



Cooperative Amphibian Monitoring Protocol for the Greater Yellowstone Network

Narrative, Version 1.0

Natural Resource Report NPS/GRYN/NRR—2013/654



ON THE COVER

Crew members survey a wetland site for amphibians in Yellowstone National Park, July 2012.

Photograph by: Andrew Ray, NPS

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Amphibian Monitoring Working Group*

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This protocol uses methods based on an established peer-reviewed protocol. Additional formal peer review was received by a subject-matter expert not directly involved in the development of the sample design and sample size analysis, and whose background and expertise put them on par technically and scientifically with the authors.

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Revision History Log

All changes to this protocol must be logged in the following table. Version numbers increase incrementally by hundredths (e.g., version 1.01, version 1.02, etc.) for minor changes that do not require a change in analytical or procedural methods. A protocol leader must review minor modifications for clarity and technical soundness, incorporate, and communicate all changes to affected and prospective users of the protocol. Major revisions that involve a change in analytical or procedural methods are designated with the next whole number (e.g., version 2.0, 3.0, 4.0). The cooperators must review and approve major modifications.

The following table lists all edits and amendments to this document since the original publication date. Information entered in the log must be complete and concise. Users of this monitoring protocol will promptly notify the protocol leader or a member of the cooperative working group about recommended and required changes. A protocol leader is responsible for completing the revision history log, changing the date and version number on the title page and in the footer of the document file(s), and managing web-based and other distribution of updated protocol materials.

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Contents

	page
Revision History Log	ii
Contents	iv
Figures.....	vii
Tables	vii
Standard Operating Procedures.....	viii
Executive Summary	ix
Acknowledgements	xi
Acronyms.....	xiii
Introduction.....	1
Brief History of Monitoring.....	2
Issues and Threats	4
Relevance to Park Managers.....	9
Sampling Design.....	11
The Sample Frame	11
Primary Sampling Units—Catchments.....	13
Secondary Sampling Units—Sites within Catchments.....	13
Observation Units	14
Sample Stratification and Randomization	15
Sample Selection and Sample Frequency	19
Occupancy and Detection Probability—Single-season Repeat Surveys	21
Seasonal Timing of Sampling.....	23
Monitoring Potential Breeding Habitat (Objective 2)	24
Detecting Levels of Change.....	25
Supplemental Design for Boreal Toads	25
<i>Occupancy, Detectability, and Timing for Boreal Toad Sampling.....</i>	<i>29</i>
Field Methods.....	30
Field Season Preparations	30

Contents (continued)

	page
<i>Permitting and Compliance</i>	30
Sequence of Field Events	30
Initial (First Time) Visits to Catchments	31
Subsequent Visits to Catchments	31
Collecting and Recording Data	31
<i>Sketching the Site</i>	32
<i>Photographing the Site</i>	32
<i>Notifying Park Officials about Amphibian Die-offs</i>	33
Post-collection Data Processing	33
End-of-season Procedures	33
Data Management, Analysis, and Reporting	34
Data Stewardship	34
<i>Data Storage and Database Applications</i>	34
<i>Data Entry</i>	35
<i>Data Backup and Security</i>	35
<i>Data Quality Assurance</i>	36
<i>Data Documentation (Metadata)</i>	36
Sensitive Information	36
<i>Data Certification, Distribution, and Archives</i>	37
Data Analysis	37
<i>Overview of Analysis Approach</i>	37
<i>Occupancy Models</i>	38
<i>Model Selection</i>	40
<i>Model Fit</i>	41
<i>Model Averaging</i>	42
<i>Occupancy Modeling Using Survey Data</i>	42
<i>Trend Analysis</i>	43
<i>Boreal Toad Data Analysis</i>	44
Data Reporting	45
Personnel Requirements	46
Roles, Responsibilities, and Qualifications	46
Training	47
Operational Requirements	49
Annual Workload and Field Schedule	49

Contents (continued)

	page
Facility and Equipment Needs	49
Budget	50
Literature Cited	51
Appendix A. National Wetlands Inventory Types Used in Sample Design	59
Excluded Types	59
Stratified Types	59
Water Regime Types, as Defined by NWI	60
Appendix B. Occupancy Models to Study Wildlife	63
Appendix C. Modeling at the Catchment level: An Example Using 2007 Data	69
Modeling Results, Goodness-of-Fit, Model Averaging, and Application of Weighted Averages to Obtain GYE Occupancy Estimates	71
<i>Tiger Salamanders</i>	71
<i>Boreal Chorus Frog</i>	74
<i>Columbia Spotted Frogs</i>	77
Appendix D. Multi-season Analysis for Tiger Salamanders (2006-2007)	79
Appendix E. Estimating Occupancy in Large Landscapes	81

Figures

Figure 1. The conceptual basis for monitoring amphibians.	6
Figure 2. Primary drivers and stressors influencing amphibian populations.	7
Figure 3. Sample frame for GRTE and YELL showing catchments containing potentially suitable wetlands areas based on analysis of National Wetlands Inventory mapping.	12
Figure 4. Sample frame for GRTE and YELL showing distribution of catchments classed as High, Medium, and Low in terms of potential habitat quality.	16
Figure 5. Sample frame for GRTE and YELL showing the major roads and a 4 km buffer.	17
Figure 6. Sample frame showing the major drainages from which catchments were selected.	18
Figure 7. Catchments selected for long-term monitoring in Yellowstone and Grand Teton national parks.	20
Figure 8. Approximate seasonal window for amphibian monitoring in GRTE and YELL catchments.	24
Figure 9. Boreal toad breeding sites in YELL and GRTE. Sites that are ± 500 m of each other are clustered as “toad breeding areas” for monitoring. A total of 39 breeding areas are currently identified.	27
Figure 10. Database structure (USGS ARMI-Rocky Mountain Region).	35
Figure 11. Conceptual tradeoff between precision (low variance, shown with red line) and bias (blue line), as a function of the number of parameters (after Burnham and Anderson 2002).	40

Tables

Table 1. The distribution by strata of 3,370 catchments containing potentially suitable wetland sites.	17
Table 2. The 40 sample catchments within accessibility strata and habitat quality strata, spatially distributed across basins.	19
Table 3. Example of catchment level detection probability (1=detection and 0=non-detection).	22
Table 4. Time envelopes for amphibian monitoring in GRTE and YELL. These time periods are based on historical sampling and may need to be altered if breeding phenology changes are documented.	23
Table 5. Stratification classes for boreal toad breeding areas.	28
Table 6. Data stewardship roles and responsibilities.	34
Table 7. Roles and responsibilities for implementing the Amphibian Monitoring Program in the GRYN.	46
Table 8. Annual budget for amphibian monitoring in YELL and GRTE. More than 50% of the amphibian monitoring budget is spent on data management activities including analysis and reporting.	50

Standard Operating Procedures

This report is linked to the following Standard Operating Procedures (SOPs), which can be found in Bennetts et al. (2013).

SOP 1: Field Safety for the Amphibian Monitoring Program

SOP 2: Pre-season Preparations and Equipment Setup

SOP 3: Daily Procedures and Checklists

SOP 4: Monitoring Catchments Not Previously Surveyed

SOP 5: Monitoring Previously Surveyed Catchments

SOP 6: Conducting Visual Encounter Surveys

SOP 7: Data Field Descriptions and Instructions for Data Entry

SOP 8: Data Analysis

SOP 9: Quality Assurance

SOP 10: Protocol Revision

Executive Summary

This document describes a protocol for monitoring amphibians and amphibian breeding sites within John D. Rockefeller, Jr. Memorial Parkway (JORO), Grand Teton National Park (GRTE), and Yellowstone National Park (YELL). Amphibians were identified as a vital sign in the Greater Yellowstone Network's (GRYN) monitoring plan (Jean et al. 2005) and as indicator taxa in the National Park Service's (NPS) climate change response strategy for high elevation parks (Bingham et al. 2010). The amphibian assemblages present in the GRYN parks and of interest for monitoring in this protocol are barred tiger salamanders (*Ambystoma mavortium*=*Ambystoma tigrinum*), boreal chorus frogs (*Pseudacris maculata*), boreal toads (*Anaxyrus boreas boreas*=*Bufo boreas boreas*), and Columbia spotted frogs (*Rana luteiventris*).

Amphibian monitoring was initiated in GRYN for multiple reasons, but principally to track and estimate changes in the distribution and occurrence of breeding amphibians within GRTE and YELL's wetlands. A secondary goal was to evaluate if this important and obligate wetland indicator group or *vital sign* could be used to assess the status and condition of wetland ecosystems and their associated biodiversity in GRTE and YELL over time. Use of amphibians as an indicator group was based on their presumed sensitivity to environmental change, broad geographic distribution, relative straightforward techniques for surveying, and ecological importance to wetland ecosystems. Our focus on amphibians, a single taxonomic group that could serve as a surrogate for numerous obligate and facultative wetland species, seemed far more tractable than studying the full expression of organisms (*sensu* Noss 1990) that use wetlands located throughout the Greater Yellowstone Ecosystem (GYE). In addition, amphibian declines have been noted worldwide and this has not only elevated their conservation significance, but increased our awareness of their sensitivity to individual and interacting stressors globally (Collins and Storfer 2003) and within the GYE (Corn 2007). Finally, amphibian monitoring efforts have highlighted the potential vulnerability of this group to a changing climate and confirmed that amphibians can serve as valuable indicators of wetland ecosystem change (Walls et al. 2013).

In the western U.S. declines have been particularly severe and native species of the widespread genus *Rana* (brown frogs) and many species of the genus *Anaxyrus* (toads) are at risk in at least a portion of their native ranges (Corn 2003 and 2007, Bradford 2005). Unexpectedly, many declines have occurred in protected and even remote natural areas, including national parks (Bradford et al. 1993, Bury 1999, Knapp and Matthews 2001, Muths et al. 2003, Fellers et al. 2007). In addition, the western U.S. has reportedly experienced widespread and abnormally high incidences of malformations in young frogs, including multiple extra limbs, missing limbs, and deformities of the body and face (Blaustein and Johnson 2003).

To ensure that GRYN adopted and employed amphibian monitoring protocols that were both robust and scientifically defensible for long-term monitoring, GRYN joined forces with university and U.S. Geological Survey (USGS) scientists to develop, test, and adapt previous amphibian monitoring approaches used in GRTE and YELL. And, what followed was a pilot study (carried out in 2004) to investigate detection probability approaches, evaluate site definitions and habitat characteristics, and fully evaluate the initial sampling design. The 2006 field season was the final year of testing and by 2007, the main sampling and data collection

strategies were developed, and the protocol was fully implemented. Strategies for analyzing current and historic data sets continue to evolve but estimates of occupancy using post-2005 datasets have been completed (Gould et al. 2012). Since 2007, the GRYN Amphibian Monitoring Program has continued to evolve to a point that appears to be financially sustainable under current budgetary realizations. A description of the current monitoring level is carefully summarized within this protocol.

The sampling design is a stratified cluster design with random selection of catchments from major subbasins within participating parks. Catchments in GRTE are located within the Snake River Headwaters subbasin; YELL contains the Madison-Gallatin, Northern Range, Yellowstone, and Snake-Henry's Fork subbasins. To minimize costs and maximize efficiency, a type of optimal allocation of catchments among these subbasins was also applied. As a result, more easily accessible than remote catchments are included in our sample targets, and more catchments in the high and medium habitat quality classes are prioritized for annual sampling.

Once a site within a catchment is identified or located, field crews have four main tasks: (1) conduct the survey for amphibians, (2) collect the habitat and amphibian data, (3) record the data, and (4) document the site with a photograph and sketch. Two-person field crews conduct surveys following standard amphibian visual encounter methodologies. In brief, this entails walking the perimeters of water bodies and walking transects through shallow ponds and wetlands. Long-handled dip-nets are used to sweep the water for amphibian larvae. Each crew member surveys the site independently without communicating observations to the other observer. This dual-observer method is critical to enable accurate estimates of species detectability.

Occupancy by breeding amphibians per species is the resource condition or state variable of interest for this protocol and occupancy can be estimated at two levels: catchments and sites. Detection of any number of eggs, larvae, or recent metamorphs (i.e., young of the year life stages) of a particular species indicates occupancy of a site, and occupancy at any site within a catchment indicates occupancy at the catchment level. Occupancy is adjusted for detection probability at both levels, and modeled using a suite of habitat and sampling covariates. This approach is similar to that used by the USGS in Glacier National Park (Corn et al. 2005b, Hossack and Corn 2007) and has been used to successfully estimate amphibian occupancy in the GYE (Gould et al. 2012). This protocol document provides comprehensive information on sampling design, survey methods, the collection and management of field data, and approaches to estimating amphibian occupancy in the GRYN parks.

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Robert Bennetts was the primary architect of the sampling design, employing a process that involved many participants from the National Park Service (including GRYN's Vital Signs program), USGS-Amphibian Research and Monitoring Initiative (ARMI), USGS-Earth Resources Observation Systems (EROS), and Idaho State University's Herpetology Laboratory. Charles Peterson's leadership of herpetological inventory, monitoring, and research efforts in the GYE provided essential baseline information and insights that have informed many aspects of the current protocol. Larissa Bailey provided assistance as consultant for sample design, statistical issues, and field methods; her involvement included visits to study sites in the GYE in 2004, participation in many discussions, and analysis of pilot data. We also thank John Sauer and James Nichols for their advice. William Gould's evaluation of sample design and data analysis methods and summarized in Gould et al. (2012) resulted in design improvements as well as enhanced understanding of the statistical issues and the first assessment of the monitoring data through modeling.

USGS-ARMI has been an essential partner for all phases of this monitoring program since its inception. We thank P. Stephen Corn for including the GYE in ARMI's regional and national programs, and for procuring funding. For assistance with sample design, statistical analyses, and field methods, in addition to Steve Corn, we thank Blake Hossack and Erin Muths. Expert database support and assistance with PDA programming was provided by Blake Hossack, Chris Brown, and Donn Holmes. For former database support during the pilot-study years, we thank Sarah Street. The USGS-EROS Data Center was an active partner during the design phase as we tested monitoring at various spatial scales, culminating with the GIS layer of catchment boundaries currently in use; we thank Robert Klaver and Alisa Gallant for their expert support as well as their patience. For diagnostic examination of amphibian specimens collected during monitoring activities, we are indebted to David Green at USGS-National Wildlife Health Center.

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The GRYN parks have provided many and diverse kinds of assistance during the pilot years and recent implementation of long-term monitoring. In particular, we thank the following people in Yellowstone: Margie Fey, Stacey Gunther, Christie Hendrix, Austin Murphy, Pat Perrotti, Daniel Reinhart, Ann Rodman, Brad Ross, Christine Smith, and Anita and John Varley; in Grand Teton National Park: Stephen Cain, Megan Callahan, and Susan Wolff. We also thank the many park

personnel not listed here who have cooperated with accomplishing the field work in a variety of ways, such as by granting permission for research activities and by providing advice.

We warmly thank the volunteers and field crews for their efforts in procuring data. Char Corkran and Dave Corkran have volunteered their expert help for more than 15 years, assisting with early testing of watershed-based amphibian monitoring in the backcountry and the monitoring of boreal toads. We thank Ann Harvey for multiple years of help with field work. Field crew members participating in the initial stages or final implementation of this protocol (since 2001) have been numerous. We appreciate and thank all past field crew members for their hard work, dedication, interest, and enthusiasm. The GRYN Inventory & Monitoring staff expresses sincere gratitude to Debra Patla for her exceptional assistance and unending support during all phases of this monitoring protocol and to Chuck Peterson for his passion and motivation to study and protect amphibians.

Acronyms

AIC	Akaike information criterion
AICc	corrected Akaike information criterion
AMMA, AMTI	<i>Ambystoma mavortium</i> , <i>Ambystoma tigrinum</i> , or barred tiger salamander,
ARMI	Amphibian Research and Monitoring Initiative
Bd	<i>Batrachochytrium dendrobatidis</i>
ANBO, BUBO	<i>Anaxyrus boreas boreas</i> , <i>Bufo boreas boreas</i> , or boreal toad
CSDGM	content standard for digital geospatial metadata
DEM	digital elevation model
DOI	Department of the Interior
EROS	Earth Resources Observation Systems
GIS	Geographic Information Systems
GPS	Global Positioning System
GRTE	Grand Teton National Park
GRTS	generalized random-tessellation stratified
GRYN	Greater Yellowstone Network
GYE	Greater Yellowstone Ecosystem
GYSCLC	Greater Yellowstone Science Learning Center
I&M	Inventory and Monitoring
ISU	Idaho State University
JORO	John D. Rockefeller, Jr. Memorial Parkway
NPS	National Park Service
NRCC	Northern Rockies Conservation Cooperative
NRMSC	Northern Rocky Mountain Science Center
NWI	National Wetlands Inventory
POA	portion of area occupied
PDA	personal data assistant
PSMA	<i>Pseudacris maculata</i> , or boreal chorus frog
QAICc	quasi-corrected Akaike information criterion
RALU	<i>Rana luteiventris</i> , or Columbia spotted frog
SOP	standard operating procedure
SPOT	Satellite personal tracker and messenger device
USGS	United States Geological Survey
UV	ultraviolet
YELL	Yellowstone National Park

1. Introduction

Amphibian declines have been noted worldwide in recent decades, manifested as population crashes and disappearances, shrinking geographic ranges, and species extinctions. The phenomenon has been the focus of extensive scientific research since its recognition as a global issue by the First World Congress of Herpetology held in Canterbury, England in 1989 (www.worldcongressofherpetology.org). In some regions, including North America, rapid declines probably began around the middle of the 20th century, and the rate of decline increased in the 1990s (Houlahan et al. 2000, Alford et al. 2001). Worldwide, 32% of amphibian species are now threatened with extinction, while 43% exhibit some form of population decrease, according to the World Conservation Union's Global Amphibian Assessment (Stuart et al. 2004). Amphibians are far more threatened and declining more rapidly than either mammals or birds, with many amphibian species at the brink of extinction (Stuart et al. 2004). And, it is now believed to be "virtually certain that many hundreds, if not thousands, of frogs, toads, salamanders, newts, and caecilians will become extinct in the wild in this century" (Norris 2007:311).

Amphibian declines have been particularly severe in the western U.S., where all native species of the widespread genus *Rana* (brown frogs) and many species of the genus *Anaxyrus* (toads) are at risk in at least a portion of their native ranges (Corn 2003 and 2007, Bradford 2005). Unexpectedly, many declines have occurred in protected and even remote natural areas, including national parks (Bradford et al. 1993, Bury 1999, Knapp and Matthews 2001, Muths et al. 2003, Fellers et al. 2007). In addition, the U.S. West is reportedly experiencing widespread and abnormally high incidences of malformations in young frogs, including multiple extra limbs, missing limbs, and deformities of the body and face (Blaustein and Johnson 2003).

Amphibian decline is a "global change" issue, similar to climate change in the sense that both are symptomatic of complex interactions (Sodhi et al. 2008) and widespread environmental changes, with a variety of local or regional manifestations and incomplete understanding of mechanisms (Mattoon 2001). The loss of amphibians, the most ancient of the Earth's land vertebrates, is seen as an example of a complex and potentially enduring phenomenon (Bury 1999) that could represent "the first whole class of animals to be globally affected by our cumulative impact on this planet" (Gascon et al. 2007:4). More specifically, and with implications at local or regional scales, amphibians can index problems of air and water pollution, drought, habitat loss and fragmentation, the introduction of non-native species, such as sport fish and bullfrogs (*Lithobates catesbeianus* = *Rana catesbeiana*), and the emergence and spread of infectious disease (Bury et al. 1995). The status and trends of amphibian populations in protected areas such as national parks may provide an opportunity to help elucidate causal mechanisms of decline (i.e. indicate if and to what extent such problems exist in the absence of some perturbations, or how resilient these areas are from threats that are being experienced by declining populations in other places). Moreover, documenting the amphibians present in wetlands and aquatic habitats of national parks will add to our understanding of the utility of parks in managing and conserving freshwater biodiversity (Lawrence et al. 2011).

"We ourselves could not have devised a better early-warning device for general environmental deterioration than a frog," observed E.O. Wilson (Wilson 2002:56). A suite of characteristics make amphibians valuable as indicators of environmental problems (Stebbins and Cohen 1995;

Sparling et al. 2003). Their moist skin, permeable to air and water, renders them potentially more vulnerable to contaminants and ultraviolet (UV) radiation than other vertebrates, and readily accumulates toxins and parasites (Wilson 2002, Sparling et al. 2003). Small-bodied and unable to move long distances, amphibians are also subject to local conditions. Their two-phased life history (including an aquatic, usually herbivorous stage and a terrestrial, carnivorous stage) exposes them to a variety of environmental conditions and renders them potentially vulnerable to even subtle changes in the environment. High fidelity to breeding sites, along with a capacity for colonizing new wetland habitats, makes it possible to track both positive and negative changes in population numbers and distribution.

1.1. Brief History of Monitoring

In 1991, the Herpetology Laboratory at Idaho State University (ISU) began a collaborative project with the National Park Service and the U.S. Fish and Wildlife Service to assess the occurrence and status of amphibians in the Greater Yellowstone Ecosystem (GYE)¹. This early effort consisted mainly of comparing the occurrence of species at sites where they had been previously documented, and then monitoring ten selected sites in the GYE. In 1995, Edward Koch and Charles Peterson published a field guide describing the distribution and life history of amphibians in Yellowstone (YELL) and Grand Teton (GRTE) national parks, based on their compilation of historical records, communications with numerous knowledgeable people, current herpetological literature, and field work including surveys and monitoring (Koch and Peterson 1995). GRTE is used here and throughout this document to describe areas located within GRTE and the John D. Rockefeller, Jr. Memorial Parkway (JORO); JORO provides a natural link between GRTE and YELL and is administered by GRTE.

In the 1990s, the ISU Herpetology Lab also conducted surveys in many portions of GRTE and YELL to provide information about road reconstruction, fish restoration, and other projects. Several graduate-level research projects on amphibians were also conducted. Findings from the 1990s (see Peterson et al. 1992, Peterson et al. 1995, Corkran 1997 and 1998, Patla 1997, Patla and Peterson 1997, Patla 1998, Patla 2000) are housed in a variety of databases, reports, and records housed at Idaho State University (ISU), various national park offices, and available from the NPS's Integrated Resource Management Application portal (<https://irma.nps.gov/App/Portal/Home>).

Investigations in the 1990s (e.g. Hill and Moore 1994, Koch and Peterson 1995) also suggested that three amphibian species are widespread and locally common in GRTE and YELL: barred tiger salamander (*Ambystoma mavortium*²=*Ambystoma tigrinum*), boreal chorus frog (*Pseudacris maculata*), and Columbia spotted frog (*Rana luteiventris*). Boreal toads (*Anaxyrus boreas boreas*²=*Bufo boreas boreas*) appear to be less widespread and abundant than in the 1950s (Carpenter 1953), but historical information is insufficient to quantify a decline. Northern leopard frogs (*Lithobates pipiens*²=*Rana pipiens*) have almost completely disappeared from

¹“Greater Yellowstone Ecosystem” (GYE) typically refers to Yellowstone and Grand Teton National Parks and the surrounding mountainous terrain in Wyoming, Idaho, and Montana. In this Protocol, “GYE” will most often be used to refer to Yellowstone and Grand Teton national parks, or the portion of the Greater Yellowstone Network (GRYN) excluding Bighorn Canyon National Recreation Area.

²Scientific and standard names of amphibians described here follow that in Crother (2008).

GRTE, where the species was well documented in the 1950s (Carpenter 1953). One non-native species, the American bullfrog, is apparently thriving in GRTE at Kelly Warm Springs, where it has resided since the 1950s (Koch and Peterson 1995). The 1990s work provided fundamental information needed for monitoring amphibians (e.g., which species occur, life history characteristics, and identification of breeding habitat in the GYE), but was insufficient to determine overall trends within YELL and GRTE.

The initial stages of long-term amphibian monitoring in the GYE began in 2000 through collaborations between the National Park Service Greater Yellowstone Network (GRYN), the U.S. Geological Survey's Amphibian Research and Monitoring Initiative (USGS-ARMI), and ISU's Department of Biological Sciences Herpetology Laboratory. From 2000 through 2003, a herpetological inventory was conducted in YELL and GRTE. This was accomplished for amphibians through surveys of potential breeding habitat in randomly-selected watershed units across YELL and GRTE (Patla and Peterson 2004). The approach was designed and implemented initially as a pilot study in 2000 under USGS-ARMI (Patla 2001). In 2001, 2002, and 2003, surveys were jointly funded by the National Park Service Inventory & Monitoring Program (NPS-I&M) and USGS-ARMI, with the majority of funding supplied by USGS-ARMI. Beginning in 2004, a sampling design for YELL and GRTE was developed, tested, and adapted from the herpetological inventory and initial ARMI projects (the sampling design is fully described in the next section). During the field season of 2004, a pilot study was also conducted to investigate detection probability, site definition, and related issues pertinent to sampling design. In 2005, the new approach was field tested, with a subset of the selected sampling units (catchments). The 2006 field season was the final year of testing. By 2007, the main sampling and data collection issues were resolved and the protocol was fully implemented with recognition of the need for adaptive modifications and further development of data analysis methodology. Since 2007, the Amphibian Monitoring Program has continued to evolve to a point that appears to be financially sustainable under current budgetary realizations. A description of the current monitoring level is carefully summarized within this protocol.

The USGS-ARMI (ARMI hereafter) was established and funded by the U.S. Congress in 2000, in response to concerns about amphibian declines and malformations. ARMI is a national program coordinated by the USGS, the science and research bureau for the Department of the Interior (DOI). Its goal is to "better understand the dynamics of amphibian population trends, including causes of declines, so that DOI agencies and other land managers have the most accurate information from which to develop effective ways to manage and conserve amphibian populations" (Corn et al. 2005a:1). ARMI's conceptual framework is a pyramid, with extensive inventory of many sites nationwide (pyramid base), more concentrated surveys at a moderate number of areas (mid-level), and intensive research at a small number of sample sites (apex) (Corn et al. 2005a). The collaborative, long-term monitoring program described in this protocol fits mostly within the mid-level of the national ARMI pyramid. Apex-level efforts (not described in this protocol) are directed at toad breeding sites and a long-term monitoring site for Columbia spotted frogs at Lodge Creek in YELL. Seven ARMI regions were defined; the GYE resides in the Rocky Mountain Region, which includes the states of Montana, Wyoming, Colorado, and New Mexico. (See the ARMI website at <http://armi.usgs.gov/>.) The ARMI Rocky Mountain Region designated the GYE as the central portion of the Great Divide Transect, a system of amphibian monitoring and research projects extending from Glacier National Park in the north to Rocky Mountain National Park in the south (Corn et al. 2005b).

The Herpetology Laboratory is located in the Biological Sciences Department of ISU, Pocatello Idaho. Headed by Dr. Charles R. Peterson, Professor and Curator of Herpetology at the Idaho Museum of Natural History, the Herpetology Lab has investigated the distribution and abundance of amphibians in the GYE and Idaho since 1989. Numerous amphibian surveys and research projects conducted by the lab and its affiliates (associates and graduate students) prior to the NPS I&M effort provided a base of natural history, occurrence, and methodological information for the current monitoring program. Under contract with GRYN and ARMI, cooperators (e.g., ISU and the Northern Rockies Conservation Cooperative or NRCC) have hired field personnel and coordinated implementation of the monitoring program with the GRYN.

