



Trends in Rocky Mountain amphibians and the role of beaver as a keystone species



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ABSTRACT

Despite prevalent awareness of global amphibian declines, there is still little information on trends for many widespread species. To inform land managers of trends on protected landscapes and identify potential conservation strategies, we collected occurrence data for five wetland-breeding amphibian species in four national parks in the U.S. Rocky Mountains during 2002–2011. We used explicit dynamics models to estimate variation in annual occupancy, extinction, and colonization of wetlands according to summer drought and several biophysical characteristics (e.g., wetland size, elevation), including the influence of North American beaver (*Castor canadensis*). We found more declines in occupancy than increases, especially in Yellowstone and Grand Teton national parks (NP), where three of four species declined since 2002. However, most species in Rocky Mountain NP were too rare to include in our analysis, which likely reflects significant historical declines. Although beaver were uncommon, their creation or modification of wetlands was associated with higher colonization rates for 4 of 5 amphibian species, producing a 34% increase in occupancy in beaver-influenced wetlands compared to wetlands without beaver influence. Also, colonization rates and occupancy of boreal toads (*Anaxyrus boreas*) and Columbia spotted frogs (*Rana luteiventris*) were ≥ 2 times higher in beaver-influenced wetlands. These strong relationships suggest management for beaver that fosters amphibian recovery could counter declines in some areas. Our data reinforce reports of widespread declines of formerly and currently common species, even in areas assumed to be protected from most forms of human disturbance, and demonstrate the close ecological association between beaver and wetland-dependent species.

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1. Introduction

Declines in amphibians exceed those of any other vertebrate class (Hoffmann et al., 2010). Amphibian declines have often affected species considered common or abundant, even in protected landscapes (Adams et al., 2013; Drost and Fellers, 1996; Muths et al., 2003). These observations accentuate the importance of providing land managers with accurate information on the status and trends of species they are responsible for conserving (Fancy et al., 2009; Wright, 1992). In response to this need, the U.S. Geological Survey's Amphibian Research and Monitoring Initiative (ARMI) began monitoring amphibian populations in

Glacier, Yellowstone, Grand Teton, and Rocky Mountain national parks in 2002 (Corn et al., 2005). Soon thereafter, the National Park Service's Greater Yellowstone Inventory and Monitoring Network made amphibians a focus (i.e., a vital sign) of their monitoring program in 2004 (Jean et al., 2005). At the same time, extensive declines of North American beaver (*Castor canadensis*) prompted its selection for monitoring in Rocky Mountain National Park (Fancy et al., 2009).

Occurrence data for amphibians in these four parks, which span the Continental Divide from Montana to Colorado, have been examined partially in the last decade. An early analysis of data from 2002 to 2003 revealed a north to south gradient of decreasing amphibian occupancy (Corn et al., 2005), which was driven in part by the well-documented declines of amphibians in the southern Rocky Mountains (Carey, 1993; Corn and Fogelman, 1984; Muths

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et al., 2003). The Corn et al. (2005) study did not assess potential causes of the decrease in occupancy from north to south, except to note that the three areas differ in climate and amount of anthropogenic influence. For example, Rocky Mountain National Park receives about five times the visitor use, adjusted for area, as the other parks and has by far the largest surrounding human population. A subsequent analysis of data collected from Yellowstone and Grand Teton national parks during 2006–2009 revealed mixed trends for species, although the short time series limited conclusions about changes in occurrence (Gould et al., 2012).

Here, we assess data collected from 2002 to 2011 from all four parks, and we incorporate the influence of summer drought and beaver to expand on previous analyses (Gould et al., 2012). Drought can negatively affect population growth of amphibians through several mechanisms, including reduced extent and duration of water in wetlands that decreases larval survival, and through negative effects on vital rates of moisture-sensitive juveniles and adults (Hossack et al., 2013a; Walls et al., 2013). Drought can also increase synchrony among local populations, subsequently increasing extinction risk (Piha et al., 2007; Ruetz et al., 2005).

As ecosystem engineers, beaver strongly affect aquatic and riparian habitats. Damming of streams creates new wetlands, can elevate the local water table, and prolongs the persistence of seasonal surface water (Hood and Bayley, 2008; Naiman et al., 1986; Westbrook et al., 2006). Beaver wetlands often have characteristics favored by many amphibians, including high insolation and shallow margins that increase water temperatures to speed growth and development of ectothermic larvae (Skelly and Freidenburg, 2000), which is especially important in regions such as the Rocky Mountains that have short growing seasons. As a result, beaver affect local abundance and dynamics of amphibians and other wetland-associated species (Dalbeck et al., 2014; Karraker and Gibbs, 2009; Rosell et al., 2005). And by increasing amount and diversity of wetland habitat, beaver can increase connectivity and buffer populations against drought and other stochastic sources of variation (Popescu and Gibbs, 2009). By incorporating information on beaver and annual variability of external stressors, we sought a better understanding of the link between beaver and amphibians, as well as how amphibian populations might respond to current and future changes in habitat conditions.

2. Materials and methods

2.1. Study system

The four national parks on the Continental Divide span approximately 8° of latitude (Fig. 1). Rocky Mountain National Park (ROMO) in Colorado is the southern-most study area and Glacier National Park (GLAC) in Montana represents the north end of the transect. Grand Teton and Yellowstone national parks, in north-west Wyoming (considered a single study area for this analysis, GRYN), are in the middle of the transect. The parks differ in size, climate, and potential degree of anthropogenic influence (Corn et al., 2005). Vegetation is similar among all three study areas (Peet, 1999). Lower-elevation montane forests are dominated by ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), or Douglas fir (*Pseudotsuga menziesii*), with western redcedar (*Thuja plicata*) and western larch (*Larix occidentalis*) in some areas. Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and white pines (*Pinus flexilis*, *Pinus albicaulis*) are the dominant trees in mid- to high-elevation subalpine forests. All study areas include alpine zones above tree line, but amphibians are rare above these elevations.

