

Multi-species amphibian monitoring across a protected landscape: Critical reflections on 15 years of wetland monitoring in Grand Teton and Yellowstone national parks

Andrew M. Ray^{a,*}, Blake R. Hossack^b, William R. Gould^c, Debra A. Patla^d, Stephen F. Spear^e, Robert W. Klaver^f, Paul E. Bartelt^g, David P. Thoma^a, Kristin L. Legg^a, Rob Daley^a, P. Stephen Corn^h, Charles R. Petersonⁱ

^a National Park Service, Greater Yellowstone Network, Bozeman, MT 59715, USA

^b U.S. Geological Survey, Northern Rocky Mountain Science Center and Wildlife Biology Program, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA

^c Applied Statistics Program, New Mexico State University, Box 30001/MS 3CQ, Las Cruces, NM 88003, USA

^d Northern Rockies Conservation Cooperative, P.O. Box 2705, Jackson, WY 83001, USA

^e U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI 54603, USA

^f U.S. Geological Survey, Coop Wildlife Research Unit, Iowa State University, Ames, IA 50011, USA

^g Department of Biology, Waldorf University, Forest City, IA 50436, USA

^h U.S. Geological Survey, Northern Rocky Mountain Science Center, Missoula, MT 59812, USA

ⁱ Department of Biological Sciences, Idaho State University, Pocatello, ID 83201, USA

ARTICLE INFO

Keywords:

Amphibian
Ecological monitoring
Greater Yellowstone Ecosystem
Long-term monitoring
Multi-species

ABSTRACT

Widespread amphibian declines were well documented at the end of the 20th century, raising concerns about the need to identify individual and interactive contributors to this global trend. At the same time, there was growing interest in the use of amphibians as ecological indicators. In the United States, wetland and amphibian monitoring programs were launched in some national parks as a necessary first step to evaluating the status and trends of amphibian populations within some of North America's most protected areas. In Grand Teton and Yellowstone national parks, a multi-species amphibian monitoring program was launched by many of the authors in 2006 and continues to this day. This Viewpoint Article serves as a self-evaluation of our journey from conception through implementation of an ongoing, long-term monitoring program. This self-evaluation should provide a framework and guidance for other monitoring programs. We address whether we are fulfilling the program's main objective of describing status and trends of the four amphibian species, discuss how a one-size-fits-all monitoring approach does not serve all species equally, and describe opportunities to bolster our core work using emerging statistical approaches and thoughtful integration of remote sensing and molecular tools. We also describe how the data generated over the program's first 15 years have been useful beyond our initial goal of characterizing status and trend. Notably, our integration of climate datasets has allowed us to describe wetland and species-specific amphibian responses to variations in climate drivers. Documenting climate links to amphibian occurrence and their primary habitats has allowed us to identify which species, habitat types, and subregions within this large, protected landscape are most vulnerable to anticipated climate change. Recognizing that tools and threats change over time, it will be important to adapt our original monitoring design to maximize opportunities and use of resulting information. Maintaining engagement by multiple stakeholders and expanding our funding portfolio will also be necessary to sustain our program into the future. Finally, collaboration has become standard for long-term, cross-jurisdictional, landscape-scale monitoring. We argue that collaborative monitoring facilitates resource sharing, leveraging of limited funds, completion of work, and mutual learning. Such collaboration also increases the efficacy of conservation.

* Corresponding author.

E-mail address: andrew_ray@nps.gov (A.M. Ray).

<https://doi.org/10.1016/j.ecolind.2021.108519>

Received 11 October 2021; Received in revised form 27 December 2021; Accepted 28 December 2021

Available online 5 January 2022

1470-160X/Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Global declines of amphibians were a well-documented phenomenon at the end of the 20th century (Wake, 1991, Green, 1997, Stuart et al., 2004). This multi-continental occurrence raised concerns about the lack of understanding of the individual and interactive drivers contributing to amphibian declines (Stuart et al., 2004). Despite uncertainty, the susceptibility of amphibians to multiple stressors (e.g., disease, introduced species, habitat alteration) and declines even on protected lands such as national parks and wilderness areas (Adams et al., 2013) generated concern that widespread declines may be foreshadowing a larger biodiversity crisis (Corn, 1994, Drost and Fellers, 1996, Knapp and Matthews, 2000). At the same time, the concept that amphibians provided gauges of ecosystem health was being promoted (Blaustein and Wake, 1990, Collins and Storer, 2003, Welsh and Ollivier, 1998).

In the United States (US), efforts to investigate and interpret amphibian declines were led by the US Geological Survey's (USGS) Amphibian Research and Monitoring Initiative (ARMI; Corn et al., 2005, Muths et al., 2005), a collaboration of government scientists from across the country. This endeavor dove-tailed with US National Park Service's (NPS) Vital Signs Monitoring Program—a program designed in the early 2000s to increase scientific information on the status or condition of a vital set of natural resources in support of science-informed management of national parks (Fancy et al., 2009, Rodhouse, et al., 2016). In total, ~50 national parks selected amphibians as indicators, which meant amphibians would be monitored consistently using standardized, peer-reviewed monitoring approaches. For each park, the sampling design and protocols for monitoring were developed through collaborative efforts that required engagement with relevant stakeholders.

Amphibians were selected as a Vital Sign to be monitored in Grand Teton (GTNP) and Yellowstone (YNP) national parks and a monitoring protocol was developed to make inference to wetlands in both parks (Bennetts et al., 2013, Gould et al., 2012). Inventories and pilot studies for multi-species amphibian monitoring in the two parks began in 2000, led initially by a collaboration of USGS and Idaho State University scientists who had been working with these parks through the 1990s on targeted amphibian surveys and associated research questions. The sampling design and survey approaches were formally implemented in 2006. The monitoring approach and protocols (see Bennetts et al., 2013) reflected efforts by USGS ARMI elsewhere in the US and by other national park-focused monitoring efforts (summarized in Halstead et al., this issue). The specific objectives were formulated to address key concerns and questions regarding widely reported amphibian declines (Corn et al., 2005, Muths et al., 2005) and to characterize the status and trends of four widespread species in GTNP and YNP (Table 1).

At the time of this writing, the monitoring effort in GTNP and YNP represents one of the longest running, multi-species amphibian monitoring programs in the entire US. The successful launching and implementation of the amphibian monitoring program in GTNP and YNP reflected significant commitment and strong collaborations among program architects (including several co-authors of this paper).

Table 1

The long-term amphibian monitoring program in Grand Teton and Yellowstone national parks specified the following objectives as part of the cooperative long-term monitoring protocol (see Bennetts et al., 2013).

Objective	Objective description
1	Estimate the proportion of catchments and wetland sites 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.
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.
3	For Western 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.

Sustaining this program will require continued support from committed stakeholders, deep connection to the original monitoring design, and preservation of institutional knowledge so that continued participation of original program designers is unnecessary (*sensu* Sergeant et al., 2012).

In this special issue of *Ecological Indicators*, we have a unique opportunity to reflect on the successes and challenges that have arisen during the conception and implementation of a long-term, multi-species monitoring program that covers a large geographic area. Through conception, pilot studies, and implementation (2000 to 2020), our understanding of the threats to amphibian populations (e.g., disease and climate change) has, unsurprisingly, grown. Management concerns and the information needed to conserve amphibians and their primary habitats (see Grant et al., 2019) have also changed and will continue to evolve during future years of monitoring.

We describe this amphibian monitoring program and offer reflections following 15 years of effort in GTNP and YNP, with an overarching objective of evaluating our approach given concerns and advances in the field of assessing ecological indicators. To that end, we address the following questions: 1) is the monitoring program fulfilling its main objective of describing status and trend of the four targeted species? (Objective 1, Table 1); 2) has the multi-scale approach to monitoring in GTNP and YNP increased our understanding of the dynamics of amphibian populations and habitats?; 3) was the original focus on status and trends too narrow in terms of what we have actually learned from the data?; 4) what new directions in monitoring are possible due to recent advances in analysis and technology?; 5) is monitoring being linked to conservation actions?; and 6) can we generalize or apply what we learned to benefit amphibian conservation in less protected portions of the Greater Yellowstone Ecosystem (GYE)? Ultimately, our goal is to benefit other long-term ecological monitoring programs by sharing this self-evaluation.

