

## INFLUENCE OF WATER CONDUCTIVITY ON AMPHIBIAN OCCUPANCY IN THE GREATER YELLOWSTONE ECOSYSTEM

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**ABSTRACT.**—Investigation of amphibian occupancy at potential breeding sites can provide information about the distribution and relative abundance of species, as well as insights into habitat relationships across large areas such as national parks. Based on previous research in the Greater Yellowstone Ecosystem (GYE), we hypothesized that the probability of amphibian occupancy increases with water conductivity. We conducted amphibian surveys with habitat measurements at 235 wetland sites in the GYE in 2002, thereby locating breeding populations of boreal toads (*Anaxyrus boreas*), boreal chorus frogs (*Pseudacris maculata*), Columbia spotted frogs (*Lithobates luteiventris*), and barred tiger salamanders (*Ambystoma mavortium*). Repeat surveys provided detection probabilities, which allowed for unbiased estimates of occupancy. The boreal chorus frog was the most common amphibian in the GYE, with breeding populations occupying approximately 48% of the sites, followed by Columbia spotted frog (35%), barred tiger salamander (14%), and boreal toad (13%). Occupancy corrected for detection probability averaged 36% higher (range 27%–50%) than naïve estimates of occupancy. Detection rates ranged from 0.65 to 0.78 for the 4 species. Modeling of habitat covariates indicated that higher conductivity was positively associated with toad occupancy but negatively associated with chorus frog occupancy; Columbia spotted frog and barred tiger salamander occupancy was little influenced by water conductivity. Fish presence had a negative effect on occupancy of barred tiger salamanders and boreal chorus frogs. These results may help managers in the GYE manage and conserve important breeding habitat for amphibians, particularly if long-term monitoring efforts indicate declines in amphibian populations.

**RESUMEN.**—La investigación sobre anfibios de ocupación de sitios potenciales de reproducción puede brindar información sobre la distribución y la abundancia relativa de las especies, y sobre la relación con el hábitat en grandes áreas, como los parques nacionales. Basados en investigaciones previas realizadas en *Greater Yellowstone Ecosystem (GYE)*, tenemos la hipótesis de que la probabilidad de ocupación de anfibios se incrementa con la conductividad del agua. En el 2002 realizamos monitoreos de anfibios con mediciones en el hábitat en 235 terrenos húmedos de GYE, y localizamos poblaciones reproductoras de sapos boreales (*Anaxyrus boreas*), *Pseudacris maculata*, ranas *luteiventris* y ajolote tigre rayado (*Ambystoma mavortium*). Los monitoreos repetidos proporcionaron probabilidades de detección, las cuales permitieron realizar estimaciones exactas de ocupación. *Pseudacris maculata* resultó ser la especie de anfibios más común en GYE, y sus poblaciones reproductoras ocupan aproximadamente el 48% de los terrenos, seguidas de las ranas *luteiventris* (35%), el ajolote tigre rayado (14%) y los sapos boreales (13%). Las estimaciones corregidas de ocupación de la probabilidad de detección tuvieron un promedio del 36% superior (rango del 27 al 50%) a las estimaciones de ocupación iniciales. Las tasas de detección oscilaron entre 0,65 y 0,78 en las cuatro especies. El modelaje de las covariables relacionadas con el hábitat indicó que una mayor conductividad se asociaba de manera positiva con la ocupación de sapos, y de manera negativa con la existencia de *Pseudacris maculata*; la ocupación de ranas *luteiventris* y de ajolote tigre rayado tuvo una pequeña influencia de la conductividad del agua. La presencia de peces tuvo un efecto negativo en la ocupación del ajolote tigre rayado y en la de *Pseudacris maculata*. Estos resultados pueden ser de utilidad para que los administradores del GYE puedan cuidar y conservar el hábitat de reproducción de los anfibios, especialmente si los monitoreos a largo plazo de las poblaciones de anfibios indican que éstas están disminuyendo.

Many amphibian populations are rapidly declining or have declined worldwide, and the proportion of amphibian species that are threatened is considerably greater than that of birds or mammals (Houlahan et al. 2000, Alford et al. 2001, Stuart et al. 2004, Hof et al. 2011). Habitat loss appeared to be the major cause of amphibian population declines and disease a main cause of extinctions (Stuart et al. 2004,

however see McCallum 2005, Ouellet et al. 2005, Gardner et al. 2007 for contrasting views). In the western United States, over 50% of anuran (frog and toad) species are in major decline, as demonstrated by substantial decreases in range or number of occupied sites, and another 20% are exhibiting some population extirpations not counterbalanced by new populations (Lannoo 2005).

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One species of concern in western North America is the boreal toad (*Anaxyrus boreas*), which has undergone large population declines throughout much of its range (Stebbins and Cohen 1995, Muths and Nanjappa 2005). In particular, boreal toads have declined in the southern Rocky Mountains since the early 1970s (Corn et al. 1989, Carey 1993, Corn 2000, Muths et al. 2003); however the decline may be more subtle in other parts of this species' range (Murphy et al. 2009, Pilliod et al. 2010, Corn et al. 2011). Boreal toads also likely declined in the Greater Yellowstone Ecosystem (GYE; Patten 1991), especially in Jackson Hole, Wyoming, where toads were described as widespread in the early 1950s (Carpenter 1953, Peterson et al. 1991, Koch and Peterson 1995).

Declines of boreal toads in the Rocky Mountains have been linked to disease. Initially, a bacterial disease caused by *Aeromonas hydrophila* was implicated (Hawk 2000), but more recent investigations point to the chytrid fungus *Batrachochytrium dendrobatidis* (Muths et al. 2008, Murphy et al. 2009, Pilliod et al. 2010, Corn et al. 2011). Current toad breeding sites in the GYE have high-conductivity water (conductivity is a measure of total number of ions and total dissolved solids) and acid-neutralizing capacity, and these sites are typically in geothermally influenced locations (Corn and Vertucci 1992, Koch and Peterson 1995, Hawk 2000). Due to permeable skins, amphibians must maintain osmotic pressure (i.e., regulation of both water and specific solutes) so that plasma concentrations may be maintained at levels greater than or equal to levels in the environment. Diseases that interfere with osmoregulation can be lethal. Because water conductivity is important for osmoregulation and amphibian development (Cameron 1940, Morris and Tanner 1969, Hovingh 1993), and because *B. dendrobatidis* (Voyles et al. 2007) affects ion transport through skin, we hypothesize that an important relationship may exist between water conductivity and toad occurrence. Toads in high-conductivity water may be better able to cope with other stresses, like disease, and may have a better immune response when challenged. The GYE is an ideal location for investigating this relationship because of the unusual abundance of geothermal and high-conductivity water bodies.

Beginning in the early 1990s, the Herpetology Laboratory of Idaho State University has

conducted amphibian surveys in the GYE. Since 2000, systematic monitoring efforts in Yellowstone and Grand Teton National Parks have been supported by the USGS Amphibian Research and Monitoring Initiative (ARMI) and the National Park Service's Inventory and Monitoring Program (Corn et al. 2005b, Gould et al. 2012). Four species of amphibians inhabit the GYE: boreal toad, boreal chorus frog (*Pseudacris maculata*), Columbia spotted frog (*Lithobates luteiventris*), and barred tiger salamander (*Ambystoma mavortium*; Peterson et al. 1991, Koch and Peterson 1995, Patla et al. 2007). One species, the northern leopard frog (*Lithobates pipiens*), is thought to have been nearly extirpated from its former small and isolated range in Grand Teton National Park since the 1950s (Koch and Peterson 1995). The extant amphibians are widely distributed and locally abundant, with all species apparently absent only from areas of steep topography that lack suitable wetlands and ponds or areas above about 2900 m elevation (Bartelt et al. 2011). Historical information and initial surveys suggest that boreal toads may have declined since the 1950s, but the other species (excepting the leopard frog) still inhabit many sites (Koch and Peterson 1995, Gould et al. 2012). Severe declines of boreal toads in Colorado and southern Wyoming, which may be linked to catastrophic die-offs from disease (Muths et al. 2003), heighten the concern for this species in the GYE.

