

Status of amphibians on the Continental Divide: surveys on a transect from Montana to Colorado, USA

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The Rocky Mountain Region of the United States Geological Survey's Amphibian Research and Monitoring Initiative is conducting monitoring of the status of amphibians on a transect that extends along the Continental Divide from Canada to Colorado and comprises four National Parks. Monitoring uses visual encounter surveys to determine site occupancy, with multiple visits to a subset of sites to estimate detection probabilities for each species. Detection probabilities were generally high (above 0.65) among species. There was a gradient in site occupancy, with most species scarce in the south and relatively common in the north. For example, *Bufo boreas* is close to extinction in Rocky Mountain National Park, was found at fewer than 5 % of sites in Yellowstone and Grand Teton National Parks in the middle of the transect, but occurs at approximately 10 % of sites in Glacier National Park. The salamander *Ambystoma tigrinum* was rare in Rocky Mountain and occurred at less than 25 % of sites at Yellowstone and Grand Teton, but *A. macrodactylum* occurred at more than 50 % of sites in Glacier. There are numerous differences among parks, such as latitude, climate, numbers of visitors, and human population density in the surrounding landscape. The degree to which these factors have influenced the current distribution and abundance of amphibians is unknown but should be a focus of additional research.

INTRODUCTION

Amphibian declines have occurred in the western United States at a disproportionate rate (BRADFORD, 2005). These declines are not restricted to areas where land use has directly

altered habitat, but have occurred on protected federal lands including national parks and wilderness areas (DROST & FELLERS, 1996; KNAPP & MATTHEWS 2000; MATTHEWS et al., 2003, MUTHS et al., 2003). To determine the status and trends of amphibian species in the Rocky Mountains, which contain some of the United States' most significant protected landscapes, the Rocky Mountain Region of the United States Geological Survey Amphibian Research and Monitoring Initiative (ARMI) has established a transect along the Continental Divide that includes four national parks as middle-level monitoring sites. The middle level refers to a pyramid of monitoring efforts, starting with base-level inventories over large geographic areas and ending with focused apex studies at a few sites (HALL & LANGTIMM, 2001; CORN et al., 2005). At the middle level, surveys are conducted within a defined study area, such as a national park, with a sampling design that allows inference about the status and trends of the amphibians within that area.

The national parks on the Continental Divide are spaced across about 8° of latitude, from Rocky Mountain in Colorado, through Grand Teton and Yellowstone in northwest Wyoming (referred to collectively as GYE for brevity and because they compose the center of the Greater Yellowstone Ecosystem), to Glacier in northwest Montana (fig. 1). The parks differ in size, climate, and potential degree of anthropogenic influence (tab. 1). All three study areas are characterized by similar zones of vegetation. At lower elevations, the coniferous montane forest is dominated by ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*) or Douglas fir (*Pseudotsuga menziesii*), with western redcedar (*Thuja plicata*) and western larch (*Larix occidentalis*) in Glacier. The mid-elevation subalpine forests are composed primarily of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and white pines (*Pinus flexilis*, *P. albicaulis*). There are also significant alpine habitats above tree line, which decreases about 100 m in elevation for every 1° north in latitude, from about 3500 m in Rocky Mountain to 2600 m in Glacier (PEET, 1988).

Amphibian declines have occurred to the greatest extent at the southern end of the transect. In Rocky Mountain National Park, the boreal toad (*Bufo boreas*) is nearing extinction (MUTHS et al., 2003) and the northern leopard frog (*Rana pipiens*) has not been observed since 1974 (CORN et al., 1997). At the northern end of the transect, surveys in Glacier have found all of the Park's resident amphibian species, and there is little suggestion of recent declines (MARNELL, 1997; ADAMS et al., 2005; PSC & BRH, unpublished). Surveys in the 1990s and in 2000 and 2001 suggest that amphibian declines in the two parks of the GYE may be intermediate between Rocky Mountain and Glacier. *Rana pipiens* has largely disappeared from the GYE, and *B. boreas* is present, but at a reduced number of locations (KOCH & PETERSON, 1995; VAN KIRK & PATLA, 2000; PATLA & PETERSON, 2001a-b).