2. Amphibian monitoring in Grand Teton and Yellowstone national parks

Six native amphibian species have been documented across GTNP and YNP: Western Tiger Salamanders (*Ambystoma mavortium*), Western Toads (*Anaxyrus boreas*), Northern Leopard Frogs (*Lithobates pipiens*), Boreal Chorus Frogs (*Pseudacris maculata*), Columbia Spotted Frogs (*Rana luteiventris*), and Plains Spadefoots (*Spea bombifrons*) (Koch and Peterson 1995; Fig. 1). All these species rely on wetlands and ponds for breeding and larval development, making it possible to monitor the four widespread species with a single program. Limited species richness is characteristic of montane regions of northern latitudes globally, but also implies that the loss of one amphibian species represents a significant event.

The relative abundance and distribution of amphibian species varies across and within the two parks. Chorus frogs and spotted frogs are widespread and relatively common throughout both parks (Gould et al., 2019, Ray et al., 2016). Tiger salamanders are widespread but are not as common as the aforementioned species. Western Toads were previously regarded as common in this region (Carpenter, 1953), but occurrence is now patchy, and they are relatively rare at our long-term monitoring sites. Northern Leopard Frogs were well documented in GTNP in the 1950s, but now appear to be extirpated, with only one documented observation in GTNP (in 1995) since the early 1950s (Koch and Peterson, 1995). The Plains Spadefoot has a large distribution in western and central North America but was only recently confirmed and is known to inhabit a single location in YNP (Schneider et al. 2015). The loss of Northern Leopard Frogs and decline of Western Toads are surprising given that GTNP and YNP are large, relatively intact national parks that sit at the core of the GYE. The larger GYE is > 90,000 km² in size and two thirds of these lands (including both park units) are managed by federal agencies. Collectively, this region represents one of the largest protected areas in the conterminous 48 states (Hansen and Phillips, 2018).

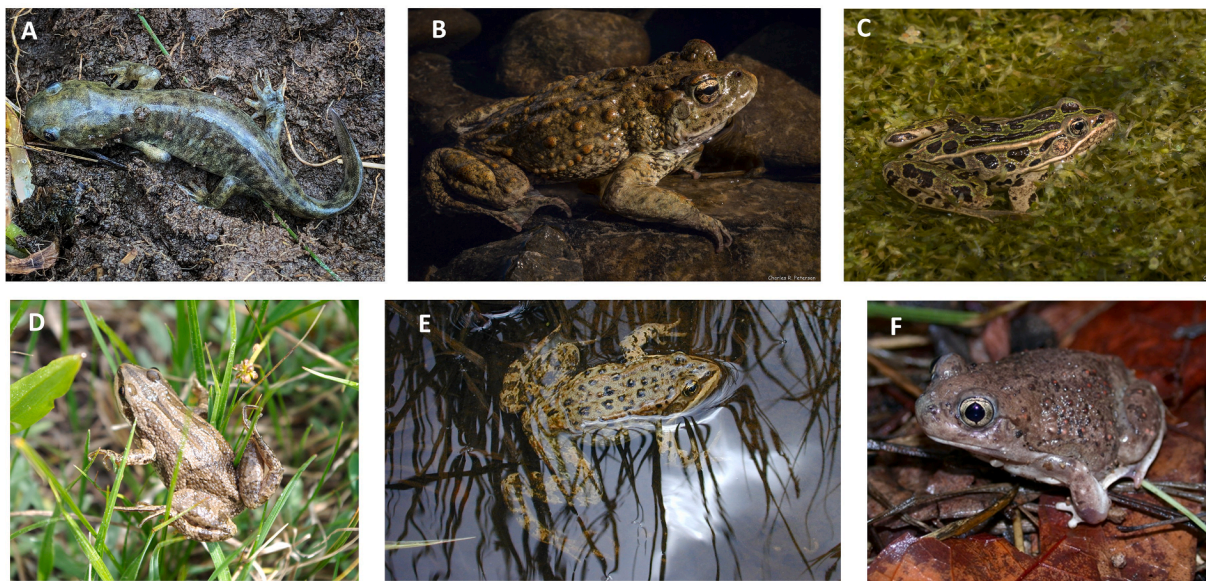


Fig. 1. Native amphibians of Yellowstone and Grand Teton National Parks: (A) Western Tiger Salamander (*Ambystoma mavortium*), (B) Western Toad (*Anaxyrus boreas*), (C) Northern Leopard Frog (*Lithobates pipiens*), (D) Boreal Chorus Frog (*Pseudacris maculata*), (E) Columbia Spotted Frog (*Rana luteiventris*), and (F) Plains Spadefoot (*Spea bombifrons*). Western Toad and Northern Leopard Frog photos by Chuck Peterson. Plains Spadefoot photo courtesy of J.D. Willson. All other photos are NPS photos.

The monitoring program was originally designed to make inference to the mapped wetland habitat present in National Wetland Inventories (see Cowardin et al., 1979) of GTNP, YNP, and the John D. Rockefeller Jr. Memorial Parkway. The John D. Rockefeller Jr. Memorial Parkway is between YNP to the north and GTNP to the south (Fig. 2). The Parkway includes a scenic highway and federally managed lands that are administered by GTNP. Hereafter, reference to GTNP refers to lands in GTNP and the adjacent John D. Rockefeller Jr. Memorial Parkway. The combined area of these adjacent national park units is $> 10,000 \text{ km}^2$ and includes some of the most topographically complex and climatologically heterogeneous protected areas in the conterminous U.S. (Tercek et al., 2012). Elevations range from 1600 m in the lowest portion of YNP to $> 4000 \text{ m}$ in the Teton Range. In conceiving the monitoring design, parks were envisioned as five hydrologic subbasins (Fig. 2); these subbasins generally represent major park drainages and differ with respect to geology, topography, elevation, climate patterns, and the existence or influence of large lakes or rivers. The GTNP subbasin was further divided into two approximately equal-sized zones, north and south, to guarantee that all sampling units were not confined to one part of GTNP. Within these subbasins, 3370 smaller watershed units (i.e., catchments), highly variable in size and averaging 200-ha, were used to define sampling unit boundaries. Catchment boundaries were established using 30 m digital elevation models and a minimum contributing area threshold of 22.5 ha (Bennetts et al., 2013); these boundaries have been respected since they were established in 2006. Although catchments contained differing numbers of, and types (e.g., permanent to ephemeral) of wetlands, they served as well-defined sampling units for selection (Corn et al., 2005). Sites — a wetland, pond, pool, or wet meadow that is capable of hosting amphibian reproduction (Gould et al., 2012) — were defined in the field by survey crews during initial visits. In contrast to catchments, the size and number of sites was expected to change from year to year depending on annual meteorological conditions.

Initially, 3370 catchments were stratified based on the type and amount of wetland contained therein (see Gould et al., 2012). In brief, catchments with higher amounts of permanent and semi-permanent wetlands were characterized as high quality ($n = 135$ catchments); three of which were randomly selected for monitoring from each subbasin. Medium quality catchments contained a lesser amount of permanent and semi-permanent wetlands ($n = 990$); another set of three

were randomly selected from each subbasin. Low quality catchments were overwhelmingly the most common in both parks ($n = 2245$) and contained limited amounts of permanent or seasonal wetlands; two were originally selected from each subbasin but these low quality catchments were later dropped due to a shortage of funding. In all monitored catchments, crews survey each wetland site each year when water is present.

The monitoring design used amphibian breeding occupancy, rather than occurrence of any life stage, as the index for statistical assessments of data collected. Breeding evidence was selected as our primary metric because it provided positive indication that a breeding population was present as opposed to individual adults with a possibly transitory or brief occurrence (Bennetts et al., 2013). Originally, 40 catchments were randomly selected, using stratifications, for inclusion in annual monitoring (see above). Since 2011, budget constraints restricted monitoring to high and medium quality catchments, confining inference to the most wetland-rich portions of the parks (Ray et al., 2016). On average, 31 catchments have been surveyed annually since 2011. The number of wetland sites surveyed varied each year (range: 246–326) due primarily to variation in the presence of surface water. Survey methods and site definition are described in more detail elsewhere (Gould et al., 2012). In brief, two observers survey each site independently on a single visit using visual observations and dip-netting to detect larvae, egg masses, or recent metamorphs as evidence of breeding. This approach allows us to account for imperfect detection and to provide statistically robust inference. While new sites were added when encountered, efforts were made (e.g., by providing site drawings and previous year photos for field crews) to retain initial site definitions and thus provide consistency.