The amphibian fauna differs among the three study areas (Appendix Table A.1). The boreal toad (*Anaxyrus boreas*) occurs in all study areas, but it was too rare in ROMO to be included in the analyses. Columbia spotted frogs (*Rana luteiventris*) occur in both GLAC and GRYN, and the wood frog (*Lithobates sylvaticus*) occurs only in ROMO west of the Continental Divide. Barred tiger salamanders (*Ambystoma mavortium*) occur in ROMO and GRYN, but the long-toed salamander (*Ambystoma macrodactylum*) occurs only in GLAC. Boreal chorus frogs (*Pseudacris maculata*) occur in all parks, but our analyses of this species include only data from ROMO and GRYN. In GLAC, this species is found only at the eastern margin of the park and was not encountered during any of our surveys (B. Hossack, unpublished data). Other species that occur only at a small number of locations in parks (the Pacific treefrog [*Pseudacris regilla*] in GLAC, the Plains spadefoot [*Spea bombifrons*] in GRYN) or that were not encountered despite historical records (the northern leopard frog [*Lithobates pipiens*] in ROMO and GRYN), were not considered in our analyses. The Rocky Mountain tailed frog (*Ascaphus montanus*) is common in GLAC, but primarily occupies headwater streams and was not encountered in our surveys of lentic habitats.

2.2. Study design

Since the beginning of our monitoring program, we have randomly selected catchments distributed across parks and then attempted to sample all accessible, mapped wetlands within each catchment. From 2002 to 2004, we sampled wetlands in a small number (<10) of large catchments that were selected randomly. After realizing that we were not achieving the desired spatial representation, we switched in 2005 (2006 in GLAC) to a sampling design based on several, small catchments that were surveyed annually (i.e., we sampled the same catchments each year). We did not monitor in GLAC in 2005 because the GIS data necessary to identify small catchments was not yet available. The sampling frames excluded areas that were not considered suitable amphibian habitat (e.g., alpine areas). Catchments were selected randomly in a spatially-balanced manner to ensure adequate geographic representation of each park. In GRYN, catchment selection was further based on three levels of habitat quality (high, medium and low) that reflected amount and permanency of wetlands. We used stratified selection to ensure sufficient samples in 'high' and 'medium' quality habitat, which represented ~33% of catchments. For this analysis, we excluded the low quality habitat stratum analyzed by Gould et al. (2012) because that analysis showed these areas provided little information useful for understanding amphibian dynamics.

2.3. Data collection

We surveyed wetlands from approximately the end of snow-melt (early June to July, depending on elevation and year) through late July to mid-August. Timing of surveys was based on our long history of working in these systems and was targeted to maximize the opportunity to detect evidence of breeding activity (e.g., presence of larvae), because a species was considered present only if breeding was detected. All species spend ≥ 6 weeks as larvae (Werner et al., 2004), providing a long time window for detection. Surveys were conducted by searching the perimeter and shallow (≤ 0.5 m) areas of each wetland, using dip-nets in areas with thick vegetation or where water clarity was poor. From 2005 to 2011, most wetlands were visited once per year by a crew of two observers, who conducted two independent dip-net surveys (i.e., replicate surveys; Gould et al., 2012). From 2002 to 2004, there were fewer replicate surveys (average of 1.2–2.3 per year; Appendix Table A.2) and they were typically conducted on different dates

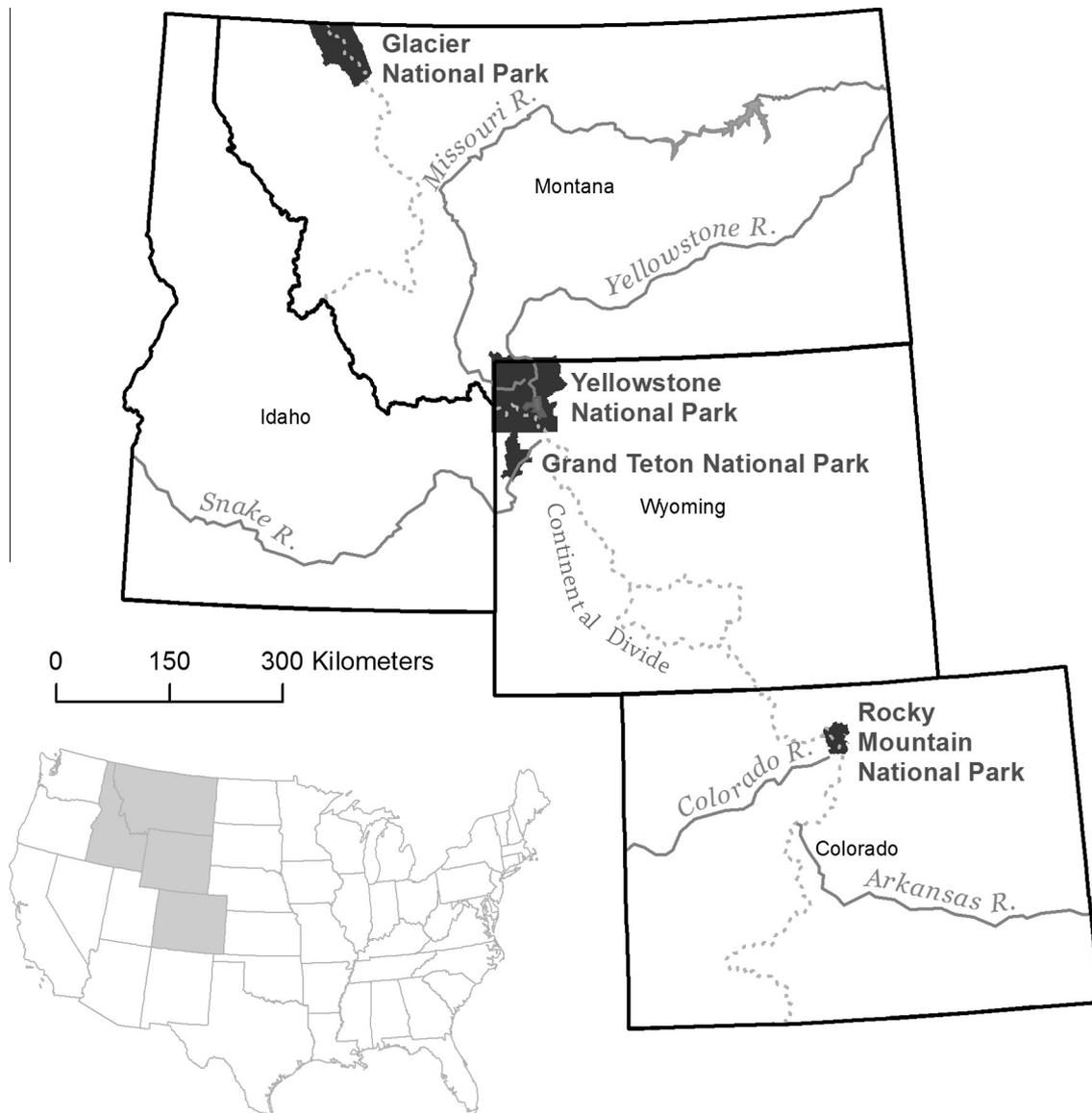


Fig. 1. Location of four national parks in the U.S.A. where we monitored wetland amphibians from 2002 to 2011. Grand Teton and Yellowstone national parks were combined for analysis.

within the year. Additional details on sampling methods are in [Corn et al. \(2005\)](#) and [Gould et al. \(2012\)](#).

