 clades, annual exponential growth rate in the 92 unrestored sites ranged from −0.374 to 0.634 (both from the northern clade) (mean $\mu = -0.003$ [SE 0.011]). Growth was greatest in the Utah clade ($\mu = 0.035$ [0.022]), followed by the Great Basin (0.025 [0.028]) and northern clades (−0.012 [0.013]) (Supporting Information). Growth estimates were negative for 7 of 19 sites in the Utah clade, 5 of 8 sites in the Great Basin clade, and 40 of 65 sites in the northern clade. On the basis

Table 2. Models fitted to annual growth rate (μ) in egg-mass counts of the Columbia spotted frog (*Rana luteiventris*) at 92 unrestored sites.[a]

Model	k	R^2	ΔAIC_c	w_i
Clade + footprint + hydroperiod + (site size × drought)	9	0.35	0.00	0.29
Clade + site size + footprint + hydroperiod	7	0.31	0.29	0.25
Clade + site size + footprint + hydroperiod + drought	8	0.32	1.95	0.11
Clade + site size + footprint + hydroperiod + site origin	8	0.32	2.08	0.10
Clade + site size + footprint + (hydroperiod × footprint)	8	0.31	2.47	0.08
Clade + footprint + (hydroperiod × site size)	8	0.31	2.63	0.08
Clade + site size + footprint + hydroperiod + site origin + drought	9	0.32	3.97	0.04
Clade + site size + footprint + (hydroperiod × drought)	9	0.32	4.10	0.004
Clade + site size + footprint + hydroperiod + (site origin × drought)	10	0.32	6.21	0.01
Clade	4	0.03	24.92	<0.01

[a]*Abbreviations: k, number of model parameters; R^2, coefficient of determination; AIC_c, Akaike information criterion; ΔAIC_c, difference in the AIC_c between a particular model and the top-ranked model; w_i, probability that a model is the best for the given set of models and data.*

of exponential growth ($N_0 e^{rT}$) (Mills 2013) and the average time series of 11 years, egg-mass abundance was predicted to have increased approximately 32% in the Great Basin and 47% in the Utah populations. In contrast, abundance was predicted to have declined by 12% over the same period in the northern populations, where the species is considered secure.

Extrinsic Factors in Unrestored Sites

The model with the interaction between site size and drought frequency (measured with a 1-year lag) explained the most variation in growth and received the most support (Table 2). Growth decreased as disturbance increased in the surrounding landscape ($b = -0.020$ [SE 0.006) (Fig. 2a) and was lower in temporary ($b = -0.095$ [0.026]) than in permanent sites (Fig. 2b). The relation between site size and drought was complex. Population growth was positively correlated with site size and negatively correlated with drought frequency, but relative to large sites, growth of populations in small sites was lower during drought (Fig. 3). Occurrence of summer drought was mostly synchronous across the region since 1990, and there was significant variation in frequency and severity among the 3 clades (Fig. 4). The simple additive effect of drought in the third-ranked model was negative but imprecise ($b = -0.058$ [0.070]) (Table 2), likely because its effect depended on site size.

The basic model with site size, hydroperiod, and human footprint index received nearly as much support as the top-ranked model (Table 2). Population growth increased strongly with site size ($b = 0.020$ [SE 0.006]) (Fig. 2c), and negative growth was predicted for sites of ≤ 0.15 ha. The predicted effects of human footprint index ($b = -0.021$ [0.006]) and hydroperiod ($b = -0.088$ [0.025]) were similar to those in the top-ranked model. The remaining models with additive or interactive effects of drought and site origin explained little additional variation compared with the basic habitat model and received weak support. Notably, growth rates were simi-

lar in human-modified ($b = -0.025$ [0.033]) and natural sites.

