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ARTICLE

Estimating Occupancy in Large Landscapes: Evaluation of Amphibian Monitoring in the Greater Yellowstone Ecosystem

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Abstract Monitoring of natural resources is crucial to ecosystem conservation, and yet it can pose many challenges. Annual surveys for amphibian breeding occupancy were conducted in Yellowstone and Grand Teton National Parks over a 4-year period (2006–2009) at two scales: catchments (portions of watersheds) and individual wetland sites. Catchments were selected in a stratified random sample with habitat quality and ease of access serving as strata. All known wetland sites with suitable habitat were surveyed within selected catchments. Changes in breeding occurrence of tiger salamanders, boreal chorus frogs, and Columbia-spotted frogs were assessed using multi-season occupancy estimation. Numerous a priori models were considered within an information theoretic framework including those with catchment and site-level covariates. Habitat quality was the most important predictor of occupancy. Boreal chorus frogs demonstrated the greatest increase in breeding occupancy at the catchment level. Larger changes for all 3 species were detected at the finer site-level scale. Connectivity of sites explained occupancy rates more than other covariates, and may improve understanding of the dynamic processes occurring among wetlands within this ecosystem. Our results suggest monitoring occupancy at two spatial scales within large study areas is feasible and informative.

Keywords Colonization · Conservation · Detection · Extinction · Trend · Wetlands

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The status of amphibian populations provides one measure for evaluating ecological integrity on management units such as National Parks (Fancy et al. 2009). Many amphibian species of the western U.S., excepting local endemics, were regarded as widespread and common until the latter part of the 20th century (Bury et al. 1995). This view has been altered given rapid amphibian population declines and range constrictions (Stebbins and Cohen 1995; Green 1997; Stuart et al. 2004). Habitat loss, fragmentation and disease are among the culprits for observed losses, but declining populations have also been observed in landscapes considered protected from environmental degradation (Drost and Fellers 1996; Muths et al. 2003; Vredenburg et al. 2010).

Determining the condition of any population is challenging. This challenge is compounded when dealing with small-bodied animals that have cryptic habits, low survival, and possibly frequent population turnover due to variable habitat conditions or high variation in vital rates (Petranka et al. 2004; Green 2005). Facing these challenges, a program to assess the

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status and trends of native amphibian species was implemented initially in Grand Teton and Yellowstone National Parks in 2000 by the U.S. Geological Survey's Amphibian Research and Monitoring Initiative (ARMI) and researchers from Idaho State University, with funding from the National Park Service (NPS) Inventory and Monitoring Program (Corn et al. 2005a). In 2004, the NPS Greater Yellowstone Inventory and Monitoring Network (GRYN) selected amphibians as one of the "vital signs" (Fancy et al. 2009) to be monitored in these two parks, finalizing the sampling design and project protocol in 2006. The parks form the core of the Greater Yellowstone Ecosystem (GYE, used hereafter to describe our study area), which occupies the middle position on an ARMI transect between Glacier National Park in the north to Rocky Mountain National Park in the south, intended to provide long-term monitoring of amphibian species in the Rocky Mountains (Corn et al. 2005a). Our effort serves as an example of landscape scale monitoring called for by others (e.g., Hamer and Mahoney 2010).

Our monitoring approach uses occupancy modeling (MacKenzie et al. 2002, 2006) to estimate the probability that a suitable habitat patch is occupied by breeding amphibians. Occupancy estimation has become a standard method to assess status and trends of amphibians and many other species (Schmidt 2005; Bailey and Nichols 2009). The use of occupancy as the primary monitoring metric has grown in part because it serves as a low-cost alternative to count indices or abundance estimates, which are prohibitively expensive or logistically impossible for large areas (Mazerolle et al. 2007). Occupancy modeling uses information from repeated observations in a manner similar to capture-recapture to estimate detectability, thereby adjusting naïve relative frequency estimates (MacKenzie et al. 2002). In our study, the resulting unbiased estimate of breeding occupancy (as defined by sites with eggs, larvae, or recently metamorphosed juveniles) is the state variable used to monitor changes in patch occupancy over time.

The appropriate spatial scale for monitoring amphibian populations is uncertain and likely differs among species (Petranka et al. 2004). Thus, we assessed amphibian breeding occupancy at two scales: catchments (portions of watersheds containing variable amounts and types of wetlands), and sites (individual ponds or wetlands within the catchments). The catchment level approximates the 'breeding population' proposed by ARMI as the feasible target for monitoring amphibian population trends in large management units such as National Parks (Corn et al. 2005b). Catchments have fixed boundaries that were identifiable a priori in our study area whereas sites were identified in the field and were expected to be dynamic over time in terms of number and size. Breeding occupancy at the site level is a finer-scale measure that allows investigation of site-specific and survey-specific variables affecting detection probability and dynamics at individual wetlands, which may differ from dynamics operating at coarser scales (Van Buskirk 2005; Werner et al. 2007).

In this paper, our primary concern is to assess the efficacy of estimating occupancy by breeding amphibians at two spatial scales to assess status and trends. Specifically, our objectives are 1) to provide baseline information on the presence of breeding amphibian populations in the GYE using occupancy in catchments over multiple years, 2) to evaluate the effectiveness of our stratified sampling approach, and 3) to consider the effects of covariates on breeding occupancy in catchments and individual wetlands to better understand the underlying dynamic processes at two spatial scales.