2.4. Covariates and analyses

We developed a priori hypotheses based on biologically relevant metrics (i.e., covariates) at a workshop attended by researchers, park employees, and statisticians ([Table 1](#)). We used a small set of covariates that we expected would affect occupancy, detection, or vital rates ([Table 2](#)). Approximate wetland size, extent of wetland vegetation, maximum depth (<1 m, 1–2 m, >2 m), and evidence of whether a wetland was modified by beaver were recorded during each survey. Recognition of old beaver wetlands can sometimes be imperfect, but we searched for multiple lines of evidence to indicate beaver influence, including chewed trees and old lodges. We also recorded information on presence of fishes, but they occurred in <10% of sampled water bodies and were excluded in this analysis. Only wetlands that contained water when surveyed were included in the analyses. For lakes >2 ha, we used GIS to exclude open water areas >10 m

Table 1

Summary of variables used to model occupancy and detection of amphibians in Glacier National Park (GLAC), Grand Teton and Yellowstone national parks (GRYN), and Rocky Mountain National Park (ROMO).

Variable	Description
Group (g)	Study area: ROMO (Rocky Mountain NP), GRYN (Yellowstone & Grand Teton NP), GLAC (Glacier NP)
Veg	Mean (across years) emergent vegetation (%)
Depth	Mean (across years) of depth estimates (<1 m, 1–2 m, >2 m)
Area	Mean (across years) of estimated wetland area (for lakes \geq 2 ha, only the area within 10 m of shoreline was included)
Beaver	Influenced by beaver activity = 1, or not = 0
Relative Elevation (elev)	Difference between wetland elevation and the lowest elevation in each park group
Landscape water (water)	Total wetland area (ha) within 1 km of a surveyed site
PHDI	Palmer Hydrological Drought Index (July, August average) each year from the appropriate climate division

Table 2

Frequency or mean (SD) of wetland variables for Glacier National Park (GLAC), Grand Teton and Yellowstone national parks (GRYN), and Rocky Mountain National Park (ROMO). See Table 1 for description of the variables.

Park group	No. unique wetlands	No. beaver wetlands	Area (ha)	Depth (m)	Relative elevation (m)	Vegetation (%)	Landscape water (ha)
GLAC	916	93	0.34 (0.86)	0.82 (0.60)	564 (341)	45.2 (33.5)	11.2 (13.6)
GRYN	824	91	0.76 (2.58)	0.71 (0.46)	706 (215)	56.0 (30.11)	60.3 (59.1)
ROMO	320	11	1.34 (2.19)	0.97 (0.70)	794 (317)	47.6 (31.22)	21.2 (27.3)

from shore, because we did not consider deep, open water as amphibian habitat. As a measure of potential connectivity among populations, we used a GIS to calculate the area of mapped wetland habitat within a 1-km buffer around each surveyed site (USFWS, 2008). Elevation of sampled wetlands ranged from 951 m to 2308 m in GLAC, 1882 m to 3093 m in GRYN, and 2326 m to 3999 m in ROMO. To standardize the effect of elevation across parks, we calculated relative elevation for each wetland based on the lowest elevation in the respective park. Drought was represented by the mean July and August Palmer Hydrological Drought Index (PHDI), a common measure of moisture conditions that reflects ground water recharge and reservoir storage (Dai et al., 2004).

To model changes in wetland occupancy, we used the multi-season explicit dynamics model in program MARK (White and Burnham, 1999). Occupancy in year 1 (initial occupancy) is the estimated probability that a species is present, and 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 defined as the probability that a wetland occupied in one year is unoccupied the next year, whereas colonization is the probability that an unoccupied wetland in one year is occupied by the species the next year. Yearly occupancy estimates ($\hat{\psi}_i$) are derived from the extinction and colonization probabilities. Assumptions of this model include closure of occupancy status between surveys within years, proper identification of species, and no unmodeled heterogeneity in detection probabilities. We are confident the first two assumptions hold and have attempted to reduce violations of the third by using covariates most pertinent to these species. Missing occurrence data are accommodated in the multi-season model, but we must assume that dynamics are similar at surveyed and unsurveyed wetlands. We included data collected from 2002 to 2011. We switched methods for selecting catchments in 2005, thereby adding spatial variation to our time series. However, the areas surveyed during 2002–2004 were selected randomly and thus the resulting estimates are unbiased.

To reduce the number of models fitted, we used a multi-stage modeling process in which initial occupancy was park-specific and dynamic parameters were park and time (year) specific, while fitting several plausible detection models that allowed for time variation or associations with covariates. Except to characterize summer drought, we used the average value of covariates measured across time (if applicable) rather than letting them vary annually (Tables 1 and 2). Once the detection parameterization was chosen, we fit models based on hypothesized relationships with biophysical characteristics, summer drought, and the influence of beaver. We constructed models so that initial occupancy allowed for additive or interactive associations with park location. At the last stage, dynamic parameters were developed as linear functions of covariates, time variation, and park that represented a priori hypotheses about primary drivers of vital rates. We measured support for models based on differences in AIC_c and Akaike weights (w_i), which represent the probability that a particular

model is the best for a set of data and fitted models (Burnham and Anderson, 2002).

We analyzed data by species (genus for salamanders; see below) using a common set of covariates across parks. We allowed relationships between species and covariates to differ among parks by fitting interactive models for some covariates in which both intercepts and slopes varied by park. We also included models that pooled data across parks (i.e., common intercepts and slopes), as well as additive models with different intercepts but common slopes for each park group. We combined data from the two salamander species (*A. macrodactylum* in GLAC, *A. mavortium* in GRYN) because they use similar habitats and because pooling produced more precise estimates than analyzing them separately. Because these species did not co-occur in our sampling areas, extracting park-specific estimates provided information at the species level.