Efficacy of Site Restoration

Because 2 models received similar support for the 92 unrestored breeding sites, we used both to measure the effect of site restoration. The base model with the addition of the restoration term received slightly more support than the comparable model with the interaction between site size and drought ($\Delta AIC_c = 0.58$), but the restoration term was similar in both models and there was clear support for greater growth in restored sites compared with unrestored sites (Supporting Information). On the basis of the top-ranked model, annual growth rate of egg masses in the 6 restored sites in the Utah and Great Basin clades exceeded growth in unrestored sites in these same clades by 17.9% (SE 8.6).

Discussion

Analyses of long-term data from 92 unrestored Columbia spotted frog breeding sites in 3 genetic clades revealed significant variation in growth that was strongly associated with patch characteristics, drought frequency, and restoration actions. Across the approximately 378,000-km^2 region, abundance of egg masses declined approximately 0.3% annually. Growth was positive in the 2 clades with greatest history of decline, however, including in the Great Basin, where the species is a candidate for listing under the Endangered Species Act. Populations in large water bodies were more likely to increase and were more resistant to drought than populations in small water bodies. We suspect negative growth rates in water bodies ≤ 0.15 ha partly reflects the greater susceptibility of small areas of habitat to environmental stochasticity (Lande et al. 2003). For example, Great Basin populations experienced the least drought but grew less than Utah populations, likely because the latter included
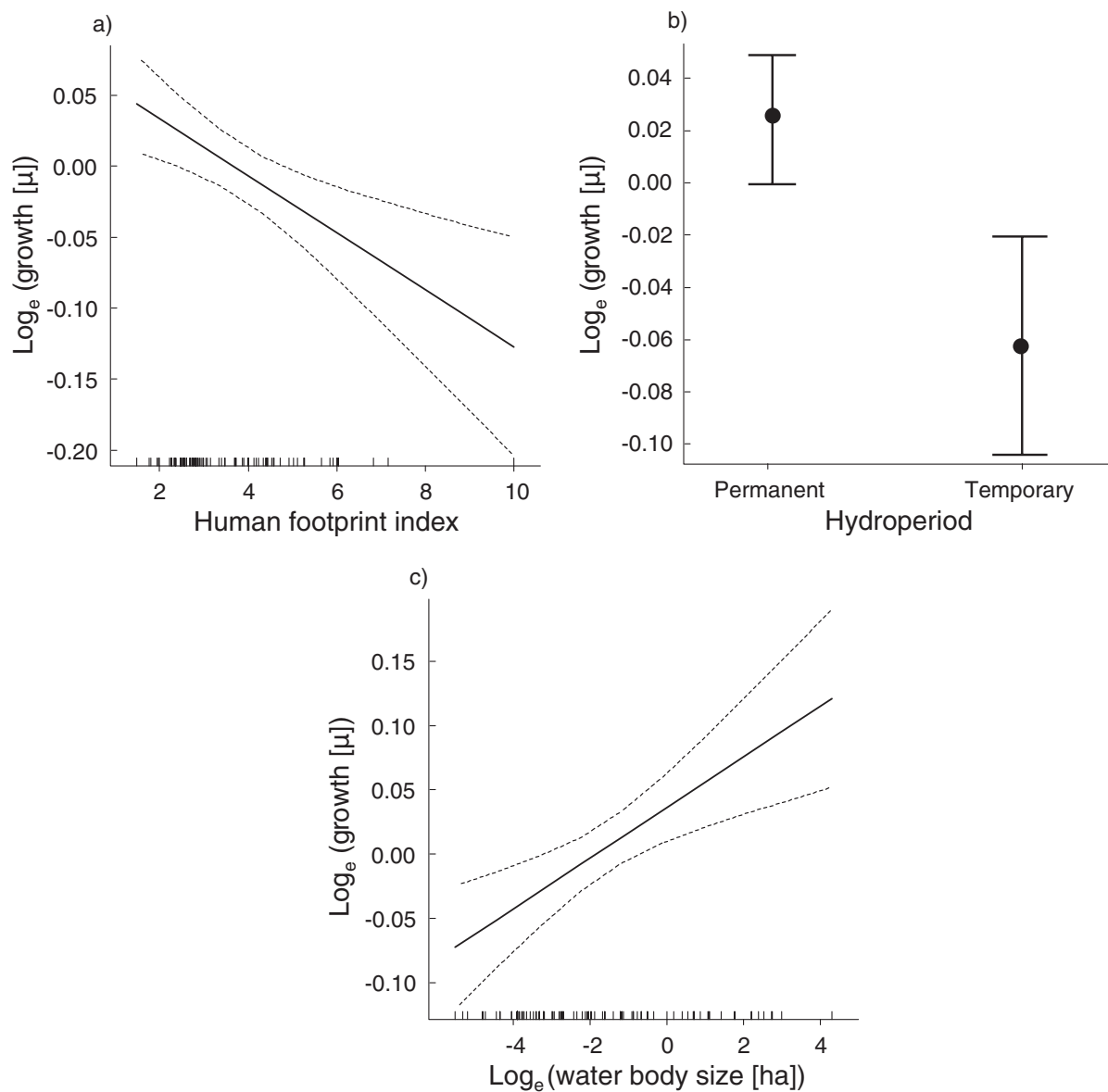
Figure 2. Predicted mean effects (95% CI) of (a) human footprint index, (b) hydroperiod, and (c) water body size on annual rate of change in number of egg masses of Columbia spotted frogs (Rana luteiventris) at 92 unrestored breeding sites. The additive effect of water body size was estimated from the second-ranked model (Table 2). In (a) and (c), hatch marks on the x-axis are values of the indicated variable. Some hatch marks represent >1 site.