In light of previous survey results indicating a relationship between water conductivity and successful breeding of boreal toads (Peterson et al. 1991, Hawk 2000), we wanted to investigate this relationship with an expanded data set that includes the other amphibian species present in the GYE. The use of randomly selected sites in this study increases our ability to make inferences to the GYE, compared to the previous exploratory investigations that used targeted sites. On the basis of existing data and previous research from selected study sites, we hypothesized that boreal toads breed most commonly at sites with high-conductivity water, in contrast to probably less restrictive patterns for the other amphibian species. We wanted to include the previously targeted sites in our analysis to determine if these sites had a higher occupancy than our randomly selected sites. If there was a difference in occupancy, did it occur for all

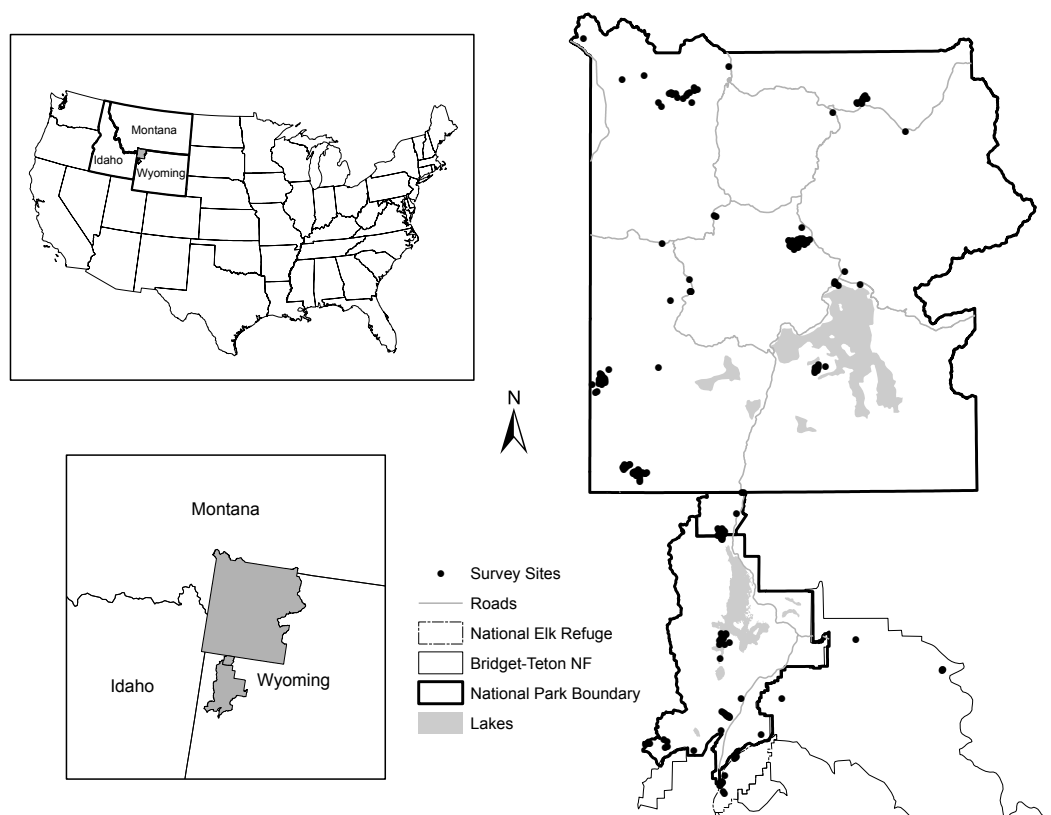


Fig. 1. Sites surveyed for the presence of breeding amphibians in the Greater Yellowstone Ecosystem in 2002.

species or just some? Finally, because the presence of fish has been implicated in the decline of amphibian populations (Pilliod and Peterson 2001), we hypothesized that fish would negatively affect amphibian occupancy. Knowledge of the relationship between amphibian breeding habitat and water conductivity may allow managers to better identify habitat components for protection and, perhaps, amphibian reintroduction.

## METHODS

### Study Area

Field work was conducted in Grand Teton National Park, Yellowstone National Park, and the National Elk Refuge and adjacent Bridger-Teton National Forest (Fig. 1), all collectively referred to here as the Greater Yellowstone Ecosystem (GYE). The study area provided an extraordinarily varied set of habitat conditions with respect to conductivity and other environmental factors, due to past and current

geothermal activity in Yellowstone, the granitic fault-block mountains of Grand Teton, dynamic river systems, and widely distributed ponds and small lakes.

### Sample Site Selection

Our approach was to survey all potential amphibian breeding habitat within randomly selected subwatersheds or catchments ( $\bar{x}$  = 879 ha,  $SD$  = 731). Catchment boundaries were delineated using the U.S. Geological Survey Elevation Derivatives for National Applications data set (Popenga and Worstell 2008). We stratified the park area into 15 blocks (10 for Yellowstone National Park; 5 for Grand Teton National Park) to achieve spatial distribution across the parks. Within the selected catchments, National Wetland Inventory (NWI) polygons were surveyed, except for those wetlands that were coded as temporarily flooded (water regime A), saturated soils (water regime B), and edges of flowing water (riverine). Field crews visited all preidentified areas and

conducted surveys at any other sites incidentally encountered within the watershed that had potential habitat for pond-breeding amphibians. Sites included ponds and lake-shores, pools in wet meadows, beaver impoundments, and oxbows and backwaters. In 2002, we surveyed 6 catchments in Yellowstone and 4 catchments in Grand Teton. Based on our spatial stratification scheme, these samples provided inference to approximately 60% of the parks' area. Additionally, due to the relative rarity of boreal toads, we surveyed some previously identified boreal toad breeding sites in the national parks, in areas surrounding Bridger-Teton National Forest, and in the National Elk Refuge, and we included the data in our analyses as "targeted sites." Multiple visits were made to approximately 20% of sites within the catchments. Because of logistic constraints, including remoteness of the catchments, a short survey season, and our inability to predict which NWI wetlands would contain surface water at the time of surveys, these resampled sites were selected nonrandomly.

#### Field Methods

At sites with suitable surface water, crews searched for the 4 amphibian species using standard visual encounter methods, including searching the perimeters of water bodies and sweeping the water with dip nets (Thoms et al. 1997). Data collected included location (recorded with GPS receivers, Garmin GPS12 map, Garmin International Inc., Olathe, KS), time spent searching, species life stage and estimated numbers of individuals, weather conditions, vegetation descriptors, water temperature, pH, and conductivity. Conductivity and pH data were collected within 1 m of the shore by using pocket-sized, microprocessor-based, calibrated instruments (ECTestr and pHTestr2, Oakton Instruments, Vernon Hills, IL). We chose 1 m from shore as a reasonable indicator of habitat for eggs and larvae. The pH meter was accurate to  $\pm 0.1$  pH; the conductivity meter was accurate to  $\pm 2\%$  of full scale (0–1990  $\mu\text{S}$ ). Instruments were calibrated weekly. We recorded fish as detected if any were observed during the survey. Surveys were conducted in the 8-week period between 5 June and 5 August. Repeat visits were separated by 1–5 days; however, some sites were also visited after 20 and 55 days.