Methods

Study Area and Species

Yellowstone and Grand Teton are adjoining National Parks located primarily in northwest Wyoming. This 1.02 million hectares are the core of the GYE, an area known for its retention of native wildlife and wilderness qualities (Noss et al. 2002). Elevation ranges from 1600 m in the lowest portion of Yellowstone to peaks over 4000 m in the Teton Range. Vegetation of the two parks includes sagebrush and grasslands at lower elevations, conifer forests at middle and upper elevations, and deciduous trees, willows, grass-sedge, and forbs in moist areas. The climate is characterized by long, cold winters and brief, cool summers, with considerable differences in annual precipitation amounts (25 cm to over 200 cm) depending on location (Wright and Gallant 2007). Most precipitation occurs as snow; snowmelt provides the main source of surface water (Despain 1990). Wetlands of the study area are diverse in size, depth, and hydroperiod, and are most prominently influenced by the water-holding capacity of associated soils (Elliott and Hektner 2000). Palustrine wetlands, which are typically used by breeding amphibians, are the most prevalent wetland type. They constitute approximately 3% of the area of the two parks. Palustrine wetlands include ponds, vernal pools, wet meadows, and marshy areas bordering lakes and rivers.

Amphibian fauna of the two parks is restricted to five native and one introduced species, reflecting the recent glacial retreat (beginning about 14,000 years ago) and cool climate (Koch and Peterson 1995). We focus on the three most common native species: barred tiger salamander (*Ambystoma mavortium*), boreal chorus frog (*Pseudacris maculata*), and Columbia spotted frog (*Rana luteiventris*). We were unable to model monitoring results for one species, the boreal toad (*Anaxyrus boreas*), because of its relatively scant occurrence. One breeding population of the non-native American bullfrog (*Lithobates catesbeianus*) inhabits a

limited area within Grand Teton National Park. The resident anurans have aquatic-obligate larvae that metamorphose and emerge from breeding ponds within 2 to 3 months after egg deposition. Tiger salamander larvae may complete metamorphosis in one season, overwinter as larvae, or obtain sexual maturity while retaining gills.

Survey Methods

On the initial survey of selected catchments, we visited all potentially suitable wetlands within catchment boundaries using National Wetland Inventory (NWI) mapping and topographic maps. We identified potential amphibian breeding sites based on the presence of non-flowing surface water, or on indicators (e.g., wetland vegetation, topographic depressions) suggesting that surface water could be present under wetter conditions. All sites were assigned a permanent identification number, and a UTM point coordinate was collected within the site using a GPS unit. We sketched and photographed sites to assist in annual relocation.

At sites with surface water, in the initial and subsequent years of monitoring, we conducted daytime encounter surveys (Crump and Scott 1994; Thoms et al. 1997) to search for all amphibian species and life stages (eggs, larvae, and adults). We visited all sites once per field season, but amphibian surveys and covariate data collection were restricted to sites with surface water capable of hosting reproduction. Two independent surveys (our form of replication) were conducted at each site by two trained observers on a single visit. Observers maintained at least 15 min separation in most cases, and did not communicate detections until both surveys were completed. Field methods were designed to satisfy two key assumptions of occupancy modeling: occupancy did not change over the course of the sampling period (due to sequential sampling), and detection histories were independent. We assumed that the target species was never detected falsely. Catchments and wetland sites were considered occupied where eggs, larvae, or recently metamorphosed juveniles were observed.

If a site was visited but not surveyed due to lack of water in a given year, a non-detection (as opposed to missing value) was recorded for both observers. Mapped NWI wetlands that were examined but never contained water in all years were removed before analysis. If new or previously-missed sites were encountered in a catchment, these were surveyed and included as targets for subsequent annual visits.

Sampling Design

We selected a stratified random sample from 3370 catchments containing wetlands with the potential for amphibian breeding presence within the two parks after delineating three levels of habitat quality (high, medium and low) from NWI definitions based on the amount and permanency of wetlands (Cowardin et al. 1979). High quality catchments were defined as those that contained large permanent/semi-permanent wetlands totaling >4 ha and seasonal wetlands totaling >2 ha. Medium quality catchments contained some permanent/semi-permanent wetlands (>0 ha and <4 ha) and >1 ha of seasonal wetlands. Low quality catchments included the remaining catchments with any amount of permanent/semi-permanent or seasonal wetlands. We stratified habitat types to ensure sufficient samples in 'high quality' habitat, given such areas represent a small portion (<5%) of catchments within the two parks (Fig. 1). Although low quality catchments comprise approximately 70% of catchments in our study area, pilot data suggested that breeding amphibians were uncommon in this stratum. Within the selected catchments, we surveyed 390 distinct wetland sites (105 permanent, 285 seasonal) over the years 2006–2009. The number of sites visited began with 296 in 2006, increasing to 335 in 2007 and 372 in 2008, decreasing to 337 in 2009.

Catchments were also stratified according to an access class ('close' ≤4 km from roads; and 'remote' >4 km) to accommodate our concern about the feasibility of surveying enough catchments in the spatially large sampling frame. Remote catchments and low quality catchments were sampled less than proportionally available, but to enable inference to the parks some samples were apportioned to both. Habitat quality and accessibility combined to act as six strata from which a stratified random sample of catchments was selected. The target population of catchments within the two National Parks consisted of 135 high quality catchments (of which 92 are close access), 990 medium quality catchments (of which 565 are close access), and 2245 low quality catchments (of which 1009 are close access).