several large spring complexes where the hydrology was relatively buffered against drought.

Only the northern clade experienced net negative growth. These populations experienced the greatest frequency and severity of summer drought, including 9 consecutive years of moderate or severe drought (PHDI $\leq$ −2.0) from 2000 to 2008 (Fig. 4). Persistent drought can reduce amount of habitat and cause decline or extirpation (Corn & Fogleman 1984). Although mechanisms are often unclear, potential causes of decline include skipped breeding opportunities and reduced survival of larvae, especially for species with slow or inflexible development (Leips et al. 2000; Daszak et al. 2005; Church et al.

2007). If failed recruitment were the primary mechanism of reduced growth for our populations, we would have expected support for our hypothesis of greater drought effects in sites with temporary hydroperiods. Instead, we found population growth in water bodies with permanent hydroperiod was approximately 9% greater than in sites that dried regularly, which is consistent with short-term studies of abundance or occupancy of Columbia spotted frogs in the Great Basin (Welch & MacMahon 2005; Wente et al. 2005). Likewise, production of juvenile wood frogs (*L. sylvaticus*) is >10 times higher in semipermanent than temporary wetlands in the northeastern United States (Karraker & Gibbs 2009).
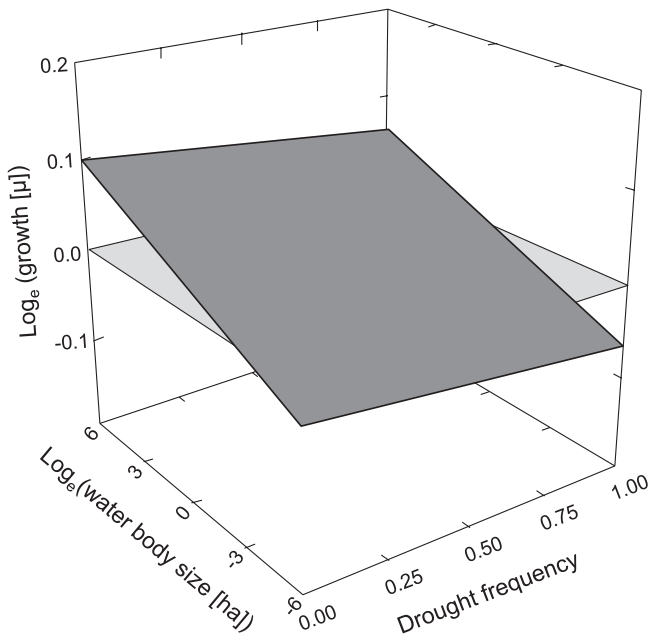
Figure 3. Predicted effect of the interaction between drought frequency and water body size (ha) on annual growth rate in number of egg masses for Columbia spotted frogs (Rana luteiventris) at 92 unrestored breeding sites (dark gray). Drought was measured as the frequency of moderate-to-severe drought (Palmer hydrological drought index ≤ −2) during the July and August before egg deposition. The light gray plane is the zero-growth line.