3. One-size-fits-all approach does not work

While this amphibian monitoring program was designed to investigate the status and trends of multiple species in two contiguous NPS units, our data confirm that not all species are equally suited for a random or stratified random sampling. Results from the many years of monitoring in GTNP and YNP indicate that the program's main goal of assessing status and trends through occupancy estimation (Objective 1; Table 1) was feasibly implemented for three species (Boreal Chorus Frogs, Columbia Spotted Frogs, and Western Tiger Salamanders), but

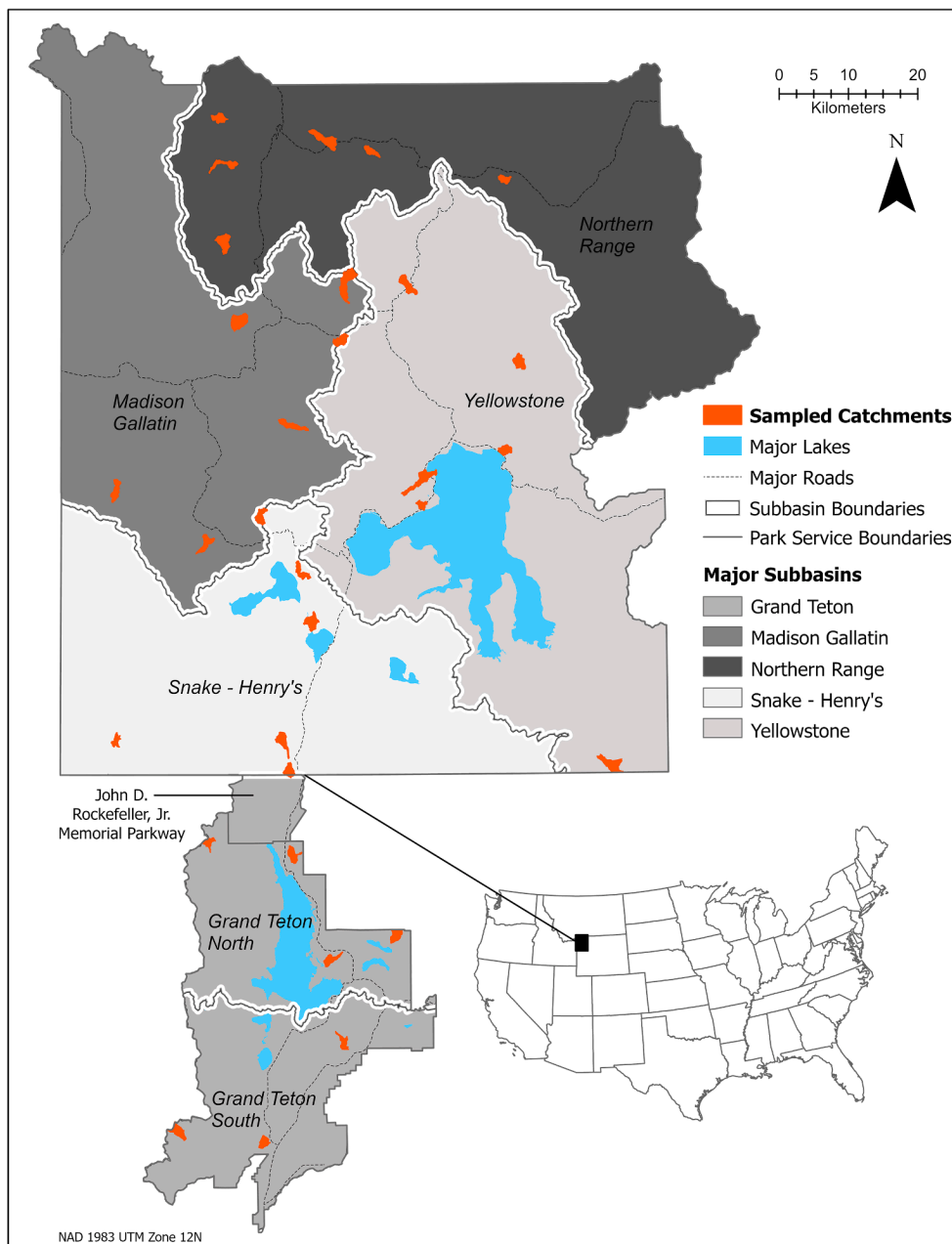


Fig. 2. Sample frame for Grand Teton (GTNP) and Yellowstone (YNP) national parks and John D. Rockefeller, Jr. Memorial Parkway (JDR) was initially divided into five subbasins. The GTNP subbasin which included JDR was further divided into north and south units. Catchments ($n = 31$) currently selected for long-term amphibian monitoring are shown in orange. All potential amphibian breeding sites within these 31 catchments are targeted annually: 24 catchments are located in YNP, and 7 are in GTNP. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

revealed that the proportion of catchments and sites occupied is restrictively small for Western Toads. Boreal Chorus Frogs and Columbia Spotted Frogs occur in most of the catchments (Fig. 3) and provide sufficient data for modeling breeding dynamics at the site level (Gould et al., 2019). Tiger salamanders, while widespread in our region, are most abundant in GTNP and YNP's Northern Range subbasin (Fig. 4). Data records in our program for salamanders are relatively few and erratic compared to chorus frogs and spotted frogs (e.g., only six breeding sites were detected in 2010; 29 breeding sites in 2014). Recent attempts to model salamander occupancy dynamics often resulted in estimation issues (Gould, 2020). To better meet Objective 1 (Table 1) for salamanders, additional catchments are needed, either in subbasins where they are most common (Fig. 4) or by including new catchments where salamanders are known to be present (see Klaver et al., 2013). A drawback to this latter approach (i.e., including locations of known breeding), is that it can limit our ability to make inference to the larger region.

Western Toads, one of the four species targeted by Objective 1, have been so rare within our sampling frame that we have been unable to use monitoring data in statistical models (Gould et al., 2012, 2019; Ray et al., 2016). Only 4 to 10 breeding sites have been detected per year. The rarity issue with toads was foreseen; Objective 3 (Table 1) directs monitoring this species annually in previously-identified breeding areas. Our efforts to implement the objective have mostly relied on opportunistic and volunteer efforts and have fallen short of our original goal for this species: some of the areas where toads were known to breed have not been surveyed for many years, and a subset that have been visited either no longer host toad populations or have been inadequately surveyed (Patla and Ray, 2020). Given the critically imperiled status of this species (NatureServe, 2021) in Wyoming (USA), the urgency to fully implement this objective increases as the baseline data age.

Finally, recent documentation of a population of Plains Spadefoot in YNP indicates this species is rare and its known occurrence is restricted to geothermally influenced wetlands in a single wet meadow of YNP