1.2. Issues and Threats

Ascertaining the cause of amphibian declines has been challenging due to the wide range of species and geographical areas affected. Of the world's rapidly declining amphibian species, 48% are victims of "enigmatic declines" or unidentified processes (Stuart et al. 2004). Complex and possibly interacting factors (Sodhi et al. 2008) are thought most likely for enigmatic declines, including disease, climate change, increased UV radiation, and long-distance chemical contamination carried by wind. Emerging infectious disease has garnered the most intense and recent concern, and particularly the disease chytridiomycosis, caused by a species of fungus that parasitizes amphibian skin (Matoon 2001, Collins and Storfer 2003, Stuart et al. 2004). In addition, amphibians face problems common to most species of wildlife in the 21st century: habitat loss and degradation, non-native species introductions (species that prey on or compete with native amphibians), over-exploitation (for food and the pet trade), and pollution. Habitat loss and degradation is considered the most critical threat to amphibians, globally and in the U.S. (Muths et al. 2006 and sources therein). And, habitat degradation along with other environmental factors may be facilitating the spread of amphibian disease (Rohr et al. 2011). Amphibian malformations, which may or may not result in significant population declines, are thought to result from several causes: infection by parasites, chemical contamination, increased ultraviolet radiation, and physical trauma (USGS NWHC 2001, Blaustein and Johnson 2003). In YELL and GRTE disease, fish stocking, and habitat modification associated with road and housing developments have been implicated in amphibian declines (Patla 1997, Patla and Peterson 2004, Corn et al. 2005b, Spear et al. 2006, Corn 2007, Patla et al. 2007) and one native species, *Lithobates pipiens*, is believed to have been extirpated from YELL (Corn 2007). Interestingly, recent evidence showed the pathogenic chytrid fungus is ubiquitous throughout the GYE (Muths et al. 2008) and although survival of adult toads is reduced in northern populations, severe declines caused by chytrid elsewhere have not occurred (Pilliod et al. 2010; Corn and Legg 2012).

1.3. Measurable Objectives

The considerations described above and conceptual models prepared by GRYN to explain the structure, function, and interconnectedness of GRTE and YELL ecosystems were carefully evaluated during the process of selecting GRYN *Vital Signs*. As a result, amphibians were selected as an indicator of biological integrity, at the level of focal species or communities (Jean et al. 2005).

To that end, amphibian monitoring was initiated in GRYN to track and estimate changes in the distribution and occurrence of breeding amphibians within GRTE and YELL's wetlands. A secondary goal was to assess whether this important and obligate wetland indicator group or *vital*

sign could be used to assess the status and condition of wetland ecosystems and their associated biodiversity in GRTE and YELL over time (Jean et al. 2005). In brief, use of amphibians as an indicator group was based on their presumed sensitivity to environmental change, broad geographic distribution, relative straightforward techniques for surveying, and ecological importance to wetland ecosystems. Our focus on amphibians, a single taxonomic group that could serve as a surrogate for numerous obligate and facultative wetland species, seemed far more tractable than studying the full expression of organisms (*sensu* Noss 1990) that use wetlands located throughout the GYE. As noted above, amphibian declines have been documented worldwide and this has not only elevated their conservation significance, but increased our awareness of their sensitivity to individual and interacting stressors globally (Collins and Storfer 2003) and within the GRTE and YELL (Corn 2007). Finally, amphibian monitoring efforts have highlighted the potential vulnerability of this group to a changing climate and confirmed that amphibians can serve as valuable indicators of wetland ecosystem change (Walls et al. 2013).

Long-term monitoring of amphibians in GRTE and YELL will not only provide insights into the status of a significant component of wetland biological diversity, but may also assist in assessing the level of overall ecological condition or stress in one of the few remaining large, relatively intact landscapes in the northern temperate zone (Schullery 1995, Gould et al. 2012). Amphibians can also serve as useful indicators to some environmental stressors (e.g. Norris 2007) that are of concern to national park managers and the public, including climate change, diseases, contaminants, habitat alteration, and introduced non-native species (Figure 1).

Amphibian populations may respond in a number of ways to these stressors and variables: occupancy and distribution patterns may change, species may disappear regionally or within administrative units, the abundance of individuals can decline or increase, outbreaks of disease and malformations may occur, and the genetic structure of populations may change. The consequences of changes in amphibian populations may be realized through effects on predators, prey, pond ecosystems, and energy or nutrient flow.

Figure 2 depicts more specifically how amphibians respond to drivers and potential stressors. All amphibian species of the GYE rely on shallow water bodies for egg deposition and larval development (Koch and Peterson 1995). Thus, factors (e.g., drought or climate change, land use, and beavers, *Castor canadensis*) affecting the location, size, and persistence of wetlands are likely to substantially affect the distribution and number of amphibian breeding populations. Some stressors have the potential to directly affect the health, survival, and abundance of amphibians: pathogens, contaminants from both local and remote sources, UV radiation, and introduced species that compete with or prey on native amphibians (such as bullfrogs, non-native fish, and introduced snails) or plant species that degrade wetland breeding habitat (Alford and Richards 1999). Some environmental factors may affect amphibians directly as well as indirectly, through their impacts on wetland habitats. For example, roads can cause high mortality rates in frogs attempting to reach their seasonal breeding or wintering habitat, and roads can also cause wetland loss.

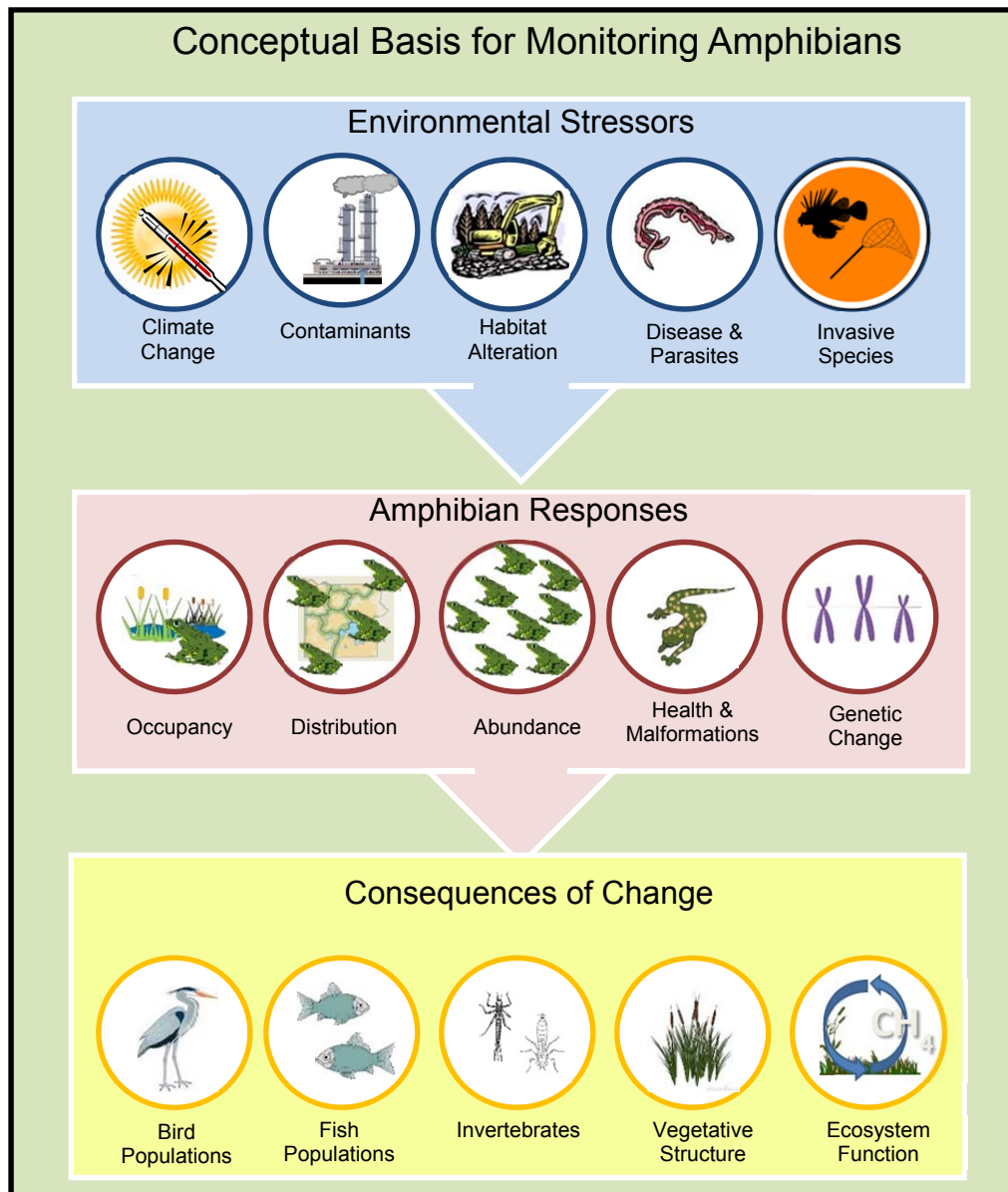


Figure 1. The conceptual basis for monitoring amphibians.

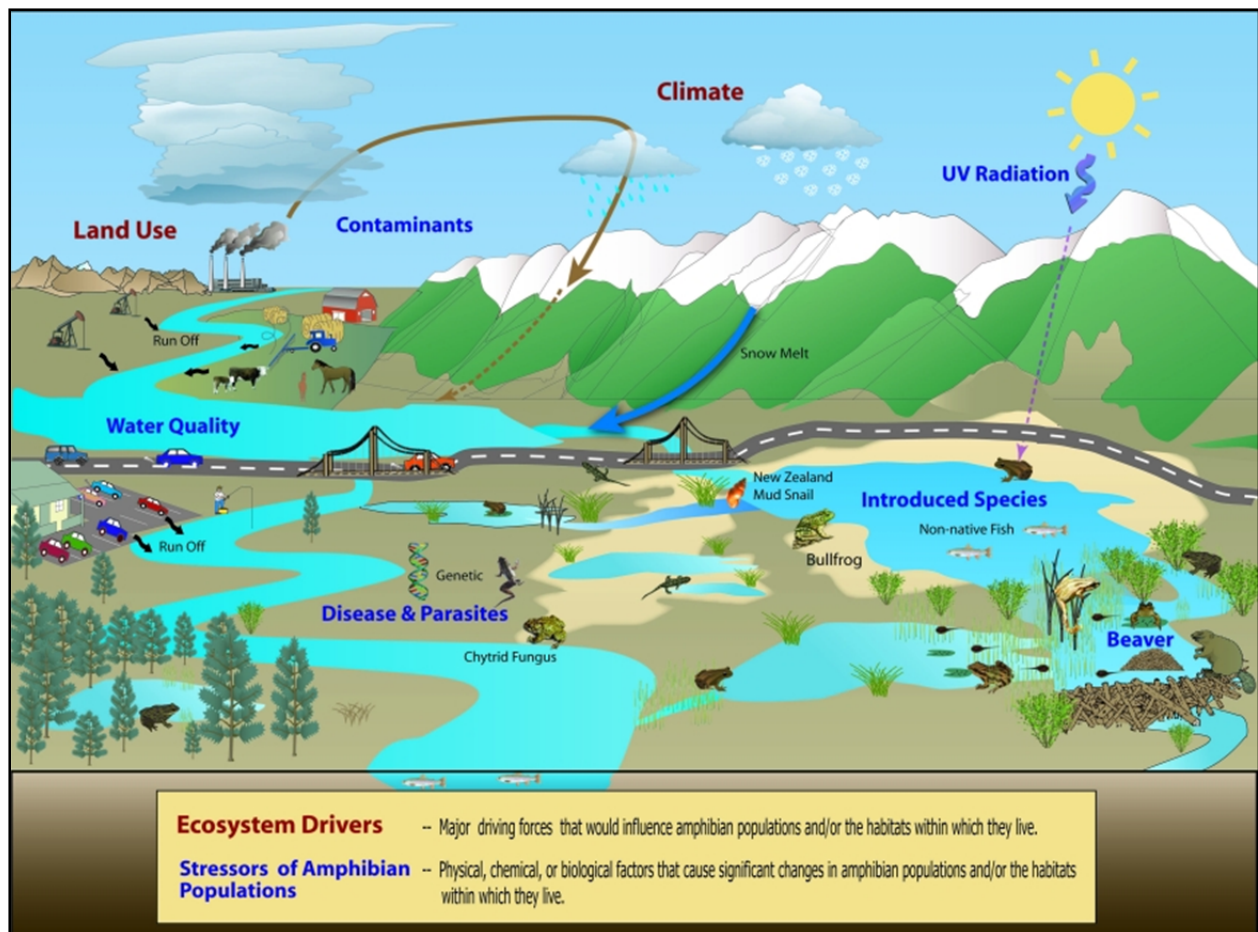


Figure 2. Primary drivers and stressors influencing amphibian populations.

Determining the abundance and trends of wildlife species can be notoriously difficult, expensive, and prone to bias due to short-term fluctuations in population sizes or methodological problems. Fortunately, the problem of how to monitor amphibians on DOI lands has been the subject of an integrated effort by senior USGS scientists with expertise in biology, cartography, hydrology, and statistics (Corn et al. 2005a). The conceptual, “mid-level” approach embraced for monitoring amphibians in selected administrative units (e.g., national parks) focuses on changes in the number of populations, as opposed to changes in the size of populations. This is based on Green’s (1997) framework for discerning declines:

A decline is the condition whereby the local loss of populations across the normal range of a species so exceeds the rate at which populations maybe established, or reestablished, that there is a definite downward trend in population number.
(Green 1997:293)

To assess amphibian status and trends in these terms, USGS scientists propose monitoring changes in the proportion of area occupied based on presence/absence data, using estimation techniques that incorporate measures of detection probability and support analyses that will draw correlations between measured environmental variables and population changes (Corn et al. 2005a). The approach assumes:

As populations increase in abundance they should expand into available habitat with a concomitant increase in occupancy. As populations decrease in size, distributions should shrink, with fewer species in the sampling units and a concomitant decline in occupancy. Thus the occupancy estimator can provide indirect information on temporal and spatial variations in species abundance. With simultaneous monitoring at sampling sites of environmental variables and stressors that can affect amphibians, correlation with possible causes of change can be established and studied. (Corn et al. 2005a:6)

The details of implementing this approach are described in the section on Sampling Design.

Although our specific monitoring objectives are targeted for inferences to the GRTE and YELL portion of GRYN, they are also intended to complement broader objectives of ARMI that seek to address objectives at more regional and national scales.

Objective 1: Estimate the proportion of catchments and wetland sites (described below) used for breeding by each of the four common, native amphibian species annually, and estimate the rate at which their use is changing over time.

Breeding sites are wetlands that are identified by the presence of eggs, larvae, or recently metamorphosed juveniles. The species under investigation in GRTE and YELL are: barred tiger salamander, boreal chorus frog, boreal toads, and Columbia spotted frog. If discovered in the future, northern leopard frogs and any other rare native species will be addressed separately.

Justification/Rationale for Objective 1: Breeding site occupancy, as opposed to the occurrence of any life stage of the species, was selected for the metric because:

- Breeding sites provide positive indication that a breeding population is present (as opposed to individual adults with a possibly transitory or brief occurrence in the unit);
- Breeding sites (i.e., wetlands) exist within relatively small and identifiable portions of the landscape;
- Breeding sites are used annually if suitable and if the species remains present;
- New breeding sites have the potential to become occupied when they become available; and
- Breeding sites are more likely to meet the closure assumption of the occupancy estimation model being used (i.e., larval amphibians are confined to wetlands where adults deposit eggs, while adults disperse to upland areas and could be absent during the surveys).

The proportion of area occupied (PAO) approach provides a measure that: (1) explicitly enables estimation of local extinctions and colonization of sites; (2) accounts for imperfect detectability of individual species; (3) enables estimation of confidence intervals; (4) is comparable across sites; and (5) has become a widely accepted approach for reliable estimates of occupancy (MacKenzie et al. 2006).

Occupancy will be assessed at two levels: catchments (portions of watersheds containing multiple potential sites; described in the section on Sampling Design), and sites (individual

ponds or wetlands). The catchment level approximates the “breeding population” identified by ARMI as the feasible target for monitoring amphibian population trends in national parks. Occupancy at this level will be the major vehicle for meeting the goal of determining if amphibians are declining, stable, or increasing in GRTE and YELL. Occupancy at the site level is a lower-scale measure that will allow one to investigate the importance of site-specific and survey-specific variables affecting detection probability and occupancy at individual wetlands. The dynamics at the site level can augment the catchment-level results to provide greater understanding of system dynamics. This approach assumes sites are independent and that individual amphibians are only breeding at a single breeding site (Gould et al. 2012).

Objective 2: Determine the total number of wetlands within sampled catchments that are suitable for amphibian breeding (i.e., have standing water during the breeding season) annually.

Justification/Rationale for Objective 2: For reliable comparisons of change in occupancy over time, the sampling frame must be the same from year to year. However, some wetlands are dry in some years, with no possibility of supporting amphibian breeding. By tracking the number of available wetlands annually (e.g., 250 of 263 wetlands/breeding sites inundated in 2011 [95%]; 206 of 270 wetlands inundated in 2012 [76%]), we can test whether amphibian occupancy changes as a function of the proportion of wetlands that are dry. And, as this objective becomes more fully developed, the integration of meteorological data may aid in identifying to what extent drought or climate change is affecting wetland and amphibian occurrence.

Objective 3: For boreal toads, estimate the proportion of previously identified breeding areas that are used annually, and estimate the rate at which their use may be changing over time.

Justification/Rationale for Objective 3: Based on pilot studies, boreal toads are potentially too rare to be adequately sampled using the same sampling scheme employed for Objectives 1 and 2. Based only on the randomly-selected catchments under Objective 1, occupancy rates for boreal toads are too low to enable reliable estimation of rates of change, or to recognize a decline if it is occurring across GRTE and YELL. Instead, our approach for monitoring boreal toads is to sample all known breeding areas annually, as a supplement to Objective 1. At this time, however, we are constrained by fiscal resources and therefore full implementation of this objective has been suspended. Our plans for monitoring boreal toads are outlined in this protocol, along with a more limited sampling scheme that can be implemented with a modest budget or the help of experienced volunteers. Partial implementation could, at a minimum, indicate if the status of toads is changing at a set of sites where toad breeding populations have been monitored for a decade or more.

1.4. Relevance to Park Managers

Amphibians have been selected as a Native Species Vital Sign in YELL because this taxonomic group is, reportedly, sensitive to environmental change and a reliable indicator of wetland ecosystem health (YCR 2011). As such, measurement of amphibian occupancy will inform park managers about the conservation status of native species (rare, common, etc.) and long-term monitoring may assist in documenting whether this status is changing relative to documented changes in climate or in response to changes in the abundance of keystone species (e.g., beaver; Smith and Tyers 2012) that create amphibian breeding habitat (Bartelt et al. 2011). Status monitoring in national parks provides critical information on the status of indicator taxa, the

composition of biological assemblages, and condition of critical ecosystems. Combined, this information will aid in the evaluation of current management practices and the ability of these practices to sustain park resource (Fancy et al. 2009). Moreover, the monitoring protocols described herein will help identify and document covariates at the catchment and site level that influence amphibian occupancy (Gould et al. 2012). Identification of key covariates will not only provide insight for future protocol planning and environmental impact analyses, it may also help develop tools that will allow park managers to mitigate future threats to parks and operate more effectively in the public arena (Fancy et al. 2009). Finally, monitoring data will aid in documenting changes in wetland breeding habitat and amphibian occupancy, and thus can help describe some of the physical and biological manifestations of drought, climate change, and disease in GRTE and YELL.

2. Sampling Design

The sampling design for GRTE and YELL uses breeding amphibian occurrences across catchments (portions of watersheds *sensu* Franken 2004) as the primary index measure with which to measure amphibian population health. Catchments were selected using a stratified-random sample design of all catchments in GRTE and YELL (see discussion of primary sampling units below). Our fixed sampling strategy, employs annual site visits to permanent catchments (i.e., primary sampling unit) and supports site-level (i.e., secondary sampling unit) surveys of breeding amphibians (i.e., observation unit). So, clustered within catchments are potential amphibian breeding sites (e.g., wetlands, ponds, wet meadows, etc.). When standing water is present, all wetlands or potential breeding sites within a catchment are surveyed by multiple observers each year. These surveys are designed to document species occurrences and breeding evidence using visual encounter surveys and dip netting. Analysis of this information yields occupancy estimates for catchments and breeding sites which can be used to elucidate coarser and finer scale processes that may affect amphibian distributions and trends within GRTE and YELL. This overall sampling strategy is based on the approach developed by ARMI (described in the Introduction) for large administrative units such as national parks, in which the status of amphibians is tracked through changes in the number of populations (Corn et al. 2005a).

2.1. The Sample Frame

A sampling frame is a geographic representation (i.e., map) or list of sampling units within the population from which a sample will be drawn (Lohr 2010). Ideally, the sample frame used for monitoring and evaluating trends in amphibians within GRTE and YELL would include all of the hydrologic units or catchments contained within these parks. However, catchments within this collection of parks vary with respect to elevation, wetland extent, and or presence of infrastructure (e.g., roads and buildings) or artificial habitats (e.g., sewage lagoons). This variation led to the exclusion of a small number of catchments from our sample frame (Figure 3). What follows is a brief discussion of criteria used to select a statistically defensible yet logistically feasible set of sampling units (Corn and Legg 2011) for our sample frame.

An initial goal was to establish sample frame based on sampling units that could be summarized using a recognized hydrologic classification system and readily available digital elevation models (DEMs) for the region. Because of the nested nature of hydrologic classification systems, another important consideration was to select an appropriate sampling unit size—one that would balance our goal of including multiple potential amphibian breeding sites within each sampling unit, while constraining it to a size that could be surveyed by field crews over a period of hours to days. To that end, the amphibian monitoring working group in collaboration with USGS-ARMI researchers set a goal to include a minimum of five to ten wetlands/amphibian breeding sites per sampling unit. Using a hybrid of the Pfafstetter system for watershed identification (Verdin and Verdin 1999) and hydrologic unit maps (see Seaber et al. 1987), the USGS-EROS Data Center developed a set of potential sampling frames whose hydrologic units were deconstructed into successively finer catchment sizes.

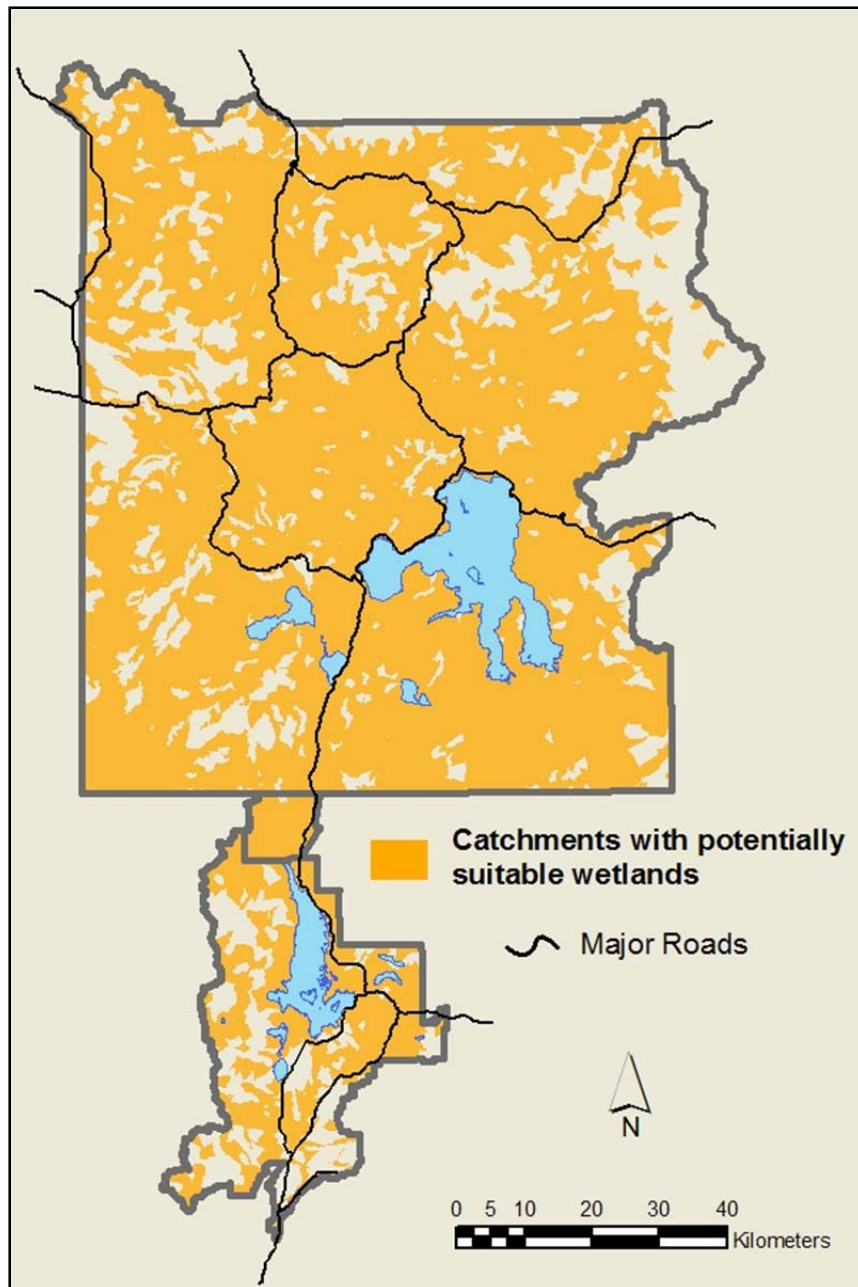


Figure 3. Sample frame for GRTE and YELL. Within this frame, 3,370 catchments averaging approximately 200 hectares have been described. Each of these catchments contain multiple National Wetland Inventory-mapped wetlands that represent potentially suitable amphibian breeding sites.

Ultimately, the selected GIS layer modeled catchments that had an average size of approximately 200 hectares, but catchments varied in size and amounts of potential amphibian breeding habitat. Catchments that were unlikely to have any wetlands suitable for amphibian breeding were excluded. The decision to exclude catchments was based on the following criteria: (1) catchments with no National Wetlands Inventory (NWI)-mapped wetlands; (2) catchments that contain only deep lakes, sewage lagoons, perennial rivers, and areas with temporary flooding or saturated soils. Appendix A contains a complete list of excluded NWI types. After excluding

catchments using the above criteria, 3,370 catchments remained and represented the sample frame for the Cooperative Amphibian Monitoring Program for the Greater Yellowstone Network (Figure 3).

2.2. Primary Sampling Units—Catchments

The primary sampling unit, catchments, is defined by topography as it relates to the flow and collection of water sources (Franken 2004, Gould et al. 2012) and using the Pfafstetter nomenclature system (Verdin and Verdin 1999) to confer information about hierarchical nestedness and general position within a drainage basin. DEM-corrected catalog units (level 4 hydrologic units; Seaber et al. 1987) were the basis for delineating catchments. Once the catchments were created a second algorithm added Pfafstetter codes to each catchment (Furnans and Olivera 2001).

Ultimately, catchments as used here were based on a minimum contributing-area threshold of 250 cells at 30-meter cell size. This distinction is important because unlike the typical Pfafstetter level, the number of digits in the Pfafstetter code can change among catchments in a catalog unit. Since the Pfafstetter code depends on the nature of the topography across the catalog unit a branch with more catchments can have more Pfafstetter digits than a branch with fewer catchments. Regardless, Pfafstetter codes do enable users to determine a basin's upstream or downstream location based solely on codes presented in tabular data (Furnans and Olivera 2001).

Catchments with an average size of approximately 200 hectares were established using a contributing area of 250 cells using 30 m DEMs; these initial polygons represented the foundation for the current catchment boundaries used throughout GRTE and YELL. Larger hydrologic units were used in GRTE and YELL prior to 2005, but these units required too much sampling time per sampling unit and provided an insufficient number of sample units for rigorous statistical analyses or for deriving inference to the parks. At the other end of the scale, using individual ponds or wetlands (sites) as primary sampling units is not practical due to the dynamic nature of these water features. For example, a distinct pool in one year may be three distinct pools in another year due to less surface water. Similarly, several distinct pools can merge into a single large water body in a year with abundant water. These kinds of changes make it difficult to consistently define and recognize sample units from year to year.