After determining the best model for each species-park combination (e.g., *R. luteiventris* in GLAC and GRYN), we estimated trends in occupancy by regressing the derived annual occupancy estimates against year. We weighted occupancy probabilities by the inverse of their standard error to account for uncertainty in estimates. To account for the two different catchment selection schemes used during 2002–2004 (few large catchments) and 2005–2011 (several small catchments), we estimated one trend for the entire time series (2002–2011) and one trend for the time series during which sampled catchments were fixed (2005–2011 in ROMO and GRYN, 2006–2011 in GLAC). We highlight cases where the trend differs according to times series.

3. Results

From 2002 through 2011, we surveyed 2060 wetlands across the three park units (Table 2). Primarily because of the change in sampling design in 2005, 70.5% of these wetlands were surveyed in 3 or fewer years; 50% were surveyed in only one year (Appendix Table A.2). Wetlands tended to be larger and deeper in ROMO, and wetlands in GRYN were shallowest with higher percentage of emergent vegetation. Wetlands in GLAC had the smallest mean area and were at lower relative elevations (Table 2). The amphibian fauna in ROMO is sparsely distributed and occupancy was too low to provide adequate data to fit models for all species but *P. maculata*.

3.1. *Ambystoma* spp. (GLAC and GRYN)

The top-ranked detection model for the two salamander species showed that detection varied by park and year (Table 3). Detection was also lower in beaver-influenced wetlands compared to non-beaver wetlands. Initial occupancy was park-specific and varied with elevation. In GLAC, initial occupancy of *A. macrodactylum* declined as elevation increased ($b = -0.004$; SE = 0.0006). In contrast, initial occupancy of *A. mavortium* in GRYN increased weakly with elevation ($b = 0.0004$ [0.0009]). For both species, initial occupancy increased with wetland depth ($b = 0.736$ [0.196]), and in GLAC, initial occupancy of *A. macrodactylum* increased with

Table 3
Top-ranked models used to estimate initial occupancy (Ψ), extinction (ε) and colonization (γ), and detection (p) of breeding amphibians in Glacier National Park (GLAC), Grand Teton and Yellowstone national parks (GRYN), and Rocky Mountain National Park (ROMO). Only models $\Delta AIC_c < 6$ are shown.

Model	k	Deviance	AIC _c	ΔAIC_c	w_i
<i>Ambystoma macrodactylum</i> (GLAC) and <i>A. mavortium</i> (GRYN)					
$\Psi(g * \text{elev} + \text{veg}[\text{GLAC}] + \text{depth} + \text{beaver}) \varepsilon(g + \text{year} + \text{depth} + \text{area} + \text{beaver}) \gamma(g + \text{year} + \text{depth} + \text{area} + \text{beaver})$ $p(g * \text{year} + \text{beaver})$	50	4881.47	4982.59	0.00	0.90
$\Psi(g * \text{elev} + \text{veg}[\text{GLAC}] + \text{depth} + \text{beaver}) \varepsilon(g + \text{year} + \text{depth} + \text{beaver}) \gamma(g + \text{year} + \text{depth} + \text{beaver}) p(g * \text{year} + \text{beaver})$	48	4888.41	4985.45	2.86	0.04
$\Psi(g * \text{elev} + \text{veg}[\text{GLAC}] + \text{depth} + \text{beaver}) \varepsilon(g + \text{year} + \text{depth} + \text{water} + \text{beaver}) \gamma(g + \text{year} + \text{depth} + \text{water} + \text{beaver})$ $p(g * \text{year} + \text{beaver})$	50	4884.86	4985.99	3.40	0.03
$\Psi(g * \text{elev} + \text{veg}[\text{GLAC}] + \text{depth} + \text{area}) \varepsilon(g + \text{year} + \text{depth} + \text{area}) \gamma(g + \text{year} + \text{depth} + \text{beaver}) p(g * \text{year} + \text{beaver})$	48	4889.62	4986.65	4.06	0.02
<i>Anaxyrus boreas</i> (GLAC and GRYN)					
$\Psi(\text{area} + \text{veg} + \text{beaver}) \varepsilon(g + \text{year} + \text{beaver} + \text{water}) \gamma(g + \text{year} + \text{beaver} + \text{water}) p(g * \text{year} + \text{area})$	47	1815.36	1910.35	0.00	0.76
$\Psi(\text{area} + \text{veg} + \text{beaver}) \varepsilon(g + \text{beaver}) \gamma(g + \text{beaver}) p(g * \text{year} + \text{area})$	30	1850.31	1910.72	0.37	0.13
$\Psi(\text{area} + \text{veg} + \text{beaver}) \varepsilon(g + \text{beaver} + \text{PHDI}) \gamma(g + \text{beaver} + \text{PHDI}) p(g * \text{year} + \text{area})$	32	1848.71	1913.18	2.82	0.04
$\Psi(\text{beaver} + \text{area} + \text{veg}) \varepsilon(g + \text{year} + \text{beaver}) \gamma(g + \text{year} + \text{beaver}) p(g * \text{year} + \text{area})$	45	1822.28	1913.19	2.84	0.04
$\Psi(\text{area} + \text{veg} + \text{beaver}) \varepsilon(g + \text{beaver} + \text{water}) \gamma(g + \text{beaver} + \text{water}) p(g * \text{year} + \text{area})$	32	1849.50	1913.96	3.61	0.02
<i>Pseudacris maculata</i> (ROMO and GRYN)					
$\Psi(g + \text{beaver} + \text{area} + \text{veg} + \text{area} * \text{veg}) \varepsilon(g * \text{year}) \gamma(g * \text{year}) p(g * \text{year} + \text{veg})$	63	3446.49	3575.17	0.00	0.48
$\Psi(g + \text{beaver} + \text{area}) \varepsilon(g * \text{year}) \gamma(g * \text{year}) p(g * \text{year} + \text{veg})$	61	3451.80	3576.32	1.15	0.27
$\Psi(g + \text{beaver} + \text{area} + \text{veg}) \varepsilon(g * \text{year}) \gamma(g * \text{year}) p(g * \text{year} + \text{veg})$	62	3451.31	3577.91	2.74	0.12
$\Psi(g + \text{beaver} + \text{area} + \text{veg} + \text{area} * \text{veg}) \varepsilon(\text{year}) \gamma(\text{year}) p(g * \text{year} + \text{veg})$	45	3488.98	3580.34	5.17	0.04
$\Psi(g + \text{beaver}) \varepsilon(g * \text{year}) \gamma(g * \text{year}) p(g * \text{year} + \text{veg})$	60	3458.01	3580.44	5.27	0.03
<i>Rana luteiventris</i> (GLAC and GRYN)					
$\Psi(\text{veg} + \text{area} + \text{beaver}) \varepsilon(g + \text{veg} + \text{area} + \text{beaver}) \gamma(g + \text{veg} + \text{area} + \text{beaver}) p(g * \text{year})$	33	4503.60	4570.10	0.00	0.94
$\Psi(\text{veg} + \text{area} + \text{beaver}) \varepsilon(g + \text{veg} + \text{area} + \text{beaver} + \text{PHDI}) \gamma(g + \text{veg} + \text{area} + \text{beaver} + \text{PHDI}) p(g * \text{year})$	35	4502.18	4572.74	2.64	0.05