For each site, amphibians present were recorded as breeding based on the occurrence of eggs, larvae, and/or recent metamorphs. If only adults and juveniles were present, we classified the site as nonbreeding because of the ability of postmetamorphic amphibians to disperse. We used Koch and Peterson (1995) for identification of eggs, larvae, and adults for the 4 species of amphibians. Field personnel were well trained and took photographs in the field for data verification and quality control.

#### Statistical Analyses

We estimated detection probability—the probability that at least one individual is detected during a sampling occasion, given that the species is present in the area and available for sampling (Boulinier et al. 1998, MacKenzie et al. 2002, 2006)—by using the ARMI protocol (Corn et al. 2005a, 2005c). Multiple visits to sites allowed us to determine the effect of variable detection probability on our inferences and thus remove the bias that results from confusing absence with a failure to detect species (Yoccoz et al. 2001, MacKenzie et al. 2002, 2006). Detection probability was known to vary for the 4 species in the GYE; typically, barred tiger salamanders were the most difficult to sample (Peterson et al. 1991, Corn et al. 2005b). Descriptive statistics were analyzed with SAS (SAS Institute Inc., Cary, NC) and expressed as means ( $\pm$ SE).

To evaluate the influence of site and sampling covariates on amphibian occupancy, we used program PRESENCE (MacKenzie et al. 2002). MacKenzie et al. (2002) defined  $\Psi$  as the probability that a site is occupied by the species and  $p_j$  as the probability of detecting the species (given that it is present) during the  $j$ th independent survey of the site. Furthermore, PRESENCE allowed us to evaluate the importance of accounting for detection probability  $< 1$  in our analyses by directly estimating it and by setting detection probability to 1.

Analyses included both site- and survey-specific covariates. Site covariates were the initial water conductivity measurement, the detection of fish (fish present = 1, fish absent = 0), and whether the site was targeted or randomly selected (targeted site = 1, random site = 0). Site-specific covariates temperature and pH were initially investigated as variables influencing site occupancy and were found to not be important predictors. Survey specific

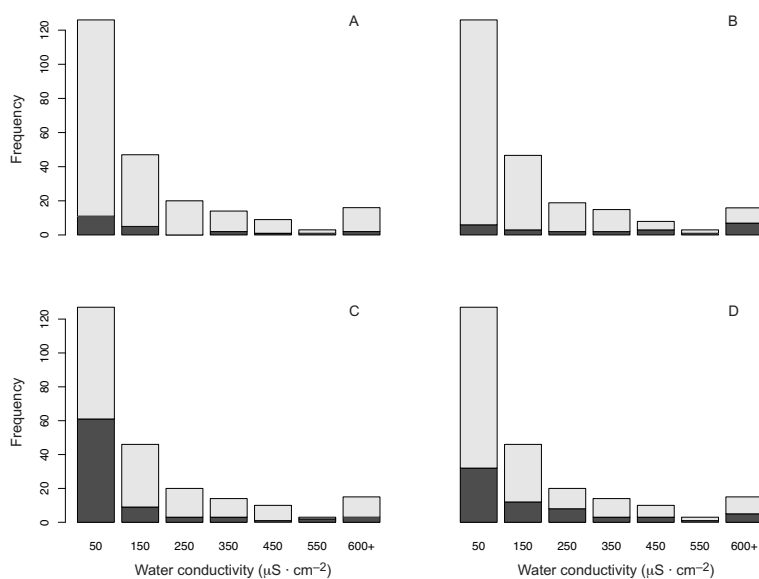


Fig. 2. Frequency of breeding (coded black) and nonbreeding sites (coded white) for barred tiger salamander (A), boreal toad (B), boreal chorus frog (C), and Columbia spotted frog (D) corresponding to water conductivity in the Greater Yellowstone Ecosystem during 2002.

TABLE 1. The number of sampling sites with detections of breeding amphibians in the Greater Yellowstone Ecosystem in relation to the presence of fish.

Species	Fish absent	Fish present
Boreal toad	11	5
Boreal chorus frog	73	4
Columbia spotted frog	38	18
Barred tiger salamander	21	0

covariates were the water conductivity at the time of the survey and the time of the season. Surveys were coded as occurring on or before 15 May, in one of the six 15-day intervals between 16 May and 15 Aug, or on 16 Aug and later. Barred tiger salamanders were not detected until 6 June 2002, so only surveys after this time were analyzed for their occurrence (MacKenzie et al. 2002).

The global model ( $\Psi[\text{Conductivity, Fish, Selection}]p[\text{Conductivity, Time}]$ ) was tested for goodness-of-fit using a parametric bootstrap procedure, where the overdispersion parameter,  $\hat{c}$ , was estimated by comparing the observed chi-squared value to the mean of the test statistics from the parametric bootstrap (MacKenzie and Bailey 2004). We did not adjust standard errors if the probability of the overdispersion parameter was  $>0.05$ . We

developed 20 candidate models for the toad and frogs and 11 models for the barred tiger salamander by using all combinations to balance our model set. Models were ranked using Akaike's Information Criteria (AIC; Akaike 1973), and AIC values were used to select models with the most support (Burnham and Anderson 2002). AIC values and differences ( $\Delta\text{AIC}$ ) between individual models and the model with the lowest AIC (i.e., most supported model) and Akaike weights ( $w_i$ ) are reported (Burnham and Anderson 2002). Differences of  $\leq 2$  are taken to indicate similar support for the corresponding model compared to the most supported model given the data set;  $\Delta\text{AIC} > 2$  and  $< 7$  indicates considerably less support for the model relative to the most supported model, whereas  $\Delta\text{AIC} > 7$  indicates little or no support compared to the most supported model (Burnham and Anderson 2002). To account for model selection uncertainty, we calculated model-averaged results (Burnham and Anderson 2002). To better demonstrate the importance of predictor variables, the relative importance of each predictor variable was calculated as the sum of the variable's Akaike weights across all models in which the variable occurred (Burnham and Anderson 2002). Model notation follows Lebreton et al. (1992).



TABLE 2. Number of breeding sites, naïve occupancy, occupancy accounting for incomplete detection, detection probability, and relationship to water conductivity for amphibian species in the Greater Yellowstone Ecosystem, 2002.

Species	Breeding sites	Occupancy			Water conductivity
		Naïve	Model average (SE)	Detection probability	
Boreal toad	24	0.10	0.13 (0.04)	0.78	Positive
Chorus frog	82	0.35	0.48 (0.06)	0.70	Negative
Columbia spotted frog	64	0.27	0.35 (0.04)	0.75	None
Barred tiger salamander	22	0.09	0.14 (0.05)	0.65 <sup>a</sup>	None

<sup>a</sup>Detection probability for the initial survey since there was a time effect in the model with the lowest AIC value

## RESULTS

We conducted amphibian surveys with water conductivity measurements at 235 sites in the GYE. Multiple visits were made at 20% of the sites ( $n = 47$ ) with 32, 9, 4, and 2 sites visited 2, 3, 4, and 6 times, respectively. Average breeding site water conductivity was  $183.6 \mu\text{S} \cdot \text{cm}^{-1}$  (SE = 16.5,  $n = 235$ ) and ranged between 10 and  $1300 \mu\text{S} \cdot \text{cm}^{-1}$  (Fig. 2). Breeding site pH averaged 7.7 (SE = 0.05), and temperature averaged  $17.6^\circ\text{C}$  (SE = 0.4). Fish were detected in 22% of the 213 sites where data were available on fish presence.