Covariates

We hypothesized that the number of sites (nsite) in a catchment would positively affect occupancy. We also predicted that the degree to which sites were connected may affect the initial probability of breeding occupancy for the catchment. Specifically, if a catchment contained several sites close to one another, then it is more likely that one or more sites would have breeding occurring than for catchments with few sites geographically distant from one another. This idea reflects predictions from metapopulation theory that connected populations have greater chances of viability than isolated ones (e.g., Prugh et al. 2009). We used averaged nearest neighbor (NN) distance among sites within the catchment as a (inversely related) surrogate for connectivity. Nearest neighbor distances were not modeled for catchment-level colonization probabilities because we could not think of a valid a priori reason for spatial arrangement within the

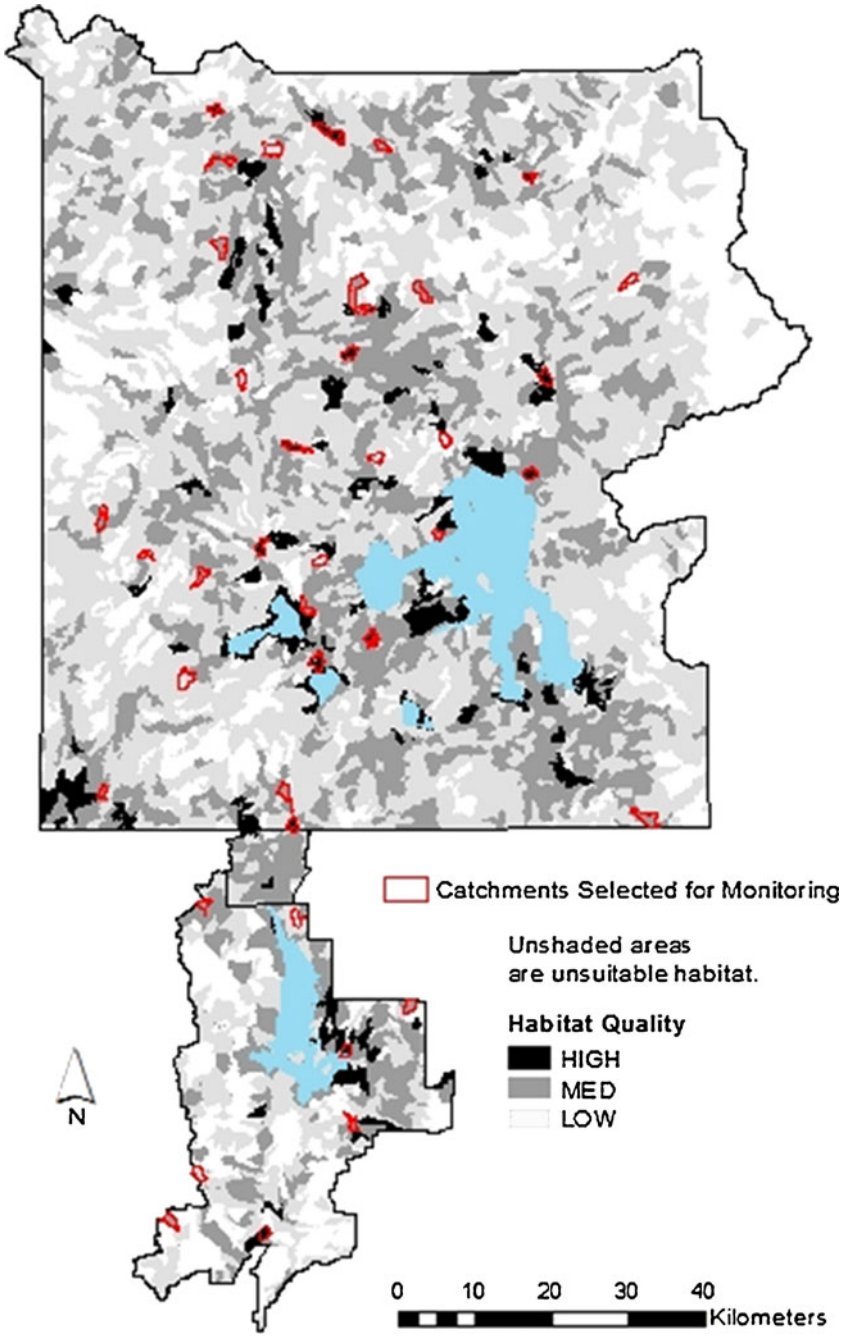

Fig. 1 Stratification of catchment habitat quality for Yellowstone and Grand Teton National Parks

catchment to be related to colonization from outside the catchment.

Using GIS-based maps, we also estimated the proportion of wetland area from high resolution (1:24,000 scale) imagery (wet; based on NWI and National Hydrology data sources completed in the early 1980's) within a 1-km buffer of all sites within the catchment with the idea that the greater wetland area available, the greater the chance a catchment would contain breeding activity. All river and lake features were included because they can facilitate amphibian movement. All covariates were year-specific because sites within catchments varied among years.

At the individual wetland scale, we included a number of site-specific covariates in our analyses. Wetland size (size; approx. length x width in meters), percent vegetation cover (veg), and percent shallow water (shal) were identified as pertinent variables likely to affect breeding status. Wetland size is expected to be positively related to occupancy (MacArthur and Wilson 1967; Hanski 1998). We computed the average distance of a site (asd) from all other sites within a catchment as a measure of site isolation, the idea being that more isolated sites are less likely to be colonized if unoccupied previously. Sites were classified as permanent/semi-permanent or seasonal based on water regime codes assigned by NWI (Cowardin

et al. 1979). Semi-permanent sites typically retain water through the amphibian larval development period, and thus were combined with permanent water bodies; seasonal sites have variable hydroperiods and some lack surface water soon after snowmelt in dry years. Percent cloud cover (cc) was considered as a potential variable that would negatively affect detectability. Our use of covariates likely reduced the potential for estimation bias due to unmodeled heterogeneity.

Analysis

We used the explicit dynamics model (MacKenzie et al. 2003) in which extinction and colonization rates are estimated to describe the mechanistic process for changes in occupancy. Extinction probabilities (ε_t) between the seasons are defined as the probability that a site occupied in season t is unoccupied by the species in season t+1. Colonization (γ_t) is the probability that an unoccupied site in season t is occupied by the species in season t+1. Direct modeling of the processes driving changes are likely to be more useful (MacKenzie et al. 2006) than yearly occupancy estimates. Yearly occupancy estimates were derived based on the extinction and colonization probabilities using program MARK (White and Burnham 1999). Each species was analyzed separately.