Key: k, number of model parameters; AIC_c, second-order Akaike information criterion; ΔAIC_c , difference in 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.

wetland vegetation ($b = 0.037$ [0.006]). Despite lower detectability in beaver ponds, initial occupancy of salamanders was higher in beaver-influenced wetlands than other wetlands, but occupancy estimates were similar for both types of wetlands by the end of the study (Fig. 2a and b). Across all years, extinction and colonization rates for both species were higher in beaver ponds, which indicated they were more dynamic than non-beaver wetlands (Table 4). Salamander populations in large ($b = -0.044$ [0.048]), deep wetlands ($b = -0.514$ [0.291]) were also less likely to go extinct. Other models lacking wetland size or models that replaced size with amount of wetland area within a 1 km buffer of a surveyed site (i.e., landscape water) received moderate support, but they did not explain additional variance in data compared with the top model (Table 3).

Both species of salamanders decreased in occupancy during the study (Table 5). In GRYN, there was a large decline in occupancy for *A. mavortium* between 2002 ($\hat{\psi}_1 = 0.315$ [0.067]) and 2011 ($\hat{\psi}_{10} = 0.052$ [0.013]; Fig. 2). However, this trend was heavily influenced by the first 3 years of sampling. Considering only the estimates for 2006 to 2011—when we sampled the same catchments annually—occupancy declined from $\hat{\psi}_1 = 0.106$ (0.017) to $\hat{\psi}_7 = 0.052$ (0.013; Fig. 2). While this is a much smaller decline in occupancy compared with the change between 2002 and 2011, it still represents a 50% loss in number of occupied wetlands. In GLAC, the rate of decline in occupancy of *A. macrodactylum* between 2002 ($\hat{\psi}_1 = 0.700$ [0.046]) and 2011 ($\hat{\psi}_{10} = 0.569$ [0.033]) was greater than decline of *A. mavortium* in GRYN (Table 5). Based only on changes between 2006 ($\hat{\psi}_1 = 0.598$, SE = 0.033) and 2011 ($\hat{\psi}_7 = 0.569$, SE = 0.033), the negative trend was much weaker but the confidence interval still excluded zero (Table 5).

3.2. *A. boreas* (GLAC and GRYN)

Detection of *A. boreas* differed by park and year and was higher in small wetlands than in large wetlands. Estimated initial occupancy was similar in GLAC and GRYN and was low

($\hat{\psi}_1 = 0.062$ [0.015] for an average-sized wetland with 50% vegetation cover). In both park units, large ($b = 1.582$ [0.362]), beaver-influenced wetlands were more likely to be occupied (Table 3 and Fig. 2c and d). Extinction and colonization varied by park, among years, and according to the presence of beaver influence. Surprisingly, extinction was positively associated with amount of wetland area within 1 km of sites ($b = 0.0153$ [0.005]), indicating that more isolated sites were less likely to go extinct. In both park units, extinction was similar in beaver and non-beaver wetlands, but colonization was ≥ 2 times higher in beaver wetlands (Table 4).

Based on the top-ranked model, occupancy of *A. boreas* declined greatly between 2002 and 2011 in GRYN (0.062 [SE = 0.016] – 0.015 [SE = 0.005]), but was there was no trend in GLAC (0.062 [SE = 0.016] – 0.063 [SE = 0.016]) (Table 5). Based only estimates for 2006–2011 only, there was no trend in occupancy in either park unit. Notably, there was nearly equal support for a model in which extinction and colonization did not vary over time or as a function of wetland area within 1 km (Table 3). Estimates from this second-ranked model indicated occupancy declined from 0.07 (0.016) to 0.02 (0.004) in GRYN, while estimates increased slightly from 0.08 (0.016) to 0.11 (0.014) in GLAC. Three additional models also received at least modest support ($\Delta AIC_c \leq 3.61$), but it was primarily because they had similar structures as the two top-ranked models.

3.3. *P. maculata* (GRYN and ROMO)

Probability of detecting boreal chorus frogs varied among years and increased with amount of vegetative cover in wetlands (Table 3). Initial occupancy was much greater for GRYN than ROMO (0.368 [SE = 0.046] vs. 0.046 [SE = 0.023], respectively) and varied based on an interaction between wetland size and extent of vegetation. Surprisingly, initial occupancy was 2–3 times greater in wetlands not influenced by beaver activity, but this effect occurred primarily in GRYN and only from 2002 to 2004 (Fig. 2e and f). Extinction and colonization varied by park unit and year, but they were not associated with any of the covariates we evaluated. For both GRYN and ROMO, trends based on data from 2002 to