Conducting surveys to determine status and trends of amphibians in all three study areas (Glacier, GYE, Rocky Mountain) provides the ability to monitor changes over an unprecedented latitudinal gradient and the opportunity to compare changes in status of amphibians to gradients in climate and habitat. Given the erratic nature of the population dynamics of many amphibian species, ARMI has chosen to follow the advice of GREEN (1997) and concentrate on detecting change in numbers of populations rather than numbers of individuals within populations (CORN et al., 2005). We determine status of each species by using the presence or absence of breeding at individual sites to estimate occupancy, expressed as the proportion of sites occupied. Trends will be assessed by examining changes in occupancy once

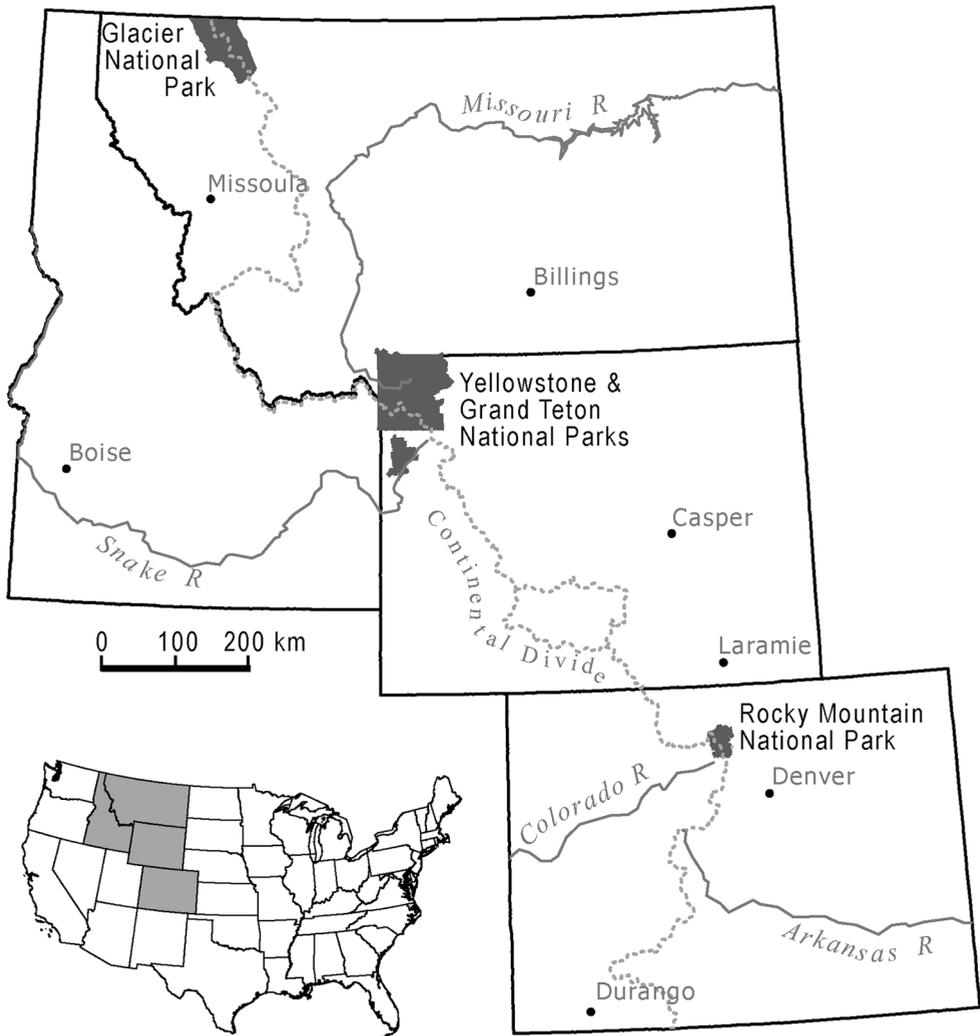


Fig. 1. – The three study areas are distributed on the Continental Divide. The scale bar refers to the four states figured and not to the inset United States map.

enough data are collected for reliable analyses. However, failure to detect presence of a species during a visit to a site may not mean that the species is absent. Therefore, we employ multiple visits to sites and recently-developed statistical tools (MACKENZIE et al., 2002, 2003) that incorporate detection probabilities to estimate occupancy.

The ultimate goal of Rocky Mountain ARMI is to conduct these surveys over the long term, in collaboration with the National Park Service. The data and analyses will provide park managers with valuable information, such as whether declines seen so far in the south are

Table 1. – Selected statistics describing the location, climate, and human influences on the three study areas on the Continental Divide. Park areas and use statistics are from ANONYMOUS (2004). Climate data are the averages of National Climate Data Center reporting stations within or at the margins of the parks.