The number of observed breeding sites varied among the 4 species. Boreal chorus frogs were the most commonly detected breeding species, with indicators of breeding found at 82 of 235 sites, followed by Columbia spotted frogs (64 of 235 sites), boreal toads (24 of 235 sites), and barred tiger salamanders (22 of 235 sites).

The observation of amphibian breeding was related to the presence of fish (Table 1). Fish were seldom detected at boreal chorus frog breeding sites and never at barred tiger salamander breeding sites. Boreal toad and Columbia spotted frog breeding was more common in sites without fish.

### Boreal Toads

Boreal toads bred in 24 of the 235 sites for a naïve estimate of occupancy of 0.10. Coefficient of variation of occupancy was 25%. Model averaged occupancy was 0.13 ( $\pm 0.04$ ), which was 27% higher than the naïve estimate of where toads were detected at least once (Table 2). Model fit of the general model was good ( $\hat{c} = 0.78$ ,  $P = 0.46$ ). Model selection uncertainty was low, with 3 candidate models having  $\Delta\text{AIC} < 2$  and 5 models having  $\Delta\text{AIC} < 7$  (Table 3). The relative importance for water conductivity, selection of sites, and fish were 0.99, 0.99, and 0.28, respectively, indicating

the importance of water conductivity and site selection to occupancy. Higher water conductivity was associated with increased occupancy. For the model with lowest AIC,

$$\text{Logit}(\Psi) = -3.14 + 0.0025(\text{Conductivity}) + 1.63(\text{Selection}).$$

The model with the lowest AIC indicated that probability of detection was constant at 0.78.

### Boreal Chorus Frogs

We found boreal chorus frogs breeding in 82 sites. Model-averaged occupancy (0.48, SE = 0.06; Table 2) was 38% higher than the naïve estimate (0.35). The coefficient of variation of occupancy was moderate at 13%. Three models had  $\Delta\text{AIC} < 2$  and 6 had  $\Delta\text{AIC} < 7$  (Table 3), with reasonable model fit of the general model ( $\hat{c} = 1.53$ ,  $P = 0.15$ ). Water conductivity was a covariate for occupancy, detection probability, or both in the top 6 models (Table 3). Relative importance of water conductivity, site selection, and fish were 0.99, 0.30, and 1.00, respectively, indicating strong support for water conductivity and fish in model selection. However, water conductivity was negatively associated with occupancy and detection probability. Fish presence was also a negative factor. For the model with the lowest AIC,

$$\text{Logit}(\Psi) = 0.34 - 2.11(\text{Fish})$$

and

$$\text{Logit}(p) = 1.44 - 0.0030(\text{Conductivity}).$$

Detection probability was 0.71 for sites with average values of water conductivity.

### Columbia Spotted Frogs

Columbia spotted frogs were found breeding at 64 sites. Model-averaged occupancy was

TABLE 3. Ranking of models  $\leq 7$   $\Delta AIC$  predicting occupancy of breeding boreal toad (*Anaxyrus boreas*), boreal chorus frog (*Pseudacris maculata*), Columbia spotted frog (*Rana luteiventris*), and barred tiger salamander (*Ambystoma macrotum*) while accounting for imperfect detection in the Greater Yellowstone Ecosystem during 2002. Models labeled with probability of detection set to 1,  $p(1)$ , indicate a model assuming perfect detection.

Model	AIC <sup>a</sup>	$\Delta AIC^b$	$w_i^c$	K <sup>d</sup>	$\Psi^e$	SE
<b>BOREAL TOAD</b>						
$\Psi(\text{Conductivity, Targeted})p(\cdot)$	165.99	0.00	0.45	4	0.130	0.032
$\Psi(\text{Conductivity, Targeted})p(\text{Conductivity})$	167.31	1.32	0.23	5	0.135	0.035
$\Psi(\text{Conductivity, Targeted, Fish})p(\cdot)$	167.76	1.77	0.19	5	0.129	0.032
$\Psi(\text{Conductivity, Targeted, Fish})p(\text{Time, Conductivity})$	169.66	3.67	0.07	7	0.137	0.036
$\Psi(\text{Targeted})p(\text{Conductivity})$	171.95	5.9	0.02	4	0.198	0.055
$\Psi(\text{Conductivity, Targeted})p(1)$	416.86	250.87	0.00	3	0.090	0.020
<b>BOREAL CHORUS FROG</b>						
$\Psi(\text{Fish})p(\text{Conductivity})$	337.44	0.00	0.37	4	0.498	0.058
$\Psi(\text{Conductivity, Fish})p(\text{Conductivity})$	338.43	0.99	0.22	5	0.460	0.081
$\Psi(\text{Targeted, Fish})p(\text{Conductivity})$	338.69	1.25	0.20	5	0.480	0.057
$\Psi(\text{Conductivity, Fish})p(\cdot)$	339.98	2.54	0.10	4	0.445	0.056
$\Psi(\text{Conductivity, Targeted, Fish})p(\text{Time, Conductivity})$	341.46	4.02	0.05	7	0.453	0.082
$\Psi(\text{Conductivity, Targeted, Fish})p(\cdot)$	341.58	4.14	0.05	5	0.445	0.057
$\Psi(\text{Conductivity, Fish})p(1)$	747.05	409.61	0.00	3	0.340	0.030
<b>COLUMBIA SPOTTED FROG</b>						
$\Psi(\text{Targeted, Fish})p(\cdot)$	324.79	0.00	0.30	4	0.352	0.043
$\Psi(\text{Targeted, Fish})p(\text{Time})$	325.89	1.10	0.18	5	0.352	0.043
$\Psi(\text{Targeted, Fish})p(\text{Conductivity})$	326.28	1.49	0.14	5	0.350	0.043
$\Psi(\text{Conductivity, Targeted, Fish})p(\cdot)$	326.39	1.60	0.14	5	0.353	0.054
$\Psi(\text{Targeted})p(\cdot)$	327.62	2.83	0.07	3	0.351	0.044
$\Psi(\text{Targeted})p(\text{Time})$	328.93	4.14	0.04	4	0.350	0.043
$\Psi(\text{Conductivity, Targeted, Fish})p(\text{Time, Conductivity})$	329.09	4.30	0.04	7	0.349	0.053
$\Psi(\text{Targeted})p(\text{Conductivity})$	329.21	4.42	0.03	4	0.349	0.043
$\Psi(\text{Conductivity, Targeted})p(\cdot)$	329.35	4.56	0.03	4	0.352	0.054
$\Psi(\text{Conductivity, Targeted})p(\text{Conductivity})$	331.11	6.32	0.01	5	0.349	0.054
$\Psi(\text{Targeted, Fish})p(1)$	786.74	461.95	0.00	3	0.251	0.028
<b>BARRED TIGER SALAMANDER</b>						
$\Psi(\text{Targeted})p(\text{Time})$	174.47	0.00	0.22	4	0.144	0.031
$\Psi(\cdot)p(\text{Time})$	175.46	0.99	0.13	3	0.139	0.018
$\Psi(\text{Targeted})p(\cdot)$	175.67	1.20	0.12	3	0.164	0.020
$\Psi(\cdot)p(\cdot)$	176.15	1.68	0.09	2	0.161	0.015
$\Psi(\text{Conductivity, Targeted})p(\text{Time})$	176.18	1.71	0.09	5	0.144	0.013
$\Psi(\text{Conductivity, Targeted})p(\text{Time, Conductivity})$	176.26	1.79	0.09	6	0.158	0.014
$\Psi(\text{Conductivity})p(\text{Time})$	177.46	2.99	0.05	4	0.139	0.007
$\Psi(\text{Conductivity, Targeted})p(\cdot)$	177.59	3.12	0.04	4	0.163	0.008
$\Psi(\text{Conductivity})p(\cdot)$	178.13	3.66	0.04	3	0.162	0.006
$\Psi(\cdot)p(\text{Conductivity})$	178.14	3.67	0.03	3	0.161	0.006

TABLE 3. Continued.