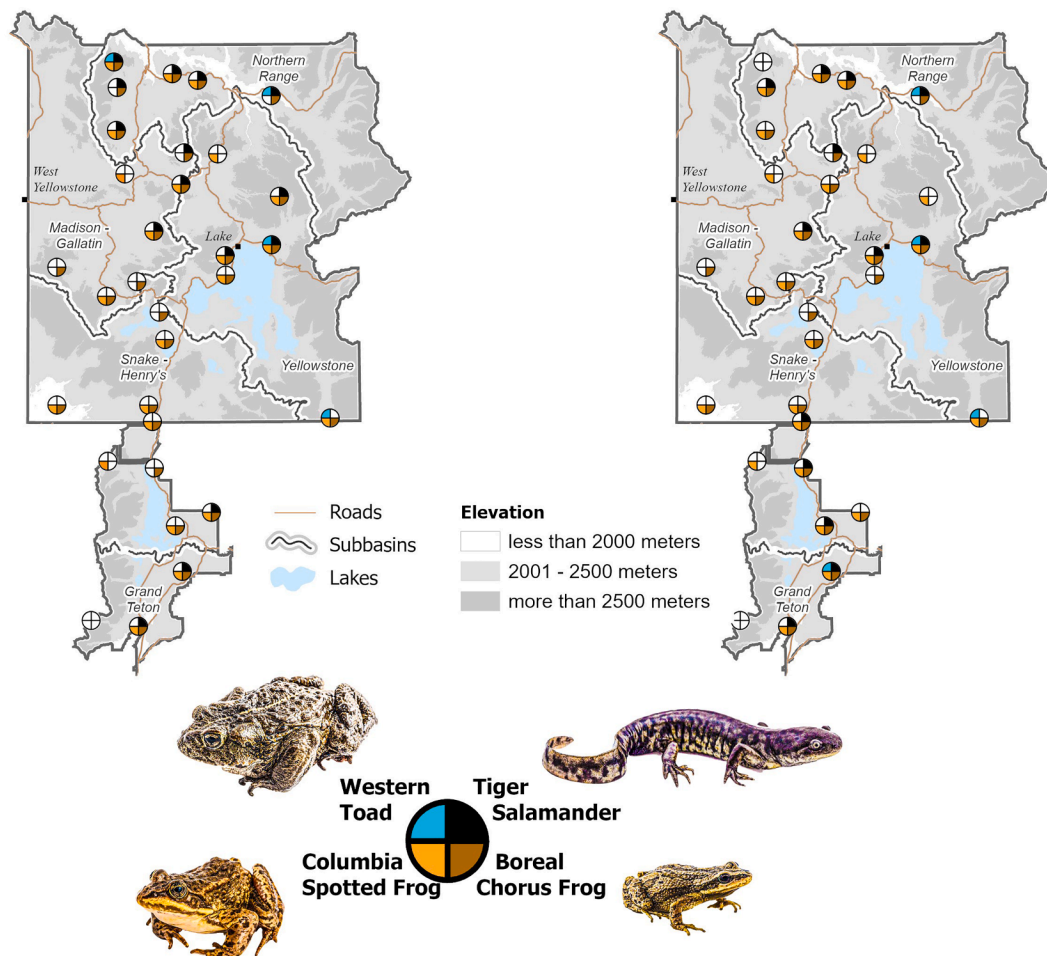


Fig. 3. An example of annual catchment-level summaries of amphibian species breeding detections from the long-term amphibian monitoring program in Grand Teton and Yellowstone national parks. The John D. Rockefeller, Jr. Memorial Parkway boundary is also shown between Grand Teton and Yellowstone national park (see Fig. 2 for further details). Two consecutive years (2017 and 2018) are shown to demonstrate the level of variation in species breeding detections within and among catchments that is common among years. Pies indicate the general location of catchments and show which amphibian species (zero to four species possible) were detected. Species color codes are shown in the legend. Elevation ranges are shown as light gray (<2000 m), medium gray (2000–2500 m), and dark gray (>2500 m). The six subbasins are separated with gray lines and indicated with labels (e.g., Northern Range).

(Schneider et al., 2015). This discovery warrants consideration of a new monitoring objective that investigates the status and trends of the spadefoot population and supports informed management of this species. Given the rareness of spadefoots, a metric other than occupancy is required—metrics that summarize abundance or key vital rates are better suited to characterize status and trends of a localized amphibian populations of high conservation interest (McCaffery et al., 2021).

4. Scale

When the original monitoring program was launched, the appropriate spatial scale for monitoring amphibian populations had not yet been clarified (e.g., Petranka et al. 2004) and not unexpectedly, much time and considerable angst were associated with planning this element of the sampling design. Since 2006, we have learned that monitoring site (or patch) occupancy across a large landscape (Howell et al., 2018) can shed important insight on occupancy dynamics at the site- and landscape-scale (Gould et al., 2019; Hossack et al., 2015; Ray et al., 2016). In a meta-analysis of 83 species and 61 study areas across North America, Grant et al. (2016) showed that amphibians respond to multiple, interacting stressors at the local (i.e., site) scale. Within climatologically and topographically heterogeneous landscapes like GTNP and YNP, there can be strong spatial autocorrelation in habitat conditions and climate exposure (e.g., temperatures, precipitation, snowmelt

runoff; e.g., Tercek et al., 2021a). Given this understanding and the need to implement a sampling design within a large landscape with challenging access, we have concluded that our use of a clustered design (sites clustered within catchments) allowed us to document amphibian use of habitat features and responses to stressors (i.e., variations in climate drivers) and to generalize those dynamic responses across management units (Hossack et al., 2015), particularly for more prevalent species (Gould et al., 2019). This approach provided an efficient strategy for maximizing the number of wetland sites surveyed each year. Not surprisingly, most analyses of the monitoring data to date have used clusters of sites as the basis for analyses (Gould et al., 2012, 2019; Hossack et al., 2015; Ray et al., 2016).

Sampling clusters of wetlands also acknowledged that amphibians could potentially shift breeding among sites depending on the flooding status of a site. While we cannot track individual movements without marking animals, we have since quantified breeding dynamics and persistence; breeding persistence at a site can be summarized as the conditional probability of breeding at sites in consecutive years given prior breeding occupancy. For chorus frogs, breeding persistence probability ranged from 80 to 96% between 2006 and 2015. For that same 10-year period, breeding persistence probability for spotted frogs ranged from 77 to 95% (Gould et al., 2019). Breeding persistence for both of these species and tiger salamanders was consistently high but also variable among years, and in the case of salamanders, among subbasins

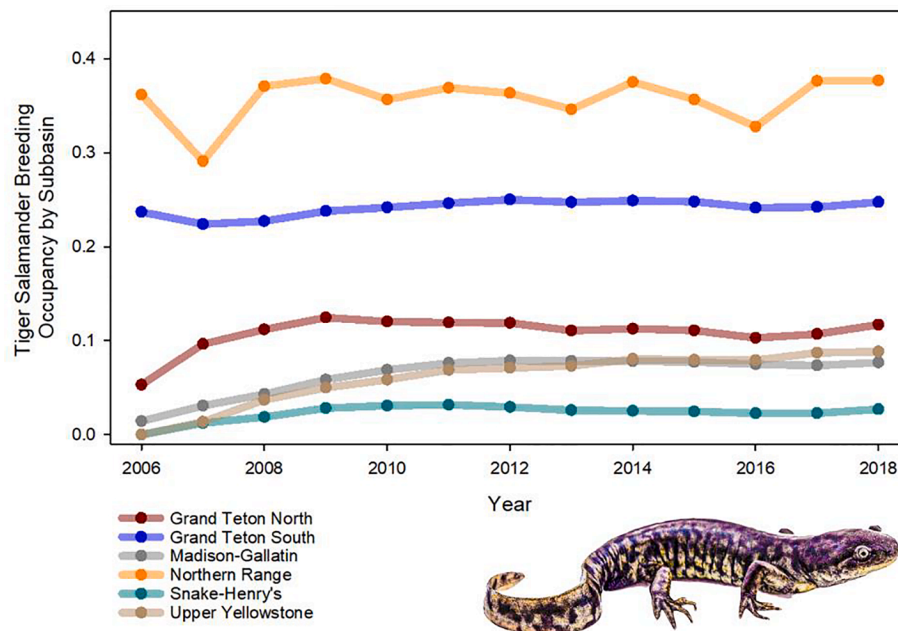


Fig. 4. Estimated salamander breeding occupancy based on site-level data and summarized by subbasin across Grand Teton and Yellowstone national parks. Subbasins are: Grand Teton North, Grand Teton South, Madison-Gallatin, Northern Range, Snake-Henry's Fork, and Upper Yellowstone (see Gould, 2020).

(Gould, 2020). Variation in breeding persistence among subbasins reflects differences in types and amount of availability of habitats, but also the subbasin-level variations in interannual drying (Fig. 5).

Tiger salamanders in the GTNP and YNP present a unique case study for examining the implications of spatial scale in status and trend analyses. From 2006 to 2018, salamander breeding site occupancy across GTNP and YNP ranged from 0.02 (SE = 0.01) in 2006 to a maximum of 0.14 (SE = 0.02) in 2014 (Fig. 6). When examined across the two parks, site colonization (current year breeding in a previously vacant or dry site) was negatively associated with runoff (Ray et al., 2016). Spatial variation, however, complicates interpretation from models of species dynamics, because the lower runoff regions of our sample frame (Northern Range and Grand Teton South subbasins; Fig. 7) also coincide with regions where salamander breeding occupancy is highest (Fig. 4) and where observations of colonization (i.e., breeding in previously dry sites) predominates. Essentially, because salamanders were more common in drier areas of these parks, we found an inverse relationship

between runoff and colonization. Hence, the negative association was valid across our sample frame but did not reflect that colonization actually occurred when site-specific runoff was higher (Fig. 8). The case study of salamanders demonstrates that the hierarchical framework of our sample design which attempts to make inference to the scale of two parks, and our pre-determined analytical approach must be carefully considered as it relates to species with a more clustered distribution and where climate drivers vary considerably across space.