Egg-mass counts in 120 ponds in Sweden showed that over ≤17 years, population growth of *R. arvalis* and *R. temporaria* increases with hydroperiod (Loman & Andersson 2007). It is possible that the large, temporary sites we sampled held water long enough to ensure larvae metamorphose in most years and thus resulted in greater recruitment in these sites than in small, temporary sites.

Drought can also reduce survival of juvenile and adult amphibians, which decreases population growth more than comparable reductions in survival of larvae (Biek et al. 2002; Church et al. 2007). In an interesting contrast to our results, a 10-year study of a high-elevation population of Columbia spotted frogs in western Montana showed years with large snowpack (wet years) result in reduced juvenile survival and population growth (McCaffery et al. 2012). One of our sites is 12 km from the site studied by McCaffery et al. (2012), but it is a low-elevation, temporary marsh, where several instances of failed recruitment followed small snowpack and early drying (Hossack 2006; B.R.H. & P.S.C., unpublished data). Our data set contained few high-elevation populations, whereas the McCaffery et al. (2012) population was near the species' elevation limit, where snowpack has the greatest affect on activity. These contrasting relations
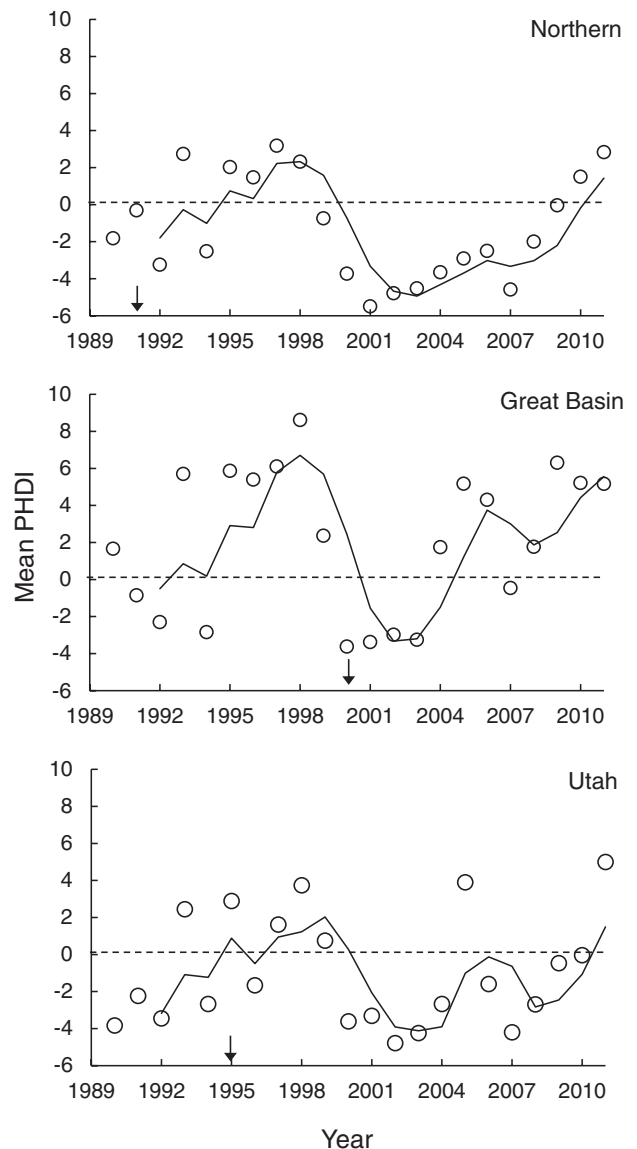

Figure 4. Mean of the July and August Palmer hydrological drought index (PHDI) during 1990–2011 in the 3 clades where we monitored abundance of Columbia spotted frog (Rana luteiventris) egg masses (solid lines, 3-year moving average; dashed lines, division between nondrought [≥−0.0] and drought [<−0.0] conditions; arrows, start of the earliest time series in each clade).

between drought and growth for populations in close proximity illustrate the importance of local patch characteristics and challenges in forecasting effects of climate change.