Trait	Glacier	GYE	Rocky Mountain
Size (ha)	410,178	1,033,389	107,577
Central latitude	48°37'N	44°22'N	40°22'N
Central longitude	113°49'W	110°33'W	105°42'W
2003 recreational visits	1,664,046	5,375,068	3,067,256
2003 backcountry overnight stays	22,958	59,036	36,012
Nearby population ¹	851,000	528,000	3,925,000
1961-1990 mean annual temperature (°C)	4.7	2.7	4.2
1961-1990 mean annual precipitation (mm)	614	527	457

¹ United States: 2000 Census, sum of county populations where the central coordinate of the county lies within 150 miles (241 km) of the central coordinate of the study area; Canada: 2001 Census, sum of Census Divisions 02 and 03 in Alberta and 01 and 03 in British Columbia (<www.statcan.ca>).

moving north, or whether amphibians that have declined are beginning to recover. Our objectives in this paper are to describe the design of surveys on the transect, report the rates of site occupancy for each species for the first two years of observations, and provide initial estimates of trend in site occupancy for *B. boreas* in Glacier.

METHODS

Our sampling units were a set of hierarchically nested drainage catchments from the USGS Elevation Derivatives for National Applications Project (KOST & KELLY, 2001). Drainages were overlaid onto National Wetlands Inventory (NWI) maps and aggregated to include 10-50 identifiable water bodies, which resulted in 40 catchments in Rocky Mountain and 80 in Glacier. There were 1060 catchments in GYE before aggregation. Because of the large number of catchments in GYE, we did not aggregate them until one was selected for sampling. We selected survey units by drawing systematic random samples in each study area to ensure spatial balance. The goal was to survey every accessible water body in selected catchments at least once, with a subset (Glacier and GYE) or all (Rocky Mountain) sites surveyed twice or more to estimate detection probabilities. Duplicate surveys were achieved by independent surveys on different days or on the same day by biologists working independently or working together at different times. For example, areas with numerous small water bodies were sometimes sampled independently by each biologist. Large sites such as wet meadows or river valleys were sampled by two biologists simultaneously. We used visual encounter surveys (HEYER et al., 1994) to search for all life stages of amphibians (embryo, larva and adult) in accessible portions of the water body, using dip nets to sample areas with

limited visibility, and recorded site (e.g., pond area, extent of emergent vegetation) and sampling covariates (e.g., temperature, date) for all surveys (ADAMS et al., 2005). A site was considered to be occupied only if breeding had occurred there, as indicated by presence of egg masses, larvae, or recently metamorphosed juveniles. Presence of adults not engaged in breeding activity was insufficient to consider a site as occupied.

We estimated detection probabilities and occupancy using the program PRESENCE (MACKENZIE et al., 2002). For this analysis, we used the simplest model, assuming constant probabilities of detection and site occupancy. Descriptions of the methods are available elsewhere (MACKENZIE et al., 2002, 2003; MACKENZIE & BAILEY, 2004).

To provide an early assessment of trends in populations of *B. boreas* in Glacier, we compared changes in numbers of occupied sites in three catchments that have been monitored each year from 1999 to 2002 (restrictions due to extensive fires in Glacier in 2003 prevented access to our sites). However, somewhat differing levels of effort among years made estimation of occupancy problematic, so we computed year-to-year estimates of trend (GREEN, 2003) as: $\text{trend} = \ln(N_t/N_{t-n})$, where N = the number of occupied sites, t = the current year, and n = a previous year (1 to 3, in this case). Only sites that were sampled in both years of the comparison were included in the calculation of trend. Positive values of trend indicate increases in site occupancy, and negative values indicate decreases.

RESULTS

We surveyed 140 (2002) and 79 (2003) sites in 15 catchments in Rocky Mountain, 183 (2002) and 189 (2003) sites in 17 catchments in GYE, and 325 (2002) and 116 (2003) sites in 17 catchments in Glacier. Species detected included *B. boreas*, wood frog (*R. sylvatica*) and boreal chorus frog (*Pseudacris maculata*) in Rocky Mountain, *B. boreas*, *P. maculata*, tiger salamander (*Ambystoma tigrinum*) and Columbia spotted frog (*R. luteiventris*) in GYE, and *B. boreas*, *R. luteiventris* and long-toed salamander (*A. macrodactylum*) in Glacier. We detected *A. tigrinum* at Rocky Mountain, but sampling was inadequate and we do not report these data here. We also observed *P. maculata*, the Pacific treefrog (*P. regilla*) and the Rocky Mountain tailed frog (*Ascaphus montanus*) in Glacier, but these species either have ranges that terminate near the border of the Park and have been found in less than 10 sites each (the hylids) or occur in habitats that we did not sample in these surveys (*A. montanus* inhabits headwater streams). Our observations of *P. maculata*, however, do represent an addition to the fauna occurring in Glacier (HOSSACK & YALE, 2002).