5. Long-term data useful beyond status and trends

When the long-term amphibian monitoring program in GTNP and YNP was launched, much emphasis was placed on quantitatively characterizing current-year status and long-term trends for each species and describing wetland inundation patterns (Table 1). However, with the accumulation of annual data, interest grew in understanding patterns and drivers of interannual variability and linking amphibian breeding

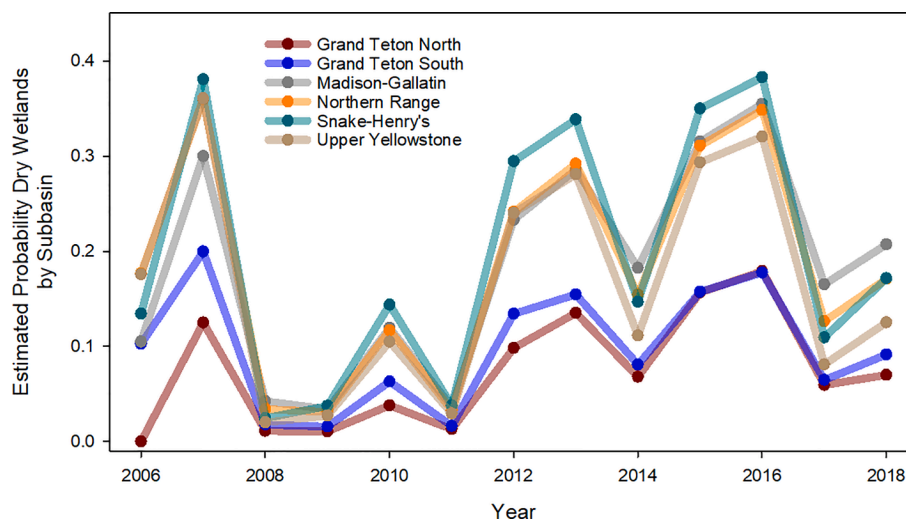


Fig. 5. Derived estimates of the proportion of dry wetlands by year for the period 2006 to 2018 and summarized by subbasins within Grand Teton and Yellowstone national parks (see Gould, 2020).

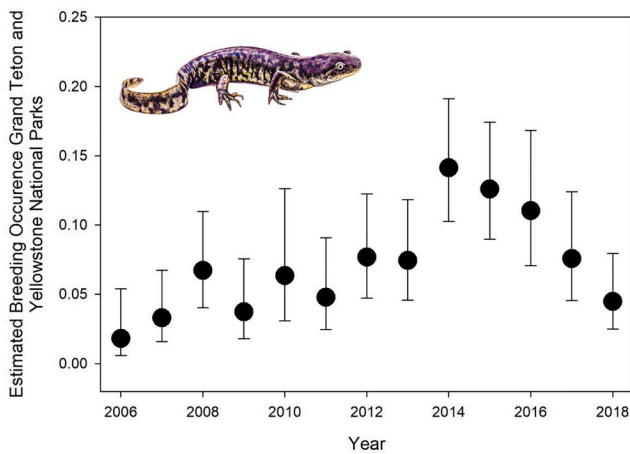


Fig. 6. Estimated site-based breeding occurrence (adjusted for detection) from a year-specific, multi-state model describing Western Tiger Salamander breeding dynamics. Error bars represent approximate 95% confidence intervals (see Gould, 2020).

occupancy and wetland drying (Fig. 8). These links further support strategies to characterize variations in indicator *sensitivity* or the degree to which indicators respond to environmental drivers (e.g., snowmelt runoff) among species and across landscapes (see Brice et al., this issue). As climate change amplifies stressors to NPS ecosystems, the value of long-term monitoring data will continue to grow as it enriches understanding of the causal factors underpinning short-term (e.g., year to year) and long-range dynamics of ecological indicators (Lindenmayer and Likens, 2010).

To provide an example of the annual variation that we have observed, we present a case study with the Boreal Chorus Frog. Chorus frogs are the most common amphibian species across GTNP and YNP. Chorus frog breeding occupancy varied year to year and ranged from 28 to 44% of monitored wetlands (Gould et al., 2019), and are present in most catchments (Fig. 9). Chorus frogs are notable among the species in this region for their widespread use of ephemeral and intermittent habitats (Bartelt et al., 2011). Given their use of ephemeral habitats, it is not surprising that occupancy patterns co-vary with wetland availability and reflect the increased availability of ephemeral wetland habitat in years with larger snowpacks (Fig. 9). Greater snowpack in a given year results in more runoff to fill shallow wetlands (Ray et al., 2019). Understanding these links provides opportunities to quantify the sensitivity

of chorus frog breeding, and wetlands, to variations in peak snowpack and provides the ability for near-term and longer-term forecasts of chorus frog occupancy based on snowpack estimates. This information could prove particularly useful for implementing conservation actions for presently common species like chorus frogs in a region predicted to have futures typified by reduced snowpacks (Tercek and Rodman, 2016).

6. Learn while doing

While flexibility is not necessarily a hallmark of all long-term monitoring programs, our experience highlights the importance of strategically building on the original objectives in a manner that follows a philosophy of learning while doing (*sensu* Lindenmayer and Likens, 2018). Even in relatively protected national park units, climate (Tercek et al., 2021b) and other major threats (disease, invasive species, anthropogenic stressors; Patla and Peterson, this issue as an example) are intensifying. Monitoring programs cannot sufficiently anticipate today the future intensification, interaction, or emergence of known and novel threats. Moreover, a narrowly-focused or inflexible approach to monitoring quickly limits a program's ability to adapt to changes and provide management relevant information that supports decisions. Therefore, we have generally followed the recommendations by Sergeant et al. (2012): prioritize the continuation of a core data set but adapt to emerging technological and analytical capabilities, unexpected threats or management needs, and promising collaborative opportunities to expand utility of monitoring.

6.1. Evolution of analytical approaches

Occupancy estimation is a standard method to assess status and trends of amphibians and other indicator species (MacKenzie et al., 2017). While early analyses focused on both site and catchment scales across GTNP and YNP (Gould et al., 2012), our recent work has focused largely on site-level estimates (Gould et al., 2019, Ray et al., 2016). In addition, the elimination of low-quality catchments from our annual visit schedule was based on funding but also on an acute awareness that the precision of catchment-level parameter estimates was limited by sample size ($n = 40$ pre-2011; $n = 31$ from 2011 to current). Additionally, we were concerned that catchment-level summaries were less sensitive in detecting declines because occupancy at the catchment level only requires detection of breeding at one wetland in a catchment.

Our original analyses relied on multi-season dynamic models that linked initial site occupancy with breeding extinction and colonization

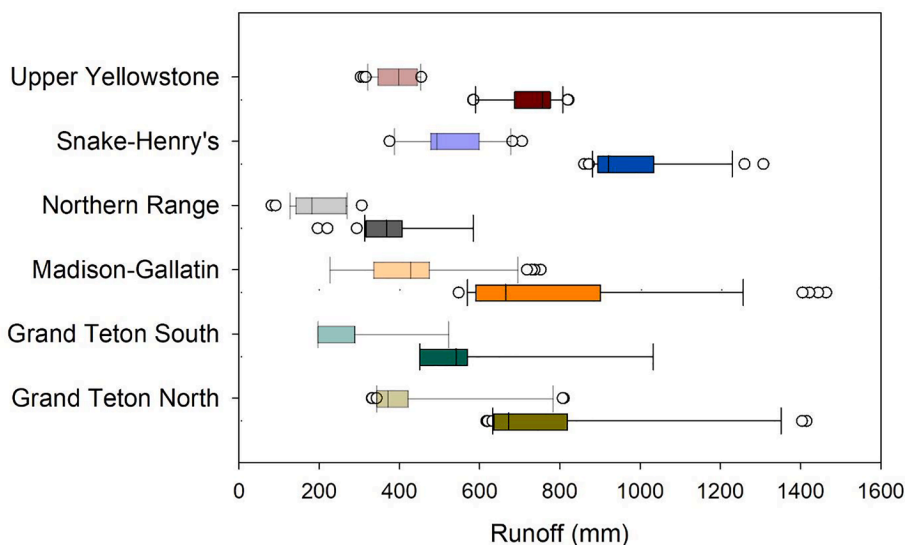


Fig. 7. Annual runoff summarized by subbasin for a dry (2007; upper, lighter bar of each pairing) and wet (2011; lower, darker bar of each pairing) year. Runoff is surplus water input after soil water-holding capacity is satisfied and includes downward infiltration plus lateral interflow and surface runoff (see Ray et al., 2016). Each box summarizes estimated annual runoff for all monitored wetlands within each subbasin and for years 2007 (low runoff year) and 2011 (high runoff year). The median of the data is shown by the interior vertical line and the interquartile range is shown by the box. Outliers are shown as hollow circles outside of the whiskers.