One important reason to use catchments as a primary unit is that the boundaries can be identified and once delineated, used consistently regardless of hydrologic state of wetlands (Gould et al. 2012). Grouping sites at the catchment level also makes biological sense, because amphibians can shift breeding areas among local sites depending on local conditions. For example, if a pond is dry, egg deposition may occur at a neighboring site. Monitoring for presence/absence at too fine a scale can be subject to large across-year variations and less biologically relevant results associated with minor spatial shifts. Clustering sites within catchments helps address variation or “noise” associated with finer-scale monitoring. Note, however, that some spatial shifting of a site may occur over catchment boundaries, particularly in areas of little topographic relief or influenced by beaver activity but catchment boundaries are respected when this occurs.

2.3. Secondary Sampling Units—Sites within Catchments

Within the sample catchments, all potential amphibian breeding sites (secondary sampling units) are surveyed. A site is defined as a pond, pool, wet meadow, or other wetland feature that is

capable of hosting amphibian eggs and larvae (Hossack and Corn 2007, Gould et al. 2012, Hossack et al. 2013).

Sites are identified using a three-step process. First, NWI mapping is initially used to identify potentially suitable wetlands within the sample catchments. Within sample catchments, target wetland sites are identified using GIS data layers depicting NWI polygons, catchment boundaries, and topographic features (1:24,000 scale). NWI functions well for this purpose based on pilot studies (2000-2004); however, some mapped wetlands turn out to be dry (e.g., due to drought, loss of beaver, changes in local hydrology) or misclassified (no wetland characteristics apparent). Less often, wetlands were missed by NWI, but are visible on topographic maps or are found in the field, in which case they are still included for monitoring. Despite efforts to define sites within the catchments and consistently survey them from year to year, comparisons of occupancy at the site level differ from year to year due to site dynamics such as size, shape, and other factors (e.g., beaver dam collapse or construction). Single-season patterns of site occupancy, however, are not subject to these problems and provide information about habitat selection by species, the effects of environmental covariates, and factors affecting detection probability.

Second, field crews navigate to identify target sites using maps and GPS coordinates and define sites during the first round of visits to a catchment following the procedures described in the next section on Field Methods. New sites and sites that were missed are added in subsequent years of survey. Guidelines for defining sites allow for the heterogeneity of conditions that are encountered in the field (e.g., multiple neighboring pools may be lumped into a single site under certain conditions). Crews may ascertain that there is one site, several sites, or no sites within a targeted NWI polygon. Defining a site entails assigning a permanent identification number for the database, sketching, and photographing the site. Geographic coordinates for sites, sketches, and site photographs (with geographic coordinates recorded at the photo points) assist field crews in finding and recognizing the sites in subsequent years. These efforts support consistent monitoring from year to year and enable recognition of changes in site conditions.

Third, decisions about the connectivity among sites/wetlands are made following initial visits to ascertain site boundaries. Admittedly, these boundaries vary by year and, specifically, inter-annual variations in hydrology change the juxtaposition and isolated nature of sites within catchments. As a result, early decisions regarding site boundaries influence annual data collection efforts. Despite these dynamics, estimated wetland area is documented each year in the field and this covariate along with nearest neighbor distances among sites (a viable surrogate for among-year variations in connectivity) can be used for modeling site-level occupancy (Gould et al. 2012).

2.4. Observation Units

The observation unit is the reproductive portion of the four native amphibian species of GRTE and YELL: barred tiger salamander, boreal chorus frog, Columbia spotted frog, and boreal toad. The rationale for focusing on reproductive portions of the populations is provided under Objective 1 of the previous section. In short, breeding populations are more feasibly monitored than total populations for practical, logistical, and biological reasons as well as for meeting the basic assumptions of currently available occupancy modeling approaches. As with other wildlife species (e.g., bald eagles [*Haliaeetus leucocephalus*], song birds), assessing the breeding portion

of an amphibian population is an effective way to monitor the status of the entire population (Corn et al. 2005b, Hossack and Corn 2007, Gould et al. 2012, Hossack et al. 2013).

2.5. Sample Stratification and Randomization

The large potential study area within our sample frame and considerable variation in amounts of amphibian habitat among catchments indicated that a simple random sample of catchments in the sample frame would not provide a sufficient number of amphibian detections to enable meaningful analyses. Most catchments in the sample frame contain small and isolated wetlands unlikely to host amphibians or to host only the species most adapted for this type of habitat (i.e., boreal chorus frogs).

Based on pilot study results, we posited that only about one third of the catchments in the sample frame were likely to support multiple potential breeding sites for multiple amphibian species. To help address these issues, each catchment was assigned one of the following habitat quality classes (Figure 4 and Table 1). These classifications were based on a thorough assessment of multi-species occupancy estimates generated from pilot study years; these results demonstrated that occupancy differed based on the extent of permanent, semi-permanent, and seasonally flooded wetlands within a catchment. For that reason, habitat classification categories were established and to ensure some high and medium quality catchments were included in our sample. The criteria for these classifications are described below.

Amphibian Habitat Quality Classification Criteria (see Appendix 1 for full definition of the NWI attribute codes and habitat classification modifiers used below):

- High quality: >4 ha of semi-permanent & permanent wetlands (NWI water regime F, G, or H), AND >2 ha of seasonally flooded wetlands (NWI water regime C).
- Medium quality: >0 ha (any amount) of semi-permanent & permanent wetlands (NWI water regime F, G, or H), AND >1 ha of seasonally flooded wetlands (NWI water regime C).
- Low quality: >0 ha (any amount) of semi-permanent & permanent wetlands (NWI water regime F, G, or H); OR >0 ha (any amount) of seasonally flooded wetlands (NWI water regime C) (i.e., all remaining catchments with potential surface water).

An additional stratification approach was applied to our sampling design and has been factored into these protocols. Due to the logistical constraints associated with accessing remote areas of GRTE and YELL, it is prohibitively expensive to use a simple random sample. Accordingly, we also stratify catchments by distance to nearest road and, each catchment is assigned an “access classification code” depending on whether any part of the catchment lies within 4 km of primary roads (Figure 5). To enable inferences to all areas included within the sample frame, a sufficient number of remote catchments are sampled (2:1 close to far; Table 2). This ratio of sampling allows us to balance resources and time available for sampling some close and far catchments, with the amount of sampling error that is tolerable in our occupancy estimates.

Finally, sample catchments need to be spatially distributed across the sample frame, because the major park drainages differ due to factors such as geology, topography, precipitation patterns, and the existence or influence of large lakes or rivers. Consequently, catchments are assigned to one of five values representing the major drainage in which they occur (Figure 6). Catchments in

GRTE, within the Snake River Headwaters subbasin, are further divided into two approximately equal zones, north and south, to guarantee that all sampling units are not confined to one part of the park. An alternative approach would have been to use a generalized random-tessellation stratified (GRTS) design (Stevens and Olsen 2004), which is well suited to achieving these goals. However, this approach requires specialized expertise and variance estimation for data analysis. Given the substantial investment of time and effort already expended in sampling at GRTE and YELL, the benefits of starting anew with an alternative design did not outweigh the loss of existing progress.

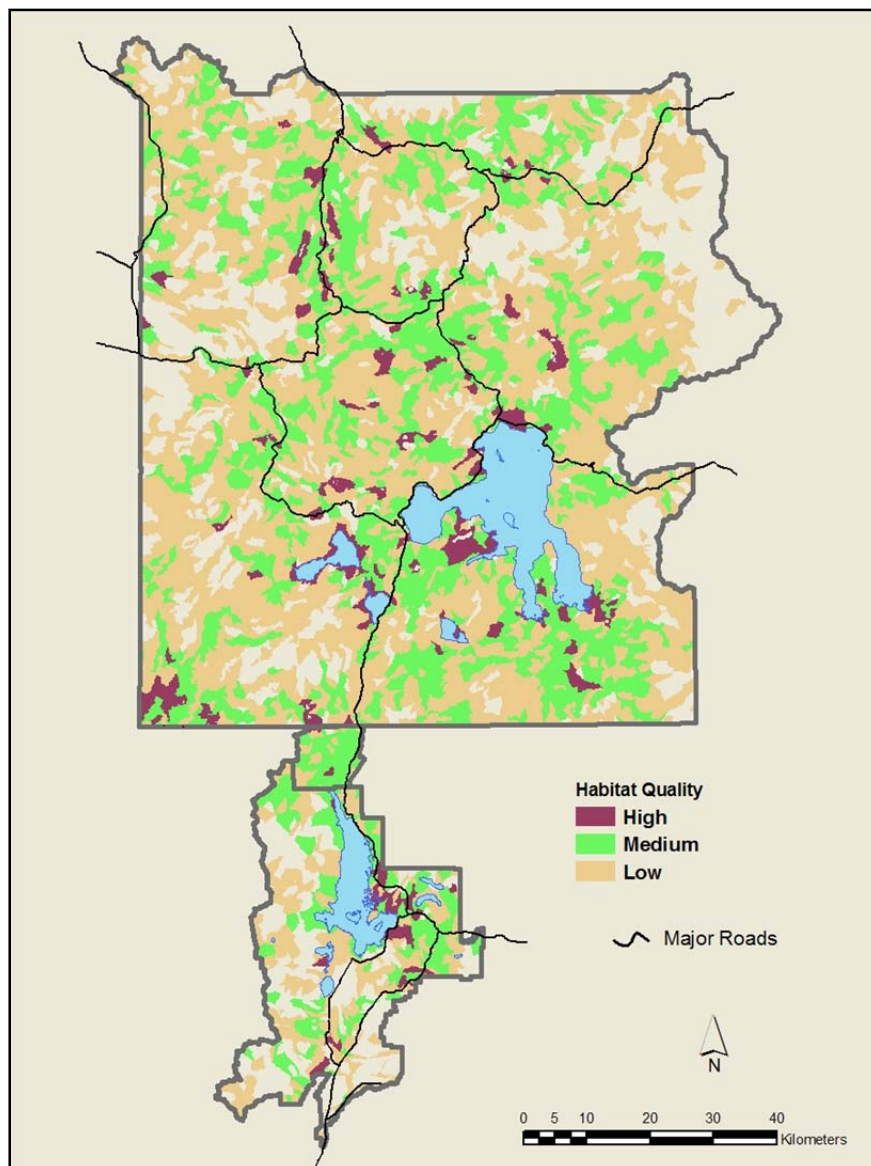


Figure 4. Sample frame for GRTE and YELL showing distribution of catchments classed as High, Medium, and Low in terms of potential habitat quality as classified above.

Table 1. The distribution by strata of 3,370 catchments containing potentially suitable wetland sites.

Habitat	Access	Number of Catchments
High	Close	92
High	Far	43
Medium	Close	565
Medium	Far	425
Low	Close	1,009
Low	Far	1,236

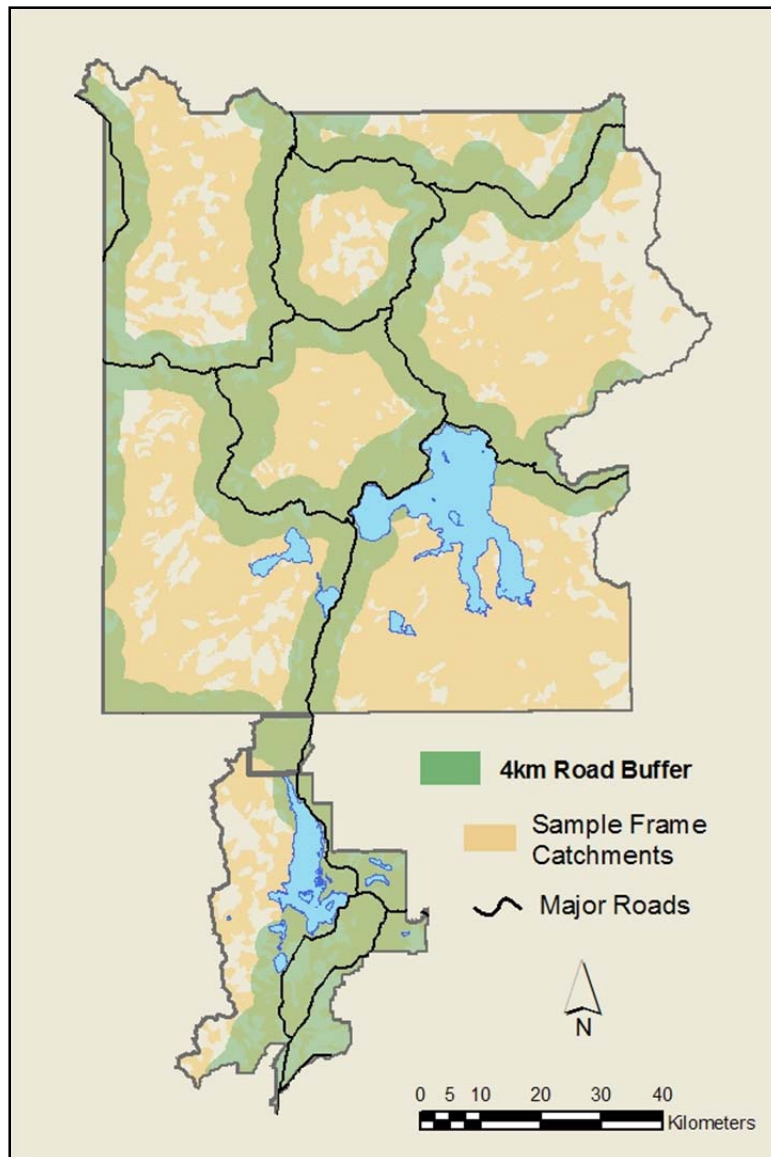


Figure 5. Sample frame for GRTE and YELL showing the major roads and a 4 km buffer.

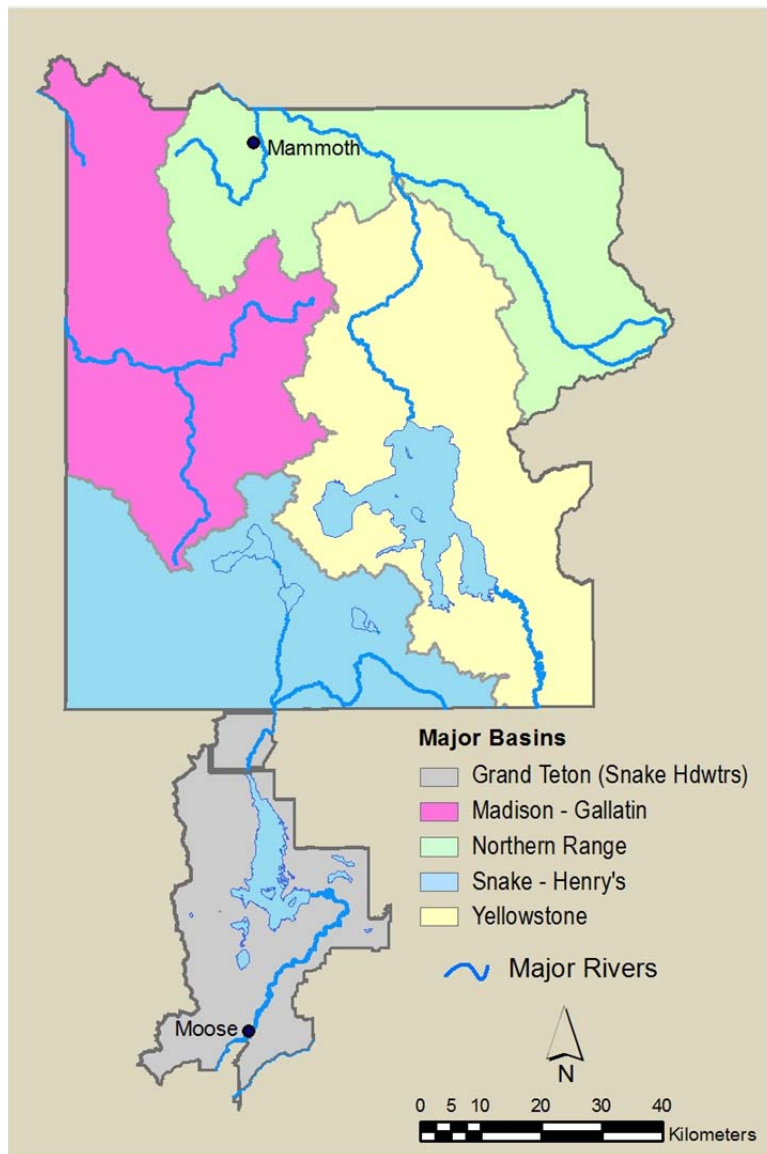


Figure 6. Sample frame showing the major drainages from which catchments were selected.

In treating the collection of catchments allocated to the major drainage basins (climatologically, geologically, and hydrologically unique river basins; Figure 6) within a habitat quality classification stratum as a simple random sample it may result in more variability within strata (e.g., high quality habitat) than among strata (e.g., high versus medium quality habitat; Gould 2008). If instead, the drainage basins are considered as an additional layer of stratification, this approach would force most strata (within a drainage basin) to have a sample size of 1, thereby eliminating straightforward variance estimation.

Deriving separate inference for each subpopulation created by the drainage basin stratifications is of secondary importance (with the possible exception of the drainages within the two national parks, where managers may desire distinct data sets and reporting of results). Rather, the intent is to find a balance between logistical considerations and sampling representative segments of the population. Since there is too small of a sample for each individual combination of

subpopulations (habitat quality class, drainage basin, and access class) to derive a reliable estimate, a model selection approach (see the section on Data Management, Analysis, and Reporting) will be used to find the most parsimonious balance of parameters.

2.6. Sample Selection and Sample Frequency

The basic sampling design for catchments is a stratified cluster design with random selection of catchments from the strata described above. Within the sample catchments (i.e., clusters), all wetlands that represent potentially suitable breeding sites are surveyed for evidence of amphibian reproduction. To minimize costs and maximize efficiency, an informal type of optimal allocation of catchments among the strata is applied, (e.g., more “close” than remote catchments and a prioritization of high and medium habitat class catchments). The sampling scheme is displayed in Table 2, and distributed in the sample frame as shown in Figure 7.

Table 2. The 40 sample catchments within accessibility strata and habitat quality strata, spatially distributed across basins.

Access Class ¹	Habitat Class ²	Basins						Total Catchments
		Northern Range	Yellowstone	Madison-Gallatin	Snake-Henry's Fork	GRTE-North ³	GRTE-South	
Close	High	2	2	2	2	1	1	10
Far	High	1	1	1	1			4
Close	Medium	2	2	2	2	1	1	10
Far	Medium	1	1	1	1	1	1	6
Close	Low	1	1	1	1	1		5
Far	Low	1	1	1	1		1	5
								40

¹Based on catchment distance ≤ or >4 km from a road.

²Based on the amount and type of wetlands in each catchment identified by the National Wetland Inventory.

³GRTE is in the Snake basin; it was divided into North and South zones to achieve better spatial representation.

Ideally, all 40 catchments would be sampled annually but this does not always occur due to periodic wildlife closures or access issues (e.g., high flows prevent obligatory river crossings). In recent years (2011 and 2012), however, we have focused our monitoring efforts and resources on the medium- and high-quality catchments (n=30; Table 2). The decision to focus on medium- and high-quality catchments was based on limited fiscal resources and because stratum-specific differences in occupancy have been documented. Gould et al. (2012) showed that medium- and high-quality habitat designations can be modeled together and are readily distinguished from occupancy estimates in low quality catchments (Gould et al. 2012). This work supports preliminary assessments (Gould 2008) and suggests that habitat strata may eventually be combined and this may produce more parsimonious models. Although a focus on medium- and high-quality catchments is more likely to reveal patterns of amphibian occurrence in catchments with more, and potentially higher quality (i.e., more permanent), wetland area, it does limit GRYN's ability to make park-wide inferences (Gould 2008). Medium-quality (29.4%) and high-quality (4.0%) catchments represent a fraction of GRTE and YELL's catchments. The revised sampling design also restricts our sample size to 30 sample units. Precision of parameter estimates is strongly dependent on species-specific detection probabilities and overall sample sizes. Any proposed or future changes to the number of sampling units (from current level of 30) included in our current design should be accompanied by studies that provide guidance about the consequences and changes to precision of resulting estimates for each of the target species.

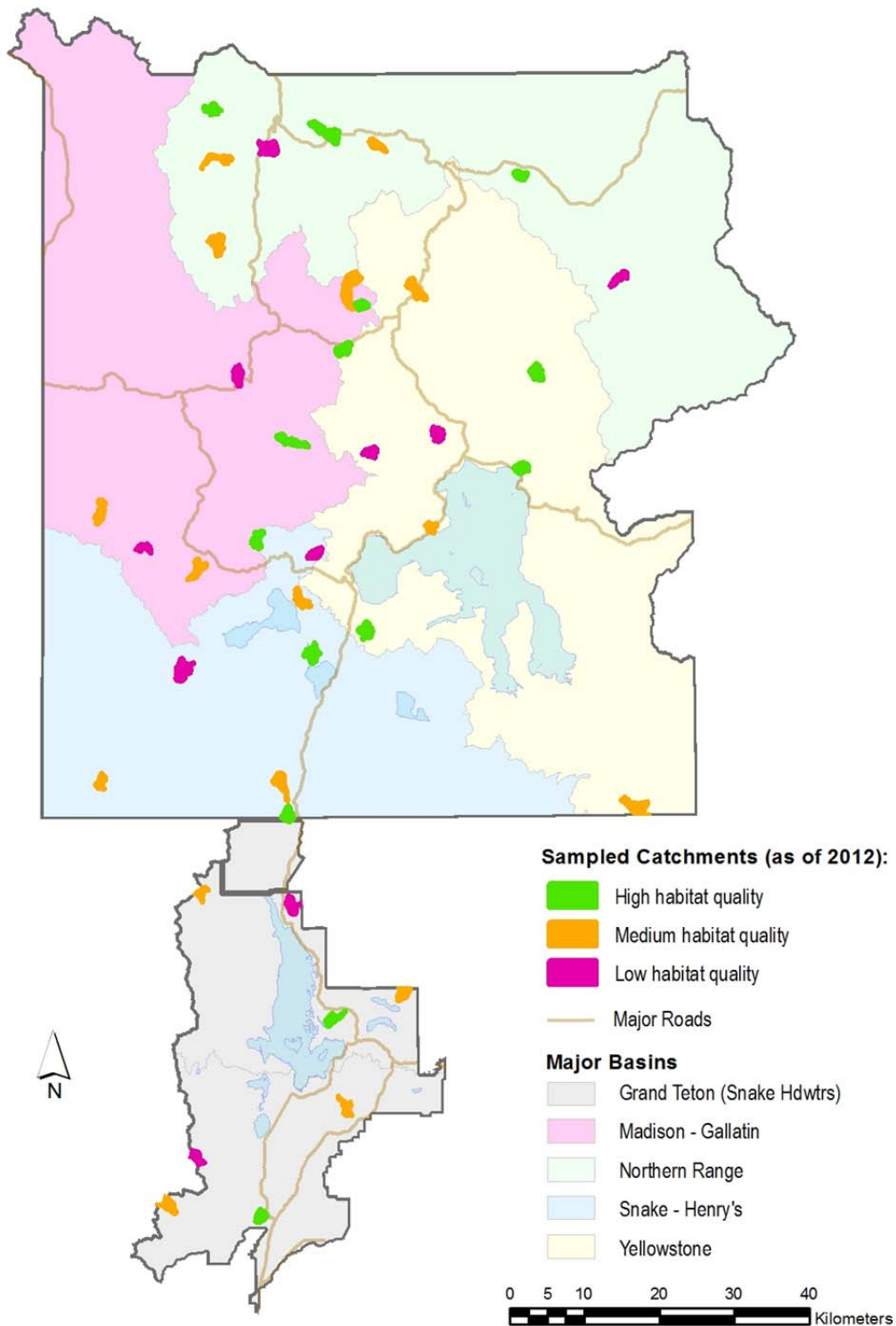


Figure 7. Catchments selected for long-term monitoring in Yellowstone and Grand Teton national parks.

A rotating panel design was considered as an alternative to dropping low-quality catchments; this approach would allow a subset of low-quality catchments to be visited each year, and subsequently revisited at a longer interval (e.g., every other year). The rotating panel approach

was initially rejected because of the potentially confounding effects of among and within year variation in this region. Among year variation in habitat availability is believed to be tightly associated with annual variations in precipitation and snowpack and the spatial variation in precipitation and snowpack throughout YELL and the GYE within years is well documented (Wilmers et al. 2013). Because of the potentially interactive nature of spatial and temporal variation, a rotating panel approach was thought to provide limited utility in isolating the effects of environmental factors that may differ from year to year. Discussion on this topic with the USGS staff at Patuxent Wildlife Research Center resulted in a small simulation that indicated a loss of precision for most parameters under the alternating year panel design compared to sampling every year (Larissa Bailey and James Nichols, pers. comm.). Because of these concerns, this approach (the rotating panel approach or split panel design) is unlikely to be used to sample low-quality catchments in the future (see below).

Catchment selection is permanent unless valid circumstances exist or occur that require dropping and replacing catchments. For example, one catchment was dropped in YELL after two years of survey due to occupation by wolves and an administrative closure to protect them. Similarly, one catchment was dropped in GRTE for administrative reasons (e.g., bear management restrictions and other wildlife closures). Although wildlife closures may only last a few weeks, the short amphibian breeding survey season can be over by the time the area is re-opened. Target sample catchments may also be dropped and replaced if no potentially suitable wetland sites are found during the initial visit. When catchments must be replaced, the original selection process is followed to select the next catchment in the list of stratum (e.g., high quality, close access, “x” basin), which contains sequentially ranked records based on original random numbering.

During trial implementation of a draft protocol in 2005-2007, a rotating panel design was used for catchments in the low habitat quality class. This was a trade-off based on logistical considerations. Data from preliminary sampling indicate very low occupancy for this kind of catchment, likely due to the limited amount of wetlands and their ephemeral nature. Higher occupancy was anticipated only in very wet years, or if climate changes lead to greater precipitation. Given limited resources for sampling, it seemed unwise to invest a large portion of those resources in visiting catchments unlikely to be occupied. As a compromise, a split-panel design was initiated in which one randomly selected catchment from the low stratum in each major drainage is visited every five years (one of which is visited in any given year), and one catchment (randomly selected at large from the low class) is visited annually. However, this approach was abandoned when internal review and expert analysis (Gould 2008, Gould et al. 2012) pointed out that inferences to all of GRTE and YELL require better representation of the low-quality strata. This point is critical because the number of catchments per habitat class is much greater for the low-quality catchments than either the high- or medium-quality catchments.

2.7. Occupancy and Detection Probability—Single-season Repeat Surveys

Occupancy by breeding amphibians per species is the resource condition or state variable of interest for this protocol, measured at two levels: catchments and sites. Detection of any number of eggs, larvae, or recent metamorphs (i.e., young of the year life stages) of a particular species indicates occupancy of a site, and occupancy at any site within a catchment indicates occupancy

at the catchment level (and by default occurrence)³. Occupancy rates based on detection of the species can be biased if failures to detect the species are equated with its absence. Occupancy rates that are not corrected for false absences (species is present, but not detected) are referred to as “naïve occupancy,” and they result in underestimation of true occupancy (MacKenzie et al. 2006). Naïve occupancy needs to be corrected for detection probability to remove this bias. Detection probability (also called detectability) is the probability that at least one individual of a species will be detected given that the species occurs in the area of interest (MacKenzie et al. 2006).

To obtain information about detection probability, temporal replication is used (i.e., repeated surveys for occupancy at the same site). From the available options to accomplish this, described in MacKenzie et al. (2006), the dual-observer, single-visit method was chosen, in which two trained observers independently survey the same site. This is the same approach used by ARMI in Glacier National Park (Corn et al. 2005b, Hossack and Corn 2007) and has been used to successfully estimate amphibian occupancy in the GYE (Gould et al. 2012). In brief, one surveyor completes the “primary” survey of a potential breeding site before the other surveyor begins the “secondary” survey approximately 15 minutes later. At large sites, both observers may work simultaneously, but try to maintain spatial and temporal separation by beginning the survey at different places. To preserve independence and avoid bias, observers do not communicate their individual findings until both surveys are complete.

