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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 $\geqslant 2$ 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 Fogleman, 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 northwest 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 snowmelt (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 $\geqslant$6 weeks as larvae (Werner et al., 2004), providing a long time window for detection. Surveys were conducted by searching the perimeter and shallow ($\leqslant$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