We used a multi-stage or hybrid modeling approach, whereby detectability was modeled while first holding all other variables in their most general form without covariates i.e., initial occupancy was allowed to vary by stratum (ψ_1(g)) and extinction and colonization rates were modeled most generally as stratum and year-specific ε(g*yr) and γ(g*yr). The highest ranked detection model was then used in subsequent evaluations of dynamic parameters in which extinction and colonization parameterizations were varied in the same manner. For example, if extinction was stratum-specific, then colonization was as well (ε(g) and γ(g)). We also considered models in which extinction and colonization rates were habitat-specific, ε(hab) and γ(hab), or access-specific ε(dis) and γ(dis). The latter case is not the result of a directional biological hypothesis. Rather, our intention was to examine if differences exist between more convenient sites and those that are more remote so as to consider if random sampling closer to roads might have inherent biases. Colonization and extinction rates were also considered as functions of the previously described covariates. The last stage of model evaluation considered different parameterizations of initial occupancy (e.g., stratum specific and reduced parameter versions as well as covariate-influenced) using the highest ranked dynamic parameter and detection probability model. A static model (in which extinction and colonization rates were fixed to zero) was also considered in the model set. Models were ranked according to Akaike's Information Criterion corrected for small sample size (AIC_c; Akaike 1973; Burnham and Anderson 2002).

We considered several biologically plausible models for detectability. For catchments, detection rates were obtained from the cumulative histories of two surveys for all sites within the catchment. Detectability was modeled as year-specific, p(yr). Year-specific differences may be caused by differing weather or personnel among years. Detectability was also modeled as year and observer-specific, i.e., model p(yr*t). Here, the 't' of p(yr*t) refers to the survey sequence, since two observers sequentially conducted surveys at each location as the means of survey replication within the season. We indicate survey-specific detectability without a year effect as $p(t)$ and constant detection probability over years and surveys as p(.). An additional model that allowed for detectability to be a function of cloud cover conditions, p(cc), was developed for site-level analyses.

To estimate occupancy for the GYE when stratum-specific models were strongly supported, we combined the stratum-level estimates according to design-based methodology (e.g., Thompson 1992). The weighted average and variance were computed as: $\overline{\widehat{\psi}} = \sum_{h=1}^{L} \frac{N_h}{N} \widehat{\psi}_h$ where h indexes each stratum, and N_h is the stratum size such that $\sum_{h=1}^{L} N_h = N$. The estimated variance is $\widehat{Var}\left(\overline{\widehat{\psi}}\right) = \sum_{h=1}^{L} \left(\frac{N_h}{N}\right)^2 \left(\frac{N_h - n_h}{N_h}\right) \widehat{Var}(\widehat{\psi}_h)$ where n_h represents the number of catchments sampled from stratum h and $\widehat{Var}(\widehat{\psi}_h)$ is the square of the estimated standard error for stratum h.

Results

Catchment-Level Analyses

The number and type of catchments used for analysis changed over the years (Table 1). Differences resulted from the decision to obtain a larger sample in the low quality stratum, and from more recent funding shortfalls. Sample sizes allocated to the low quality stratum were small because occupancy in these sites was thought to be low or absent, resulting in an inefficient use of limited resources for field work. Effort was increased in low quality catchments in the latter years to better estimate occupancy within this stratum.

The top ranked model for the tiger salamander supported habitat-specific differences (high and medium quality pooled versus low quality) for initial (first-year) catchment occupancy, extinction and colonization rates (Online Table S1). Occurrence was not detected at any of the low-quality sites, so extinction rates were fixed to zero for low quality habitats. Estimated detection probabilities were constant over years and surveys within years ($\widehat{p} = 0.79$, SE=0.07). Estimated occupancy for high and medium quality catchments ranged from

Table 1 Numbers of catchments in the 6 strata formed by 3 habitat classes (high, medium, and low) and 2 access classes (close and remote); and numbers of catchments surveyed in each stratum per year, 2006–2009

	Sample Frame	2006	2007	2008	2009
High-Close	92	9	10	10	9
High-Remote	43	4	4	4	2
Medium-Close	565	10	10	10	10
Medium-Remote	425	4	5	6	6
Low-Close	1009	2	3	5	5
Low-Remote	1236	1	1	5	5
Total Catchments	3370	30	33	40	37

approximately 32% (SE=9.0%) initially in 2006 to 39% (SE=9.0%) in 2009, based on underlying dynamic of extinction and colonization rates. Estimated extinction rate for high and medium quality sites ($\widehat{\varepsilon} = 0.184$; SE=0.107) was higher than estimated colonization rate ($\widehat{\gamma} = 0.134$, SE=0.054), but there were more unoccupied than occupied catchments, hence an overall increase in occupancy was observed. In essence, $0.134*(1-\psi)>0.184*(\psi)$. However, because low quality catchments represent the majority of GYE catchments, park-wide estimates increased only slightly over the 4-year study period (Fig. 2).

There was moderate support (Online Table S1) for the model which considered initial occupancy as a function of the average nearest neighbor distance among sites within the catchment. Specifically, the probability of a catchment being initially occupied in 2006 was higher for those catchments with the smaller NN distances (Fig. 3). Models that allowed connectivity of sites to affect extinction probability had little support.