At the catchment level, detection probability is based on a species observation records from the primary and secondary surveys within the catchment. For example, Table 3 simulates a case in which breeding evidence for Columbia spotted frogs (RALU, young of the year) was detected during both primary and secondary surveys, so detection probability for Catchment X is 100%.

Table 3. Example of catchment level detection probability (1=detection and 0=non-detection).

Sites in Catchment X	Detection of RLU Primary Survey	Detection of RLU Secondary Survey
X-1	1	0
X-2	0	0
X-3	1	1
X-4	0	0
X-5	0	0
X-6	0	0

At the site level (considering six sites in Table 3), the species was detected at two sites during the primary survey, but at only one site during the secondary survey. Detection probability for the sites is 0.67. In this case, naïve occupancy is 0.33 (two out of six sites), but occupancy adjusted for detection (using program Presence, see the section on Data Management, Analysis, and Reporting) is 0.37, with a standard error of 0.24.

³Detection of juvenile and adult amphibians is also recorded during field surveys, and may be used in future analysis when the capability to handle multiple life stages is incorporated into existing software. The transitory presence of post-metamorphic (juvenile and adult) amphibians at wetlands presents problems in interpreting results if these life stages are included.

It is important to note that occupancy and detectability are scale-dependent measures. That is, where catchments contain multiple wetland sites, the probability of detection and occupancy is higher at the catchment scale than at the site scale. Thus, catchment and site occupancy are reported and analyzed separately (see the section on Data Management, Analysis, and Reporting). For rare species, such as boreal toads, catchment occupancy and the number of occupied sites per catchment are so low (e.g., one occupied site per one occupied catchment) that detection probability may be similar at both scales.

2.8. Seasonal Timing of Sampling

Surveys are scheduled to take place after amphibian egg laying and prior to larval metamorphosis. This period normally begins in mid-June and lasts about eight weeks in GRTE and YELL, but site-specific conditions and the larval occupancy period can vary greatly even within the same catchment. For instance, boreal toad surveys (discussed below) may commence in mid-May in accessible areas with a thermal influence. We also acknowledge that monitoring windows must be flexible and may be adjusted in the future if breeding phenology changes are documented. In scheduling surveys, two main factors are considered when timing of surveys is not defined by management constraints: proximity to rivers (which flood potential amphibian sites during snowmelt run-off) and elevation. Access constraints are also considered within this period due to bear management restrictions, eagle nests, and other wildlife closures. Some areas are not accessible until later in the summer due to high water in rivers that must be crossed on foot. Guidelines and considerations for scheduling surveys are defined in Table 4 and depicted in Figure 8. These guidelines are applied with flexibility to allow for late snowmelt or other unusual weather patterns that will occur in some years. In recent drought years, for example, monitoring was completed by July 25. To reduce some of the variability in available wetland habitat, catchments are normally surveyed at roughly the same time each summer; for example, a catchment surveyed in mid-June one year is normally scheduled for mid-June the next year. Completing the catchment surveys in the very short survey season while following the guidelines and respecting the various resource management closures is one of the most challenging aspects of implementing this protocol.

Table 4. Time envelopes for amphibian monitoring in GRTE and YELL. These time periods are based on historical sampling and may need to be altered if breeding phenology changes are documented.

Type*	Elevation	Start	End	Notes
Non-riverine	<2,070 m	June 15	July 7	Northern Range in YELL and lowest elevation catchments in GRTE. End date is constrained by pool drying.
Non-riverine	2,070-2,440 m	June 15	July 24	Majority of catchments are in this category.
Non-riverine	>2,440 m	June 21	August 1	Target high-elevation catchments with permanent ponds during last ten days of survey period, if possible.
Riverine	<2,200 m	June 21	July 21	Lamar River, Snake River GRTE. Postpone start date as needed to allow for waters to recede after peak flow.
Riverine	>2,200 m	July 7	July 24	Upper Yellowstone River, Lewis River.

*Riverine refers to catchments with potential amphibian breeding habitat adjacent to third order or higher streams. Time frames were based on USGS peak flow data for rivers in YELL and GRTE (1994-2005) as well as our evaluation of conditions encountered during the pilot study.

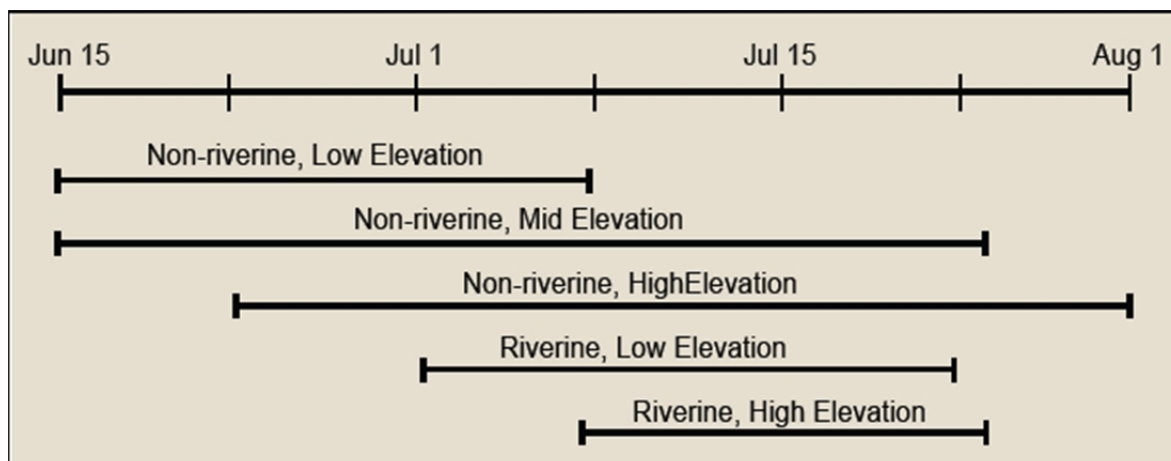


Figure 8. Approximate seasonal window for amphibian monitoring in GRTE and YELL catchments.

As a final note regarding timing, it is understood that breeding occupancy can change during the duration of the field season, despite efforts to compress the field season and schedule surveys at suitable times. For example, boreal chorus frog tadpoles might metamorphose and disperse from a site before a survey occurs. This would violate the assumption in occupancy modeling that occupancy is closed (does not change) over the duration of the sampling period. If such events occur at all sites in some catchments in some years or under some conditions, this will cause an unknown bias in occupancy estimation at the catchment level. Additional investigation outside the scope of this protocol is needed to determine if this issue could significantly influence occupancy estimates in GRTE and YELL.

2.9. Monitoring Potential Breeding Habitat (Objective 2)

Determining the number of potential breeding sites within sampled areas that are suitable for amphibian breeding (irrespective of actual use), is an objective that is accomplished concurrently with amphibian monitoring in the sample catchments. Field crews document the existence of surface water at NWI wetlands and any unmapped wetlands encountered, estimate the size of the water body (length and width in meters), and also estimate depth class (<0.5 m, 0.5-1 m, 1-2 m, >2 m); these metrics will be used to document how much a site may change in size and depth from year to year (see the next section on Field Methods). NWI sites that have wetland indicators (e.g., hydrophytic vegetation, hydric soils; wetland indicators are further described in Field Methods), but lack surface water are marked as “potentially suitable in the future, not surveyed” due to the current lack of standing water available for amphibian breeding. The set of “potentially suitable” habitat sites per catchment is identified the first year that the catchment is visited and represents the minimum number of sites that will be visited and reassessed each year to document its potential suitability for amphibian breeding. “Potentially suitable” sites that consistently lack surface water over the course of both dry and wet years are categorized as “not suitable” and are not targeted for visits in subsequent years.

The wetland or breeding site data collected may be used in one of the four following analysis approaches, with respect to integrating amphibian occupancy (Objective 1) and descriptions of wetland inundation patterns:

1. Assess amphibian occupancy for *all* potential breeding sites, regardless of whether or not they are suitable for amphibian breeding in a given year (see Chapter 10.2 in MacKenzie et al. 2006, Gould et al. 2012).
2. Assess occupancy considering only available, suitable sites. This approach could mask a decline in the actual number of occupied wetlands. The advantage of this approach is that it accurately indicates detection rates. Including dry sites could bias detection rates given that amphibian larvae have no probability of occurring, unlike wet sites where the species may either be detected, truly absent, or falsely described as absent.
3. Model habitat histories (as opposed to species detection histories) per site, based on suitable/not suitable status each year. This would allow estimation of the parameters relevant to habitat suitability and dynamics, with inference to the sample frame considering the stratifications in random selection of catchments. A separate model for occupancy dynamics could be developed that would be conditional on the habitat histories, and joint likelihood for habitat and occupancy dynamics would be provided by the product of these components (Chapter 10.2 in MacKenzie et al. 2006).
4. Model habitat suitability along with occupancy histories. Joint habitat/occupancy modeling may prove useful for situations in which habitat does not remain suitable from year to year (Chapter 10.2 in MacKenzie et al. 2006).

2.10. Detecting Levels of Change

Same-year estimates for the number of catchments and sites occupied that year by each species (adjusted for detection probability) will be produced, along with estimates of the number of apparently suitable sites. Between-year comparisons of the annual summaries reflect only the catchments and sites surveyed and do not summarize across-year variability of amphibian breeding sites for the entire park unit or units (GRTE and YELL) or the GYE. Because catchments contain multiple sites, relative stability is expected in the year-to-year number of catchments occupied per species, and dynamism is expected primarily to occur in the year-to-year number of sites occupied (see Gould et al. 2012). To understand changes and patterns of change throughout GRTE and YELL, an information theoretic approach to model selection will be used, with application of weighted averages to elucidate the effects of the stratified random sampling design described above. Power analysis was evaluated during the development of this protocol, but the data from pilot studies were too limited to support a reliable analysis (Gould 2008). Given that amphibians may exhibit considerable year-to-year fluctuation in breeding efforts and success, multiple years of monitoring data are needed to understand if change, measured as increases or decreases in occupancy, is occurring within GRTE and YELL. Evaluation of multi-year patterns is planned for regular, multi-year intervals (see Gould et al. 2012 for four-year summary) to help inform whether changes in the number of amphibian populations can be explained by changes in habitat (changes in the number of suitable sites and their characteristics), or if other factors that directly affect amphibian populations (e.g., disease) may be in operation.

2.11. Supplemental Design for Boreal Toads

The paragraphs that follow apply only when funding and survey crews are available and after work associated with Objectives 1 and 2 has been completed.

Based on previous studies and results from the first years of this program, the probabilistic sampling design described above is not sufficient for boreal toads due to their relative scarcity. Boreal toads are of management concern due to their rarity, possible decline in the GYE since the 1950s (Koch and Peterson 1995), and dramatic declines elsewhere that may be associated with pathogenic disease (Muths et al. 2003). A dual-frame sampling design is recommended for this species, in which previously identified boreal toad breeding sites in GRTE and YELL are monitored in addition to the probabilistic (catchment) sampling. The dual frame method, combining independent samples from an “area frame” and a “list frame,” is useful for monitoring wildlife populations where breeding individuals have highly visible territories that tend to be stable over years (Haines and Pollock 1998). The dual frame is a special case of a stratified sample for which standard estimation techniques for single frame can be applied (Bankier 1986).

The list frame for boreal toads includes the locations and characteristics of all breeding sites identified for this species in previous year(s). The list frame is presumed to be incomplete due to undiscovered or new sites, and can be updated annually by adding active sites discovered in the previous year (Haines and Pollock 1998). The area frame corresponds to the sample frame described above and employed for catchment sampling. The area frame is assumed to be completely enumerated in any given year; that is, all active sites within the sampling units are visited. Elements on the list frame also belong to the area frame, because the area frame covers the entire target population through probabilistic sampling. Haines and Pollock (1998) describe how the “screening estimator” can be applied to estimate the total number of active sites, combining the list frame (overlap domain) and area frame (non-overlap). Other estimators are described by Hartley (1962), Bosecker and Ford (1976), Groves and Lepkowski (1985), and Bankier (1986). Further discussion is needed to determine which estimator would be most useful for characterizing the status boreal toads in GRTE and YELL given the historical datasets.

All known boreal toad breeding sites in GRTE and YELL are included in the list frame, based on a variety of sources including Koch and Peterson (1995) and sources used therein, sites discovered during amphibian surveys conducted by the ISU Herpetology Lab, sites discovered during Herpetological Inventory and pilot studies for the current monitoring program (2000-2004), sites reported by park staff or visitors and then confirmed by cooperators, and sites encountered opportunistically (e.g., while hiking to catchments). Breeding sites are defined by the presence of toad eggs, mating adults, tadpoles, or recent metamorphs⁴. A recent depiction of boreal toad breeding sites in GRTE and YELL is displayed in Figure 9. A comprehensive list of toad breeding sites is maintained by the GRYN.

⁴Because this species is known to make long overland movements, the finding of lone juveniles or adults is not regarded as useful for monitoring purposes. Consistent or frequent observations of juvenile or adult toads in an area in which no breeding sites have been identified, however, indicate that this area should be considered a potential breeding area that should be searched for sites.

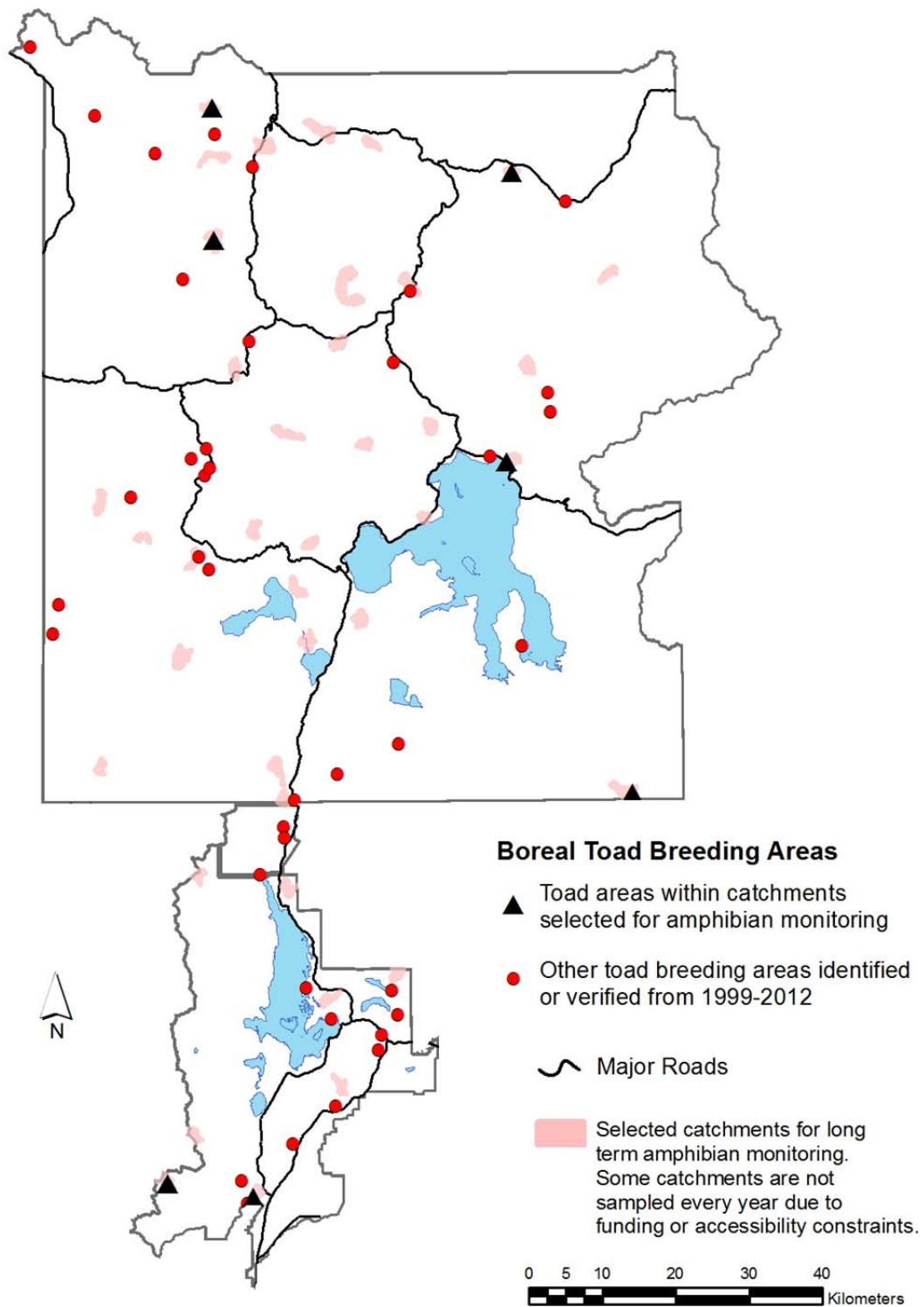


Figure 9. Boreal toad breeding sites in YELL and GRTE based on information available in 2012. Sites that are ± 500 m of each other are clustered as “toad breeding areas” for monitoring. Approximately 45 breeding areas were identified by 2012.

Because multiple breeding sites in a local area may reflect small spatial shifts in egg deposition locations, and are likely populated by closely related individuals, sites are grouped into “boreal toad breeding areas.” The breeding areas are comprised of sites that are in the same drainage and within approximately 500 meters of each other. There are approximately 45 known toad breeding areas including ten areas that were found within catchments selected at random as sampling units for amphibian monitoring (Figure 9). Breeding areas are classified by accessibility: easy (<2 km from roads), day-hike, and backpack. They are also classified by major or minor status as breeding areas. Major areas host thousands of tadpoles and have been active in all or most years when surveys were conducted; minor areas were documented with few tadpoles (<100, and often <10) and (in most cases) in only one year. The 35 areas of the list frame confirmed as of 2008 were distributed among these strata as shown in the Table 5:

Table 5. Stratification classes for boreal toad breeding areas; example summary as of 2008.

Status	Access			Totals
	Easy	Day-hike	Backpack	
Major	12	6	4	22
Minor	4	2	7	13
Totals	16	8	11	35

Although a principal goal of our monitoring is to describe the status of native amphibians in GRTE and YELL, tightening of resources prevents us from fully implementing the strategy needed to monitor boreal toads using the unique sampling strategy described above. Recognizing these limitations, boreal toad monitoring efforts described here will only be implemented once all work needed to address Objectives 1 and 2 have been completed for all amphibians within a given year. When time and resources allow, the amphibian monitoring program partners will leverage existing resources by fostering partnerships with park biologists and university partners and take advantage of trained volunteers to monitor toad sites using the approach described above.

If additional or new funding becomes available, sampling of all known toad sites should be completed annually in order to carefully evaluate Objective 3. If partial resources allow, GRYN may consider the following approach to initiating toad sampling in GRTE and YELL at known/historic breeding sites.

Site classified in the “major-easy” categories (see Table 5) should always receive first priority sampling for several reasons: (1) to provide a consistent window on the status of this species at historic sites where many years of monitoring data exist; (2) to help determine if site-specific causes of decline may be in operation (e.g., shrinking wetlands, construction projects); (3) to bring attention to the need for more intensive, dedicated monitoring of all known toad breeding areas if these flagship areas show a trend of decline; and (4) to provide information for planners and managers to help identify and mitigate potential effects of human development in or near breeding areas. For the strata where random selection is applied, we will rotate through the areas, disqualifying areas that were surveyed in the previous year(s) until all areas have been visited. Newly discovered toad breeding areas (e.g., those identified in 2012) will be added to the list of toad breeding sites and may be added to the list frame if, for some reason, the catchment is dropped from sampling (e.g., due to administrative closure).

Major-Easy: Sample all (alternatively, random selection of 5-10 depending on resources available for survey)

Minor-Easy: Sample 1 (random selection)

Major-Day-hike: Sample 2 (random selection)

Minor-Day-hike: Sample 1 (random selection)

Major-Backpack: Sample 1 (random selection). *Not attainable with existing resources.*

Minor-Backpack: Sample 1 (random selection). *Not attainable with existing resources.*

2.11.1. Occupancy, Detectability, and Timing for Boreal Toad Sampling

Boreal toad breeding areas are considered occupied if at least one of the member breeding sites has eggs, tadpoles, or recent metamorphs. Detectability is known to be high in the “major” areas, but variable at “minor” areas where only a few tadpoles may be present. Despite these differences between major and minor sites, if toad breeding site monitoring is initiated, we will employ dual observers, similar to the catchment monitoring, to independently survey each area. If two surveyors are not available, repeat visits later in the same year may be made. This latter approach is not desirable both because of its deviation from our multi-park protocols, but also because of safety considerations. The sampling period is late-May to mid-July for this species, with visits to minor sites confined to the most reliable period of mid-June to mid-July.

3. Field Methods

3.1. Field Season Preparations

A primary goal of the GRYN Amphibian Monitoring Program is to ensure the safety of its staff and partners while conducting inventory and monitoring activities in GRTE and YELL. To that end, a Safety Plan has been assembled for the GRYN (GRYN 2012). This document, along with the associated safety protocols (SOP 1: Field Safety for the Amphibian Monitoring Program; Bennetts et al. 2013), should be reviewed annually and prior to the field season. Several other important tasks must be completed prior to each field season including: procuring necessary permits, hiring field crews, readying equipment, ordering supplies, scheduling surveys, preparing the “catchment folders” to guide field crews (navigation and site identification aids), and preparing training materials. Specific instructions, lists, and recommended dates are found in SOP 2: Pre-season Preparations and Equipment Setup (Bennetts et al. 2013). Careful preparation and organization is very important to the success of a very short field season in June and July.

3.1.1. Permitting and Compliance

All research, inventory, and monitoring activities in national park units require a research and collecting permit before field work can be conducted. GRTE and YELL each require such permits. In addition to the national guidelines for research permitting in national park units, each park has additional requirements that must be addressed. Initial permit applications for amphibian monitoring in the two parks, under field protocols similar to those presented here, were submitted by ISU in 2000 and subjected to the review process, including peer review. Since then, applications for permit renewal have been submitted annually to GRTE and YELL, following NPS and park-specific instructions on the NPS Research Permit and Reporting System internet site. Permit renewal includes submitting an Investigators Annual Report. The annual report and permit renewal application are due by March 31 each year. In addition, we comply with YELL’s requirements for a Field Research Survey that documents where work was conducted in the previous field season, and copies of reports, papers, and other documentation related to the work.

3.2. Sequence of Field Events

All high and medium sample catchments are visited each field season, assuming adequate funding. One field crew, composed of two trained surveyors, is normally sent to each catchment, although multiple crews are occasionally used when this is deemed most efficient (e.g., large or very remote catchments). Each catchment survey requires one to four days of field crew time, depending on catchment size, location, and number of wetland sites. Within one week prior to scheduled surveys, the field coordinator notifies district rangers about the date and location of survey activities, as required by the research permit office. Rangers may provide information about hazards or problems, stipulate requirements, such as wearing bright orange vests when working in areas visible to the public, or deny access for safety or resource management concerns. For backcountry camping, field crews pick up the camping permit from the appropriate backcountry office on the day prior to the trip.

In addition to the standard catchment surveys, field crews or trained volunteers may survey for boreal toads if the funding is available and if the field coordinator determines that time is available and regular sampling targets are being met. The daily sequence of tasks listed below is further specified in SOP 3: Daily Procedures and Checklists (Bennetts et al. 2013).

- Assemble items needed for the survey: catchment folder (with maps and photos), equipment and supplies, and personal gear, such as drinking water and rainwear.
- Drive to trailhead, hike to catchment, and navigate to sites.
- Conduct survey and collect data.
- At the end of the day or backpack trip, download data and sanitize field gear.

3.3. Initial (First Time) Visits to Catchments

On the first visit to a sample catchment, a thorough effort is made to identify all potential amphibian breeding sites within catchment boundaries. As of 2008, most of the catchments selected for long-term monitoring received their initial visits. If a sample catchment needs to be abandoned due to an administrative closure and a new catchment added, the procedures for first-time visits and defining sites are used and detailed in SOP 4: Monitoring Catchments not Previously Surveyed (Bennetts et al. 2013).

3.4. Subsequent Visits to Catchments

The main task of field crews in subsequent visits (i.e., in years following the initial surveys) is to find and correctly identify known sites; however, any sites previously missed should be added (SOP 4: Monitoring Catchments not Previously Surveyed; Bennetts et al. 2013). Procedures for subsequent visits to catchments are detailed in SOP 5: Monitoring Previously Surveyed Catchments (Bennetts et al. 2013).

3.5. Collecting and Recording Data

Once a site is identified or located, there are four main tasks: (1) conduct the survey for amphibians, (2) collect the data, (3) record the data, and (4) document the site with a photograph and sketch. Two-person field crews conduct surveys following standard amphibian visual encounter methodology (Thoms et al. 1997). This entails walking the perimeters of water bodies and walking transects through shallow ponds and wetlands. In large wetlands, expansive meadows, or within tall willows, the transect should be spaced such that you are able to maintain good visual coverage of the wetland including the areas between transects. Long-handled dip-nets are used to sweep the water for amphibian larvae. Each crew member surveys the site independently without communicating observations to the other observer. This dual-observer method is critical to enable accurate estimates of species detectability. Survey procedures are detailed in SOP 6: Conducting Visual Encounter Surveys (Bennetts et al. 2013).

Crew members typically enter data directly into a field computer during and immediately after site surveys, with a paper field log form as a back-up record of sites visited and species found. Crews may use a paper field data sheet under special circumstances or in case of electronic failure (available in SOP 7: Data Field Descriptions and Instructions for Data Entry; Bennetts et al. 2013). Controls built in to the electronic forms prevent entering values out of range or values other than those available from pick lists. Data on the field computers are backed up at least twice each day; once or more in the field on a memory card and immediately upon returning to the field operations base when crew members synchronize their handheld field computer with a laptop computer to automatically transfer survey data to a Microsoft Access database. For detailed instructions refer to SOP 3: Daily Procedures and Checklists (Bennetts et al. 2013). The

following list summarizes the measurements, observations, and other information collected and recorded during surveys for each individual survey site.

Wetland survey data:

- catchment and site number
- date and start and end times of primary and replicate surveys
- total minutes of search time (primary and replicate surveys)
- percent of site perimeter searched
- site photo frame, UTM coordinates of photo point, and bearing of photo

Weather/condition data:

- air and water temperatures
- cloud cover, wind, precipitation

Habitat data:

- habitat type
- maximum water depth
- percent of site at 50 cm or less water depth
- water body length and width
- number of discrete water bodies
- presence of fish
- evidence of beaver activity
- percent of water body with emergent or aquatic plants
- dominant wetland macrophyte
- dominant substrate

Amphibian species data:

- species and life stage
- number of animals per species and life stage
- detection method
- number of dead found per species per life stage or other comments

3.5.1. Sketching the Site

On the initial site visit and survey, crew members sketch the site on a paper form with a grid so that scale can be defined (SOP 7: Data Field Descriptions and Instructions for Data Entry; Bennetts et al. 2013). The sketch shows orientation (north arrow); the shapes and spatial relationships of the pools; vegetative features, such as emergent vegetation and surrounding forest or shrub stands; adjacent features, such as roads or trails; and location of site UTM collection and photo points. On subsequent visits in following years, the site should be sketched again or annotated if the existing site sketch is no longer representative of field conditions.

3.5.2. Photographing the Site

On the initial site visit and survey, crew members establish a photo point that provides a good overview of the surveyed area. If the site is dry and no survey is conducted, a photo is taken from

the target site UTM. The photo point UTMs and UTM accuracy are read from the GPS unit and recorded on a paper data form, along with the compass bearing of the camera direction. Electronic forms provided by USGS do not support photographic data records. Site photos are retaken on subsequent visits from the previously defined photo point and using the same camera direction bearing.