Detection probabilities were high for all species (tab. 2), with the exception of one anomalous value for *P. maculata*. We are unsure of the cause of this low value, but we consider it to be an outlier. Anurans tended to have higher detection probabilities (mean 0.84, not including *P. maculata* in 2003 at Rocky Mountain) than did salamanders (mean 0.68). Estimated occupancy for each species varied between 0 and 0.57 and decreased from north to south (tab. 2). The highest occupancy observed in Rocky Mountain was 0.10 for *R. sylvatica* in 2003, but this species has a restricted distribution in the Park. In contrast, the only occupancy below 0.10 in Glacier was for *B. boreas* in 2002, and *A. macrodactylum* occurred at

Table 2. – Site occupancy and detection probabilities of amphibians in the three study areas. Dashes indicate parameters that could not be estimated due to sparse data.

Study area / Species	2002				2003			
	Occupancy (naïve)	Detection probability	Occupancy (adjusted)	Standard error	Occupancy (naïve)	Detection probability	Occupancy (adjusted)	Standard error
Glacier								
<i>Ambystoma macrodactylum</i>	0.38	0.68	0.53	0.058	0.48	0.75	0.57	0.062
<i>Bufo boreas</i>	0.06	0.90	0.07	0.027	0.12	0.74	0.15	0.041
<i>Rana luteiventris</i>	0.14	0.79	0.17	0.028	0.23	0.92	0.24	0.042
GYE								
<i>Ambystoma tigrinum</i>	0.12	0.64	0.18	0.135	0.16	0.62	0.24	0.048
<i>Bufo boreas</i>	0.05	-	0.05	0.016	0.02	-	0.02	0.01
<i>Pseudacris maculata</i>	0.38	0.88	0.43	0.05	0.30	0.94	0.32	0.037
<i>Rana luteiventris</i>	0.20	0.75	0.26	0.051	0.14	0.95	0.14	0.026
Rocky Mountain								
<i>Bufo boreas</i>	0.01	-	-	-	0	-	-	-
<i>Pseudacris maculata</i>	0.02	0.71	0.02	0.013	0.09	0.29	0.18	0.118
<i>Rana sylvatica</i>	0.03	-	0.03	0.032	0.10	0.87	0.10	0.055

less than 50 % of sites. Occurrence of amphibian species in GYE was intermediate between Rocky Mountain and Glacier.

There was no apparent trend in numbers of breeding sites of *B. boreas* in Glacier between 1999 and 2002 (tab. 3). There was no trend between 1999 and 2000, an increase in site occupancy between 2000 and 2001, followed by a decrease in occupancy of the same magnitude between 2001 and 2002. Trend over greater intervals shows less variability. Comparing 2001 to 1999, there was only a slight increase in site occupancy, and there was no trend between 1999 and 2002.

DISCUSSION

Results of our surveys in 2002-2003 confirm data from earlier studies that amphibian occurrence is greatly reduced in the southern Rocky Mountains. The cause of the decline of *B. boreas* in Rocky Mountain and elsewhere in the southern Rocky Mountains is thought to be the result of infection by the fungus *Batrachochytrium dendrobatidis* (MUTHS et al., 2003; CAREY et al., 2005). Although *B. dendrobatidis* has been detected in *R. sylvatica* and *P. maculata* in Rocky Mountain (RITTMANN et al., 2003; GREEN & MUTHS, 2005), we do not know how or whether these species have been affected.

There has been relatively little direct physical alteration of amphibian habitats in any of the parks. However, the high visitor use and the greater size of the nearby human population at Rocky Mountain suggests that it is reasonable to hypothesize that anthropogenic influences have contributed directly or indirectly to the low occupancy of amphibians there. For example, DAVIDSON et al. (2002) found an anthropogenic influence (amount of agriculture

Table 3. – Annual trends in populations of *B. boreas* in three catchments in Glacier National Park. The highlighted diagonal shows the comparisons between each year (columns) and the previous year (rows). Values above the diagonal show comparisons between sites sampled both in the year of each column and 2 or 3 years before.

Year	Sites surveyed	Sites with breeding	Year-to-year trend		
			2000	2001	2002
1999	12	8	0.00	0.12	0.00
2000	18	12	–	0.22	0.08
2001	28	23	–	–	-0.24
2002	41	28	–	–	–

upwind) was correlated with reduced occurrence of four species of amphibians in California. Adjusted for area, Rocky Mountain receives about five times the visitor use, both in the backcountry and by visitors touring the parks by automobile, than do Glacier or the parks in the GYE (tab. 1). Rocky Mountain is the smallest of the parks in the transect, but has the greatest number of people living nearby and may be less buffered from outside influences. For example, land use change (urbanization and agricultural development) on the Colorado piedmont east of the park has resulted in cooler and wetter summers in Rocky Mountain (STOHLGREN et al., 1998), and increased nitrogen deposition from urban and agricultural sources has altered the diatom communities of Alpine lakes (WOLFE et al., 2001). We can offer no direct evidence that human influences have affected the occurrence of amphibians in Rocky Mountain, but this topic deserves further research.