Model	AIC <sup>a</sup>	$\Delta AIC^b$	$w_i^c$	K <sup>d</sup>	$\Psi_e$	SE
$\Psi(\text{Conductivity})p(\text{Time, Conductivity})$	178.80	4.33	0.02	5	0.141	0.003
$\Psi(\text{Targeted})p(1)$	531.42	356.95	0.00	2	0.073	0.017
$\Psi(\text{Conductivity, Targeted})p(1)$	533.20	358.73	0.00	3	0.073	0.017
$\Psi(\cdot)p(1)$	536.53	362.06	0.00	1	0.073	0.018
$\Psi(\text{Conductivity})p(1)$	538.51	364.04	0.00	2	0.073	0.018

<sup>a</sup>Akaike information criteria (Log Likelihood + 2K)

<sup>b</sup>Difference between the AIC of the "best model" and the current model ( $AIC_{\text{best}} - AIC_i$ )

<sup>c</sup>Akaike weight

<sup>d</sup>Number of parameters

<sup>e</sup>Occupancy

0.35 ( $\pm 0.04$ ; Table 2), 28% higher than the naïve estimate of occupancy (0.27). The coefficient of variation of occupancy was moderate at 13%. Model selection uncertainty was higher than for boreal toads and boreal chorus frogs, with 4 models having  $\Delta AIC < 2$  and 10 models having  $\Delta AIC < 7$  (Table 3). However, model fit was good for the general model ( $\hat{c} = 0.66$ ,  $P = 0.67$ ). Relative importance of water conductivity, site selection, and fish were 0.40, 0.98, and 0.81, respectively. For the model with the lowest AIC,

$$\text{Logit}(\Psi) = -1.11 + 1.23(\text{Selection}) \\ + 0.92(\text{Fish})$$

with constant detection. Detection probability for this model was 0.75.

#### Barred Tiger Salamanders

We found barred tiger salamanders breeding at 22 sites. Model-averaged occupancy (0.14, SE = 0.053; Table 2) was 50% higher than the naïve estimate of occupancy (0.09). Coefficient of variation of occupancy was high at 38%. Model uncertainty was highest for barred tiger salamanders compared to the other species; 6 models had  $\Delta AIC < 2$  and 11 models had  $\Delta AIC < 7$  (Table 3). However, model fit was good for the global model ( $\hat{c} = 1.10$ ,  $P = 0.11$ ). There was some support of time variation in detection probability, indicating that salamanders were more detectable later in the season. Relative importance of water conductivity and site selection were 0.37 and 0.56, respectively. For the model with lowest AIC,

$$\text{Logit}(\Psi) = -1.62 - 1.18(\text{Selection})$$

and

$$\text{Logit}(p) = -2.84 + 0.76(\text{Time}).$$

Probability of detection was 0.65 for the initial survey.

#### Assuming Perfect Detection

We evaluated the importance of incorporating imperfect detection by fixing the probability of detection to 1 within the analysis of occupancy. For all species, assuming perfect detection (i.e., logistic regression) was a poor method compared to accounting for imperfect



detection (Table 3). Compared to the highest-ranking model, logistic regression models had  $\Delta\text{AIC} > 250$ , resulting in model weights of 0. Occupancy estimated assuming perfect detection averaged 57% lower (range 40%–98%) than the adjusted estimate after accounting for detection probability. Moreover, occupancy estimated assuming perfect detection was less than the naïve estimates of occupancy, with standard errors approximately one-half of the standard error accounting for detection probability. The largest differences occurred for barred tiger salamanders, which had the lowest detection probability.

#### DISCUSSION

The results from this study strongly support previous work (Peterson et al. 1991, Koch and Peterson 1995, Hawk and Peterson 1999, Hawk 2000), indicating a positive association between high-conductivity water and active toad breeding sites. It is interesting that when Peterson et al. (1991) resurveyed 2 historical breeding areas for boreal toads (Carpenter 1953, Carpenter unpublished field notes), they found sites with low-conductivity water no longer occupied.

For the past decades, we have wondered whether high-conductivity water may be somehow protecting amphibians from diseases (Koch and Peterson 1995). Originally, in seeking the causes of toad declines, investigators focused on bacterial disease and compromised immune systems (Carey 1993). Field and laboratory investigations of boreal toads in the GYE provided clues to the relationship between toad breeding sites, water conductivity, and water temperature. Tadpoles raised in the laboratory in low-conductivity water were more susceptible to infection by *A. hydrophila* than tadpoles raised in high-conductivity water or in low-conductivity water treated with tetracycline (Hawk 2000). Boreal toad tadpoles appeared to be protected from bacterial infection by developing in high-conductivity water (Hawk 2000).

Of recent concern in the GYE is the occurrence of *B. dendrobatidis*. Toads with the presence of *B. dendrobatidis* at enzootic levels and also toads dying of *B. dendrobatidis* infection were both found in the GYE (Corn 2007, Muths et al. 2008). Boreal toads at a site in Grand Teton National Park had a high incidence

of *B. dendrobatidis* and a negative population growth rate, but did not experience the population crash or extinction observed in other populations with high prevalence of *B. dendrobatidis* (Corn et al. 2011). Murphy et al. (2009) hypothesized that, although toads in Wyoming were widely infected, they may escape chytridiomycosis due to innate resistance or because their native habitat hinders *B. dendrobatidis* growth or provides more opportunities to behaviorally reduce pathogen loads than other parts of their range. Blaustein et al. (2005) reported that boreal toad tadpoles were more susceptible to *B. dendrobatidis* infection than other amphibian species. We hypothesize that amphibians in high-conductivity water may be better able to cope with stressors or have a better immune response when challenged, especially since chytridiomycosis causes death by disrupting osmotic balance through electrolyte loss (Voyles et al. 2007). Furthermore, we hypothesize that *B. dendrobatidis* and possibly other diseases are less lethal because amphibians are less stressed (with respect to osmoregulation) in a high-conductivity aquatic environment, perhaps rendering *B. dendrobatidis* less virulent or even ameliorated in high-conductivity water. Prior to *B. dendrobatidis* appearance in the GYE, toads may have formerly occupied low-conductivity sites, which may be why they appear to have declined since the 1950s (Carpenter 1953, Koch and Peterson 1995).