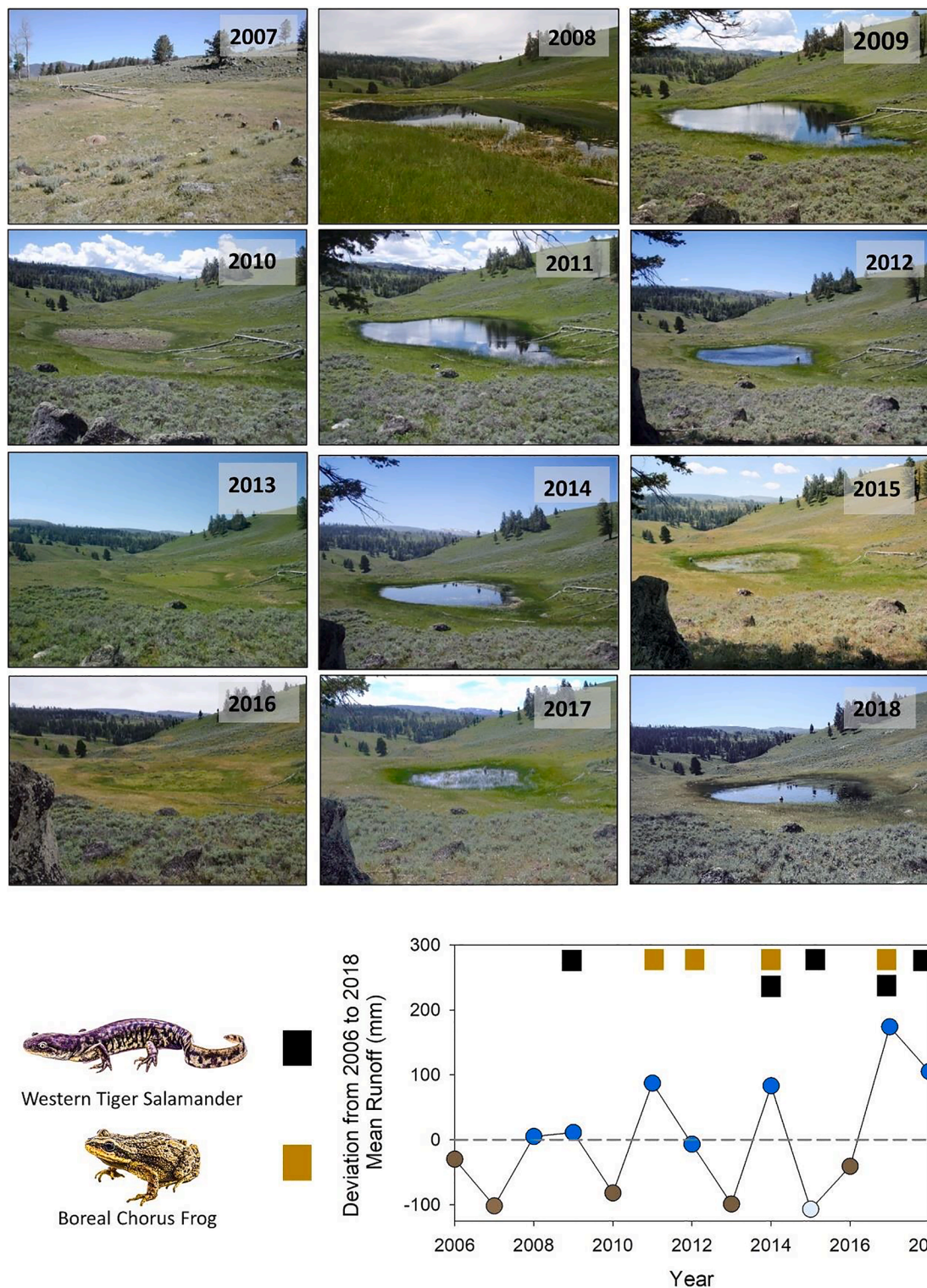


Fig. 8. Photographs taken during annual visits to an isolated wetland in Yellowstone National Park's Northern Range subbasin. This wetland was dry during early July sampling visits in 2006, 2007, 2010, 2013, and 2016. The deviation of annual runoff from the 2006 to 2018 average is shown in the lower right graph. Years in which crews observed dry conditions at this site are summarized with brown circles; blue circles indicate the presence of standing water (including in 2015 when runoff levels would have predicted dry conditions). The long-term mean runoff used to summarize annual deviation in runoff is represented with a dashed line. Species-specific breeding evidence during surveys are shown using colored squares: Western Tiger Salamanders (black) and Boreal Chorus Frogs (brown). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

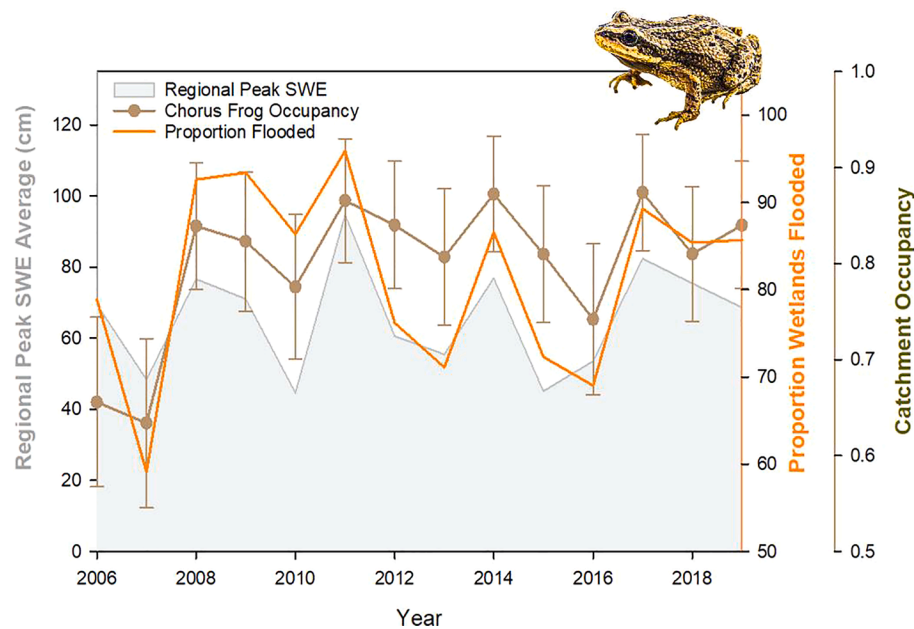


Fig. 9. Relationship between regional snowpacks (estimated as Snow Water Equivalent; SWE shown as grayed area), the proportion of sites inundated with water (orange line), and the proportion of monitored catchments with chorus frog breeding (brown line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

processes (Gould et al., 2012, Hossack et al., 2015). Categorical site covariates such as “permanent” or “seasonal” have been replaced with time varying covariates such as “maximum depth”. Breeding was modelled as a simple binary response where breeding was either detected or not—non-detects did not differentiate between flooded sites with no breeding and dry sites, which effectively reduced the estimated detection probability and introduced a positive bias in our occupancy estimates. Because amphibian breeding is conditional on the availability of suitable breeding habitat (wetlands with surface water), we recently adopted a multistate occupancy approach that jointly models wetland intermittency and amphibian breeding dynamics (Gould et al., 2019, MacKenzie et al., 2009) and simultaneously addresses two of our programmatic objectives (Objectives 1 and 2; Table 1). Our multi-state approach included the following states: 1) the wetland was dry (and thus no breeding with certainty), 2) the wetland contained water but was without breeding, and 3) the wetland contained standing water and supported amphibian breeding by the species under analysis. Our current analytical approach estimates year to year colonization transitions from previously dry and previously wet sites as well as breeding retention (the conditional probability of maintaining breeding given breeding in the prior year). Extinction probabilities are derived from breeding retention.