Differences in climate among study areas could influence the patterns we observed. Rocky Mountain is warmer than the GYE, but receives the least precipitation of the three study areas. Climate and extreme weather events can directly affect amphibian populations (CAREY & ALEXANDER, 2003), and the interactions between climate and anthropogenic influences have received little study.

Whether the levels of habitat occupancy seen in GYE and Glacier represent declines of any species is unknown. It is suspected that *B. boreas* should occur at a greater number of potential breeding sites than has been observed recently (KOCH & PETERSON, 1995; MAXELL et al., 2003). Alternatively, the Rocky Mountains have low diversity of amphibians, and it may be that low species diversity and low habitat occupancy are linked. Unfortunately we lack knowledge of historical habitat occupancy rates for any species. The recent data from Glacier indicate no trend since 1999, but this is still too brief a time series to draw firm conclusions.

The goal of Rocky Mountain ARMI is to collect data over the long term, so that we will be able to draw conclusions about trend for each species within the national parks, and patterns across the region. Longer time series will allow the use of more sophisticated models to estimate detection probabilities and occupancy, including rates of population turnover (MACKENZIE et al., 2003). During the first years of monitoring, the effort in each study area was constrained somewhat by funding, resulting in uneven allocation of effort based on size of study areas. Beginning in 2005, we will use size of the areas in allocating samples, which will

result in increased effort at GYE. Future analyses will also incorporate covariates in the estimation of detection probabilities and site occupancy. Site-specific covariates do not change across sampling occasions within years (e.g., many habitat variables), whereas sampling covariates (e.g., date or weather) may change for each sampling occasion. Both site and sampling covariates can influence detection probabilities, but only site covariates are used to model occupancy probabilities. Analyses of trend also will need to include covariates. For example, annual precipitation may determine the number of available breeding sites. Paradoxically, some species may have higher occupancy in dry years, because there are fewer sites available. The increase in occupancy by *B. boreas* in Glacier in 2001, a year with extremely low winter snowpack, may be an illustration of this phenomenon. We need to be able to distinguish changes in occupancy caused by variation in natural conditions, such as habitat changes due to drought and wildfire or outbreaks of infectious disease, from changes caused by anthropogenic influences, such as introduction of a novel pathogen.

RÉSUMÉ

Les chercheurs de la Rocky Mountain Region de l'United States Geological Survey's Amphibian Research and Monitoring Initiative ont effectué une étude sur le statut des amphibiens le long d'un transect qui suit la ligne de partage des eaux du Canada au Colorado et qui comprend quatre parcs nationaux. L'étude s'est appuyée sur des inventaires par contact visuel pour déterminer l'occupation des sites, avec des visites multiples à un sous-ensemble de sites pour estimer les probabilités de détection pour chaque espèce. Pour chaque espèce, les probabilités de détection ont été généralement élevées (plus de 65 %). Un gradient d'occupation des sites a été mis en évidence, la plupart des espèces étant rares dans le sud et relativement communes dans le nord. Par exemple, *Bufo boreas* est proche de l'extinction dans le Rocky Mountain National Park, présent dans moins de 5 % des sites dans les parcs nationaux de Yellowstone et du Grand Teton au milieu du transect, mais présent dans environ 10 % des sites dans le Glacier National Park. La salamandre *Ambystoma tigrinum* est rare à Rocky Mountain et présente dans moins de 25 % des sites à Yellowstone et au Grand Teton, mais *A. macrodactylum* a été observée dans plus de 50 % des sites à Glacier. Il y a de nombreuses différences entre les parcs, telles que la latitude, le climat, l'abondance des visiteurs et la densité de la population humaine dans la région avoisinante. Le degré auquel ces facteurs ont influencé la distribution et l'abondance actuelles des amphibiens est inconnu et devrait faire l'objet de recherches complémentaires.

ACKNOWLEDGMENTS

Surveys were funded by the US Geological Survey and the National Park Service. We thank the administrative, natural resource management, and ranger staffs of Glacier, Grand Teton, Rocky Mountain, and Yellowstone national parks for their cooperation and assistance.

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Corresponding editor: C. Kenneth DODD, Jr.