Previous investigations have provided mixed support for the suitability of modified water bodies for amphibians, particularly for species with specific requirements or that perform poorly in permanent water bodies (Pechmann et al. 2001; Petranka et al. 2007; Shulse et al.

2010). We expected lower growth in modified water bodies because these sites often host more predators or parasites than natural water bodies and because they tend to be in disturbed landscapes (Adams 2000; Johnson et al. 2002; Pearl et al. 2005), and modified water bodies have contributed to decline of amphibians in some areas (Johnson et al. 2013). However, population trends of Columbia spotted frogs were similar in modified and natural sites. Similar growth rates in modified and natural water bodies and greater growth in permanent compared with temporary water bodies may be explained, in part, by the absence of non-native predators from most of our sites.

We found a strong, negative effect of human disturbance on growth rates, but it was a local rather than a regional effect. For example, some of the largest declines occurred near developed areas inside Yellowstone National Park, an otherwise intact landscape. Site origin and human footprint index were weakly correlated ($r = 0.08$), which may have contributed to the small difference in growth between modified and natural sites. Constructed ponds have been critical to conservation of amphibians in some arid landscapes (Wente et al. 2005; Shoo et al. 2011). Positive long-term growth for Columbia spotted frogs and other species in human-modified water bodies is meaningful because these water bodies are likely to become an increasingly important resource as habitat is lost and climate changes.

Habitat restoration is often a critical component of conservation and was effective in our study system. Wetland restoration and habitat management were essential to the recovery of endangered natterjack toads (*Bufo calamita*) in England and species of concern in other aquatic systems (Denton et al. 1997; Gray et al. 2002), yet the long-term efficacy of restoration actions is rarely measured (Campbell et al. 2002; Petranka et al. 2007). In the Utah and Great Basin clades, sites that received management actions intended specifically to enhance habitat for frogs or other native species had 18% greater population growth than unrestored sites. The effects of restoration were especially substantial for the isolated Great Basin populations. Three restoration sites in southwestern Idaho initially had no egg masses detected. All these sites had positive growth, one of which contained >100 egg masses within 5 years.

It has been >20 years since the widespread decline of amphibians was identified as a clear example of the global biological diversity crisis and highlighted the need for long-term monitoring (Wyman 1990). Since then, there have been assessments of long-term changes in amphibian abundance across species (Houlahan et al. 2000; Adams et al. 2013) and for single populations or study sites (Bell et al. 2004; Daszak et al. 2005; Corn et al. 2011), but there are still few long-term studies of rates of change across multiple populations of a single species. Analyses such as ours from a large, climatically diverse region are critical for assessing status and trends and for identifying factors linked to abundance and extinction risk. Our results underscore the importance of large habitats in regional trends, but they also underscore the greater vulnerability of small habitats to drought and other forms of environmental stochasticity. Our data also provide encouraging results, such as net positive growth in the 2 clades where the Columbia spotted frog previously experienced the greatest declines. However, knowledge of vital rates and population trends from some areas where the species is most imperiled is still lacking. Although it is critical to continue monitoring, comparable long-term growth rates in modified and natural water bodies and rapid, positive responses to targeted conservation actions suggest pond construction and other forms of habitat management can be effective mitigation against drought.

Acknowledgments

Supporting Information

Summaries of estimated annual exponential growth rate, process variance, and sampling variance (Appendix S1) and models used to measure the efficacy of wetland restoration (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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