In addition to simultaneously meeting multiple objectives (Objective 1 and 2; Table 1), another advantage of our current multi-state modeling approach is that it produces less biased occupancy estimates. However, these models are notably parameter heavy or ‘data hungry’ and are best suited for species that are more prevalent and for monitoring programs with a large number of sites. For example, a recent effort was made to model Western Tiger Salamander dynamics, but the sparseness of detections prevented us from incorporating meaningful model complexity (i.e., year-specific breeding transitions). The evolution of analytical approaches continues; multi-species models (Devarajan et al., 2020) and dynamic extensions of N-mixture models (Rossman et al., 2016) offer promise in integrating count and detection data that have been collected by our program over years and in providing new dimensions to understanding amphibian occurrence.

Multi-species occupancy models also provide a strategy for modeling rare species and could potentially improve the precision of

parameter estimates of individual species. Oja et al. (2021) used a multi-species model in a Bayesian framework to generate occupancy estimates for Western Toads despite a scant number of observations. Multi-species models also accommodate documented biological interactions among species within a community (Devarajan et al., 2020) that may not be beneficial in our species-poor region but could be useful elsewhere. Finally, considering approaches that enable simultaneously evaluating changes in abundance at select sentinel sites as part of broad-scale monitoring program may be critical for understanding slowly unfolding declines (McCaffery et al., 2021). The former provides insight on trends within occupied sites and may offer clues on the cause of local change that may not be represented in more traditional multi-season occupancy summaries.

6.2. Environmental DNA

One methodological advancement that has occurred since the amphibian monitoring program began is the use of environmental DNA (Ficetola et al., 2008, Thomsen et al., 2012). Environmental DNA (eDNA) monitoring involves assessing sites for the presence of DNA of target species as evidence for species presence. Results from eDNA surveys may increase or better estimate detection of target species compared to visual search or other field methods (Fediajevaite et al., 2021, Smith and Goldberg, 2020). The caveat with using eDNA to increase detection is the resulting data are not directly comparable because eDNA cannot distinguish the presence of adults or transitory individuals from breeding presence (the index for amphibian status and trends summaries in GTNP and YNP). This concern could be alleviated by sampling for eDNA after adults have left the breeding site, although this would still be problematic for species such as Columbia Spotted Frogs that move among wetland sites across the active season.

Given the uncertainty with respect to breeding, inclusion of eDNA may be most useful by adding complementary data to the amphibian monitoring program. For instance, eDNA sampling can increase the number of sites surveyed as water collection takes less time than two independent observer visual surveys at a site. An increase in sampling efficiency (i.e., more sites and greater detection capabilities) could especially benefit monitoring for tiger salamanders and Western Toads

as more sites with detections are needed to model changes in these species' populations. Second, eDNA can be effective for pathogen monitoring (e.g., Sieber et al., 2020). Recent eDNA work for ranaviruses, a significant disease threat for amphibians in the GYE (Muths et al., this issue, Patla et al., 2016), has been relatively successful, with multiple instances of detection at sites with die-offs (Miaud et al., 2019, Vilaça et al., 2019). Finally, eDNA samples could be used to inventory new or existing long-term monitoring sites. For sampling new sites, inventories could be targeted in regions where rare species such as Western Toads, Plains Spadefoots, or Northern Leopard Frogs may be detected. New sites identified through eDNA could be followed by visual searches to confirm breeding activity by these species of interest. Inventories could also be established to characterize the broader wetland community through metabarcoding approaches; the goal of this approach is to sequence comprehensively DNA fragments that can be amplified by primers designed to capture the diversity of broader taxonomic groups (Deiner et al., 2017). Ultimately, a well-designed metabarcoding study has the potential to address several biotic drivers of amphibian population dynamics, particularly pathogens, introduced predators (e.g., fish), and changes in trophic interactions.

6.3. Population genetic monitoring

Genetic monitoring is a complementary tool that can enhance ongoing monitoring and provide insight into species' ecology, evolution, and population trends (Schwartz et al., 2007). Genotypic data can be used to assess ecological implications of connectivity through the field of landscape genetics (Storfer et al., 2006, Watts et al., 2015), estimate effective population size and identify population bottlenecks, detect evidence of inbreeding, and more recently, study adaptive differentiation among populations (Hohenlohe et al., 2021). In YNP, population genetic structure of Western Tiger Salamanders and Western Toads was examined in the 2000 s around the time the vital signs amphibian monitoring effort was initiated (McMenamin and Hadly, 2012, Murphy et al., 2010, Spear et al., 2005). These studies demonstrated that environmental factors had important impacts on genetic connectivity and provided inference related to ecological associations of each species. Additionally, genetic monitoring of tiger salamanders suggested recent declines at some sampled sites (Spear et al., 2005). For all species monitored, baseline genetic data can help inform how many biologically-based management units or evolutionary significant units occur within GTNP and YNP, which can provide important context for interpreting trends from the monitoring data. Relatedly, genetic diversity and estimates of effective population size can provide important complementary data to ongoing estimates of occupancy and the impact of drought and climate change on populations (Nunziata and Weisrock, 2018). Furthermore, the existence of previous genotypic data for tiger salamanders in YNP's Northern Range and Western Toads would be especially useful for estimating any trends in genetic diversity (using common loci) over the past 15–20 years.

If genome-wide markers are used to complement ongoing efforts, it is possible to examine if there is evidence of adaptation to climate change factors observed during monitoring, and better predict if each species will be able to adapt to changing environmental conditions. Within the past decade, high throughput sequencing platforms have allowed for genotyping across hundreds to thousands of single nucleotide polymorphism (SNP) loci that have increased resolution and genomic coverage (Andrews et al., 2016) relative to work conducted in the early 2000 s. Such high-resolution SNP datasets can be used to identify associations between specific loci and environmental variables that may represent adaptation. Adaptive genetic monitoring can give important insights into amphibian population responses to environmental change such as climate change effects and habitat fragmentation (Cayuela et al., in press).

6.4. Remote sensing

Remote sensing data sources and methods are evolving rapidly and are being increasingly used in concert with ground-based observations to complement and expand monitoring capabilities (Brice et al., this issue, Kissel et al., 2020, Shive et al., 2010). The benefits of integrating remote sensing monitoring with traditional, field-based monitoring techniques are numerous including expanded and more complete spatial coverage, increased number of wetland observations available within a year or season, extended observation record, and the ability to characterize other features of the habitat. As an example, hyperspectral data have been used to identify and differentiate the spectral signatures of certain habitat types or objects within wetlands that support amphibian breeding. By pairing ground-based and hyper-spectral datasets, Shive et al. (2010) effectively predicted which wetlands were used by Columbia Spotted Frogs for breeding in high elevation basins of Idaho, USA. The authors determined that hyperspectral data was used to correctly identify ponds where spotted frogs bred and within breeding ponds the locations of egg masses were correctly identified in most cases. Finally, the repeated use of hyperspectral data over the lifespan of a monitoring program can complement ongoing monitoring work by quantifying changes in spectral properties of wetlands for spotted frogs or other species that have strong habitat associations for breeding, foraging, or overwintering.

Brice et al. (this issue) provide an example of how Landsat imagery can serve as a platform for reconstructing wetland hydrographs in YNP's Northern Range. Landsat has 30-m spatial resolution and modest temporal (16-day) resolution for characterizing dynamics of individual wetlands. Since Landsat's imagery dates back to 1984, it can provide a longer historical perspective of wetland dynamics (Pasquarella et al., 2016, Sall et al., 2020) than is available through most ground-based programs. Spectral mixture analysis and other sub-pixel techniques offer further opportunities to reconstruct wetland hydroperiods at sub-30 m resolution (Halabisky et al., 2016). Finally, high resolution (<1 m), Light Detection and Ranging (LiDAR) delineations of wetland catchments and discharge points is providing opportunities to calculate storage capacity and runoff modulation of individual wetlands across entire landscapes (Huang et al., 2011, Wu et al., 2019). Together, these examples offer insight on how remotely sensed data are already being used to enhance the understanding of hydrobiological components of wetlands. Importantly, the fine-scale information generated from ground-based observations provides insight on species, life stage, and genetics that cannot be identified from satellites (Turner, 2014). Therefore, integration of ground-based with remotely sensed observations will better address information needs at management relevant scales.