The top ranked model for the boreal chorus frog supported habitat-specific differences (high and medium quality pooled versus low quality) for initial occupancy, extinction and colonization rates (Online Table S2). Estimated detection probabilities were high and constant over years and surveys within years ($\widehat{p} = 0.96$, SE=0.01). Estimated occupancy for high and medium quality catchments ranged from approximately 66% (SE=9.0%) in 2006 to 81% (SE=7.0%) in 2009. These occupancy rates are more than double those estimated for low quality catchments which ranged from 16.3% (SE=13.0%) in 2006, to 30.3% (SE=14.6%) in 2009. These estimates are based on underlying estimates of extinction rate (<5.0%) and colonization rates ($\widehat{\gamma} = 31\%$, SE=9.2%, for high and medium quality sites; $\widehat{\gamma} = 5.9\%$, SE=5.4% for low quality sites).

Models with covariates that received moderate support (ΔAICc<4) included one that demonstrated a positive relationship of initial occupancy with connectivity of sites within a catchment and one with a positive relationship with the number of sites in a catchment. Both of these results were in the anticipated direction, but were not as strongly supported as the habitat-specific model.

The top ranked model for the Columbia spotted frog supported habitat-specific differences (high quality versus medium quality versus low quality) for initial occupancy, extinction and colonization rates and the nearest neighbor distance among sites within a catchment (Online Table S3). Estimated detection probability was high and constant over years and surveys within a year ($\widehat{p} = 0.96$, SE=0.01). A negative relationship between initial occupancy and nearest neighbor distances of sites within catchments was detected (Fig. 4), suggesting that spatial pattern of wetland sites may affect catchment-level occupancy. Derived occupancy rates mirrored habitat quality rankings, with occupancy increasing with habitat quality (Fig. 5). For low quality catchments, occupancy rates were constant (31.0%; SE=21.6%) due to no observed colonization or extinction over the 4-year period. Occupancy estimates for the GYE declined from 41.3% (SE=9.9%) in 2006 to 37.4% (SE=10.2%) in 2009 (Fig. 2), but given the uncertainty a decline is not definitive.

Site Level Analyses

The top ranked model for the tiger salamander supported wetland-specific differences (permanent or seasonal) for

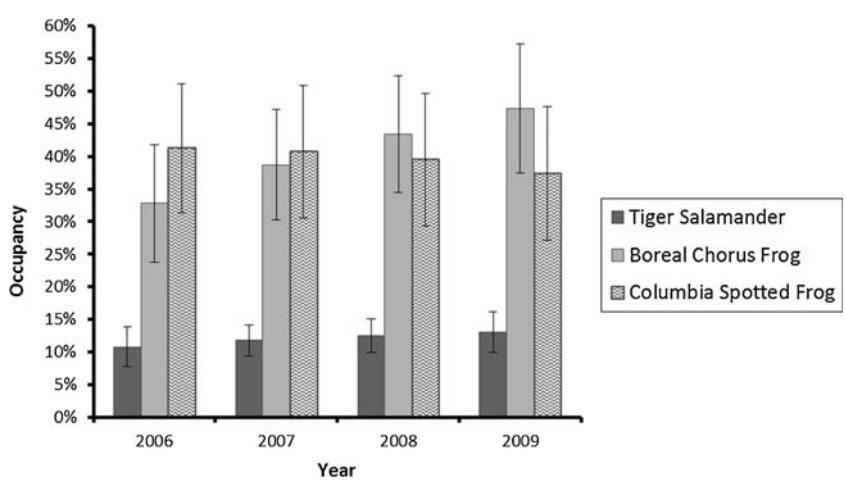

Fig. 2 Derived occupancy estimates (±SE) from the top ranked models for the tiger salamander, boreal chorus frog and Columbia spotted frog catchment-level data analysis

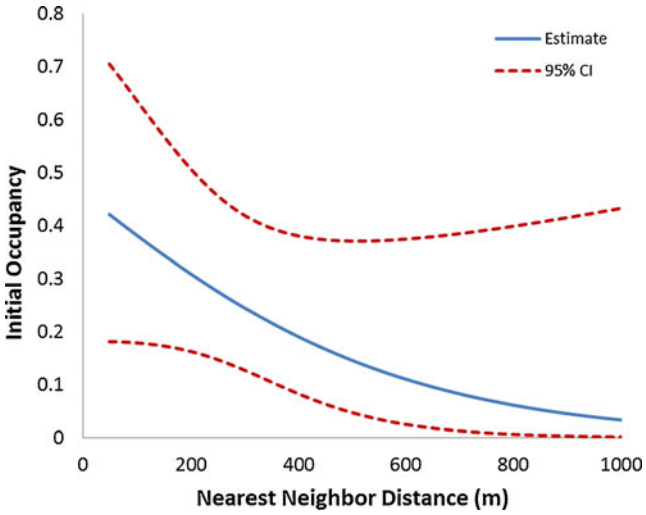

Fig. 3 Initial occupancy probability of tiger salamanders for catchments as related to average nearest neighbor distances (NN) within catchments

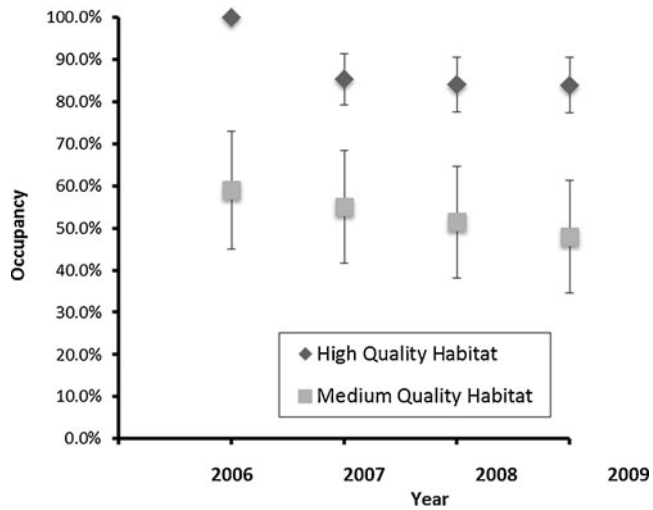

Fig. 5 Derived occupancy estimates (±SE) from the top ranked model {ψ (hab+NN) ε(hab) γ(hab) p(.)} for the Columbia spotted frog (2006–2009) catchment-level data analysis. Initial occupancy is estimated for the average nearest neighbor (NN) distance of wetland sites within catchments. Low quality catchments (not shown) had a constant estimated occupancy of 31.0% (SE=21.6%)