Given the widespread occurrence of *B. dendrobatidis* in the GYE (Muths et al. 2008), several questions arise: Does high-conductivity and geothermal water provide protection against *B. dendrobatidis*? If so, what factors account for this protection? Does high-conductivity and geothermal water directly affect *B. dendrobatidis*? Or do the water properties influence the immune system of the toads or the amount of osmoregulatory stress the toads experience? Water conductivity is important for osmoregulation and amphibian development (Cameron 1940, Morris and Tanner 1969, Hovingh 1993). *Batrachochytrium dendrobatidis* also affects ion transport through amphibian skin and can cause reduced plasma solute concentrations in amphibians (Voyles et al. 2007). Environmental stressors may compromise the immune response of amphibians (Carey et al. 1999), and *B. dendrobatidis* infections occur more frequently at cold temperatures (Carey

2000). Field and laboratory experiments demonstrated that *B. dendrobatidis* ceases growth at temperatures  $>28^{\circ}\text{C}$  (Piotrowski et al. 2004, Forrest and Schlaepfer 2011). Laboratory studies of tadpoles and recent metamorphs of boreal toads exposed to *B. dendrobatidis* under different environmental conditions are needed to address these questions (e.g., Garner et al. 2009, Muths et al. 2011).

The relationship between boreal chorus frogs and water conductivity was the opposite of that for boreal toads. Boreal chorus frogs appeared to have higher occupancy and detection probability with lower water conductivity at breeding sites. Bartelt et al. (2011) also found a negative relationship with water conductivity and occurrence of boreal chorus frogs in Yellowstone National Park. For Columbia spotted frogs, Bartelt et al. (2011) reported a weak but statistically significant positive relationship with water conductivity in Yellowstone National Park. In Utah, Columbia spotted frogs were both positively and negatively associated with water conductivity, depending on the landscape context (Welch and MacMahon 2005). Frogs were positively associated with water conductivity in the riverine valleys and negatively associated with conductivity in spring-fed valleys. When data were pooled statewide, evidence of a relationship between frog occurrence and water conductivity disappeared.

#### Fish Presence

The presence of fish had a large influence on amphibian occupancy within the GYE. No barred tiger salamanders were found in sites with fish, perhaps due to barred tiger salamanders having a minimum 10-week aquatic life stage, with some larval overwintering and metamorphosing the following spring (Lannoo and Phillips 2005). These results corroborate previous studies that found a negative relationship between the co-occurrence of predatory fish, especially introduced salmonids and pond-breeding amphibians in the Rocky Mountains (Pilliod and Peterson 2001, Patla and Lannoo 2005). Boreal toads may be less affected by fish because the toads' eggs and larvae produce a mild toxin that renders them unpalatable (Brodie et al. 1978, Gunzburger and Travis 2005, Muths and Nanjappa 2005). We acknowledge that we may have misclassified ponds with fish; however, our results are robust and support previous research.

The relationship between the presence of fish and occupancy by boreal chorus frogs and Columbia spotted frogs was most likely related to these species' preference for different types of wetlands. Occupancy for boreal chorus frogs had a negative relationship with fish sites. Boreal chorus frogs generally breed in ephemeral wetlands (Koch and Peterson 1995, Moriarty and Lannoo 2005, Bartelt et al. 2011), where fish cannot live; thus, the negative relationship with the presence of fish was expected. In contrast, Columbia spotted frog occupancy was positively related to the presence of fish. Although spotted frogs also breed in ephemeral water bodies, they frequently use permanent water bodies, which have a higher likelihood of fish presence (Reaser and Pilliod 2005). Spotted frogs have also apparently adapted to coexisting with these predators in the GYE, perhaps by occupying ponds with floating vegetation and vegetation dominated by graminoids (Reaser and Pilliod 2005, Bartelt et al. 2011). This seems not to be the case in other portions of this species' range (e.g., Pilliod and Peterson 2001).

#### Detection Probability

Variation in detection probabilities limits the inferences that may be drawn from surveys (Yoccoz et al. 2001, MacKenzie et al. 2002, Moilanen 2002, Pollock et al. 2002, McDonald 2003, Gu and Swihart 2004, Mazerolle et al. 2005); therefore, monitoring programs and habitat selection studies should estimate species-specific detection probabilities (Pollock et al. 2002). Failure to include probability of detection in models can lead to "predicting the probability of detecting a species, given a set of habitat conditions, not necessarily its true abundance of presence," thus hindering model accuracy (Stauffer 2002). Gu and Swihart (2004) found when detection probability was  $<1$  that parameter estimates from logistic regression were biased, depending on the sign of the coefficient. If a coefficient was positive, the parameter was underestimated; conversely, when a coefficient was negative, the parameter was overestimated.

Probability of detection of breeding varied by species (boreal toads  $>$  Columbia spotted frogs  $>$  boreal chorus frogs  $>$  barred tiger salamander) and ranged between 0.78 and 0.65 (Table 2). Columbia spotted frogs were associated with high emergent vegetation cover

(Munger et al. 1998, Pilliod et al. 2002, Welch and MacMahon 2005), which lowered detection probability (Hossack and Corn 2007). Occupancy models not accounting for imperfect detection (i.e., logistic regression) were not supported for any species. As expected, barred salamanders, with the lowest detection probability, had the greatest difference of the 4 species between the estimates of occupancy based on assuming perfect and imperfect detection. However, estimates of occupancy for all species were biased low with overly small standard errors when perfect detection was assumed as compared to both naïve estimates and occupancy when imperfect detection was assumed.

Previous monitoring included known sites for boreal toads. We were able to test if there was a difference in occupancy between these targeted sites and the random locations for each species. As expected, occupancy of boreal toads was higher in targeted than in random sites. This observation was also true for Columbia spotted frogs. However, occupancy was lower for barred tiger salamanders in targeted sites than in random sites. The covariate for targeted versus random site selection was not in the model with lowest AIC for boreal chorus frogs. These results emphasize the need for statistically valid sampling methods in making valid inferences for monitoring so that state variables will not be biased either high or low. By including these targeted sites in our analysis, results from previous monitoring programs perhaps could be incorporated into the current program, thus extending the time series.

Numerous organizations (e.g., U.S. Geological Survey Amphibian Research and Monitoring Initiative, Declining Amphibian Populations Task Force, and U.S. state and federal agencies) are promoting long-term programs for amphibians, especially for species believed to be at risk. Detailed, site-specific water quality information such as that presented here, combined with broader-scale breeding habitat models (e.g., Murphy et al. 2010, Bartelt et al. 2011, Gould et al. 2012), can provide substantial help in identifying new and probable breeding habitats for monitoring. We encourage others to investigate the relationship between water conductivity and amphibian occurrence (e.g., Beebee 1985, Beebee et al. 1990, Glooschenko et al. 1992, Hecnar and

McLoskey 1996). We heartily endorse the recommendation of Mazerolle et al. (2005) for estimating the probability of detection in amphibian field surveys to increase survey quality and conservation potential.