3.5.3. Notifying Park Officials about Amphibian Die-offs

Amphibian die-offs have been observed at some breeding locations within GYE. Large die-offs could occur when breeding sites dry prior to tadpoles metamorphosing. However, die-offs can also be caused by amphibian disease or other stressors. Both ranavirus and *Batrachochytrium dendrobatidis* (*Bd*) have been identified inside the GRYN, and during the 2010 breeding season die-offs were documented in more than ten breeding sites in YELL (NPS 2012). Field crews and individual surveyors will document and report any unusual symptoms (e.g., severe hemorrhages in ventral skin) or amphibian die-offs to the field coordinator or to park officials as soon as possible. If park officials request specimens, collections should be carried out following instructions provided by GRTE's and YELL's wildlife ecologists.

3.6. Post-collection Data Processing

When field crews return to the field operations base, the handheld computers are synchronized with the computer and survey records are automatically stored in a database developed by USGS-ARMI. Crew members immediately verify the transferred data to ensure that all survey, site, and species data are correctly entered in the master database. Photos are downloaded to the computer and sorted according to catchment. The field coordinator interviews field crews each week to document or resolve data collection issues, and also checks the database for handheld interface or other problems.

3.7. End-of-season Procedures

At the end of the field season, equipment is collected and inventoried. Electronic equipment is sent to GRYN as directed. Database verification and validation are completed, as described in SOP 9: Quality Assurance (Bennetts et al. 2013). Unresolved issues with data collection procedures and equipment are documented and communicated to GRYN and ARMI data management personnel. The final, validated database is submitted to GRYN and ARMI. Boreal toad data forms are collected and compiled. Site and species validation photos are named, resized, and stored according to SOP 3: Daily Procedures and Checklists (Bennetts et al. 2013). Photos are reviewed to evaluate field crew decisions on site suitability. The overall field season is evaluated retrospectively to evaluate procedures, troubleshoot problems, and to recommend improvements for protocol components such as field crew training, data collection procedures, equipment performance, and catchment survey scheduling.

4. Data Management, Analysis, and Reporting

This section describes the overall plan for data handling, analysis, and report development for this monitoring protocol. Detailed instructions are found in standard operation procedures. The GRYN Data Management Plan (Daley 2005) and the national Inventory and Monitoring Data Management Plan (NPS 2008) are also useful resources for more comprehensive philosophy and general guidance on data management.

4.1. Data Stewardship

The management and stewardship of data is coordinated among cooperating entities and the NPS GRYN (Table 6). To achieve the required level of data organization, quality, and documentation, staff members are expected to spend approximately one third of their time overall, on data stewardship activities. This is in addition to time spent collecting (observing and measuring) data and includes data entry, reviewing and verifying data values, addressing and explaining errors and deviations, reporting on quality control and assurance activities and results, and ensuring the data are structured, stored, and maintained to prevent loss and to support analysis and reporting activities.

Table 6. Data stewardship roles and responsibilities.

Data Stewardship Responsibility	Role	Organization
Master copy of monitoring protocol	Ecologist/Protocol Leader	NPS GRYN
USGS-ARMi national master database	Data Manager	USGS ARMI
Rocky Mountain ARMI master database	ARMi-Rocky Mountain Regional Representative	USGS Northern Rocky Mountain Science Center
GRYN copy of Rocky Mountain ARMI database	Data Manager	NPS GRYN
GRYN seasonal/annual field database	Field Coordinator	NPS GRYN/Active Cooperator
USGS/NPS database coordination	Data Manager	NPS GRYN
Security and back-up plan for GRYN database	Data Manager	NPS GRYN
Verification of data in GRYN database	Field Coordinator/Field Crew Members	NPS GRYN/Active Cooperator
Validation of data in GRYN database	Protocol Leader/Subject Matter Expert	NPS GRYN/Active Cooperator
Original data sheets/field forms	Field Coordinator	NPS GRYN/Active Cooperator
Documentation for data structure and database application	Data Manager	USGS ARMI

4.1.1. Data Storage and Database Applications

Survey data are processed, stored, and managed using a system developed and supported by staff of the USGS-ARMi. The GRYN data manager works with the Rocky Mountain Region ARMI representative and the field coordinator to maintain and distribute current versions of database application files and database content. The GRYN data manager and the field coordinator may make cosmetic changes to the electronic data forms (Pendragon® Software Corporation) from Rocky Mountain ARMI in order to facilitate data collection and management activities at GRTE and YELL.

Survey data for all years of the program are stored in a Microsoft Access database developed by ARMI. The data tables in this file (Figure 10) are populated automatically when portable data recorders (handheld computers) containing field data entered by crew members are synchronized

to a laptop computer. A separate (front end) Access file provides an interface to the survey data for basic quality control functionality such as identifying several types of orphaned records, and for generating summary data for export. Current and past versions of the Rocky Mountain ARMI data and interface files for GRTE and YELL survey data are stored on the GRYN server.

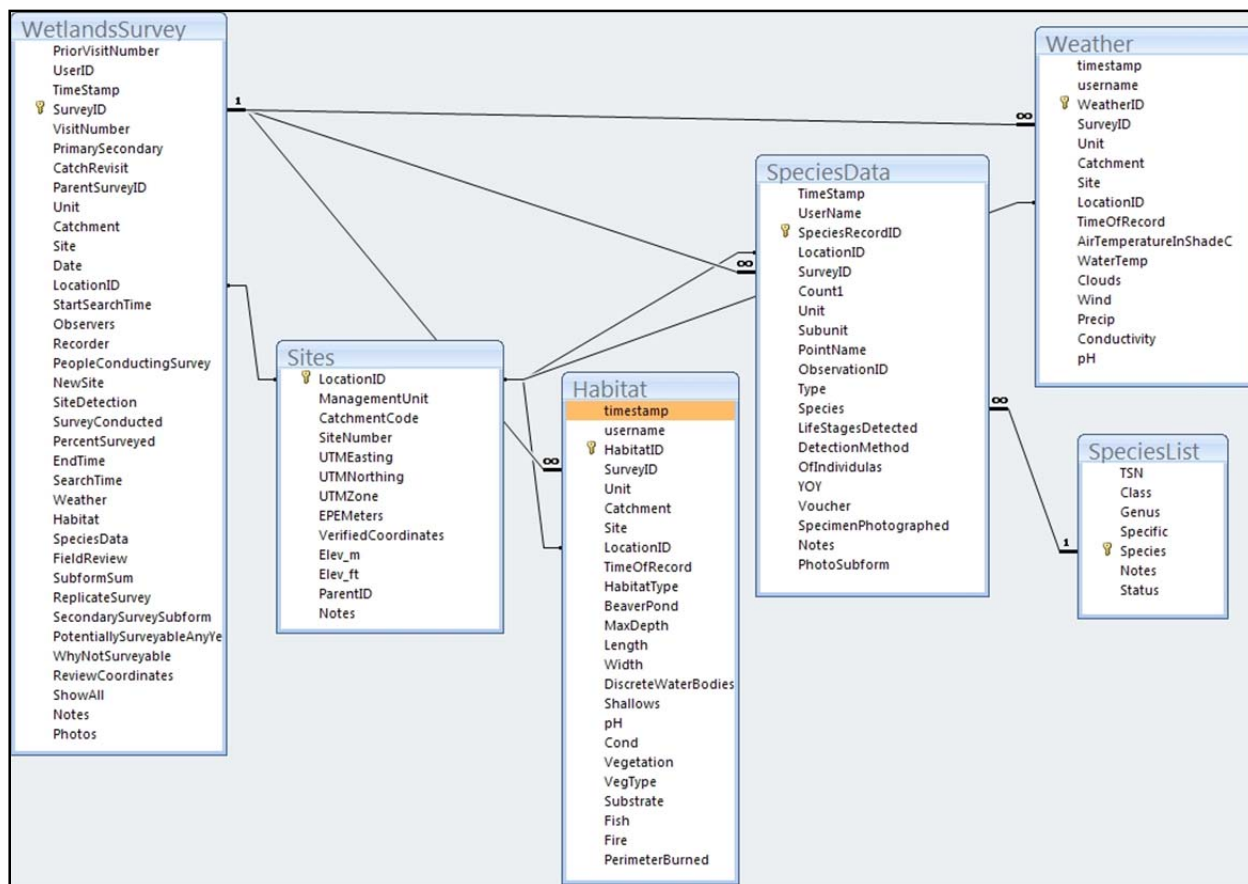


Figure 10. Database structure (USGS ARMI-Rocky Mountain Region).

The master data source for the monitoring sample frame is a GIS layer representing catchment features (polygons) with attributes for hydrologic units (“basins”), accessibility, and wetland habitat quality classes (described in the section on Sampling Design). The master data source for the monitoring sample selection is an Excel worksheet with columns for the catchment identifier, randomized and ranked selection order, and selection status. Both data sources are stored on the GRYN server file system under the Amphibians vital sign folder.

4.1.2. Data Entry

(Refer to the previous section on Field Operations, Collecting, and Recording Data.)

4.1.3. Data Backup and Security

In the field, crew members back up electronic field data at least once each day to a memory card in the handheld computer. Paper copies of data forms are always carried as a backup to electronic equipment. Data recorded on paper are entered and backed up on a working handheld computer as soon as possible. Records on the handheld computer should be backed up twice daily, once in the field to a flash drive and then at the end of each field day. Records will also be

uploaded to a laptop computer and synchronized with the database at the completion of field work in each catchment. Data on the handheld computers are retained for several days after transfer to the main database to provide for data recovery if the laptop computer fails. Crew members back up the master database on the laptop computer as often as practical given the schedule of field activities. The backup includes a full copy of all data on at least one hard disk, as well as a second full backup copy on a different hard disk, USB flash drive or verified backup media (CD or DVD). The field coordinator takes a copy of the laptop database during visits to the field operation base, approximately every two weeks during the field season.

4.1.4. Data Quality Assurance

Crew members are responsible for accurate and complete electronic data entry using the data forms provided on the handheld computer, and for legible, accurate written entries on hardcopy forms (when used), in logbooks, and in notebooks. Crew members visually inspect and verify written and electronic data values at the time of data collection and entry. On a daily or weekly basis, as allowed by the schedule and duration of field visits, the field coordinator verifies the completeness, accuracy, and legibility of all data, and works with crew members to explain and correct any issues. After crew members verify that observed and measured data values are recorded and entered completely, legibly, and accurately, the field coordinator validates the logical and structural integrity of the database overall. Data validation by the qualified subject matter expert (field coordinator) is normally a bi-weekly assessment of data value distribution and values out of acceptable range, or inconsistent with expected values. Post-season review of spatial data is coordinated between the field coordinator and the GRYN data manager to ensure that all survey points based on coordinates obtained during field work are located as expected within the sample frame. Annual assessment of data structural integrity (e.g., data types, relationships, consistency) is coordinated between ARMI representatives, the GRYN data manager, and the field coordinator. The field coordinator ensures that all errors identified during data verification and validation activities are corrected and documented appropriately. Documentation includes hand-written annotations on paper records, and memo column/field entries for electronic data, accompanied by a simple written explanation of the data review process (date, name of subject matter expert, methods used), and a description of the “quality control” values used.

4.1.5. Data Documentation (Metadata)

Documenting the sample design and survey data sources and the methodology by which the data are acquired establishes the basis for interpreting and appropriately using data and results from this long-term amphibian monitoring program. Metadata for the GIS layer representing sample units (water catchments) is stored in Federal Geographic Data Committee Content Standard for Digital Geospatial Metadata (CSDGM) format with the GIS files on the GRYN server.

Documentation for the random sample selection data source is in a worksheet titled “Read Me” stored in the Microsoft Excel file containing the MASTER LIST of sample catchments.

Monitoring survey data field documentation is found in SOP 7: Data Field Description and Instructions for Data Entry (Bennetts et al. 2013). The field coordinator and GRYN data manager share responsibility for reviewing and updating data documentation when and where necessary.

4.2. Sensitive Information

The protocol leader, working with a park resource manager, determines whether existing or potential sensitive information from this protocol needs to be identified and addressed for rare,

threatened, or endangered species. While the presence of sensitive information is not anticipated for this monitoring protocol, identified cases that may occur are documented in writing and communicated to the data manager, who will help identify sensitive records in the database and prevent their release. Only the park resource manager, superintendent, or other appropriate authority may authorize the release of sensitive data after following appropriate review procedures and distribution restrictions for sensitive information.

4.2.1. Data Certification, Distribution, and Archives

Data certification is a data quality assurance process resulting in a signed, written statement from the protocol leader/ecologist, data manager, and program manager confirming that a set of data complies with NPS Director's Order #11B, Ensuring Quality of Information Disseminated by the National Park Service (Mainella 2002). Certification is not an absolute guarantee that data are completely free of errors or inconsistencies. The protocol leader is responsible for completing written certification of data collected each year as a prerequisite to using or sharing data from that year. Electronic archives for data are maintained on the GRYN server. All data on the server are restricted for read/write access and receive daily differential and monthly full backups stored on site and quarterly backups stored off site. At the end of each field season, all physical program materials, including field data collection forms, site sketches, and log books, and other materials are submitted by the protocol leader for filing with the protocol record in the GRYN office. Paper data sheets, when used, are managed as permanent records and kept on file with other protocol materials. Certified data and related reports are stored on the GRYN server, posted to the GRYN website, and uploaded to the NPS online national database for resource information. The NPS master database for biodiversity is updated annually as new or additional information about species is discovered from this monitoring effort.

4.3. Data Analysis

4.3.1. Overview of Analysis Approach

In this study, we use presence/absence data from multiple surveys and proven statistical methods to estimate the probability that sampling units (catchments and sites) are occupied by each amphibian species (see Gould et al. 2012). Our approach uses occupancy as the primary indexing analysis because this approach has become the “gold standard” method to assess status and trends of amphibians across large landscapes (Bailey et al. 2004; Bailey and Adams 2005; Corn et al. 2005a; Schmidt 2005). In brief, occupancy modeling relies on presence and absence data collected during multiple surveys of a wetland site. These survey results or detection histories can be used to estimate the 1) probability of detecting a species given its documented detectability and the 2) probability that a site or catchment is occupied by the target species (Bailey and Adams 2005). Occupancy can be modeled for a single species in a single season, for a single species over multiple seasons, or for multiple species over single or multiple seasons⁵ (MacKenzie et al. 2006). Our ultimate goal is to examine whether occupancy estimates for different species vary across years, habitat quality classes, access classifications, and major park subbasins (see Sampling Design section above). Detection of differences in occupancy across years can facilitate trend monitoring and can be achieved in multiple ways. For example, an evaluation of species-level occupancy trends can be completed using an explicit dynamics

⁵“Season” refers to the sampling season of a given year. For this protocol, which targets early life stages as indicators of breeding, a single season is equivalent to a single year, and “multi-season” refers to >1 year of sampling.

modeling approach that incorporates a time component, varies by habitat class, access class, and major subbasin, and ultimately produces probabilities of occupancy that may change across years (MacKenzie et al. 2006). Alternatively, annual estimates of occupancy can be examined together using recognized regression approaches, and the slope (β_i) of the line estimates the trend parameter across years using a logit link function (MacKenzie et al. 2006). A description of the occupancy framework employed for amphibian monitoring within GRTE and YELL follows and an example of the application of this framework is provided in Appendix E.

The decision to use presence/absence data and the occupancy framework, rather than population estimates, is based on both practical and biological reasons. Practically speaking, population estimates are difficult, expensive, and nearly impossible to apply with acceptable accuracy to small animals over large areas. Biologically, the highly variable nature of amphibian populations results in large yearly fluctuations, resulting in low power to detect change (Corn et al. 2005a). Occupancy, as an alternative to estimating abundance, has a long history of use in wildlife studies. It can reveal changes in species status over large areas and is thought to be appropriate for species with wide, short-term population fluctuations (Bailey and Adams 2005, Gould et al. 2012).

Either annual or biennial data summary reports provide estimates of amphibian species occupancy at the catchment and site level. Data summaries include the number of catchments and sites visited, the number of suitable wetland sites surveyed, the number of dry but potential sites (which may be available in the future under different conditions), the number of catchments and breeding sites where the species were detected, and field effort in terms of the number of crew-days used to accomplish the work. Based on analysis that goes well beyond the data summaries, occupancy per species are modeled and reported at two levels, catchments and sites (see Gould et al. 2012). Occupancy models allow for analysis of covariates potentially affecting occupancy (e.g., habitat class), and covariates affecting detectability (e.g., observer). The analysis philosophy is optimization, based on evaluating which model or set of models best explains patterns of detectability and occupancy, rather than the elimination of models using hypotheses testing. Information theoretic methods (Akaike's Information Criteria [AIC] differences and weights) are used to evaluate the models, and the principle of parsimony is applied. This is followed by model averaging, which allows one to incorporate the model uncertainty into the estimation process as well as providing unconditional variance estimation. Occupancy modeling will be applied, as described below and in SOP 8: Data Analysis (Bennetts et al. 2013) using software programs PRESENCE (<http://www.mbr-pwrc.usgs.gov/software/presence.html>) or MARK (<http://www.phidot.org/software/mark/>).

Our goal is to summarize trends from our occupancy monitoring every five years. The first such report summarized monitoring years 2006 through 2009 (see Gould et al. 2012). Although trends from just four years of monitoring should be examined with caution, this first multi-year summary provided an initial look at the status of three native amphibians (barred tiger salamanders, boreal chorus frogs, and Columbia spotted frogs) and identified habitat and environmental covariates that influence occupancy in GRTE and YELL.

4.3.2. Occupancy Models

In brief, occupancy refers to the proportion of sites or habitat units occupied by a species. The use of occupancy modeling framework has gained support because it can be distinguished from

simple occurrence estimates based on observed presence/absence (or detection/non-detection). Use of presence/absence to report occurrence is problematic because “absence” may in fact be a failure to detect the species rather than a true absence. In other words, non-detection can result from two situations: (1) the species is truly not present, or (2) the species was there, but was not seen by observers. The reasons for missing species can be influenced by factors that vary over space and time. “Naïve occupancy,” not corrected for detectability, is biased and underestimates the true occupancy of the study area, unless species are perfectly detected (MacKenzie et al. 2003, Bailey and Adams 2005, Hossack and Corn 2007, Gould et al. 2012).

Occupancy modeling allows estimating and accounting for detectability, thus accounting for the bias that comes from imperfect detection. To do this, the models use information from multiple visits or multiple observers (detection histories of the target species), and apply a technique similar to population estimation using mark-recapture data to estimate occupancy. Bailey and Adams (2005; Appendix B) provide a concise description of the approach and its underpinnings as well as a glossary of terms. Basically, detection histories are mathematically assessed using maximum likelihood techniques to estimate the model parameters, occupancy, and detectability.

Using models developed by MacKenzie et al. (2002, 2006), occupancy modeling allows for the investigation of how characteristics of the site and the survey affect the parameters (occupancy and detectability). Potential influences on parameter estimates are incorporated into analysis as two kinds of covariates, site and sampling. Site covariates are constant for a site within a season; examples include habitat type, distance to nearest road, or generalized time patterns such as year. Sampling covariates are those that may change with each survey of a site, for example, local environmental conditions such as water temperature, precipitation, time of day, or observer. Detection probabilities may be functions of either site or sampling covariates (e.g., detection could be affected by habitat type as well as time of day), while occupancy is considered as a function of site covariates only (e.g., occupancy by amphibian larvae is not influenced by the time of day at which the survey was conducted, but may depend on habitat type). Occupancy is not considered in relation to sampling covariates because one of the model assumptions is that occupied sites are occupied for the duration of season (e.g., all sampling occasions within a given year).

Occupancy can be modeled for a single species in a single season, for a single species over multiple seasons, or for multiple species over single or multiple seasons⁶ (MacKenzie et al. 2006). At this point, we envision single-species, single-season analyses annually, and single-species, multi-season analyses at least every five years (see Gould et al. 2012 for an example of our first multi-year summary). With more experience and future insights, we may consider combining data from all the amphibian species under study to assess occupancy at the multi-species (community) level (as described in MacKenzie et al. 2006), to assess patterns and trends of amphibian species richness in GRTE and YELL.

⁶“Season” refers to the sampling season of a given year. For this protocol, which targets early life stages as indicators of breeding, a single season is equivalent to a single year, and “multi-season” refers to >1 year of sampling.

4.3.3. Model Selection

Generally, our approach to occupancy modeling will apply recognized techniques to select a single or multiple models that characterize patterns in amphibian species occupancy of catchments and sites across years. To achieve this, we will use model selection techniques that examine the goodness of fit for a set of candidate models. Simply, these techniques will evaluate the accuracy and complexity (i.e., parsimony) of each model. In statistics, the principle of parsimony is to find a model, from a pool of potential models, that summarizes the behavior (or variation) of the dataset with the smallest possible number of parameters⁷. So, a parsimonious model is one which retains only those parameters that are warranted and eliminates excessive parameters (Figure 11). The Akaike's Information Criteria or AIC is a tool commonly used to evaluate a set of candidate models (Bolker et al. 2009). Model selection based on information theory is relatively new in biology and considerably different from methods based on null hypothesis testing (Burnham and Anderson 2002).

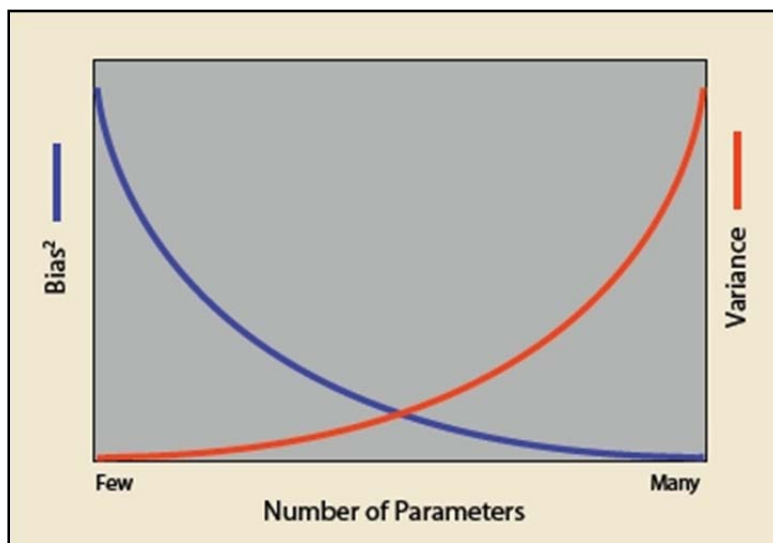


Figure 11. Conceptual tradeoff between precision (low variance, shown with red line) and bias (blue line), as a function of the number of parameters (after Burnham and Anderson 2002).

AIC provides an objective, relatively simple tool that can be used to select the most parsimonious model, balancing model fit and parameter precision (e.g., as shown in Appendix B, Bailey and Adams Fact Sheet). The properties and benefits of using AIC as a model selection tool have been extensively documented (Shibata 1989, Anderson et al. 1994, Burnham and Anderson 2002). AIC is defined as: $-2 \ln(L) + 2k$, where $\ln(L)$ is the log-likelihood function evaluated at the maximum likelihood estimates, and k is the number of parameters in the model. The first term, $-2 \ln(L)$, is called the relative deviance and is a measure of goodness-of-fit of the model. The second term ($2k$), called the penalty term, is the cost of adding additional parameters (Lebreton et al. 1992). A correction for small samples, AICc, is often applied (including in the

⁷Parameters are defined as quantities to be estimated under an assumed model structure. We are most interested in the parameter occupancy, which may be further parameterized into groups (e.g., for different habitat strata). In terms of understanding trends in amphibian populations, detectability is a “nuisance” parameter that must be accounted for and understood.

analysis software we are using, see SOP 8: Data Analysis (Bennetts et al. 2013), in which the penalty term becomes $2k\{n/(n-k-1)\}$, where n is the effective sample size.

We emphasize that the notion of finding one “true” model for complex biological data is unlikely, and often more than one model may be indicated as appropriate for a given data set (Burnham and Anderson 2002). Anderson et al. (1994) suggest viewing model selection in the analogous context of confidence intervals, rather than point estimation, such that the selection process often indicates a range of models that are appropriate, rather than a single model. Thus, as the differences in AIC become smaller, so does the statistical basis for distinguishing among alternative models (Burnham and Anderson 1992). Models in a set are compared to the model with the minimum AIC (or AICc) by using a table of differences in AIC (see Appendix B). Sakamoto et al. (1986) suggests that AIC differences of less than or ≈ 2 should not be considered as statistically different, although this is not typically viewed as if it were a hypothesis test. As a rough rule of thumb, all models with AIC differences of less than 2 are viewed as having a substantial level of empirical support, differences of 4-7 have substantially less support, and greater than 10 have essentially no support (MacKenzie et al. 2006). However, models with close AIC differences greater than 2 may still warrant consideration, such as by using AIC weights for deriving parameter estimates from model averaging (see below).

4.3.4. Model Fit

While providing a valuable tool for selecting among alternative models, model selection statistics such as AIC do not provide a basis for whether or not any of the models being considered describe the data well. As MacKenzie and Bailey (2004) suggest, the “best” model is not necessarily a “good” model. For this assessment, some form of goodness-of-fit is needed. A general strategy that is often recommended is that the most global model⁸ be tested for goodness-of-fit, based on the logic that the global model will theoretically be the best-fitting model and that all other models can be considered as special cases of this model (Lebreton et al. 1992, Burnham and Anderson 2002).

MacKenzie and Bailey (2004) recently evaluated assessment of goodness-of-fit for occupancy models and found that the global model often fit the data poorly, however, especially when this model contained a large number of parameters. Thus, an overdispersion factor ($\hat{c}$) should be calculated. This factor is calculated as the observed chi-square goodness-of-fit statistic for the global model divided by its degrees of freedom. If there is no overdispersion or lack of fit, then $\hat{c}$ should be approximately 1, because the expected value of a chi-square statistic is equal to its degrees of freedom (MacKenzie et al. 2006). MacKenzie and Bailey (2004) further describe a procedure by which Pearson’s chi-square statistic is calculated and a parametric bootstrap is used to determine whether the observed statistic is unusually large and whether an inflation factor is warranted. This assessment is incorporated into the current version 5.3 of PRESENCE (Hines 2006). A similar test is contained within the current version 6.2 of MARK (White et al. 2001), although based on the deviance, rather than Person’s chi-square, and is not available for models with individual covariates (MacKenzie and Bailey 2004).

⁸The “global model” is the most general model in the model set, the one with most parameters.

When overdispersion is present (i.e., there is more variance than is accounted for with the model structure being used), then a modification of AICc is used, based on quasi likelihood theory, QAICc.

$$\text{QAICc} = - \left[2 \log(L(\hat{\theta})/\hat{c}) \right] + 2k + \frac{2k(k+1)}{n-k-1}$$

PRESENCE has a Model Fit option for determining if overdispersion is a problem using a parametric bootstrap approach (Hines 2006).

4.3.5. Model Averaging

During any modeling endeavor, there is always uncertainty associated with the model selection process (Burnham and Anderson 2002). This will become particularly important as data accumulate and potential effects such as space, time, scale, and covariates are incorporated into models. To account for this uncertainty, Buckland et al. (1997) proposed a procedure for deriving parameter estimates based on an average of several plausible models, rather than a single “chosen” one. This approach weights the models according to AIC (or AICc) values; thus the most plausible models receive the highest weight, while the least plausible models receive little or no weight.

When multiple models in the model set are reasonable and a best model is not apparent, the AICc weights of the candidate models can be used to obtain a weighted average of the individual parameter estimates. An estimate of the variance of the model-averaged estimator allowing for model uncertainty can also be calculated; this is an advantage of model averaging (Burnham and Anderson 2002, MacKenzie et al. 2006).