occupancy that differed by the extent to which the site is isolated (asd), and extinction and colonization rates that varied by year and amount of shallow water (Online Table S4). Detection probabilities were allowed to vary over years and by survey within year and increased with increasing cloud cover. Estimated initial occupancy for permanent wetland sites was notably higher ($\widehat{\psi} = 15.4\%$; SE=3.8%) than for seasonal sites ($\widehat{\psi} = 1.2\%$; SE=0.8%) using the average isolation measure (Fig. 6). A positive relationship with site isolation was demonstrated for permanent sites, but not for seasonal sites.

The top ranked boreal chorus frog model allowed for wetland-specific initial occupancy (permanent or seasonal) both of which increased with increased vegetation cover (Fig. 7). Extinction and colonization rates were year-specific (Online Table S5) as were detection probabilities, which varied between 0.83 and 0.93 (SE~0.03). Estimated occupancy for permanent sites (Fig. 8) was notably higher than for seasonal sites based on the average amount of vegetation cover (64%).

The top ranked Columbia spotted frog model (Online Table S6) supported wetland-specific differences (permanent or seasonal) for initial occupancy that increased with vegetation cover for permanent sites (Fig. 9), but this relationship was not observed for seasonal sites. Extinction and colonization rates were also wetland-specific and had differing relationships with site isolation (asd). Detection probability was constant over years and surveys ($\widehat{p} = 0.84$ SE=0.024). Estimated

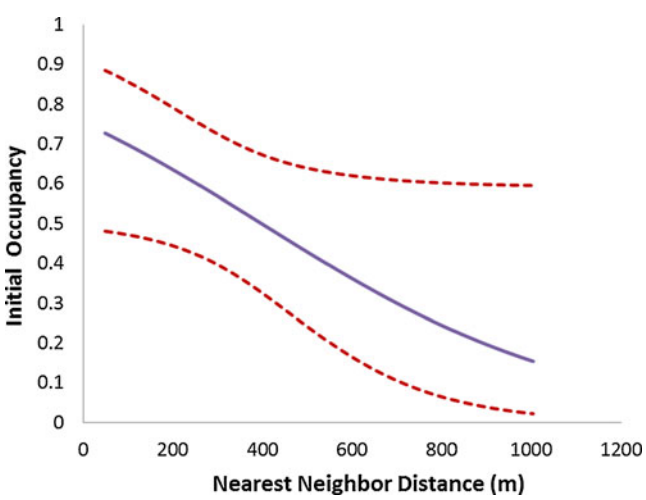

Fig. 4 Columbia-spotted frog initial occupancy of catchments as related to the average nearest neighbor distance among sites within catchments

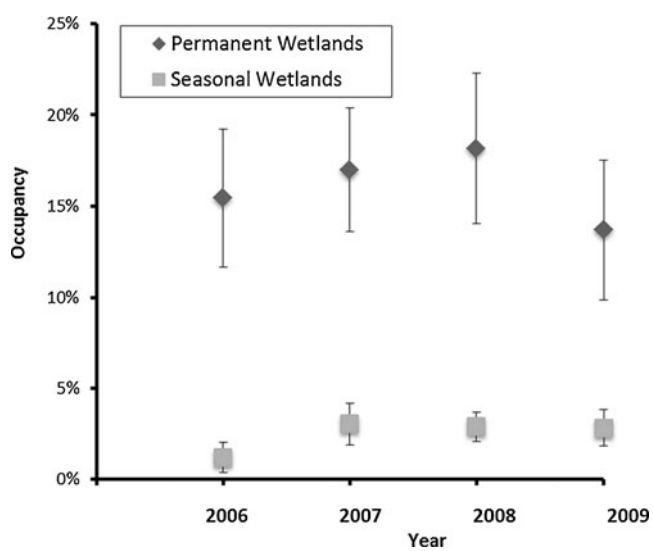

Fig. 6 Derived occupancy estimates (±SE) from the top ranked model {ψ (g*asd) ε (yr+shal) γ (yr+shal) p(t*yr+over)} for tiger salamander (2006–2009) site-level data analysis. Estimated occupancy for the first year is presented for permanent and seasonal wetland types using the average isolation measure among sites within catchments

occupancy rates (2006–2009) were more than double for permanent ($\widehat{\psi} = 34 - 29\%$; SE=0.05) than seasonal ($\widehat{\psi} = 12 - 10\%$; SE=0.02) sites. Estimated occupancy decreased over the 4-year period because estimated extinction rates (permanent: 0.15, seasonal: 0.27) were substantially higher than colonization rates (permanent: 0.05, seasonal: 0.03). The derived site occupancy rates were based on the average vegetation cover for the first year and the average (across all catchments) of the average distances among sites within catchments in later years.