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#### LITERATURE CITED

- AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in B.N. Petrov and F. Csaki, editors, Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- ALFORD, R.A., P.M. DIXON, AND J.H.K. PECHMANN. 2001. Global amphibian population declines. *Nature* 412: 499–500.
- BARTELT, P.E., A.L. GALLANT, R.W. KLAVER, C.K. WRIGHT, D.A. PATLA, AND C.R. PETERSON. 2011. Predicting breeding habitat for amphibians: a spatiotemporal analysis across Yellowstone National Park. *Ecological Applications* 21:2530–2547.
- BEEBEE, T.J.C. 1985. Discriminant analysis of amphibian habitat determinants in southeast England UK. *Amphibia-Reptilia* 6:35–44.
- BEEBEE, T.J.C., R.J. FLOWER, A.C. STEVENSON, S.T. PATRICK, P.G. APPLEBY, C. FLETCHER, C. MARSH, J. NATKANSKI, B. RIPPEY, AND R.W. BATTARBEE. 1990. Decline of the natterjack toad *Bufo calamita* in Britain—paleoecological, documentary and experimental evidence for breeding site acidification. *Biological Conservation* 53:1–20.
- BLAUSTEIN, A.R., J.M. ROMANSIC, E.A. SCHEESSELE, B.A. HAN, A.P. PESSIER, AND J.E. LONGCORE. 2005. Inter-specific variation in susceptibility of frog tadpoles to

- the pathogenic fungus *Batrachochytrium dendrobatidis*. *Conservation Biology* 19:1460–1468.
- BOULINIER, T., J.D. NICHOLS, J.R. SAUER, J.E. HINES, AND K.H. POLLOCK. 1998. Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* 79:1018–1028.
- BRODIE, E.D., JR., D.R. FORMANOWICZ, AND E.D. BRODIE III. 1978. The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. *Herpetologica* 34:302–306.
- BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, NY.
- CAMERON, J.A. 1940. Effects of fluorine on hatching and hatching stage in *Rana pipiens*. *Ecology* 21:288–292.
- CAREY, C. 1993. Hypothesis concerning the causes of the disappearance of boreal toads from the mountains of Colorado. *Conservation Biology* 7:355–362.
- \_\_\_\_\_. 2000. Infectious disease and worldwide declines of amphibian populations, with comments on emerging diseases in coral reef organisms and in humans. *Environmental Health Perspectives* 108:143–150.
- CAREY, C., N. COHEN, AND L. ROLLINS-SMITH. 1999. Amphibian declines: an immunological perspective. *Developmental and Comparative Immunology* 23:459–472.
- CARPENTER, C.C. 1953. An ecological survey of the herpetofauna of the Grand Teton–Jackson Hole area of Wyoming. *Copeia* 1953:170–174.
- CORN, P.S. 2000. Amphibian declines: review of some current hypotheses. Pages 663–696 in D.W. Sparling, G. Linder, and C.A. Bishop, editors, *Ecotoxicology of amphibians and reptiles*. SETAC Press, Pensacola, FL.
- \_\_\_\_\_. 2007. Amphibians and disease. *Yellowstone Science* 15:11–16.
- CORN, P.S., M.J. ADAMS, W.A. BATTAGLIN, A.L. GALLANT, D.L. JAMES, M. KNUTSON, C.A. LANGTIMM, AND J.R. SAUER, EDITORS. 2005a. Amphibian Research and Monitoring Initiative: concepts and implementation. Scientific Investigations Report 2005-5015 edition, U.S. Geological Survey, Reston, VA.
- CORN, P.S., B.R. HOSSACK, E. MUTHS, D.A. PATLA, C.R. PETERSON, AND A.L. GALLANT. 2005b. Status of amphibians on the Continental Divide: surveys on a transect from Montana to Colorado, USA. *Alytes* 22:85–94.
- CORN, P.S., E. MUTHS, M.J. ADAMS, AND C.K.J. DODD. 2005c. The United States Geological Survey's Amphibian Research and Monitoring Initiative. *Alytes* 22:65–71.
- CORN, P.S., E. MUTHS, AND D.S. PILLIOD. 2011. Long-term observations of boreal toads at an ARMI apex site. The 10th Biennial Scientific Conference on the Greater Yellowstone Ecosystem. 11–13 October 2010. William D. Ruckelshaus Institute of Environment and Natural Resources, University of Wyoming, Laramie, WY; Mammoth Hot Springs Hotel, Yellowstone National Park, WY.
- CORN, P.S., W. STOLZENBURG, AND R.B. BURY, EDITORS. 1989. Acid precipitation studies in Colorado and Wyoming: interim report of surveys of montane amphibians and water chemistry. Biological Report 80(40.26) edition, USDI Fish and Wildlife Service, Washington, DC.
- CORN, P.S., AND F.A. VERTUCCI. 1992. Descriptive risk assessment of the effects of acidic deposition on Rocky Mountain amphibians. *Journal of Herpetology* 26: 361–369.
- FORREST, M.J., AND M.A. SCHLAEFFER. 2011. Nothing a hot bath won't cure: infection rates of amphibian chytrid fungus correlate negatively with water temperature under natural field settings. *PLoS ONE* 6:e28444.
- GARDNER, T.A., J. BARLOW, AND C.A. PERES. 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biological Conservation* 138:166–179.
- GARNER, T.W.J., S. WALKER, J. BOSCH, S. LEECH, J.M. ROWCLIFFE, A.A. CUNNINGHAM, AND M.C. FISHER. 2009. Life history tradeoffs influence mortality associated with the amphibian pathogen *Batrachochytrium dendrobatidis*. *Oikos* 118:783–791.
- GLOOSCHENKO, V., W.F. WELLER, P.G.R. SMITH, R. ALVO, AND J.H.G. ARCHBOLD. 1992. Amphibian distribution with respect to pond water chemistry near Sudbury, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 49:114–121.
- GOULD, W.R., D.A. PATLA, R. DALEY, P.S. CORN, B.R. HOSSACK, R. BENNETTS, AND C.R. PETERSON. 2012. Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the Greater Yellowstone Ecosystem. *Wetlands* 32:379–389.
- GU, W.D., AND R.K. SWIHART. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* 116:195–203.
- GUNZBURGER, M.S., AND J. TRAVIS. 2005. Critical literature review of the evidence for unpalatability of amphibian eggs and larvae. *Journal of Herpetology* 39:547–571.
- HAWK, J.E. 2000. Amphibian declines in the Greater Yellowstone Ecosystem: do thermally influenced waters protect boreal toads from bacterial disease? Master's thesis, Idaho State University, Pocatello, ID.
- HAWK, J.E., AND C.R. PETERSON. 1999. Amphibian declines in the Greater Yellowstone Ecosystem: does thermally influenced water provide boreal toads with protection from bacterial disease? Pages 2–3 in H. Harlow, editor, Annual Report. University of Wyoming–National Park Service Research Station, Laramie, WY.
- HECNAR, S.J., AND R.T. MCLOSKEY. 1996. Amphibian species richness and distribution in relation to pond water chemistry in south-western Ontario, Canada. *Freshwater Biology* 36:7–15.
- HOF, C., M.B. ARAUJO, W. JETZ, AND C. RAHBEK. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480:516–NIL\_137.
- HOSSACK, B.R., AND P.S. CORN. 2007. Responses of pond-breeding amphibians to wildfire: short-term patterns in occupancy and colonization. *Ecological Applications* 17:1403–1410.
- HOULAHAN, J.E., C.S. FINDLAY, B.R. SCHMIDT, A.H. MEYER, AND S.L. KUZMIN. 2000. Quantitative evidence for global amphibian population declines. *Nature* 404: 752–755.
- HOVINGH, P. 1993. Aquatic habitats, life history observations, and zoogeographic considerations of the spotted frog (*Rana pretiosa*) in Tule Valley, Utah. *Great Basin Naturalist* 53:168–179.
- KOCH, E.D., AND C.R. PETERSON, EDITORS. 1995. Amphibians and reptiles of Yellowstone and Grand Teton