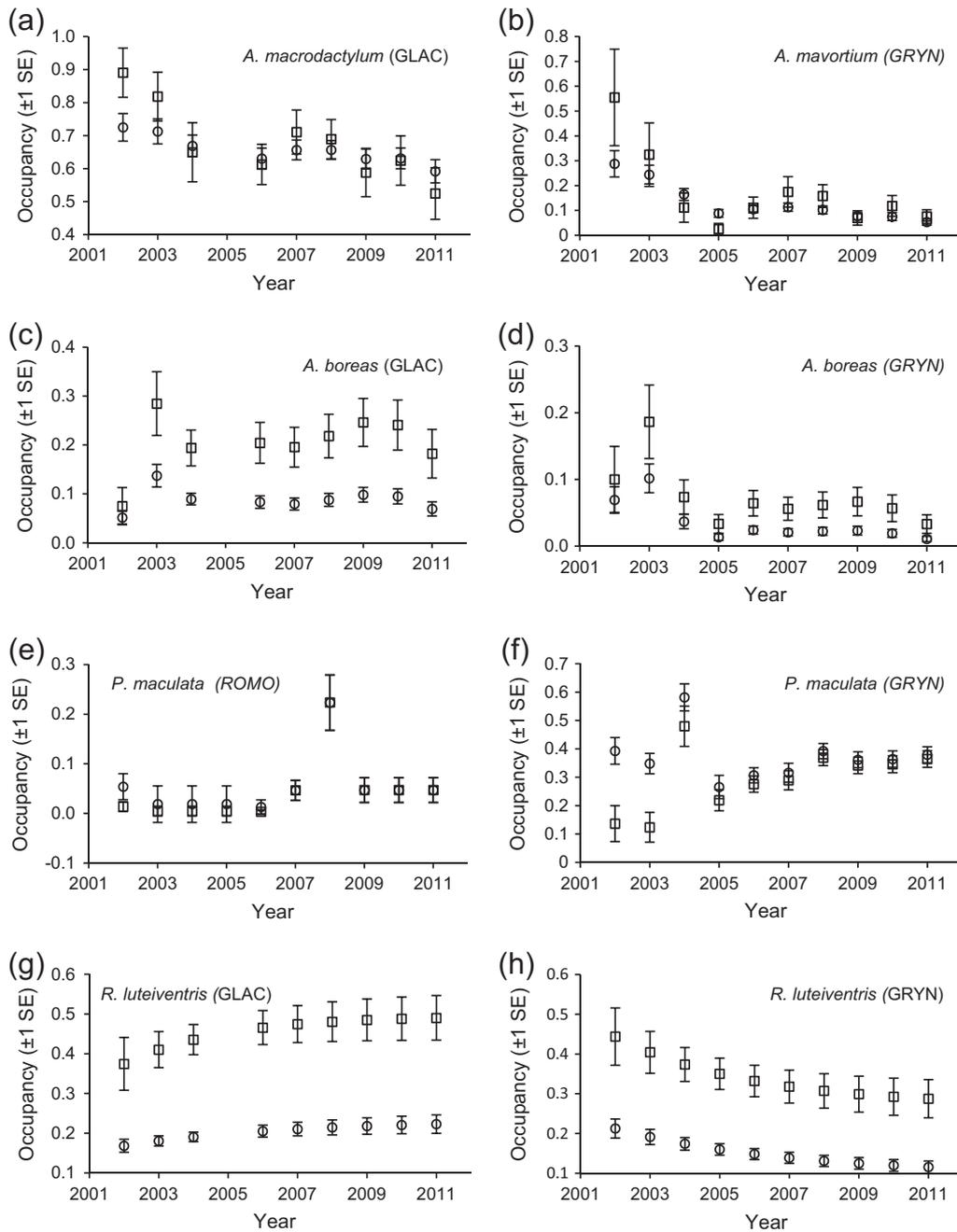


Fig. 2. Annual estimates of the probability of wetland occupancy by amphibians in beaver-influenced (squares) and wetlands not influenced by beaver (circles). Beaver-influenced wetlands were uncommon in Glacier National Park (GLAC) and were rare in Grand Teton and Yellowstone national parks (GRYN) and Rocky Mountain National Park (ROMO) (see Table 2), so estimates for other wetlands more closely represent the mean and trends in occupancy. Estimates were derived from the top-ranked model for each species.

Table 4

Mean annual extinction and colonization rates (SE) of amphibians in wetlands influenced by beaver (beaver = 1) or not influenced by beaver (beaver = 0) in Glacier National Park (GLAC) and Grand Teton and Yellowstone national parks (GRYN). Mean vital rates were derived from the top-ranked model for each species (see Table 3). *Pseudacris maculata* is not listed because its vital rates were not associated with presence of beaver.

Species	Park	Beaver = 0		Beaver = 1	
		Extinction	Colonization	Extinction	Colonization
<i>A. macrodactylum</i>	GLAC	0.042 (0.017)	0.056 (0.021)	0.210 (0.144)	0.144 (0.063)
<i>A. mavortium</i>	GRYN	0.258 (0.075)	0.012 (0.005)	0.531 (0.124)	0.055 (0.028)
<i>A. boreas</i>	GLAC	0.154 (0.050)	0.024 (0.009)	0.140 (0.059)	0.065 (0.026)
<i>A. boreas</i>	GRYN	0.369 (0.080)	0.009 (0.004)	0.349 (0.096)	0.025 (0.012)
<i>R. luteiventris</i>	GLAC	0.149 (0.024)	0.045 (0.006)	0.150 (0.037)	0.147 (0.031)
<i>R. luteiventris</i>	GRYN	0.166 (0.023)	0.018 (0.004)	0.167 (0.042)	0.062 (0.018)

Table 5
Annual rate of change (trend; 95% CI in parentheses) in wetland occupancy of breeding amphibians in Glacier National Park (GLAC), Grand Teton and Yellowstone national parks (GRYN), and Rocky Mountain National Park (ROMO). For each species, we estimated one trend for the entire time series (2002–2011) and one trend for the time series during which sampled areas were fixed.

Period	GLAC	GRYN	ROMO
<i>Ambystoma macrodactylum</i> (GLAC) and <i>A. mavortium</i> (GRYN)			
2002–2011	–0.0315 (–0.0407, –0.0224)	–0.0229 (–0.0294, –0.0164)	–
2006–2011	–0.0177 (–0.0223, –0.0130)	–0.0155 (–0.0196, –0.0114)	–
<i>Anaxyrus boreas</i>			
2002–2011	–0.0014 (–0.0085, 0.0057)	–0.0041 (–0.0082, –0.0001)	–
2006–2011	–0.0019 (–0.0109, 0.0070)	–0.0005 (–0.0034, 0.0024)	–
<i>Pseudacris maculata</i>			
2002–2011	–	0.0004 (–0.0195, 0.0203)	0.0043 (–0.0076, 0.0162)
2005–2011	–	0.0174 (0.0038, 0.0311)	0.0073 (–0.0191, 0.0334)
<i>Rana luteiventris</i>			
2002–2011	0.0086 (0.0065, 0.0108)	–0.0103 (–0.012, –0.0082)	–
2006–2011	0.0048 (0.0037, 0.0060)	–0.0075 (–0.0090, –0.0060)	–

2011 indicate <3% total change in occupancy. Based on 2005–2011 estimates, there was a positive trend in occupancy in GRYN but no trend in ROMO (Table 5).