4.3.6. Occupancy Modeling Using Survey Data

It is important to recognize that the parameter estimates reported for this program are in the context of a given model. The basic model for occupancy includes 1) estimates of the probability that a given sample unit is occupied by the target species (ψ), and 2) the probability that the target species is detected on survey (j) given that it is present (p_j) (i.e., detectability) (MacKenzie et al. 2006) (see also Bailey and Adams 2005, Appendix B). The ideas presented above, with regards to the basic philosophy and principle of parsimony, come into play when these basic parameters are modeled in relation to groups or covariates that might influence these basic probabilities. For example, we have sampled units from three classes of habitat quality: high, medium, and low. If each of these classes were equally likely to be occupied, then we would only need to estimate a single parameter for occupancy. If however, we had reason to believe (which in this case we do, based on prior data) that each of these classes were not equally likely to be occupied, then we need to estimate a separate parameter for the probability of each class being occupied (ψ_{high} , ψ_{medium} , and ψ_{low}). The same consideration might be made for whether or not detectability is likely to differ among high, medium, or low quality sites.

It helps to think about these decisions in terms of how tradeoffs are made in the number of parameters being estimated. Model selection entails a balance between too many parameters in a given model (over fitting) or too few (under fitting). This can also be thought of as a balance between the specific and the general. If separate parameters exist for each point in space and time, then the model will fit the data perfectly. The problem is that we have made no

generalizations about the patterns or processes that can help us to interpret the data. The goal is to find the right balance between over-fitting and under-fitting the model.

As indicated in the section on Sampling Design, we assigned samples to subpopulations based on habitat quality (three classes), access (two classes), and drainage basin (five classes). However, estimating separate parameters for occupancy and detectability for each class would likely result in an over-parameterized model (i.e., too many parameters). Thus, we fully anticipate finding a more parsimonious model, but prefer to do so based on the data, rather than an *a priori* decision from how we sampled. Our intention is to consider whether estimating parameters for each of the subpopulation classes is warranted, and to estimate parameters only for those that are supported by the data, using model selection processes described above.

What follows is a step-by-step approach to modeling occupancy for a single species in a single year.

Extract detection histories and covariate data from the amphibian database using the Interface Tool provided by USGS-ARMI (see SOP 8: Data Analysis (Bennetts et al. 2013)) section entitled *Extracting Presence/Absence Data from the Amphibian Database*).

Use PRESENCE, MARK, or other recognized programs/software to run models that will estimate occupancy and detectability, including the effects of selected covariates (see SOP 8: Data Analysis (Bennetts et al. 2013) for a description of these programs and how to enter data).

Estimate occupancy and detectability at the catchment level, using (at a minimum) candidate models with two habitat strata (high- and medium-quality habitat) and the two access classes (close and remote) that were used in stratifying and selecting catchments for monitoring.

Determine candidate models for site-level occupancy and run the models.

Use AICc differences and weights to evaluate the candidate models.

Apply goodness-of-fit testing to the most general model (the one with the most parameters) to see if model fit was adequate.

Consider model uncertainty and apply model averaging.

Compute occupancy per species in GRTE and YELL with a formula that considers the weight of the strata and provides an estimate of variance.

An example of the analysis process is provided in Appendix C: Modeling at the Catchment Level using 2007 data summaries. A summary of a multi-year analysis (2006 and 2007) for tiger salamanders, and 2006 through 2009 for all species are included as Appendices D and E, respectively.

4.3.7. Trend Analysis

In many monitoring programs, the rate of occupancy change over time is often of equal or greater importance than any absolute level of occupancy in a given year (MacKenzie et al. 2006). A primary goal of the GRYN amphibian monitoring program is to use long-term monitoring data (2005 to present) for all native species to determine whether trends in occupancy are observed.

To facilitate trend analysis, detection histories from all available breeding seasons (breeding seasons and years can be used synonymously here) can be used to model patterns in occupancy at the catchment and site level over the period of record.

For trend analysis, we will use the multi-season approach described in MacKenzie et al. (2006) in which the processes of extinction and colonization are modeled explicitly and can be used to derive seasonal occupancy estimates for each of our four native amphibian species. Yearly occupancy estimates will be derived based on seasonal extinction and colonization probabilities. The rate of change in occupancy among years can be considered using the ratio of occupancy in successive years or using odds ratios that are

$$\lambda'_t = \frac{\varphi_{t+1}/(1-\varphi_{t+1})}{\varphi_t/(1-\varphi_t)} \text{ (see MacKenzie et al. 2006).}$$

Although the estimation of trends does not inform of the causes of changes, it does result in information that will inform the type of management actions (if any) might be implemented. Direct modeling of the processes driving changes are likely to be more useful (MacKenzie et al. 2006). An example of this approach with data from 2006-2009 is summarized in the initial multi-season analysis of three species of amphibians (barred tiger salamanders, boreal chorus frogs, and Columbia spotted frogs; Gould et al. 2012; Appendix E). This multi-year and multi-species analysis provides the first estimates of extinction and colonization rates in GRTE and YELL. Although this dataset is based on only four years of survey results, additional years of trend monitoring data will provide stronger inferential capabilities and, we hope, more partitioning of model support.

Another potential approach uses model selection with candidate models in which occupancy varies over time (years). Several models could be developed, including one that assumes occupancy is constant, and one that allows occupancy to vary over time, for example, a model whereby the logit(Ψ) = $\beta_0 + \beta_1(t)$. MacKenzie et al. (2006) discuss an implicit dynamics modeling approach, but cautions that this approach makes fairly restrictive assumptions regarding extinction and colonization rates.

4.3.8. Boreal Toad Data Analysis

As described in the section on Sampling Design, data on boreal toad breeding areas outside of sample catchment boundaries will be collected if funding or qualified volunteers are available. If sufficient data are collected, we will apply dual frame analysis (e.g., Haines and Pollock 1998). In our case, the “area frame” would refer to the probabilistic catchment sampling (Objective 1), and the “list frame” would refer to all other toad breeding areas, which have been identified in a variety of ways over the past years. Remaining questions and issues include: selection of the most applicable dual frame methodology, clarification of what should be maintained on the list frame (e.g., should areas that have not been occupied for several years be dropped or retained?), and the level of effort needed to provide useful results with this type of analysis (e.g., would surveying a rotating panel of five or ten list frame members per year be adequate?).

Alternatively, occupancy at previously identified boreal toad breeding areas (including both the area and list frames) will be tracked using resources available and summarized annually. In this case, we recognize the set of toad areas as a “population of interest.” While these results do not

provide statistical inference to the status of boreal toads across GRTE and YELL, continued monitoring of this relatively uncommon amphibian species at known sites may have important benefits for conservation (e.g., habitat protection and mitigation measures if development occurs nearby), education (active breeding sites serve as field trip sites for park staff and amphibian natural history classes), and research (e.g., quick identification of study sites for disease or genetics work).

4.4. Data Reporting

A summary report will be produced after each year of data collection and will:

- Provide a summary history of the samples taken during each year of the study, tabulating numbers of samples for the sample frame, by subbasin, by habitat quality and accessibility stratum, and graphically illustrating summaries using GIS.
- Provide summary status statistics and interpretation of the biological meaningful results.
- Evaluate data quality and identify any data quality concerns or deviations from protocols that affect data quality and interpretation.
- Evaluate and identify suggested or required changes to the protocol.

A more in-depth trend report will be produced every five years. This analysis may include climate data or other relevant data (e.g., surface water temperature) as explanatory covariates. This report will provide greater analytical and interpretive detail, and will evaluate the relevance of findings to long-term management. The report will also evaluate operational aspects of the monitoring program, such as whether catchment boundaries need to be changed or the sampling period remains appropriate (the optimal sampling season could conceivably change over time in response to climate change). The report will also evaluate if there are new management concerns that might dictate some reallocation of effort or additions to the indicator metrics or covariates that are routinely examined annually.

Annual reports and five-year analyses of status and trend will follow guidelines for the NPS Natural Resource Publications Series and use a pre-formatted Microsoft Word template document based on current NPS formatting standards. Template guidelines and documentation of the NPS publication standards are available at the following address:

<http://www.nature.nps.gov/publications/nrpm/index.cfm>.

Current versions of the protocol, resource briefs, and annual and five-year reports will be made available on the GRYN website (<http://science.nature.nps.gov/im/units/gryn/index.cfm>). The protocol and technical reports will also be available from the national NRPM website (<http://www.nature.nps.gov/publications/NRPM/index.cfm>).

5. Personnel Requirements

5.1. Roles, Responsibilities, and Qualifications

Amphibian monitoring requires a team of knowledgeable and skilled individuals from administrative to technical, all of whom work together to ensure that data are collected using appropriate methods, and that results and derived products are thoroughly documented, credible, and available for analysis and reporting. The GRYN program manager, ecologist, and data manager have first-level responsibility for protocol administration and management, data analysis, synthesis and interpretation, and communication of monitoring results. This team works with partners and cooperators to meet the amphibian monitoring objectives (see section on Measurable Objectives). For management purposes, the protocol leader is a GRYN staff member who ensures that the monitoring follows the procedures outlined in this protocol. Field operations are coordinated and scheduled through seasonal hiring or cooperative agreements.

The USGS-ARMI and other cooperators (currently the Northern Rockies Conservation Cooperative) collaborate with GRYN to implement the amphibian monitoring protocol in GRTE and YELL. The primary positions needed to successfully implement this protocol are described in Table 7. Several responsibilities, especially data management and reporting, overlap among positions.

Table 7. Roles and responsibilities for implementing the Amphibian Monitoring Program in the GRYN.

Role	Responsibilities
Protocol Leader	Implement protocol annually Track progress toward meeting protocol objectives Identify budget needs Identify when specialists are needed to complete different phases of the protocol Facilitate communications between NPS and cooperator(s) Coordinate and update changes to protocol Coordinate training of field teams Certify each season's data for quality and completeness Perform data summaries and analyses Complete reports, metadata, and other products according to schedule Maintain and archive protocol records
Field Coordinator	Provide supervision of technicians Main contact for crew daily check-in Implement safety training for technicians Work in coordination with the protocol leader to implement the following: Plan and execute field visits Oversee data collection and entry, verify accurate data transcription into database Acquire and maintain field equipment Facilitate crew logistics (camping, vehicle use, etc.) Obtain research permit
Technician(s)	Perform fieldwork in remote backcountry areas in grizzly bear country Collect, record, enter, and verify data Lead maintains field notes, highlighting points of interest for trip report Take photographs and manage photo library

Table 7. Roles and responsibilities for implementing the Amphibian Monitoring Program in the GRYN (continued).

Role	Responsibilities
Data Manager	Prepare database, field forms, GPS for upcoming field season Consultant on data management activities Facilitate check-in, review, and posting of data, metadata, reports, and other products to national databases and clearinghouses according to schedule Maintain and update database application Provide database training as needed Consultant on GPS use Work with protocol leader to analyze spatial data and develop metadata for spatial data products Primary steward of Access database and GIS data and products Coordinate with ARMI on database updates
Network Program Manager	Protocol oversight Administration and budget Consultant on all phases of protocol review and implementation Review of annual and five-year reports Provide technician supervision if field coordinator is unavailable
Park Contact	Consultant on all phases of protocol implementation Facilitate logistics planning and coordination Communicate management plans and needs related to protocol to protocol leader Review reports, data, and other protocol deliverables Provide examples of how data have been used in management decisions
Cooperator(s)	Assist with tasks as identified through agreements: field coordination, data collection and management, report preparation, trend analysis

5.2. Training

Training is conducted at the beginning of the field season each year to make sure that field crews are competent in all required skills and can work safely and efficiently in the field. Training is a critical component of quality assurance. Correct identification of amphibian species at all life stages is a required skill for individuals involved in field data collection, and the competency of observers is a critical component of the sampling protocol. Annual training includes the following:

Safety and communication to make sure field work is conducted safely and communication is effective (SOP 1: Field Safety for the Amphibian Monitoring Program, Bennetts et al. 2013).

Review of the monitoring protocol and associated SOPs to become familiar with the monitoring objectives, data collection methods (SOP 3: Daily Procedures and Checklists, Bennetts et al. 2013), and personnel roles and responsibilities.

Amphibian species identification, especially larvae stage, to ensure no species is falsely identified. Several field guides are available (see Koch and Peterson 1995) for the amphibians present in GRTE and YELL. All reference guides provide information and tips for identifying amphibians in this region.

Navigating to catchments and sites using GPS and topographic maps to make sure the sample design is followed (SOP 2: Pre-season Preparations and Equipment Setup, Bennetts et al. 2013).

Equipment handling and use including proper care and sanitization to keep equipment in operable condition and eliminate the incidental spread of disease and aquatic nuisance species (SOP 3: Daily Procedures and Checklists, Bennetts et al. 2013).

Data collection methods to make sure data are collected and recorded according to established procedures (SOP 3: Daily Procedures and Checklists, SOP 6: Conducting Visual Encounter Surveys, and SOP 7: Data Field Descriptions and Instructions for Data Entry; Bennetts et al. 2013).

Use of handheld field computer including data entry, storing, and backing up data onto a computer (SOP 3: Daily Procedures and Checklists and SOP 7: Data Field Descriptions and Instructions for Data Entry; Bennetts et al. 2013).

Equipment calibration (e.g., pH and conductivity meters [when applicable]) to establish and document known measurement quality (SOP 2: Pre-season Preparations and Equipment Setup, Bennetts et al. 2013; ONLY if applicable).

6. Operational Requirements

6.1. Annual Workload and Field Schedule

The minimum amount of personnel needed to implement this monitoring is the protocol leader, field coordinator, and four to six field technicians, depending on availability of the two coordinators to work in the field.

The annual workload for amphibian monitoring includes pre-season preparation and end-of-season procedures related to monitoring activities, which normally take place in June and July. Preparing for the field season starts in January when recruitment for summer personnel begins and research permits are renewed. SOP 2: Pre-season Preparations and Equipment Setup (Bennetts et al. 2013) lists detailed pre-season activities by timeframe and includes the steps followed by the field coordinator before amphibian monitoring can begin.

A number of significant variables affect field operations, including weather, the dynamic nature of wetlands within catchments in a given year, the time involved in initial or first-year catchment surveys, crew abilities, and catchment replacement strategies. With these variables in mind, and based on experience from previous field seasons, the field coordinator spends approximately 800 hours throughout the year (January-December) on duties that include coordinating field operations, managing and validating survey data, recruiting, hiring, training, overseeing, and supervising crew members, performing surveys as a crew member, and coordinating volunteer activities for boreal toad surveys. It takes an estimated 1,400 person-hours in June and July to survey catchments in teams of two, organized as three field crews. The amount of time required for field surveys and field coordination may be revised depending on available funds to implement the protocol and network staff (i.e., protocol leader).

If boreal toad surveys are conducted, 42 crew-days are required to survey known toad breeding areas outside of sample catchments. Areas that are easy to access are calculated as half days, considering three hours for the survey and an average of two hours for driving and hiking time. A minimum of 11 days, and up to 17 days, are required for partial implementation of boreal toad surveys, as described in the section on Sampling Design, and depending on which areas are randomly selected. Coordinating volunteers requires approximately four days, and includes preparing maps and forms, making work assignments, and communicating with volunteers. When new volunteers participate in surveys, the field coordinator requires two additional days of training for each new person or group. After the surveys, data compilation takes approximately four days and data analysis takes up to eight additional days, depending on analysis requirements.

6.2. Facility and Equipment Needs

Amphibian monitoring takes place outdoors and requires no facilities except a small amount of space for off-season storage of monitoring equipment. Park housing (bunk-style dorm or mobile trailers) provides an efficient base location for accessing amphibian catchments which are distributed throughout GRTE and YELL. Park housing provides a dry environment for daily computer entry and back-up and a location to charge equipment. Alternatives to park housing (if not available) include camping or staying in commercial lodging facilities.

Field crews work in two-person teams. Each team requires transportation (normally a 2-wheel drive vehicle) and a full set of field equipment. Government-issued SPOT locator beacons and handheld radios for each crew are critical pieces of safety equipment provided by the GRYN office. The field coordinator requires access to a portable laptop computer. A detailed list of equipment and supplies is found in SOP 2: Pre-season Preparations and Equipment Setup (Bennetts et al. 2013).

6.3. Budget

Currently, fiscal and personnel resources support the goal of sampling all medium- and high-quality catchments (approximately 30) included in Table 2. This level of effort is consistent with the sampling intensity completed in recent years (2011 and 2012) but is below the 40 catchments sampled in 2010.

Table 8 details the annual operating budget to implement this protocol and reflects 2012 costs. If the target number of sample catchments is not attained for three consecutive years, the sample design will be reevaluated and scaled such that the design is commensurate with the funds available.

Table 8. Annual budget for amphibian monitoring in YELL and GRTE. More than 50% of the amphibian monitoring budget is spent on data management activities including analysis and reporting.

Greater Yellowstone Network Amphibian Monitoring Budget				
Expenditures	Time Allotted	% Time for Data Management	Cost in Dollars for Data Management	Total Costs in Dollars
Network Program Manager (GS-13)	1/2 week to review report; manage budget	50%	\$575	\$1,150
Network Data Manager (GS-12)	1 week field season preparation & crew training; 2 weeks QA/QC, data archiving, and close out	100%	\$5,700	\$5,700
Protocol Leader (GS-11)	4 weeks pre- and post-season (logistics, coordinating cooperators, parks); 6 weeks field training & sampling assistance; 2 weeks data analysis & reporting; close out	60%	\$11,800	\$19,700
Field Coordinator (GS-9)	9 weeks to hire, supervise & coordinate crews, train, and provide safety check-ins (could also be supported through contractors/cooperators)	50%	\$11,350	\$22,700
Seasonal Personnel: 4 Biological Technicians (GS-5)	6 weeks training, sampling, data validation in the field, and close out (could also be supported through contractors/cooperators)	50%	\$9,675	\$19,350
<i>Park Personnel</i>	1 week field work prep & assistance; verify data questions; housing logistics; report reviews		\$ -	IN-KIND
<i>Contracts/Cooperators</i>	Assistance with protocol implementation and may include being the field coordinator; data QA/QC, analysis; field work; reporting (contracts/agreements vary by year and need)		\$ -	\$
<i>Operations/Equipment</i>	Field gear, safety equipment,		\$ -	\$1,000
<i>Housing/lodging</i>	Government Housing (rent)		\$ -	\$1,400
<i>Vehicle</i>	Fuel/rental vehicle			\$2,000
<i>Travel</i>	Per diem		\$ -	\$1,500
<i>Other (contingency)</i>			\$ -	\$500
TOTAL			\$39,100	\$70,600

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8. Appendix A. National Wetlands Inventory Types Used in Sample Design

Documentation is available online for full definitions of the National Wetlands Inventory (NWI) attribute codes and habitat classification used below

(<http://www.fws.gov/wetlands/Data/Wetland-Codes.html>, accessed 12/10/2012).

8.1. Excluded Types

In constructing the sample frame, NWI polygons with the following attributes were excluded on the basis of being highly unlikely to include habitat for breeding amphibians.

U (upland)

L1ABH, L1UBH, L1UBHh (deep lakes with unconsolidated bottom)

PABKx, PUBKx, PABGx (mostly sewage lagoons; one exception we kept is the Kelly Warm Springs feature in GRTE)

R2UBH, R3ABH, R3UBF, R3UBH, R3USA, R3USC, R3RBH, R3UBG (perennial river waters with unconsolidated bottom)

Lakes and rivers may have shoreline areas that are suitable for amphibian breeding, but such areas are classified with different NWI codes than above. Some catchments were classed as non-qualifying based on water regimes (described below) and thus, were excluded from the sample frame.

8.2. Stratified Types

Catchment strata used in sample design were based on non-excluded NWI wetland types and amounts with respect to water regime, as follows:

High; refers to relatively high suitability as amphibian breeding habitat based on the amount and type of wetland areas inside catchment boundaries. Defined as containing four or more hectares of NWI mapped wetlands with water regime types of F, G, or H (semi-permanently flooded [F], intermittently exposed [G], or permanently flooded [H]), AND two or more hectares of water regime type C (seasonally flooded).

Medium; refers to relatively moderate suitability as amphibian habitat. Defined as containing some (any amount of) water regime types F, G, or H (types as described above), AND one or more hectares of type C.

Low; refers to relatively low suitability as amphibian habitat. Defined as containing any amount of water regimes F, G, H, or C; pertaining to catchments not captured by the High and Medium strata.

Non-qualifying; refers to catchments not captured by the above stratifications and containing only water regime types A (temporarily flooded) and/or B (saturated) and/or J (intermittently

flooded). These were not used for catchment selection, and should be considered as excluded from the sample frame.

8.3. Water Regime Types, as Defined by NWI

This information is from NWI documentation for freshwater non-tidal systems.

[A] *Temporarily Flooded*. Surface water is present for brief periods during the growing season, but the water table usually lies well below the soil surface. Plants that grow both in uplands and wetlands may be characteristic of this water regime.

[B] *Saturated*. The substrate is saturated to surface for extended periods during the growing season, but surface water is seldom present.

[C] *Seasonally Flooded*. Surface water is present for extended periods, especially early in the growing season, but is absent by the end of the growing season in most years. The water table after flooding ceases is variable, extending from saturated to the surface to a water table well below the ground surface.

[D] *Seasonally Flooded/Well Drained*. Not used.

[E] *Seasonally Flooded/Saturated*. Surface water is present for extended periods, especially early in the growing season and when surface water is absent; substrate remains saturated near the surface for most of the growing season. (Not used in GRTE/YELL)

[F] *Semi-permanently Flooded*. Surface water persists throughout the growing season in most years. When surface water is absent, the water table is usually at or very near the land's surface.

[G] *Intermittently Exposed*. Surface water is present throughout the year except in years of extreme drought.

[H] *Permanently Flooded*. Water covers the land surface throughout the year in all years.

[J] *Intermittently Flooded*. Substrate is usually exposed, but surface water is present for variable periods without detectable seasonal periodicity. Weeks, months, or even years may intervene between periods of inundation. The dominant plant communities under this regime may change as soil moisture conditions change. Some areas exhibiting this regime do not fall within our definition of wetland, because they do not have hydric soils or support hydrophytes. In areas mapped as intermittently flooded, refer to regional guidelines for specific applications.

[K] *Artificially Flooded*. The amount and duration of flooding is controlled by means of pumps or siphons in combination with dikes or dams. The vegetation growing on these areas cannot be considered a reliable indicator of water regime. The Artificially Flooded modifier should be used with water and waste-water treatment facilities. Neither wetlands within or resulting from leakage from man-made impoundments, nor irrigated pasturelands supplied by diversion ditches or artesian wells are included under this modifier. Artificially Flooded can be used with any non-tidal water regime. The Artificially Flooded (K) symbol should always be listed before other water regime codes (e.g., PUBKF).

[U] *Unknown*. The water regime is unknown. This designation is not used in GRTE/YELL.

9. Appendix B. Occupancy Models to Study Wildlife



Occupancy Models to Study Wildlife

Abstract

Many wildlife studies seek to understand changes or differences in the proportion of sites occupied by a species of interest. These studies are hampered by imperfect detection of these species, which can result in some sites appearing to be unoccupied that are actually occupied. Occupancy models solve this problem and produce unbiased estimates of occupancy and related parameters. Required data (detection/non-detection information) are relatively simple and inexpensive to collect. Software is available free of charge to aid investigators in occupancy estimation.

Response Variables in Wildlife Studies

Studies of wildlife populations often attempt to understand patterns of distribution and abundance. Estimating abundance can be a costly endeavor, and other state variables¹ like species richness or occupancy² may be more appropriate and less expensive. Occupancy is an alternative that has a long history of use in ecological and wildlife studies. Two of the most noticeable areas where occupancy information is used include: (1) studies of species distribution and range where investigators seek to understand the factors that determine whether or not a species will exist at a location (e.g., habitat modeling, Scott et al. 2002) and (2) metapopulation dynamics (Hanski 1992) where site (or patch) occupancy is related to patch, or site-specific, characteristics. For the latter case, extinction and colonization probabilities can also be modeled in relation to patch characteristics. Monitoring occupancy can reveal changes in the status of a species over broad

areas and may be appropriate for species that exhibit wide population fluctuations over short time periods. For example, occupancy has been the most influential state variable in describing world-wide amphibian declines (Green 1997).

The Problem

Wildlife species are rarely detected with perfect accuracy, regardless of the technique employed. Non-detection does not necessarily mean that a species was absent unless the probability of detecting the species (detectability³) was 100%. This leads to a fundamental problem: the measure of occupancy (presence/absence at a set of sites) is confounded⁴ with the detectability of the species. More specifically, an observed "absence" occurs if either the species was present at the site but not detected, or the species was truly absent. Detectability may vary among study sites and may be related to characteristics of a survey on a particular day, such as weather conditions. Because of this variation in detectability, it is insufficient to simply analyze detection/non-detection data as if they are truly presence/absence data. The proportion of sites where a species is detected will always underestimate the true occupancy level in the study area when detection is imperfect. Therefore, inferences regarding the influences of site characteristics on occupancy will be difficult or impossible to discern reliably (e.g., Gu and Swihart 2004).



Imitator Salamander

The Solution

New classes of models, called occupancy models, were developed to solve the problems created by imperfect detectability (MacKenzie et al. 2002, 2003, 2004). These models use information from repeated observations at each site to estimate detectability. Detectability may vary with site characteristics (e.g., habitat variables) or survey characteristics (e.g., weather conditions), whereas occupancy relates only to site characteristics. Repeated observations can take many forms, but the most obvious is simply surveying each site repeatedly. In some cases, traps, coverboards, transects, and surveys by independent observers can be treated as repeated observations for a local sample area or site. For example, data from 10 minnow traps in each of 30 ponds could be treated as 10 observations at each pond if there is some possibility that the species of interest could be caught in each of the traps.

How Does This Work?

The technique is very similar to estimating abundance from mark-recapture data but does not require any marking of animals. Necessary information for occupancy models is

simply a record of whether a species was detected or not detected during each survey of each site (Box 1). These records, termed detection histories, can be converted to mathematical statements. Assuming the sites are independent, the product of all the mathematical statements (one for each possible detection history) forms the model likelihood⁵ for the observed data, and maximum likelihood techniques are then used to estimate model parameters⁶. Parameter estimates (occupancy or detectability) can be related to various site and survey characteristics using the logistic equation or logit-link function⁷. The details of this and other variations on occupancy estimation are described in a series of journal articles (see MacKenzie et al. papers under Further Reading).

Two software packages will help you do an occupancy analysis. PRESENCE was created exclusively for occupancy analysis and is available at <http://www.mbr-pwrc.usgs.gov/software.html>. Occupancy analysis has also been incorporated into MARK, which is available at <http://www.cnr.colostate.edu/~gwhite/software.html>. Examples using occupancy models include Corn et al. (2005), Olson et al. (2005), and O'Connell et al. (2005).

Assumptions

All models have assumptions, and occupancy models are no exception. Critical assumptions for data collected during a single sampling season include:

(1) Occupancy state is "closed."

Species are present at occupied sites for the duration of the sampling season. Occupancy does not change at a site within the sampling season, but it can change between sampling seasons.

(2) Sites are independent. Detection of the target species at one site is independent of detecting the species at other sites. This might be a problem if your sites are closely spaced, allowing animals to move

Box 1: Details of occupancy estimation

Parameters of interest:

ψ is the probability a site is occupied by the target species.
 p_j is the probability of detecting the species during the j th survey, given it is present (detectability).