Discussion

Our work represents the application of occupancy modeling to determine multi-year breeding presence of three amphibian species across a remote area of great size and habitat complexity. Such efforts are important to provide long-term, unbiased baseline data with which to judge snap-shot observations about changes in species' distributions (e.g., McMenamin et al. 2008). These long-term estimates are also critical for evaluating the role of suspected drivers in changes to amphibian occupancy across the landscape, including links between wetland habitat and precipitation. For example, quality and interconnectivity of sites appeared to be positively associated with catchment-level occupancy. The sample design was constructed with consideration of the species' biological characteristics (e.g., short period of larval residence in wetlands), logistical constraints, efficiency, and costs. It is one of the only programs that consistently and annually monitors small-bodied vertebrates (other than fish or pika) across Yellowstone and Grand Teton National Parks, implementing a protocol that was developed through more than a decade of field studies. The program also monitors wetland dynamics (e.g., documenting the number of seasonal wetlands that are dry each year), which may provide a window on climate change effects.

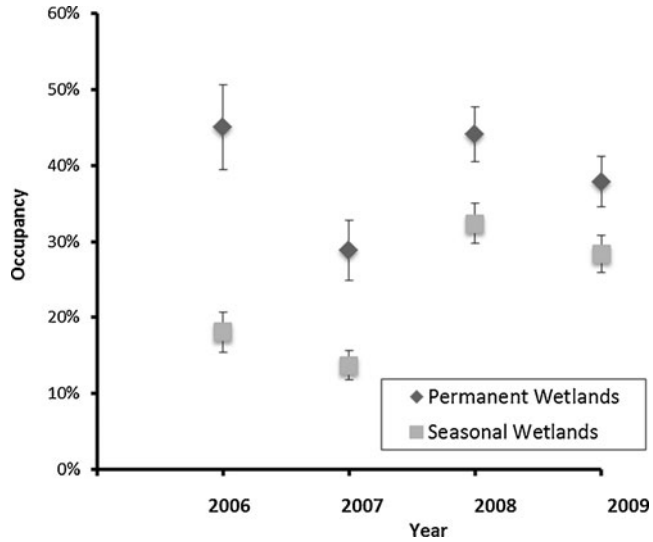

Fig. 8 Derived occupancy estimates (±SE) from the top ranked model {ψ (g+veg) ε (yr) γ (yr) p(yr)} for the boreal chorus frog (2006–2009) site-level data analysis. Estimated occupancy for the first year is presented for permanent and seasonal wetland type using the average vegetation cover among sites within catchments

Catchment Scale

Catchment occupancy by barred tiger salamanders averaged only about 12% of catchments with potentially suitable habitat. Considering that less than 70% of the total number of catchments in the parks (3370 of 4835 catchments) contain potentially suitable habitat, this species appears to be considerably less common than the other amphibians we studied.

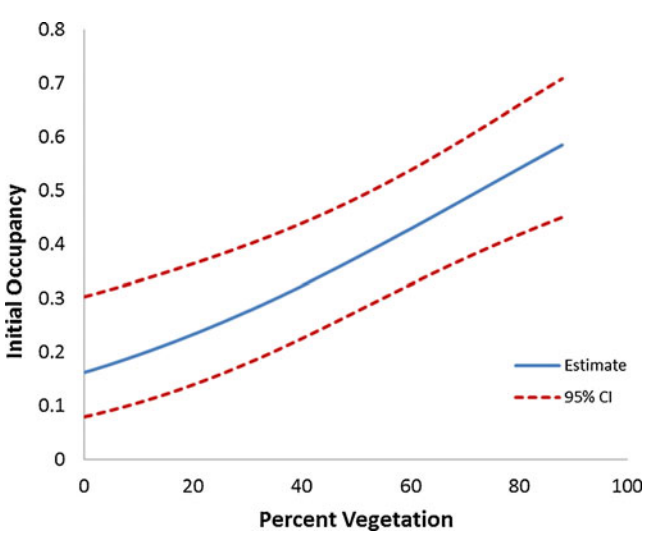

Fig. 7 Boreal chorus frog initial occupancy of permanent wetlands as related to vegetation cover at a site

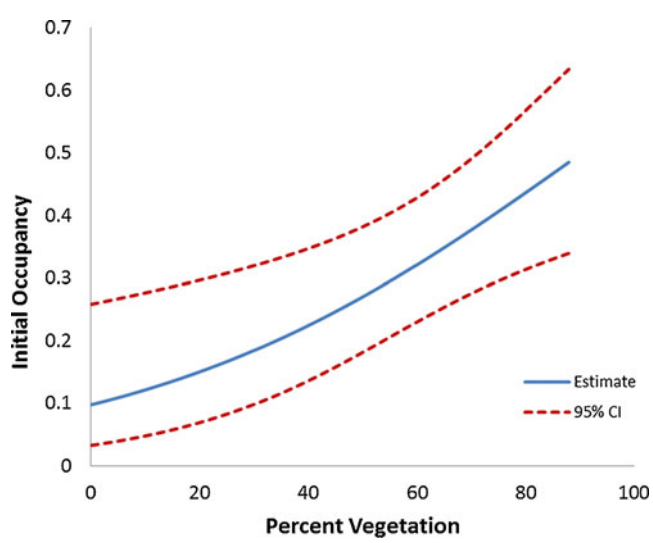

Fig. 9 Columbia-spotted frog initial occupancy of permanent wetlands as related to vegetation cover at a site

Boreal chorus frogs and Columbia spotted frogs averaged about 40% occupancy of potentially suitable catchments and thus are fairly widespread throughout the parks.

The only species with a notable positive change at the catchment level over the 4-year period was the boreal chorus frog, which showed small annual increases. Extinction rates were consistently low and colonization rates consistently high at the catchment level. In contrast, the slight negative decline in occupancy by Columbia spotted frogs is inconclusive given the estimated uncertainty. Our precision of yearly occupancy estimates was typical of many biological studies (coefficient of variations ranging from 20% to 30%). A larger sampling effort (> 40 catchments) would result in greater precision, but fiscal limitations will likely preclude additional effort. For all species, models that demonstrated time varying occupancy were strongly supported over static models for the 4-year period.