3.4. *R. luteiventris* (GLAC and GRYN)

Detection probabilities for *R. luteiventris* differed by park unit and year, but initial occupancy did not differ between the park units (Table 3). *R. luteiventris* was most likely to breed in large, beaver-influenced wetlands with extensive vegetation. Occupancy in each park was approximately twice as high in beaver-influenced wetlands than in wetlands not modified by beaver (Fig. 2g and h). Extinction and colonization (especially) were park-specific and both increased with wetland size (extinction: $b = 0.048$, $SE = 0.0023$; colonization: $b = 0.609$, $SE = 0.094$). As for *A. boreas*, extinction of *R. luteiventris* was similar in beaver and non-beaver wetlands, but colonization was much more likely in beaver wetlands (Table 4).

Trends in occupancy of *R. luteiventris* differed between the two park units (Table 5). In GLAC, occupancy increased by 39% between 2002 and 2011 (0.207 [0.019] – 0.286 [0.025]). In GRYN, occupancy decreased by ~50% during that same time period (0.207 [0.019] – 0.108 [0.015]). Based on estimates for 2006 to 2011, the patterns were the same, but the respective trends were weaker.

4. Discussion

Despite widespread awareness of global amphibian declines, there is still little information on long-term trends or ecological factors associated with trends across broad spatial scales, even for most widely-distributed species. Our analysis of occurrence of breeding populations for five species of amphibians in four national parks in the U.S. Rocky Mountains corroborates earlier results on their status—amphibians generally increase in occurrence from south to north, a pattern that at least partially reflects declines in recent decades (Corn et al., 2005). Based on estimates for the entire time series of data from 2002 to 2011, trends in amphibian occupancy of wetlands were negative for 4 combinations of species and park, changed little for 3 species-park combinations, and was positive for only 1 species-park combination.

Our results indicate a decline in occupancy for the two species of salamanders regardless of time period examined, although the magnitude of decline varied with time. The negative trends for salamanders were heavily influenced by the first 3 years of sampling, when we selected new monitoring areas annually. Compared to sampling the same areas each year, selecting new sampling areas increases spatial variation and reduces power to

detect change (MacKenzie et al., 2006). However, based only on estimates from 2006 to 2011—when we sampled the same catchments annually—occupancy of *A. mavortium* in GRYN declined by 50%. Declines for both salamander species occurred most commonly in shallow wetlands and, for *A. macrodactylum* in GLAC, at high elevations. These patterns of decline in shallow wetlands are consistent with the analysis of 2006–2009 data in GRYN that indicated *A. mavortium* was >3 times as likely to be present in permanent wetlands as in seasonal wetlands (Gould et al., 2012). We did not attempt to distinguish between permanent and seasonal wetlands in the current analysis, but maximum depth captures much of this information. We suspect the relationship between salamander occupancy and depth reflects more consistent availability of breeding habitat and greater recruitment of salamanders from deep water bodies, possibly resulting in larger local subpopulations that are less prone to extinction. Deep water bodies are especially important at high elevations, where larvae often must overwinter at least once to complete metamorphosis.

Trends in wetland occupancy by *R. luteiventris* differed greatly between GLAC and GRYN. Occupancy increased in GLAC, but decreased by ~50% between 2002 and 2011 in GRYN. The decline of *R. luteiventris* in GRYN concurs with a recent synthesis of long-term trends in abundance across several populations. Trends in abundance of egg mass counts (a surrogate for number of breeding females) between 1991 and 2010 at 98 breeding sites varied across the northwestern U.S., but they declined 1.2% per year in the northern Rocky Mountains (Hossack et al., 2013a). One formerly-large population (>1000 adults) in central Yellowstone NP that was included in the Hossack et al. (2013a) analysis declined >80% between the 1950s and 1990s and now appears close to extirpation (Turner, 1960; Patla and Peterson, 1999; Patla, unpublished data). Across the northwest U.S., declines in abundance of egg masses were linked with frequency of moderate-to-severe droughts, especially for small, temporary wetlands. In our current analysis, *R. luteiventris* occupancy and colonization increased with wetland size. But surprisingly, wetland depth and drought severity were not important predictors of occupancy or vital rates for any species, even though summer conditions in GLAC and GRYN transitioned from severe drought during early years of monitoring to average or moister conditions during the last 3 years of monitoring (Appendix Fig. A.1). Our use of average site characteristics such as depth rather than dynamic site-level covariates may have limited our ability to discern climate-driven effects on extinction and colonization.

There is now a long history of documented amphibians declines in our region, but identifying causes has been challenging, in part because many declines have occurred on protected landscapes with little human disturbance. The amphibian chytrid fungus,

Batrachochytrium dendrobatidis (Bd), is present throughout the region and has reduced survival of adult *A. boreas* at a location near Grand Teton NP (Muths et al., 2008; Pilliod et al., 2010). This fungus has likely had a role in the long-term decline of *A. boreas* in the southern Rocky Mountains (Carey, 1993; Muths et al., 2003), and it is plausible it contributed to long term declines elsewhere in the region. The fungus also infects *R. luteiventris* and species in the tiger salamander complex (*A. tigrinum*, *A. mavortium*), sometimes at greater prevalence than for *A. boreas* (Davidson et al., 2003; Hossack et al., 2013b), but we cannot link it with declines for these species. Histological examinations and cultures of individuals from mortality events have also confirmed mortality of amphibians from ranavirus (family Iridoviridae, genus *Ranavirus*) infection in GRYN (USGS, 2007). Ranaviruses infect reptiles, amphibians, and fishes and can be transmitted among classes (Brenes et al., 2014). There is increasing evidence linking ranaviruses with amphibian declines (Price et al., 2014), but how often they are a primary cause of decline vs. an opportunistic infection in animals with already-weakened immune systems is unclear (Robert, 2010). Thus, the potential role of ranaviruses in population declines merits further research in this region.