Necessary information: Detection histories

Detection histories are just a record of whether or not the target species was detected on each survey of each site. For example, suppose 30 sites were each sampled four times

within a season. The following table could be the resulting detection histories, where each row represents a site and each column represents one of the four surveys:

	Surveys			
	1	2	3	4
Site 1	1	0	0	1
Site 2	0	0	0	0
Site 3	1	1	0	0
...				
Site 30	0	0	0	0

Each site has its own detection history that can be represented by an intuitive mathematical equation. In the above case, the target species was detected at Site 1 during the first and last survey occasions (1001). The site was occupied (ψ), and the species was detected on the first and last surveys (p_1 and p_4) and not detected on the second and third surveys. We can write the probability of this detection history as:

$$\Pr(H_i = 1001) = \psi \times p_1 (1 - p_2)(1 - p_3) p_4$$

Sites 2 and 30 represent a case where the target species was never detected (detection history = 0000). These sites could either be unoccupied, which mathematically is $(1 - \psi)$, or they could be occupied but we never detected the target species, which mathematically is:

$$\psi(1 - p_1)(1 - p_2)(1 - p_3)(1 - p_4) \text{ or } \psi \prod_{j=1}^4 (1 - p_j)$$

Thus, we can write the probability of detection history (0000) as:

$$\Pr(H_i = 0000) = \psi \prod_{j=1}^4 (1 - p_j) + (1 - \psi)$$

Mathematical statements of all detection histories are combined into model likelihood, such as:

$$L(\psi, p | H_1, \dots, H_{30}) = \prod_{i=1}^{30} \Pr(H_i)$$

Maximum likelihood methods incorporated in program PRESENCE or program MARK are used to obtain estimates of occupancy and detectability (see MacKenzie et al. 2002).



among sites and be detected at multiple sites.

- (3) **No unexplained heterogeneity in occupancy.** Probability of occupancy is the same across sites or differences in occupancy can be explained with site characteristics (covariates) that have been quantified for inclusion in the model.
- (4) **No unexplained heterogeneity in detectability.** Detectability at occupied sites is the same across all surveys and sites, or differences in detectability can be explained with site or survey characteristics that have been quantified for inclusion in the model.

Approaches to Meeting Assumptions

Investigators can use design-based or model-based approaches to meet these assumptions. A design-based approach involves collecting data in a way that assures the assumptions will be met. For example, natural history information may aid in scheduling surveys during times when the closure assumption is most likely to hold. In addition, a scientist may use existing movement information to ensure that sample sites are dispersed across the sample area in a manner that maintains independence.

Sites should be chosen according to some type of probability-based sampling⁹ (e.g., simple-random sample, stratified-random sample, etc.) to ensure that estimates of occupancy apply to the area of interest. Sampling may be standardized to try to minimize differences in detection probability caused by variation in environmental conditions or time of day. Unfortunately, it is impossible to control for all possible factors that can affect detectability or occupancy. When design-based approaches cannot reduce all of the variation (sometimes termed heterogeneity) in either occupancy or detectability, model-based approaches might help. Investigators should collect information about factors they believe could cause heterogeneity in either of these two parameters and then incorporate these covariates into the estimation process. For example, it may be impractical and wasteful to only sample amphibian breeding ponds during sunny days, but larvae are more difficult to see on cloudy days; thus, investigators should record weather conditions during each survey. The variation in detection probabilities caused by cloud cover can easily be incorporated to obtain unbiased estimates of occupancy.

Biases Caused by Assumption Violations

If the assumptions mentioned above are not met, estimates of occupancy and detectability can be biased¹⁰ and inferences about factors that influence these parameters may be flawed (e.g., Gu and Swihart 2004). If the target species is not present at sites throughout the entire study season, then estimates of occupancy may still be unbiased if the species moves randomly in and out of a sampling unit. Interestingly, the interpretation of occupancy changes to the proportion of sites *used* by the target species in this case. Likewise the probability of detecting the species at occupied sites is now a combination of two different components: the probability that the species was present at the sampling unit and the probability of detecting the species given it was present. If movement in and out of the sampling unit is not random, the occupancy estimator will likely be biased. For example, non-random movement occurs if the target species was not initially at the site when sampling commenced, then moves into the sample unit and stays for the duration of the season. The direction of the occupancy bias depends on the direction of the movement (see Kendall 1999 for more details and possible solutions).

Little work has been done involving the impact of variation in occupancy probability among sites that cannot be associated with covariates (occupancy heterogeneity). It is possible that the overall average occupancy estimate may still be unbiased, but more research on the impacts of occupancy heterogeneity is needed.

Heterogeneity in detection probability will often result in occupancy estimates that are low (negatively biased). This problem is further exacerbated in studies involving a small number of sites, few repeated surveys at each site, or species with exceptionally low detection probabilities. Anticipating variation and minimizing its effects either through study

design or collecting relevant covariates to model it is essential for good performance of these methods.

Finally, if detection is not independent among sites, the standard error estimates are usually too low. In these instances, the number of independent sites is actually smaller than the total number of sites surveyed. There are existing model-based methods that aid in detecting and correcting this problem (MacKenzie and Bailey 2004).

Occupancy and Terrestrial Salamanders

Approximately 10% of the world's salamander species are found in the southern Appalachian region, with 31 species occurring inside the boundaries of Great Smoky Mountains National Park (GSMNP; Dodd 2003). Despite this rich diversity, large-scale or long-term studies of terrestrial salamanders in this region are almost nonexistent (but see Hairston and Wiley 1993). An area of interest involves the impact of various forms of disturbance on terrestrial salamander populations (Petrunka et al. 1993, Ash 1997, Petrunka 1999, Ash and Pollock 1999). Some areas within GSMNP incurred heavy human use in the form of logging or settlement prior to the park's establishment in 1934. In this example analysis, we ask if previous disturbance history affects the probability of occurrence for salamanders of the *Desmognathus imitator* complex in GSMNP. We caution that this analysis is meant as an example only, and we remind readers that there is always an inherent danger in inferring biological process from spatial patterns.

Data: Salamanders were sampled using two methods: an area-constrained natural-cover transect (50 x 3 m) and a 50 m coverboard transect, consisting of 5 coverboard stations spaced at 10 m intervals. The two transects were parallel to one another and separated by approximately 10 m. Together, the area sampled by these transects constituted a site or sample

Box 2: Results of model selection for salamanders of the *Desmognathus imitator* complex in Great Smoky Mountains National Park

The models we considered assume occupancy was either constant across sites $\psi(\cdot)$, or varied according to the sites' previous disturbance history, $\psi(\text{dist})$. Detectability was either constant across all surveys and sites $p(\cdot)$, or it varied among surveys $p(t)$, or across sites according to previous disturbance history $p(\text{dist})$, or both $p(\text{dist}+t)$. Model selection was based on Akaike's Information Criteria for small sample size (AIC_c), which selects the most parsimonious model, balancing model fit and parameter precision. Models with lower AIC_c are considered best. ΔAIC_c is the difference between the AIC_c of the best model and a subsequent model. As a general rule, models with $\Delta AIC_c < 2.0$ have substantial support and should be considered when making inferences or reporting parameter estimates. Another way of assessing model support is with Akaike weight (w), which can be interpreted as the weight of evidence for a particular model. All weights sum to 1.

Model	Parameters	AIC_c	ΔAIC_c	Weight (w)
$\psi(\text{dist}) p(\text{dist}+t)$	7	89.68	0.00	0.32
$\psi(\text{dist}) p(t)$	6	90.27	0.59	0.24
$\psi(\text{dist}) p(\text{dist})$	4	91.03	1.35	0.16
$\psi(\text{dist}) p(\cdot)$	3	91.47	1.78	0.13
$\psi(\cdot) p(\text{dist}+t)$	6	92.25	2.57	0.09
$\psi(\cdot) p(\text{dist})$	3	93.54	3.86	0.05
$\psi(\cdot) p(t)$	5	100.36	10.68	0.00
$\psi(\cdot) p(\cdot)$	2	102.01	12.33	0.00

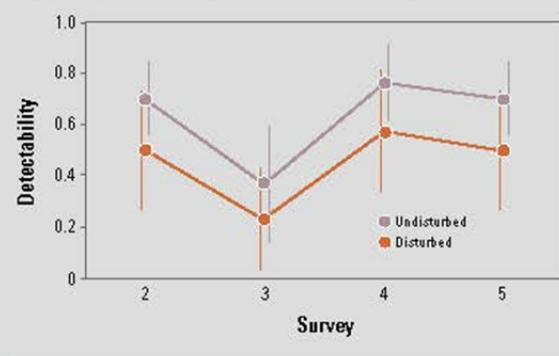


Figure 1. Model-averaged estimates of detectability across surveys and among sites with different disturbance histories.

unit. Sample units were near trails and located approximately 250 m apart to ensure independence among sites. Thirty-nine sites were sampled once every two weeks from April to mid-June when salamanders were believed to be most active and near the surface. However, we detected no salamanders of the *Desmognathus imitator*



complex during the first survey. Thus, we eliminated this survey from the analysis because we assume the salamanders had not emerged from their winter retreats and were unavailable for capture during this survey occasion. This left a total of four surveys for the analysis.

Analysis, Model Selection, and Interpretation: Salamanders of the *Desmognathus imitator* complex were detected at 10 of the 39 sites, yielding a naive occupancy estimate of 0.26; however, we suspected that salamanders may be more likely to occupy undisturbed sites compared to disturbed sites. In addition, we thought detectability might vary among surveys due to environmental conditions such as rainfall or temperature. Thus, we consider all combinations of models in which occupancy probability is assumed to be constant for all sites (denoted as $\psi(\cdot)$) or varied among sites according to the site's previous disturbance history ($\psi(\text{dist})$); detection probability was either constant ($p(\cdot)$), different among surveys ($p(t)$), or varied among sites according to previous disturbance history ($p(\text{dist})$).

Models that fit the data best with the least number of parameters are favored. We do not have room to explain the details of this parsimoni-

Glossary:

1. State variable: variable used to characterize the status of the wild-life system of interest; the system being studied.
2. Occupancy: the proportion of sites, patches, or habitat units occupied by a species.
3. Detectability: the probability of detecting a species during a single survey, given it is present at the site.
4. Confounded: an inability to separate multiple factors potentially contributing to an observed pattern.
5. Likelihood function: a functional expression of unknown parameters, given observed data and an assumed model structure.
6. Parameters: quantities to be estimated, such as occupancy or detectability, under an assumed model structure.
7. Logit function: an equation that converts a sigmoid relationship (logistic) between two factors to a linear relationship. The logit function involving detectability may be: $\text{logit}(p) = \ln(p/(1-p)) = y$.
8. Heterogeneity: Often used synonymously with variation. Here, it is used to refer to unexplained variation in the parameters of interest.
9. Probability-based sampling: a sampling scheme in which every sample unit (site) has a known probability of being selected (see Thompson et al. 1998).
10. Biased: describes an estimator that, over repeated trials, exhibits a non-random (directional) difference from the true value being estimated.
11. Parsimonious model selection: given a set of candidate models, selecting those model(s) that describe the information content of the data adequately with the fewest number of parameters possible.
12. Weighted average: an average where the contribution of the values being averaged is unequal. For example, the unweighted average of 5, 3, and 9 is $(5+3+9)/3 = (0.33(5)+0.33(3)+0.33(9)) = 5.7$. However, if we wanted the contribution of those three values to be 0.1, 0.4, and 0.5 respectively, we would calculate a weighted average of $(0.1(5)+0.4(3)+0.5(9)) = 6.2$.

ous process of model selection,¹¹ but Burnham and Anderson (2002) have written a comprehensive book on the subject. Using the software PRESENCE and methods they describe, our analysis highlighted four models as the best models representing our salamander data (see Box 2). There is some uncertainty as to which model is the best, so our parameter estimates are essentially a weighted average¹² among all four models. Together these models suggest that occupancy

indeed differs between previously disturbed and undisturbed sites; all of the top models include previous disturbance history as a covariate in the occupancy estimate. Model-averaged occupancy estimates were 0.19 (SE = 0.15) and 0.70 (SE = 0.15) for previously disturbed and undisturbed sites, respectively. Detectability also varied among surveys and possibly among sites with different disturbance histories (Figure 1, Box 2).

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Photo: *Bufo boreas*, Susanne L. Collins

10. Appendix C. Modeling at the Catchment level: An Example Using 2007 Data

The analysis that follows was structured to investigate if the stratifications used in random sampling resulted in real distinctions, using a model selection approach in which the strata are maintained or collapsed. The 2007 catchment-level data were analyzed considering the six strata-combinations that were used in sample selection: three habitat strata (high, medium, low) and two access strata (close, far). Based on the presumed similarity between high- and medium-quality habitat strata, consideration also was given to models with only two habitat categories (high+medium, versus low). Also included were models allowing for variation in detection probability between the primary and secondary surveys.

The models based on these distinctions are considered *a priori* models. A set of eight candidate models was used. The most general model allowed detection probability to vary between survey occasion (the first and second survey within a year) and occupancy to vary among the six strata combinations of habitat quality (three levels) and access (two levels).

Information theoretic methods (Burnham and Anderson 2002) were used for evaluating models in the set. With this approach, more than one model may be supported, and model uncertainty is considered when making inferences.

The following steps were taken:

1. Akaike's information criterion with a correction for small samples (AICc) was applied (Burnham and Anderson 2002). Differences in $\Delta AICc$ of less than three were taken as indicating that the model had substantial support, while AICc weights provided the probability or relative likelihood of the model, given the data. Model uncertainty was indicated when the weights were similar for several high-ranked models, and thus none of the models was clearly superior.
2. Modeling was followed by goodness-of-fit testing, performed for the most general model (the one with the most parameters) to see if model fit was adequate. The parametric bootstrap feature within MARK was used to accomplish this task in which the model deviance and estimated chat were compared to generated values under the most general model.
3. Model averaging was applied to occupancy estimates (for model sets exhibiting uncertainty). This provided estimates of occupancy for each of the six strata (e.g., high quality habitat-close access; high-far, etc.).

4. A weighted average of the stratum-specific estimates was computed:

$$\bar{\hat{\psi}} = \sum_{h=1}^L \frac{N_h}{N} \hat{\psi}_h \text{ where } h \text{ indexes each stratum and } N_h \text{ is the stratum size such that } \sum_{h=1}^L N_h = N$$

With variance computed as:

$$\hat{Var}(\bar{\hat{\psi}}) = \sum_{h=1}^L \left(\frac{N_h}{N} \right)^2 \left(\frac{N_h - n_h}{N_h} \right) \hat{Var}(\hat{\psi}_h) \text{ where } n_h \text{ represents the number of catchments sampled}$$

from stratum h .

Stratum size was obtained from the catchment GIS layer used in the sample design (total number of catchments=3,370):

Habitat	Access	Number of Catchments
High	Close	92
High	Far	43
Medium	Close	565
Medium	Far	425
Low	Close	1,009
Low	Far	1,236

In the sections below, we provide the results of modeling, model averaging, and occupancy estimation with inference to GYE for 2007. The models were applied to the 2007 catchment-level data for tiger salamanders, boreal chorus frogs, and Columbia spotted frogs. Data for boreal toads were considered too sparse for modeling.

Notations used below:

P or p=detection probability

(.)=constant, does not change during the analysis period or differ among strata

(t)=varies survey time, first or second survey

Psi or Ψ =occupancy

(hab)=the three habitat strata (high, medium, low)

(2hab)=habitat strata collapsed into high+medium and low

(distance)=the two access strata (close or ≤ 4 km from roads; far or > 4 km from roads)

(g)=groups, or the six combined strata (three habitat x two access)

AICc=Akaike's information criteria, with small-sample correction

Delta AICc=AICc differences, relative to the smallest AICc value in the set of models

AICc Weight=the relative likelihood of the model, given the data. These are normalized to sum to 1 and interpreted as probabilities.

#Par=number of parameters

10.1. Modeling Results, Goodness-of-Fit, Model Averaging, and Application of Weighted Averages to Obtain GYE Occupancy Estimates

10.1.1. Tiger Salamanders

A. Model rankings for the 2007 tiger salamander data. Parameter estimates from the four top-ranked models follow the model rankings.

Model	AICc	Δ AICc	AICc Weight	Model Likelihood	#Par	Deviance
{P(.)psi(2hab)}	60.662	0.00	0.26651	1.0000	3.00	53.834
{P(.)psi(hab)}	60.726	0.06	0.25806	0.9683	4.00	51.298
{P(.)psi(.)}	60.983	0.32	0.22694	0.8515	2.00	56.583
{P(t)psi(hab)}	62.474	1.81	0.10773	0.4042	5.00	50.251
{P(.)psi(distance)}	63.013	2.35	0.08225	0.3086	3.00	56.186
{P(t)psi(distance)}	64.568	3.91	0.03781	0.1419	4.00	55.139
{P(.)psi(2hab2dist)}	65.864	5.20	0.01978	0.0742	5.00	53.641
{P(t)psi(g)}	71.981	11.32	0.00093	0.0035	8.00	49.981

Real Function Parameters of {P(.)psi(2hab)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.7142857	0.1369021	0.4016686	0.9030076
2:Psi	0.3379310	0.0978744	0.1780012	0.5460920
3:Psi	0.2700260E-14	0.3834242E-07	-0.7515115E-07	0.7515115E-07

Real Function Parameters of {P(.)psi(hab)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.7142857	0.1369021	0.4016686	0.9030076
2:Psi	0.5025641	0.1565226	0.2284802	0.7751156
3:Psi	0.2041667	0.1076657	0.0654239	0.4845797
4:Psi	0.2517355E-14	0.3702107E-07	-0.7256130E-07	0.7256131E-07

Real Function Parameters of {P(.)psi(.)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.7142857	0.1369021	0.4016686	0.9030076
2:Psi	0.2969697	0.0881276	0.1558934	0.4913924

Real Function Parameters of {P(t)psi(hab)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.8333333	0.1521452	0.3687380	0.9771683
2:p	0.6250000	0.1711633	0.2848446	0.8745944
3:Psi	0.4923077	0.1519781	0.2274858	0.7615179
4:Psi	0.2000000	0.1051454	0.0645055	0.4754540
5:Psi	0.3046066E-15	0.1274586E-07	-0.2498188E-07	0.2498188E-07

B. Goodness of fit

Goodness-of-fit testing for the most general model indicated no evidence of lack of fit (observed deviance=49.81 at 75th percentile, average deviance=42.68: chat=1.17 or observed chat=3.12 vs. average chat=3.29).

C. Model averaged estimates of occupancy; tiger salamander 2007

Occupancy (Psi) High-Close Parameter 13

Model	Weight	Estimate	Standard Error
{P(.)psi(2hab)}	0.26651	0.3379310	0.0978744
{P(.)psi(hab)}	0.25806	0.5025641	0.1565226
{P(.)psi(.)}	0.22694	0.2969697	0.0881276
{P(t)psi(hab)}	0.10773	0.4923077	0.1519781
{P(.)psi(distance)}	0.08225	0.3314010	0.1082191
{P(t)psi(distance)}	0.03781	0.3246377	0.1051618
{P(.)psi(2hab2dist)}	0.01978	0.3629630	0.1162016
{P(t)psi(g)}	0.00093	0.5333333	0.1732763
Weighted Average	0.3873879	0.1181845	Unconditional SE 0.1495225

95% CI for Wgt. Ave. Est. (logit trans.) is 0.1553551 to 0.6849451
Percent of Variation Attributable to Model Variation is 37.52%

Occupancy (Psi) High-Far Parameter 14

Model	Weight	Estimate	Standard Error
{P(.)psi(2hab)}	0.26651	0.3379310	0.0978744
{P(.)psi(hab)}	0.25806	0.5025641	0.1565226
{P(.)psi(.)}	0.22694	0.2969697	0.0881276
{P(t)psi(hab)}	0.10773	0.4923077	0.1519781
{P(.)psi(distance)}	0.08225	0.2177778	0.1389784
{P(t)psi(distance)}	0.03781	0.2133333	0.1358576
{P(.)psi(2hab2dist)}	0.01978	0.2722222	0.1683065
{P(t)psi(g)}	0.00093	0.3555555	0.2915170
Weighted Average	0.3718750	0.1230151	Unconditional SE 0.1634075

95% CI for Wgt. Ave. Est. (logit trans.) is 0.1306378 to 0.6999308
Percent of Variation Attributable to Model Variation is 43.33%

Occupancy (Psi) Med-Close Parameter 15

Model	Weight	Estimate	Standard Error
{P(.)psi(2hab)}	0.26651	0.3379310	0.0978744
{P(.)psi(hab)}	0.25806	0.2041667	0.1076657
{P(.)psi(.)}	0.22694	0.2969697	0.0881276
{P(t)psi(hab)}	0.10773	0.2000000	0.1051454
{P(.)psi(distance)}	0.08225	0.3314010	0.1082191
{P(t)psi(distance)}	0.03781	0.3246377	0.1051618
{P(.)psi(2hab2dist)}	0.01978	0.3629630	0.1162016
{P(t)psi(g)}	0.00093	0.1939394	0.1248835
Weighted Average	0.2785789	0.1004864	Unconditional SE 0.1171652

95% CI for Wgt. Ave. Est. (logit trans.) is 0.1096635 to 0.5476400
Percent of Variation Attributable to Model Variation is 26.44%

Occupancy (Psi) Med-Far Parameter 16

Model	Weight	Estimate	Standard Error
{P(.)psi(2hab)}	0.26651	0.3379310	0.0978744
{P(.)psi(hab)}	0.25806	0.2041667	0.1076657
{P(.)psi(.)}	0.22694	0.2969697	0.0881276
{P(t)psi(hab)}	0.10773	0.2000000	0.1051454
{P(.)psi(distance)}	0.08225	0.2177778	0.1389784
{P(t)psi(distance)}	0.03781	0.2133333	0.1358576
{P(.)psi(2hab2dist)}	0.01978	0.2722222	0.1683065
{P(t)psi(g)}	0.00093	0.2133333	0.1914725
Weighted Average	0.2632491	0.1052691	Unconditional SE 0.1213387

95% CI for Wgt. Ave. Est. (logit trans.) is 0.0948875 to 0.5491084
Percent of Variation Attributable to Model Variation is 24.73%

Occupancy (Psi) Low-Close Parameter 17

Model	Weight	Estimate	Standard Error
{P(.)psi(2hab)}	0.26651	0.0000000	0.0000000
{P(.)psi(hab)}	0.25806	0.0000000	0.0000000
{P(.)psi(.)}	0.22694	0.2969697	0.0881276
{P(t)psi(hab)}	0.10773	0.0000000	0.0000000
{P(.)psi(distance)}	0.08225	0.3314010	0.1082191
{P(t)psi(distance)}	0.03781	0.3246377	0.1051618
{P(.)psi(2hab2dist)}	0.01978	0.0000000	0.0000000
{P(t)psi(g)}	0.00093	0.0000000	0.0000000
Weighted Average	0.1069241	0.0328761	Unconditional SE 0.1213387

95% CI for Wgt. Ave. Est. (logit trans.) is 0.0047204 to 0.7513893
Percent of Variation Attributable to Model Variation is 95.63%

Occupancy (Psi) Low-Far Parameter 18

Model	Weight	Estimate	Standard Error
{P(.)psi(2hab)}	0.26651	0.0000000	0.0000000
{P(.)psi(hab)}	0.25806	0.0000000	0.0000000
{P(.)psi(.)}	0.22694	0.2969697	0.0881276
{P(t)psi(hab)}	0.10773	0.0000000	0.0000000
{P(.)psi(distance)}	0.08225	0.2177778	0.1389784
{P(t)psi(distance)}	0.03781	0.2133333	0.1358576
{P(.)psi(2hab2dist)}	0.01978	0.0000000	0.0000000
{P(t)psi(g)}	0.00093	0.0000000	0.0000000
Weighted Average	0.0933709	0.0365665	Unconditional SE 0.1447968

95% CI for Wgt. Ave. Est. (logit trans.) is 0.0035911 to 0.7463776
Percent of Variation Attributable to Model Variation is 93.62%

D. Application of weighted averages to compute estimated occupancy for tiger salamanders in GYE

There are five models that have some support ($\Delta AIC < 3$). Model averaged estimates of occupancy (see above) for the six habitat-access strata arranged from high quality-close access to low quality-far access are 0.3873879 (SE=0.1495225), 0.3718750 (SE=0.1634075), 0.2785789 (SE=0.1171652), 0.2632491 (SE=0.1213387), 0.1069241 (SE=0.1572971), and 0.0933709 (SE=0.1447968).

Estimated occupancy for GYE is

$$\hat{\psi} = 0.387(92/3370) + 0.372(43/3370) + 0.279(565/3370) + 0.263(425/3370) + 0.107(1009/3370) + 0.093(1236/3370) = 0.161 \quad (SE = 0.075)$$

This estimate differs from that assuming the 3rd ranked model is correct, in which occupancy is assumed to be constant (and estimated as 0.297). Model averaging allows one to incorporate the model uncertainty into the estimation process as well as providing unconditional variance estimation.

10.1.2. Boreal Chorus Frog

A. Model rankings for the 2007 boreal chorus frog data. Parameter estimates from the six top-ranked models follow the model rankings.

Model	AIC	ΔAIC_c	AICc Weight	Model Likelihood	#Par	Deviance
{p(.)psi(.)}	58.609	0.00	0.26467	1.0000	2.00	54.209
{p(.)psi(2habonly)}	59.044	0.44	0.21292	0.8045	3.00	52.216
{p(t)psi(.)}	59.650	1.04	0.15725	0.5941	3.00	52.823
{p(t)psi(2hab)}	60.259	1.65	0.11600	0.4383	4.00	50.830
{p(.)psi(habitat)}	60.968	2.36	0.08134	0.3073	4.00	51.540
{p(.)psi(distance)}	61.002	2.39	0.08000	0.3023	3.00	54.174
{p(t)psi(distance)}	62.217	3.61	0.04358	0.1647	4.00	52.788
{p(t)psi(hab)}	62.376	3.77	0.04024	0.1520	5.00	50.154
{p(.)psi(g)}	67.581	8.97	0.00298	0.0113	7.00	49.101
{p(t)psi(g)}	69.715	11.11	0.00103	0.0039	8.00	47.715

Real Function Parameters of {p(.)psi(.)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.9729730	0.0270172	0.8277566	0.9963056
2:Psi	0.5761785	0.0861010	0.4051702	0.7307002

Real Function Parameters of {p(.)psi(2habonly)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.9729730	0.0270172	0.8277566	0.9963056
2:Psi	0.6211434	0.0901727	0.4361903	0.7765106
3:Psi	0.2501827	0.2166649	0.0335236	0.7624448

Real Function Parameters of {p(t)psi(.)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.9473684	0.0512278	0.7061303	0.9926383
2:p	1.0000000	0.3512237E-08	1.0000000	1.0000000
3:Psi	0.5757576	0.0860340	0.4049280	0.7302194

Real Function Parameters of {p(t)psi(hab2g)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.9473684	0.0512278	0.7061303	0.9926383
2:p	1.0000000	0.0000000	1.0000000	1.0000000
3:Psi	0.6206897	0.0901022	0.4359466	0.7760132
4:Psi	0.2500000	0.2165064	0.0335101	0.7621677

Real Function Parameters of {p(.)psi(habitat)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.9729730	0.0270172	0.8277566	0.9963056
2:Psi	0.5388551	0.1383675	0.2817784	0.7768020
3:Psi	0.6880026	0.1159672	0.4333759	0.8640902
4:Psi	0.2501827	0.2166649	0.0335236	0.7624447

Real Function Parameters of {p(.)psi(distance)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	0.9729730	0.0270172	0.8277566	0.9963056
2:Psi	0.5656306	0.1034454	0.3632735	0.7482453
3:Psi	0.6004386	0.1550351	0.2974876	0.8420920

B. Goodness of fit

Goodness-of-fit testing for the most general model indicated no evidence of lack of fit (observed deviance=47.695 at 80th percentile, average deviance=40.94: chat=1.16 or observed chat=4.77 vs. average chat=5.89).