- National Parks. University of Utah Press, Salt Lake City, UT.
- LANNOO, M. 2005. Amphibian declines: the conservation and status of United States species. University of California Press, Berkeley, California, USA.
- LANNOO, M.J., AND C.A. PHILLIPS. 2005. Tiger salamander. Pages 636–639 in M. Lannoo, editor, Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, CA.
- LEBRETON, J., K.P. BURNHAM, J. CLOBERT, AND D.R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- MACKENZIE, D.I., AND L.L. BAILEY. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, & Environmental Statistics* 9:300–318.
- MACKENZIE, D.I., J.D. NICHOLS, G.B. LACHMAN, S. DROEGE, J.A. ROYLE, AND C.A. LANGTIMM. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MACKENZIE, D.I., J.D. NICHOLS, J.A. ROYLE, K.H. POLLOCK, L.L. BAILEY, AND J.E. HINES, EDITORS. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Burlington, MA.
- MAZEROLLE, M.J., A. DESROCHERS, AND L. ROCHEFORT. 2005. Landscape characteristics influence pond occupancy by frogs after accounting for detectability. *Ecological Applications* 15:824–834.
- MCCALLUM, H. 2005. Inconclusiveness of chytridiomycosis as the agent in widespread frog declines. *Conservation Biology* 19:1421–1430.
- MCDONALD, T.L. 2003. Review of environmental monitoring methods: survey designs. *Environmental Monitoring and Assessment* 85:277–292.
- MOILANEN, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos* 96:516–530.
- MORIARTY, E., AND M.J. LANNOO. 2005. Striped (upland, New Jersey, western, boreal) chorus frog. Pages 485–488 in M. Lannoo, editor, Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, CA.
- MORRIS, R.L., AND W.W. TANNER. 1969. The ecology of the Western spotted frog, *Rana pretiosa* Baird and Girard, a life history study. *Great Basin Naturalist* 24:45–81.
- MUNGER, J.C., M. GERBER, K. MADRID, M.A. CARROLL, W. PETERSEN, AND L. HEBERGER. 1998. US National Wetland Inventory classifications as predictors of the occurrence of Columbia spotted frogs (*Rana luteiventris*) and Pacific treefrogs (*Hyla regilla*). *Conservation Biology* 12:320–330.
- MURPHY, M.A., J.S. EVANS, AND A. STORFER. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91:252–261.
- MURPHY, P.J., S. ST-HILAIRE, S. BRUER, P.S. CORN, AND C.R. PETERSON. 2009. Distribution and pathogenicity of *Batrachochytrium dendrobatidis* in boreal toads from the Grand Teton area of western Wyoming. *EcoHealth* 6:109–120.
- MUTHS, E., P.S. CORN, A.P. PESSIER, AND D.E. GREEN. 2003. Evidence for disease-related amphibian decline in Colorado. *Biological Conservation* 110:357–365.
- MUTHS, E., AND P. NANJAPPA. 2005. Western toad. Pages 392–396 in M. Lannoo, editor, Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, CA.
- MUTHS, E., D.S. PILLIOD, AND L.J. LIVO. 2008. Distribution and environmental limitations of an amphibian pathogen in the Rocky Mountains, USA. *Biological Conservation* 141:1484–1492.
- MUTHS, E., R.D. SCHERER, AND D.S. PILLIOD. 2011. Compensatory effects of recruitment and survival when amphibian populations are perturbed by disease. *Journal of Applied Ecology* 48:873–879.
- OUELLET, M., I. MIKAELIAN, B.D. PAULI, J. RODRIGUE, AND D.M. GREEN. 2005. Historical evidence of widespread chytrid infection in North American amphibian populations. *Conservation Biology* 19:1431–1440.
- PATLA, D.A., AND M. LANNOO. 2005. Protecting amphibians while restoring fish populations. Pages 275–276 in M. Lannoo, editor, Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, CA.
- PATLA, D.A., C.R. PETERSON, AND R.A. BENNETTS. 2007. Amphibian monitoring in the Greater Yellowstone Network: 2006 annual report. [Cited September 2008]. Available from: [http://greateryellowstonescience.org/files/pdf/Amphibian\\_2006\\_Project\\_Report.pdf](http://greateryellowstonescience.org/files/pdf/Amphibian_2006_Project_Report.pdf).
- PATTEN, D.T. 1991. Defining the Greater Yellowstone Ecosystem. Pages 19–25 in R.B. Keiter and M.S. Boyce, editors, The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, CT.
- PETERSON, C.R., E.D. KOCH, AND P.S. CORN. 1991. Monitoring amphibian populations in Yellowstone and Grand Teton national parks. University of Wyoming National Park Service Research Center Annual Report 15:39–47.
- PILLIOD, D.S., E. MUTHS, R.D. SCHERER, P.E. BARTELT, P.S. CORN, B.R. HOSSACK, B.A. LAMBERT, R. MCCAFFERY, AND C. GAUGHAN. 2010. Effects of amphibian chytrid fungus on individual survival probability in wild boreal toads. *Conservation Biology* 24:1259–1267.
- PILLIOD, D.S., AND C.R. PETERSON. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. *Ecosystems* 4:322–333.
- PILLIOD, D.S., C.R. PETERSON, AND P.I. RITSON. 2002. Seasonal migration of Columbia spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. *Canadian Journal of Zoology* 80:1849–1862.
- PIOTROWSKI, J.S., S.L. ANNIS, AND J.E. LONGCORE. 2004. Physiology of *Batrachochytrium dendrobatidis*, a chytrid pathogen of amphibians. *Mycologia* 96:9–15.
- POLLOCK, K.H., J.D. NICHOLS, T.R. SIMONS, G.L. FARNSWORTH, L.L. BAILEY, AND J.R. SAUER. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105–119.
- POPENGA, S.K., AND B.B. WORSTELL. 2008. Elevation-derived watershed basins and characteristics for major rivers of the conterminous United States. Scientific Investigations Report 2008-5153, U.S. Geological Survey, Reston, VA.
- REASER, J.K., AND D.S. PILLIOD. 2005. Columbia spotted frog. Pages 559–563 in M. Lannoo, editor, Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, CA.

- STAUFFER, D.F. 2002. Linking populations and habitats: where have we been? Where are we going? Pages 53–61 in J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Hauffer, M.G. Raphael, W.A. Wall, and F.B. Samson, editors, *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, DC.
- STEBBINS, R.C., AND N.W. COHEN, EDITORS. 1995. *A natural history of amphibians*. Princeton University Press, Princeton, NJ.
- STUART, S.N., J.S. CHANSON, N.A. COX, B.E. YOUNG, A.S.L. RODRIGUES, D.L. FISCHMAN, AND R.W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- THOMS, C., C.C. CORKRAN, AND D.H. OLSON. 1997. Basic amphibian survey for inventory and monitoring in lentic habitats. Pages 35–46 in D.H. Olson, W.P. Leonard, and R.B. Bury, editors, *Sampling amphibians in lentic habitats*. Society for Northwestern Vertebrate Biology, Olympia, WA.
- VOYLES, J., L. BERGER, S. YOUNG, R. SPEARE, R. WEBB, J. WARNER, D. RUDD, R. CAMPBELL, AND L.F. SKERRATT. 2007. Electrolyte depletion and osmotic imbalance in amphibians with chytridiomycosis. *Diseases of Aquatic Organisms* 77:113–118.
- WELCH, N.E., AND J.A. MACMAHON. 2005. Identifying habitat variables important to the rare Columbia spotted frog in Utah (USA): an information-theoretic approach. *Conservation Biology* 19:473–481.
- YOCCOZ, N.G., J.D. NICHOLS, AND T. BOULINIER. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16:446–453.

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