Uncertainty around estimates of distribution or vital rates such as extinction (or the inability to even generate estimates) has added to the challenge of identifying causes of declines for some species. For example, there was much uncertainty in estimates for *A. boreas*, the rarest species for which we were able to estimate occupancy. All point estimates suggested a decline in occupancy regardless of the time series examined, but only the 2002–2011 time series in GRYN differed from zero, and then barely so. Surprisingly, increasing isolation, as measured by amount of wetland habitat within 1 km, reduced the probability of extinction. We suspect this relationship may reflect local shifts in breeding sites by small populations where there are several suitable wetlands, whereas individuals from populations in areas with fewer wetlands are more loyal to a particular breeding site. Positive associations between isolation and population size of amphibians have been documented previously, which might result from concentrated breeding efforts by individuals when there are fewer potential sites to choose among (Hossack et al., 2013c; Veysey et al., 2011). The lack of clear trend in *A. boreas* occupancy in GLAC and GRYN should not be interpreted as evidence that the species is secure. We lack historical information on the distribution and abundance of toads in GLAC, but historical accounts for GRYN and ROMO indicate extensive declines in occurrence and abundance (Carey, 1993; Corn et al., 1997; Koch and Peterson, 1995). These declines may have stabilized, but they have not reversed.

Although our results for *P. maculata* do not indicate decline in ROMO, we were unable to incorporate data from the three other formerly-widespread amphibian species in that park. In our study, catchments selected randomly for sampling in ROMO often failed to include locations where amphibian populations persist. The lack of observations in ROMO and the resulting inability to include most species in our analyses likely reflects real and serious decline of amphibians in the southern Rocky Mountains (Corn and Fogleman, 1984; Carey, 1993; Muths et al., 2003). For example, data from repeat visits in 2000 (Muths, unpublished) to sites surveyed during 1988–1990 (Corn et al., 1997) suggest long-term, continuing declines for at least 2 species: naïve (unadjusted for detection) occupancy declined from 6% to 3% for *A. boreas* and from 26% to 12% for *P. maculata* between the 1988–1990 and 2000 surveys. Naïve occupancy of *L. sylvaticus* (6%) and *A. mavortium* (7–9%) differed little between the 1988–1990 and the 2000 surveys. Given the overall low occurrence of amphibians in ROMO after 2000, it is not surprising that much of the data were too sparse to analyze. In contrast, a study focused on the west (and wetter) side of ROMO indicated that *L. sylvaticus* and *P. maculata* were common in some

areas that had extensive beaver ponds (Scherer et al., 2012), but these areas were not selected with our sampling strategy.

Even though the only species in ROMO we could incorporate into our analyses (*P. maculata*) was not positively associated with beaver, we expect that restoration of beaver could be a key part of maintaining and recovering amphibians and other aquatic species throughout the region. Aside from common habitat associations such as wetland size and vegetation, influence of beaver was the only biophysical variable that was consistently linked with amphibian occurrence and dynamics. The importance of beaver-influenced wetlands to amphibians was evinced by its presence as a parameter describing initial occupancy or extinction and colonization in the top-ranked model for every species. Averaged across all species and parks and years, amphibian occupancy was 34% higher in beaver-influenced wetlands than in wetlands without beaver influence (0.283 vs. 0.211, respectively). Beaver influence was especially important for occupancy of *A. boreas* (0.139 in beaver-influenced wetlands vs. 0.061 in other wetlands) and *R. luteiventris* (0.399 in beaver-influenced wetlands vs. 0.178 in other wetlands). These differences were driven primarily by much higher rates of colonization in beaver ponds, rather than differences in extinction, and might reflect the preference by these species for open, warm wetland habitats.

Notably, other studies have found even larger effects of beaver on amphibian occupancy (e.g., Popescu and Gibbs, 2009). And several studies in North America and Europe have documented increased population size or production of juvenile amphibians in beaver ponds (e.g., Dalbeck et al., 2014; Karraker and Gibbs, 2009). To our knowledge, previous studies have examined effects of beaver on amphibian abundance or dynamics only over short time periods (≤ 3 years). Here, we show persistent effects of beaver that fundamentally alter local communities and extinction risks over several generations. Further, the effects of beaver are disproportionate to their relative abundance across the landscape (9.5% of sampled wetlands), consistent with the definition of a keystone species (Naiman et al., 1986; Power et al., 1996).

The strong association between beaver and amphibians suggests recent increases in beaver colonies in GRYN have likely benefited amphibians at least at local spatial scales (Smith and Tyers, 2012). For example, ponds that beaver constructed in two areas in Grand Teton NP during summer 2011 were colonized and used for breeding by *A. boreas* in 2012, even though we had not detected *A. boreas* breeding in that area since monitoring began in 2005. We are unaware of data on trends in beaver colonies in GLAC, but the relationship between beaver and amphibians is especially critical on the arid, east side of the park. Despite the strong positive effect of beaver on occupancy for four of five amphibian species, we are uncertain if beaver are common enough to significantly affect trends across the broad spatial scale we sampled. But at local scales that are most relevant to managers, enhancing beaver populations can create habitat favorable to many wetland species (e.g., extend hydroperiods, increase water temperatures) and increase population connectivity (Hood and Bayley, 2008; Popescu and Gibbs, 2009; Scherer et al., 2012). Reintroduction of beaver has been linked with recovery of rare amphibians and other wetland species (Dalbeck et al., 2007), and is now being used as a management tool specifically for rare species (Hossack et al., 2013a; Shoo et al., 2011).

Our results from 11 years of monitoring in four large national parks revealed more declines than increases in wetland occupancy but highlight the critical role of beaver in creating or favorably modifying wetland habitat. The declines we identified seem especially prevalent in GRYN. However, the prevalence and extent of declines in GRYN are likely exceeded by those in ROMO, where most species were too rare to include in our analyses due to declines in the last 30 years. A recent assessment of trends in

amphibian occupancy across the U.S. showed habitat preservation provided by national parks and other protected lands does not shield amphibians from decline (Adams et al., 2013), as exemplified by the apparent extinction of *L. pipiens* in GRYN and ROMO several decades ago (Ray et al., 2014). Indeed, declines of formerly common species in national parks and other protected areas are one of the hallmarks of the amphibian decline phenomenon (e.g., Drost and Fellers, 1996; Corn et al., 1997). Our data, representing a view at the regional level, are consistent with this assessment. We provide additional evidence of continuing declines and—in the case of *A. boreas*, continuing rarity—in putatively pristine areas.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.05.005>.

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