We pre-stratified catchments of the sample frame by access class (close and remote) and by habitat quality (high, medium, and low). Access had little or no effect in the modeling results, supporting our decision to increase efficiency by putting less effort in catchments that take the most time for field crews to reach. We estimate that stratifying catchments by access class allowed us to monitor 23% additional catchments per year than if we had used simple random selection. In contrast, habitat quality stratification was valuable not only for assuring sampling in the relatively rare high quality habitats, but also increased precision of the estimators. Our sampling effort was admittedly deficient in the low stratum, i.e., a maximum of 10 catchments per year and only three in the initial year. Unless sampling effort can be greatly increased, surveys may be limited to high and medium quality habitats in the future. This would restrict inference to those strata (rather than park-wide) but would be the most efficient use of limited resources in assessing amphibian status and trend.

Habitat is one of the keys to understanding the causes of amphibian decline, particularly with respect to connectivity and metapopulation dynamics (Pechmann and Wilbur 1994), and it is a primary component in the analysis of patterns of amphibian occupancy (Van Buskirk 2005). We identified the connectivity of wetland sites within catchments as affecting initial catchment occupancy. For all three species, smaller NN distances (high connectivity) resulted in higher probabilities of catchment-level occupancy, which is consistent with metapopulation theory (e.g., Hanski 1998). Our result echoes that of Hamer and Mahoney (2010), which found that smaller nearest neighbor distances increased the likelihood of initial occupancy for the golden bell frog (*Litoria aurea*). Similarly, the number of wetland sites per catchment was positively related to the initial occupancy probability in upper ranked models for two of our three species. Hartel and Ollerer (2009) found the number of temporary ponds in the landscape positively influenced both the persistence of permanent pond populations (individual species) and the number of species.

Our pilot studies in the GYE (Corn et al. 2005a and unpublished data) and the recommendations by Petranka et al. (2004) suggest that monitoring a set of single sites is inadequate to understand amphibian status across a large area, due in part to localized spatial shifts in active breeding sites that can occur in response to annually variable conditions (Werner et al. 2007; Church 2008). The use of catchments as primary sampling units helps to avoid this. We hypothesize that by sampling all potential breeding sites in watershed units distributed widely among the main drainages of the GYE, we can determine the presence and dynamics of breeding populations, given that active breeding sites signify the persistence of a population in the area. Widespread amphibian declines would be manifested by a declining number of occupied catchments for the affected species (Green 1997).

Wetland Scale

Our results suggest that monitoring at the site level augments catchment-level results by revealing finer-scale dynamics. For example, permanent and seasonal wetland sites had notably different occupancy rates. Such information may be useful in identifying which occupied catchments are more likely to become unoccupied in the future. Site-level analysis also offers larger sample sizes with which to examine trends, resulting in higher precision. Furthermore, a substantial reduction in wetland sites containing breeding occurrence within catchments could occur but this loss would not be noticed if only catchment-level occupancy was considered. For example, at the site level, extinction rates exceeded colonization over the 4 years for the Columbia spotted frog resulting in a weak negative trend in occupancy. These colonization rates were ~40% lower than those from a comparable study in Glacier National Park, where wetland occupancy of Columbia spotted frogs was stable over 6 years (Hossack and Corn 2007). Based on our results and outbreaks of ranavirus affecting larvae and adults of this species in the GYE (Corn 2007 and unpublished data), continued monitoring of Columbia spotted frogs is warranted.

For site occupancy, percent vegetation cover and site isolation (as measured by its average squared distance from other sites within the catchment to which it belongs) were two covariates that were commonly found in our top ranked models. As vegetation cover increased, initial occupancy rates also increased, a common result for pond-breeding amphibians (e.g., Gorman et al. 2009; Adams et al. 2011). In our study, as seasonal sites became more isolated, they were less likely to be colonized by Columbia spotted frogs. Similarly, Werner et al. (2009) demonstrated colonization probabilities for western chorus frogs (*P. triseriata*) at the pond level were positively related to pond connectivity.

Conclusions

The three species assessed here have been regarded as "common to abundant" in the two National Parks, based on recent observations (Koch and Peterson 1995), but systematic monitoring of amphibians in the GYE began only in the past decade. Public concern for the status of amphibians in the GYE increased after research concluded that drought and subsequent lack of surface water resulted in severe, recent declines of amphibian populations (McMenamin et al. 2008). Methodological problems with their study, including how populations were defined and nonrandom sampling in a small portion of Yellowstone, suggest that strong conclusions about the status of amphibians in the GYE were not appropriate (Patla et al. 2009). However, McMenamin et al. (2008) did present a convincing relationship between precipitation and suitable habitat. Given that future climate conditions are likely to be warmer and drier (Pederson et al. 2011), developing an accurate assessment of the status of amphibians in the GYE is an important task.

To our knowledge, this study represents the first systematic monitoring of the status of amphibians in a large, remote landscape. Our data support earlier conclusions about the relative status of amphibians in the Rocky Mountains, which depicted a range of amphibian occupancy across the region from Glacier National Park in the north to Rocky Mountain National Park in the south, with the GYE intermediate in occupancy (Corn et al. 2005a). We also provide a case study on the value of stratifying sampling areas, especially in large, remote landscapes where habitat quality varies substantially. Stratifying based on wetland abundance and type (i.e., habitat quality) allowed us to put the majority of our field effort (~70%) into monitoring catchments most likely to host multiple species, thus increasing sampling efficiency and information gained. These increases will be important for prioritizing monitoring and conservation efforts in a climate of shrinking budgets and water resources.

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