C. Model averaged estimates of occupancy; boreal chorus frog 2007

Occupancy (Psi) High-Close Parameter 13

Model	Weight	Estimate	Standard Error
{p(.)psi(.)}	0.26467	0.5761785	0.0861010
{p(.)psi(hab2g)}	0.21292	0.6211434	0.0901727
{p(t)psi(.)}	0.15725	0.5757576	0.0860340
{p(t)psi(hab2g)}	0.11600	0.6206897	0.0901022
{p(.)psi(habitat)}	0.08134	0.5388551	0.1383675
{p(.)psi(distance)}	0.08000	0.5656306	0.1034454
{p(t)psi(distance)}	0.04358	0.5652174	0.1033665
{p(t)psi(hab)}	0.04024	0.5384615	0.1382642
{p(.)psi(g)}	0.00298	0.5003655	0.1582311
{p(t)psi(g)}	0.00103	0.5000000	0.1581139
Weighted Average	0.5846699	0.0962011	Unconditional SE 0.1017038

95% CI for Wgt. Ave. Est. (logit trans.) is 0.3825062 to 0.7618541
Percent of Variation Attributable to Model Variation is 10.53%

Occupancy (Psi) High-Far Parameter 14

Model	Weight	Estimate	Standard Error
{p(.)psi(.)}	0.26467	0.5761785	0.0861010
{p(.)psi(hab2g)}	0.21292	0.6211434	0.0901727
{p(t)psi(.)}	0.15725	0.5757576	0.0860340
{p(t)psi(hab2g)}	0.11600	0.6206897	0.0901022
{p(.)psi(habitat)}	0.08134	0.5388551	0.1383675
{p(.)psi(distance)}	0.08000	0.6004386	0.1550351
{p(t)psi(distance)}	0.04358	0.6000000	0.1549193
{p(t)psi(hab)}	0.04024	0.5384615	0.1382642
{p(.)psi(g)}	0.00298	0.6671540	0.2723662
{p(t)psi(g)}	0.00103	0.6666667	0.2721655
Weighted Average	0.5896385	0.1030321	Unconditional SE 0.1102096

95% CI for Wgt. Ave. Est. (logit trans.) is 0.3704550 to 0.7782000
Percent of Variation Attributable to Model Variation is 12.60%

Occupancy (Psi) Med-Close Parameter 15

Model	Weight	Estimate	Standard Error
{p(.)psi(.)}	0.26467	0.5761785	0.0861010
{p(.)psi(hab2g)}	0.21292	0.6211434	0.0901727
{p(t)psi(.)}	0.15725	0.5757576	0.0860340
{p(t)psi(hab2g)}	0.11600	0.6206897	0.0901022
{p(.)psi(habitat)}	0.08134	0.6880026	0.1159672
{p(.)psi(distance)}	0.08000	0.5656306	0.1034454
{p(t)psi(distance)}	0.04358	0.5652174	0.1033665
{p(t)psi(hab)}	0.04024	0.6875000	0.1158781
{p(.)psi(g)}	0.00298	0.6368288	0.1451497
{p(t)psi(g)}	0.00103	0.6363636	0.1450407
Weighted Average	0.6033466	0.0934257	Unconditional SE 0.1015199
95% CI for Wgt. Ave. Est. (logit trans.) is 0.3984308 to 0.7774497			
Percent of Variation Attributable to Model Variation is 15.31%			

Occupancy (Psi) Med-Far Parameter 16

Model	Weight	Estimate	Standard Error
{p(.)psi(.)}	0.26467	0.5761785	0.0861010
{p(.)psi(hab2g)}	0.21292	0.6211434	0.0901727
{p(t)psi(.)}	0.15725	0.5757576	0.0860340
{p(t)psi(hab2g)}	0.11600	0.6206897	0.0901022
{p(.)psi(habitat)}	0.08134	0.6880026	0.1159672
{p(.)psi(distance)}	0.08000	0.6004386	0.1550351
{p(t)psi(distance)}	0.04358	0.6000000	0.1549193
{p(t)psi(hab)}	0.04024	0.6875000	0.1158781
{p(.)psi(g)}	0.00298	0.8005848	0.1790200
{p(t)psi(g)}	0.00103	0.8000000	0.1788854
Weighted Average	0.6083031	0.0999351	Unconditional SE 0.1093067
95% CI for Wgt. Ave. Est. (logit trans.) is 0.3872311 to 0.7923807			
Percent of Variation Attributable to Model Variation is 16.41%			

Occupancy (Psi) Low-Close Parameter 17

Model	Weight	Estimate	Standard Error
{p(.)psi(.)}	0.26467	0.5761785	0.0861010
{p(.)psi(hab2g)}	0.21292	0.2501827	0.2166649
{p(t)psi(.)}	0.15725	0.5757576	0.0860340
{p(t)psi(hab2g)}	0.11600	0.2500000	0.2165064
{p(.)psi(habitat)}	0.08134	0.2501827	0.2166649
{p(.)psi(distance)}	0.08000	0.5656306	0.1034454
{p(t)psi(distance)}	0.04358	0.5652174	0.1033665
{p(t)psi(hab)}	0.04024	0.2500000	0.2165063
{p(.)psi(g)}	0.00298	0.5003655	0.3538126
{p(t)psi(g)}	0.00103	0.5000000	0.3535534
Weighted Average	0.4275957	0.1480978	Unconditional SE 0.2279085
95% CI for Wgt. Ave. Est. (logit trans.) is 0.1074803 to 0.8225041			
Percent of Variation Attributable to Model Variation is 57.77%			

Occupancy (Psi) Low-Far Parameter 18

Model	Weight	Estimate	Standard Error
{p(.)psi(.)}	0.26467	0.5761785	0.0861010
{p(.)psi(hab2g)}	0.21292	0.2501827	0.2166649
{p(t)psi(.)}	0.15725	0.5757576	0.0860340
{p(t)psi(hab2g)}	0.11600	0.2500000	0.2165064
{p(.)psi(habitat)}	0.08134	0.2501827	0.2166649
{p(.)psi(distance)}	0.08000	0.6004386	0.1550351
{p(t)psi(distance)}	0.04358	0.6000000	0.1549193
{p(t)psi(hab)}	0.04024	0.2500000	0.2165063
{p(.)psi(g)}	0.00298	0.0000000	0.0000000
{p(t)psi(g)}	0.00103	0.0000000	0.0000000
Weighted Average	0.4298911	0.1480978	Unconditional SE 0.2347971

95% CI for Wgt. Ave. Est. (logit trans.) is 0.1033983 to 0.8313790
Percent of Variation Attributable to Model Variation is 57.51%

D. Application of weighted averages to compute estimated occupancy for chorus frogs in GYE

The 2007 boreal chorus frog analysis resulted in a lack of strong support for any particular model. There are six models that have some support ($\Delta AIC < 3$). Model averaged estimates of occupancy (above) for the six habitat-access strata arranged from high quality-close access to low quality-far access are 0.5846699 (SE=0.1017038), 0.5896385 (SE=0.1102096), 0.6033466 (SE=0.1015199), 0.6083031 (SE=0.1093067), 0.4275957 (SE=0.2279085), and 0.4298911 (SE=0.2347971).

Estimated occupancy for GYE is:

$$\hat{\psi} = 0.585(92/3370) + 0.590(43/3370) + 0.603(565/3370) + 0.608(425/3370) + 0.427(1009/3370) + 0.430(1236/3370) = 0.487 \quad (SE = 0.112)$$

This estimate differs from that assuming the 1st ranked model is correct, in which occupancy is assumed to be constant (and estimated as 0.576). Model averaging allows one to incorporate the model uncertainty into the estimation process as well as providing unconditional variance estimation.

10.1.3. Columbia Spotted Frogs

A. Model rankings for the 2007 Columbia spotted frog data. Parameter estimates from the two top-ranked models follow the model rankings.

Model	AIC	ΔAIC_c	AICc Weight	Model Likelihood	#Par	Deviance
{p(.)psi(2hab)}	42.751	0.00	0.63080	1.0000	3.0000	35.924
{p(.)psi(hab)}	44.644	1.89	0.24487	0.3882	4.0000	35.215
{p(t)psi(hab)}	47.438	4.69	0.06058	0.0960	5.0000	35.215
{p(.)psi(.)}	48.652	5.90	0.03301	0.0523	2.0000	44.252
{p(.)psi(distance)}	50.411	7.66	0.01370	0.0217	3.0000	43.583
{p(t)psi(.)}	51.079	8.33	0.00981	0.0156	3.0000	44.252
{p(t)psi(distance)}	53.012	10.26	0.00373	0.0059	4.0000	43.583
{p(.)psi(g)}	53.458	10.71	0.00299	0.0047	7.0000	34.978
{p(t)psi(g)}	56.978	14.23	0.00051	0.0008	8.0000	34.978

Real Function Parameters of {p(.)psi(2hab)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	1.0000000	0.2356080E-08	1.0000000	1.0000000
2:Psi	0.6896552	0.0859091	0.5029475	0.8299433
3:Psi	0.4088797E-15	0.1429825E-07	-0.2802456E-07	0.2802456E-07

Real Function Parameters of {p(.)psi(hab)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:p	1.0000000	0.0000000	1.0000000	1.0000000
2:Psi	0.7692308	0.1168545	0.4784491	0.9237344
3:Psi	0.6250000	0.1210307	0.3772319	0.8209747
4:Psi	0.2753602E-15	0.1173372E-07	-0.2299809E-07	0.2299809E-07

P(t) models estimated both P at 1.0 so did not include.

B. Goodness of fit

Goodness-of-fit testing for the most general model indicated no evidence of lack of fit (observed deviance=34.97 at 75th percentile, average deviance=30.24: chat=1.16 or observed chat=8.74 vs. average chat=7.56).

C. Model averaged estimates of occupancy; Columbia spotted frog 2007

Only two models are reasonably well supported. In this case, the top model was selected given its substantial support, and similarity to the second-ranked model. A model-averaged estimate of occupancy would have produced an estimate similar to the top model (psi=0.69)

D. Application of weighted averages to compute estimated occupancy for Columbia spotted frogs in GYE

$$\hat{\psi} = 0.689(1125/3370) + 0.0(2245/3370) = 0.230$$

$$\text{With estimated variance} = \hat{V}ar(\hat{\psi}) = \left(\frac{1125}{3370}\right)^2 \left(\frac{1125-29}{1125}\right) 0.086^2 + \left(\frac{2245}{3370}\right)^2 \left(\frac{2245-4}{2245}\right) 0.00^2 = 0.0008030 \text{ (SE= 0.028)}$$

Note the difference in this estimate as compared to the estimated occupancy of 0.606 with estimated SE=0.085 when assuming occupancy is constant among habitat types. In cases where stratum-specific estimates are strongly supported, these differences will occur and are significant. Note the improvement in precision in this case as well, with the habitat-specific model. Estimates reported in the 2006 annual report assume no differences among strata. These estimates might be biased toward the high- and/or medium-quality strata unless the constant occupancy model is strongly supported.

11. Appendix D. Multi-season Analysis for Tiger Salamanders (2006-2007)

This appendix summarizes multi-season survey data to model occupancy of barred tiger salamanders in GRTE and YELL. Specifically, we describe habitat-specific occupancy (three-levels (high, medium, and low quality) indicated by habitat (hab)), or two levels (high+medium and low quality) indicated by (hab2), and time (t) and/or year (2006 and 2007) differences in capture probability. Parameter estimates from the five top-ranked models are included after the initial model rankings.

Model	AIC	ΔAIC_c	AICc Weight	Model Likelihood	#Par	Deviance
{psi(hab2)eps(.)Gamma(.)p(t)}	101.967	0.00	0.19387	1.0000	6.0000	88.519
{psi(hab2)eps(.)Gamma(.)p(.)}	102.398	0.43	0.15626	0.8060	5.0000	91.381
{psi(.)eps(.)Gamma(.)p(t)}	102.453	0.49	0.15202	0.7841	5.0000	91.436
{psi(.)eps(.)Gamma(.)p(.)}	103.014	1.05	0.11485	0.5924	4.0000	94.348
{psi(hab2)eps(hab2)Gamma(hab2)p(t)}	103.771	1.80	0.07868	0.4058	7.0000	87.806
{psi(hab)eps(.)Gamma(.)p(t)}	104.008	2.04	0.06987	0.3604	7.0000	88.043
{psi(hab2)eps(hab2)Gamma(hab2)p(.)}	104.165	2.20	0.06460	0.3332	6.0000	90.717
{psi(.)eps(.)Gamma(.)p(year)}	104.350	2.38	0.05889	0.3038	5.0000	93.333
{psi(.)eps(.)Gamma(.)p(t*year)}	105.479	3.51	0.03349	0.1727	7.0000	89.514
{psi(hab2)eps(hab2)Gamma(hab2)p(year)}	105.667	3.70	0.03048	0.1572	7.0000	89.702
{psi(hab2)eps(hab2)Gamma(hab2)p(t*year)}	107.156	5.19	0.01448	0.0747	9.0000	85.883
{psi(hab)eps(hab)Gamma(hab)p(t)}	107.192	5.23	0.01422	0.0733	10.000	83.118
{psi(hab)eps(hab)Gamma(hab)p(.)}	107.471	5.50	0.01237	0.0638	9.0000	86.198
{psi(hab)eps(hab)Gamma(hab)p(year)}	109.589	7.62	0.00429	0.0221	10.000	85.515
{psi(hab)eps(hab)Gamma(hab)p(t*year)}	111.521	9.55	0.00163	0.0084	12.000	81.521

Real Function Parameters of {psi(hab2)eps(.)Gamma(.)p(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:Psi	0.3048630	0.0860502	0.1651913	0.4929020
2:Psi	0.1274480E-15	0.7569682E-08	-0.1483658E-07	0.1483658E-07
3:Epsilon	0.2198283	0.1499651	0.0483139	0.6099688
4:Gamma	0.0788672	0.0592236	0.0170287	0.2973390
5:p Session 1	0.9207282	0.0761952	0.6001650	0.9889958
6:p Session 1	0.7040862	0.1112100	0.4552816	0.8713579

Real Function Parameters of {psi(hab2)eps(.)Gamma(.)p(.)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:Psi	0.3114627	0.0883164	0.1679177	0.5034694
2:Psi	0.2286853E-15	0.1016550E-07	-0.1992437E-07	0.1992437E-07
3:Epsilon	0.2044109	0.1537173	0.0387327	0.6209699
4:Gamma	0.0743046	0.0613743	0.0137720	0.3157230
5:p Session 1	0.7962733	0.0823212	0.5911066	0.9135509

Real Function Parameters of {psi(.)eps(.)Gamma(.)p(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:Psi	0.2657828	0.0770755	0.1430398	0.4397978
2:Epsilon	0.2341465	0.1548217	0.0532894	0.6241423
3:Gamma	0.0809668	0.0592599	0.0181602	0.2955934
4:p Session 1	0.9230769	0.0739053	0.6094198	0.9892808
5:p Session 1	0.7058824	0.1105102	0.4581430	0.8719999

Real Function Parameters of {psi(.)eps(.)Gamma(.)p(.)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:Psi	0.2705933	0.0786954	0.1451577	0.4476592
2:Epsilon	0.2202848	0.1585520	0.0442224	0.6330395
3:Gamma	0.0778336	0.0609974	0.0157068	0.3086425
4:p Session 1	0.8000000	0.8000000	0.6001990	0.9142207

Real Function Parameters of {psi(hab2)eps(hab2)Gamma(hab2)p(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:Psi	0.3037113	0.0855819	0.1648059	0.4908815
2:Psi	0.1038124E-16	0.2300616E-08	-0.4509207E-08	0.4509207E-08
3:Epsilon	0.2216904	0.1500664	0.0492420	0.6103604
4:Epsilon	0.5044337	0.0000000	0.5044337	0.5044337
5:Gamma	0.0966982	0.0702610	0.0216460	0.3412182
6:Gamma	0.4024830E-15	0.1434921E-07	-0.2812445E-07	0.2812445E-07
7:p Session 1	0.9230769	0.0739053	0.6094198	0.9892808
8:p Session 1	0.7058824	0.1105102	0.4581430	0.8719999

12. Appendix E. Estimating Occupancy in Large Landscapes

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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

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

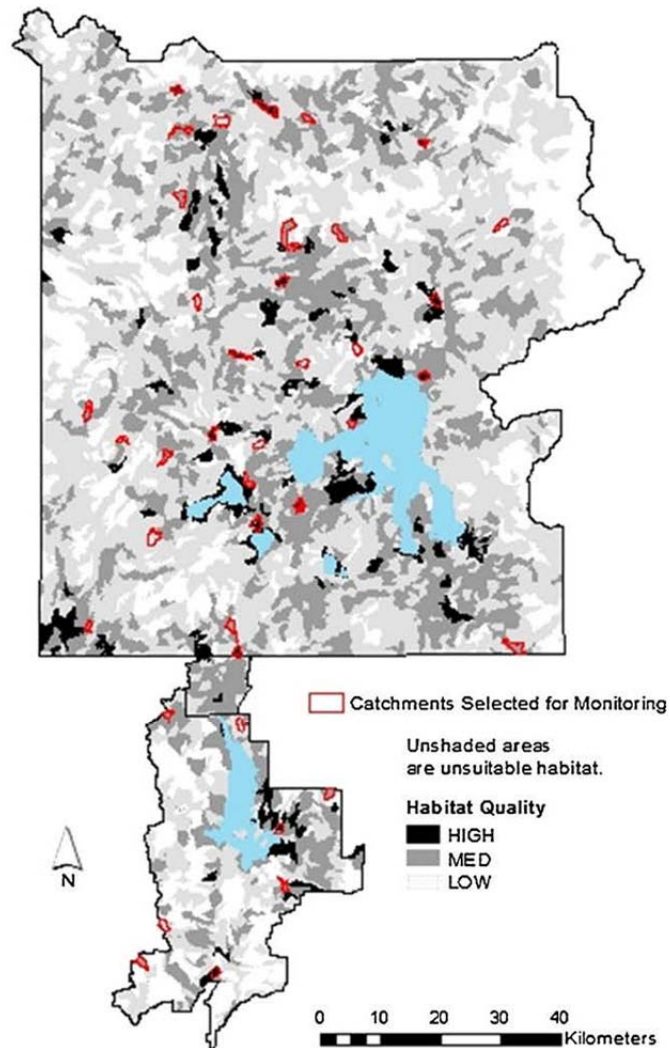
habitat quality (high, medium and low) from NWI definitions based on the amount and permanency of wetlands (Cowardin et al. 1979). High quality catchments were defined as those that contained large permanent/semi-permanent wetlands totaling >4 ha and seasonal wetlands totaling >2 ha. Medium quality catchments 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 ($\psi_1(g)$) and extinction and colonization rates were modeled most generally as stratum and year-specific $\varepsilon(g*yr)$ and $\gamma(g*yr)$. 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 ($\varepsilon(g)$ and $\gamma(g)$). We also considered models in which extinction and colonization rates were habitat-specific, $\varepsilon(hab)$ and $\gamma(hab)$, or access-specific $\varepsilon(dis)$ and $\gamma(dis)$. 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: $\bar{\psi} = \sum_{h=1}^L \frac{N_h}{N} \hat{\psi}_h$ 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 $V\hat{ar}(\bar{\psi}) = \sum_{h=1}^L \left(\frac{N_h}{N}\right)^2 \left(\frac{N_h - n_h}{N_h}\right) V\hat{ar}(\hat{\psi}_h)$ where n_h

represents the number of catchments sampled from stratum h and $V\hat{ar}(\hat{\psi}_h)$ 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 ($\hat{p} = 0.79$, $SE=0.07$). 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 ($\hat{\epsilon} = 0.184$; SE=0.107) was higher than estimated colonization rate ($\hat{\gamma} = 0.134$, 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 ($\hat{p} = 0.96$, 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 ($\hat{\gamma} = 31\%$, SE=9.2%, for high and medium quality sites; $\hat{\gamma} = 5.9\%$, SE=5.4% for low quality sites).

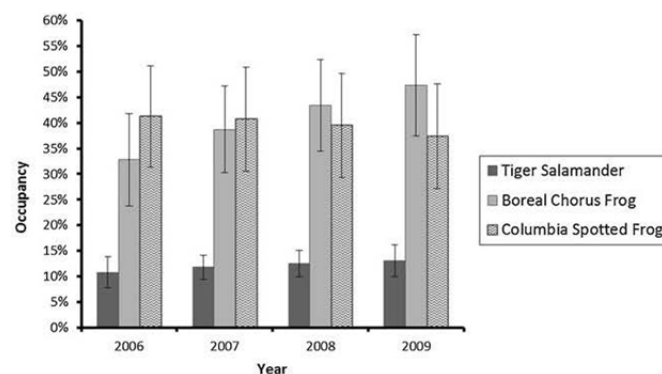
Models with covariates that received moderate support ($\Delta AIC_c < 4$) included one that demonstrated a positive relationship of initial occupancy with connectivity of sites within a catchment and one with a positive relationship with the number of sites in a catchment. Both of these results were 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 ($\hat{p} = 0.96$, 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 ($\pm$ SE) from the top ranked models for the tiger salamander, boreal chorus frog and Columbia spotted frog catchment-level data analysis



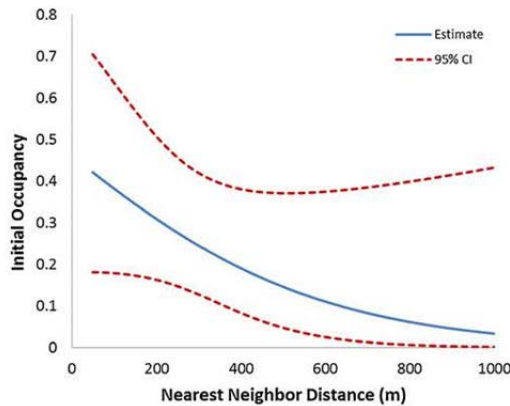


Fig. 3 Initial occupancy probability of tiger salamanders for catchments as related to average nearest neighbor distances (NN) within catchments

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 ($\bar{\psi} = 15.4\%$; $SE=3.8\%$) than for seasonal sites ($\bar{\psi} = 1.2\%$; $SE=0.8\%$) 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 ($SE \sim 0.03$). Estimated occupancy for

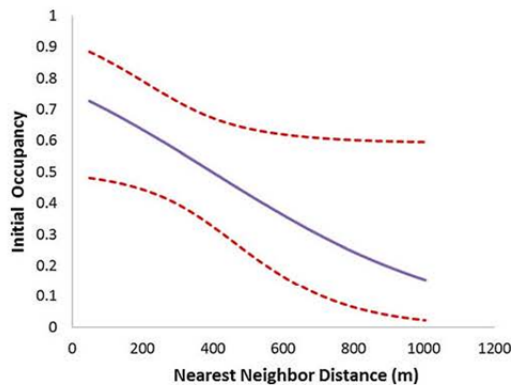


Fig. 4 Columbia-spotted frog initial occupancy of catchments as related to the average nearest neighbor distance among sites within catchments

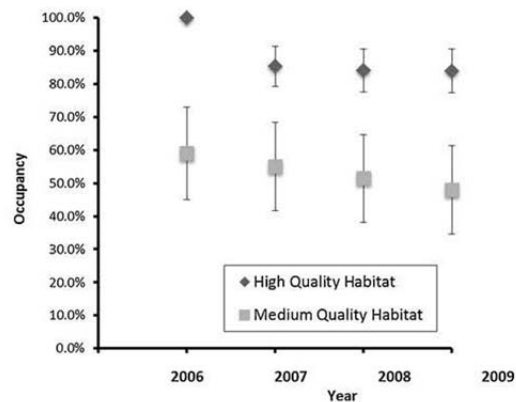


Fig. 5 Derived occupancy estimates ($\pm SE$) from the top ranked model $\{\psi(hab+NN) \varepsilon(hab) \gamma(hab) p(\cdot)\}$ for the Columbia spotted frog (2006–2009) catchment-level data analysis. Initial occupancy is estimated for the average nearest neighbor (NN) distance of wetland sites within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

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 ($\bar{p} = 0.84$ $SE=0.024$). Estimated

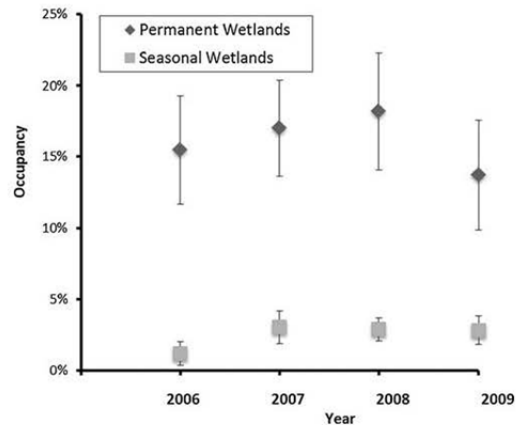


Fig. 6 Derived occupancy estimates ($\pm SE$) from the top ranked model $\{\psi(g*asd) \varepsilon(yr+shal) \gamma(yr+shal) p(t*yr+over)\}$ for tiger salamander (2006–2009) site-level data analysis. Estimated occupancy for the first year is presented for permanent and seasonal wetland types using the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

occupancy rates (2006–2009) were more than double for permanent ($\hat{\psi} = 34 - 29\%$; $SE=0.05$) than seasonal ($\hat{\psi} = 12 - 10\%$; $SE=0.02$) 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 inter-connectivity 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

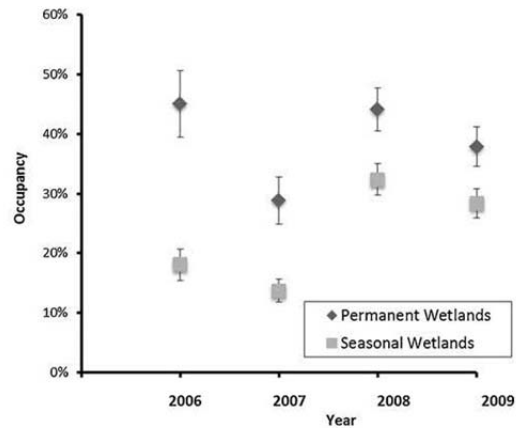


Fig. 8 Derived occupancy estimates ($\pm SE$) from the top ranked model $\{\psi(g+veg) \varepsilon(yr) \gamma(yr) p(yr)\}$ for the boreal chorus frog (2006–2009) site-level data analysis. Estimated occupancy for the first year is presented for permanent and seasonal wetland type using the average vegetation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

the number of seasonal wetlands that are dry each year), which may provide a window on climate change effects.

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.

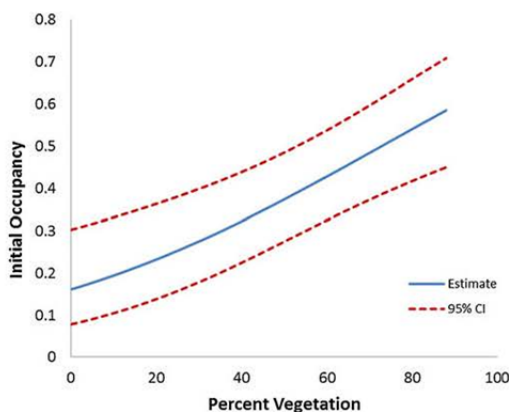


Fig. 7 Boreal chorus frog initial occupancy of permanent wetlands as related to vegetation cover at a site

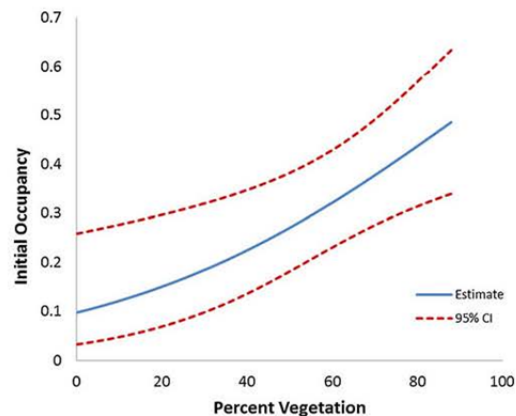


Fig. 9 Columbia-spotted frog initial occupancy of permanent wetlands as related to vegetation cover at a site

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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