6.5. Climate data and water balance models

At the time our monitoring program was conceived, climate change was widely discussed as a possible driver of population declines (Carey and Alexander, 2003, Corn, 2005). However, disease-related concerns, landscape attributes, importance of interacting species (e.g., fish and beaver), and characterizations of habitat types associated with breeding received more attention in early attempts to launch broad-scale amphibian monitoring on public lands (Muths et al., 2005). Additionally, availability and access to fine-scale regional climate information (Giorgi and Hewitson, 2001) was limited. These prevailing paradigms and the general state of circumstances at that time guided program development and analyses during the monitoring program's early years (Gould et al., 2012).

Still, the original long-term monitoring protocol for GTNP and YNP noted that the integration of meteorological data into our annual workflow would aid in identifying to what extent drought or climate change was affecting amphibian occurrence (Objective 1) and wetland inundation patterns (Objective 2). Since the program's inception,

awareness of climate change has grown and climate-related disruptions to wetland ecosystems and reorganization of their biological communities have intensified (e.g., [McMenamin et al., 2008](#)). Our own understanding expanded when evaluating the influence of climate and habitat covariates—models incorporating local climate drivers tended to outperform occupancy models based solely on habitat information or landscape attributes ([Ray et al., 2016](#), [Gould et al., 2019](#)). We found the strongest relationships with variables derived from water balance (e.g., snowmelt runoff) that are more proximal indicators of habitat condition than temperature and precipitation alone.

Water balance models integrate temperature and precipitation with local topography and site-specific factors (storage of water in soils) to estimate runoff and evapotranspiration—factors directly related to wetland filling and drying ([Bardecki, 1991](#)) that provide context for habitat conditions necessary for breeding, larval survival ([Cayuela et al., 2014](#)), and adult movement ([Bartelt et al., this issue](#)). High resolution gridded datasets ([Tercek et al., 2021b](#)) are now integrated into all our analyses (see [Gould et al., 2019](#), [Ray et al., 2016](#); [Ray et al., 2019](#)). In our experience, water balance models represent a straightforward approach to determining how individual and interactive changes in climate drivers alter the balance of hydrologic inputs and losses for individual wetlands used by amphibians ([Thoma et al., 2020](#)).

6.6. Ecological forecasting

One of the most exigent needs for the climate-informed management of parks and protected areas is to develop accurate forecasts about ecosystem and biological responses to future climate change ([Urban et al., 2016](#)). [Dietze et al. \(2018\)](#) argue that forecasting and prediction should become integral to the scientific process; we recommend that this should be extended to long-term ecological monitoring. When setting up a long-term ecological monitoring program, there should be clear intention to integrate monitoring data with forecasts of climate drivers. Ecological forecasting, the process of predicting the future state of ecosystems ([Clark et al., 2001](#)), is essential to supporting decisions concerning ecosystem integrity and human safety ([Tercek, 2019](#)). Forecasting is particularly crucial for comprehending and managing anticipated changes to species dependent on freshwater wetlands—some of the most climate-sensitive, but biologically rich habitats ([Ryan et al., 2014](#)).

There is a growing literature that calls for integration of long-term monitoring of ecological indicators ([Clark et al., 2001](#), [Honrado et al., 2016](#), [Lindenmayer and Likens, 2018](#)) with climate forecasts to generate ecological forecasts. Monitoring datasets that encompass large, climatologically diverse landscapes or regions are uniquely suited for developing ecological forecasting capabilities. Within GTNP and YNP, 15 years of repeated observations on amphibian breeding and wetland filling and drying patterns across 31 catchments and >300 wetland sites represent a dataset that is particularly well-suited for integration with downscaled climate forecasts. While our work to integrate climate forecasts with long-term monitoring data is just beginning in GTNP and YNP, doing this will help resource managers anticipate the locations most immediately affected and the widespread nature of future change. Forecasting will also help to conceive and implement systematic conservation plans for GTNP, YNP, and across the GYE, and serve as a justification for targeted conservation action ([Ray et al., 2019](#)).

7. Linking monitoring activities with conservation action – A path forward

From our experiences, translating information learned through monitoring into action is a challenging endeavor, particularly for widespread or common species that are not typically management priorities. Despite these challenges, monitoring information that is relevant, timely, and credible, is essential to support management decisions ([Cook et al., 2013](#)). Monitoring results from GTNP and YNP indicate that

amphibian occupancy and wetland dynamics are responsive to important climate drivers (e.g., snowpack and runoff generated from snowmelt) and that deeper more permanent ponds are associated with higher levels of spotted frog and tiger salamander occupancy ([Ray et al., 2016](#)). Chorus frog occupancy is related to vegetative cover and annual evaporation rates, the latter being strongly correlated to air temperatures ([Gould et al., 2019](#)). It is also clear that breeding persistence (breeding detected in consecutive years) for our most common species (chorus frogs, spotted frogs, and tiger salamanders) is $\geq 75\%$ —indicating detection in any year is a strong indication of the species breeding in subsequent years. Through our monitoring, we have also learned the tiger salamander occupancy is greatest in two of the six subbasins of the sample frame. Subbasin level summaries also indicate the wetlands in the Snake-Henry's subbasin (see [Fig. 2](#)) are more sensitive to measured variations in runoff across previously monitored years ([Ray et al., 2019](#)). At the scale of individual wetlands, [Brice et al. \(this issue\)](#) show that wetlands across the Northern Range subbasin varied in their drying frequency since 1984 and their sensitivities to changes in snowmelt runoff. Warming temperatures across the GYE ([Sepulveda et al., 2015](#)) indicate snowmelt runoff in this region is likely to occur earlier resulting in longer ice-free periods, increased evapotranspiration losses, and increased meltwater to dry soils. Combined, this information generated through our monitoring program can be used to design mitigation wetlands or restore previously impacted wetlands with anticipated climate effects and habitat features in mind ([Howell et al., 2020](#), [Oja et al., 2021](#), [Swartz et al., 2019](#)). The information can also assist with prioritizing conservation actions for populations, species, and wetlands at greatest risk to climate-induced change.

Monitoring data from this program, and across the GYE, show that amphibians quickly colonize beaver impoundments ([Hossack et al., 2015](#), [Zero and Murphy, 2016](#), this issue) and indicate that most native amphibians use beaver impoundments for breeding. Documenting associations with beaver also provides an opportunity to link our monitoring with park-wide monitoring of beaver habitats in YNP (since 1996) that shows recent expansion of beaver activity throughout several regions of the park ([Smith and Tyers, 2012](#)). This information, along with findings from [Law et al. \(2016, 2017\)](#), who documented increases in wetland habitat heterogeneity and plant and invertebrate richness following beaver reintroduction, provide support for the use of beavers or beaver dam analogs in restoration actions that benefit amphibians.

Despite documented expansion of beaver in some areas of YNP, beaver impoundments remain relatively localized in our amphibian monitoring catchments. Beaver impoundments were recently documented in only two of 24 of our monitored catchments in YNP and three of seven in GTNP ([Patla and Ray, 2020](#)), and fluctuations in beaver activity can cause considerable annual variation in wetland size. Regardless of this, sustained beaver activity generally makes wetlands more resistant to drying ([Zero and Murphy, this issue](#)). In these relatively pristine parks, where heavy-handed management options are limited, beaver flooding and damming activities represent one of the only natural methods available for reversing local wetland-reducing effects of climate change. For that reason, the expansion of studies on the benefits of beaver to native amphibians and monitoring of beaver throughout the GYE are likely to contribute to conservation efforts.

Fish introductions in naturally fishless waters pose problems for amphibians at the site and basin levels (e.g., [Pilliod et al., 2010a](#); [Pilliod et al., 2010b](#)). Previous monitoring in the GYE found a strong negative influence of fish on amphibian occupancy, particularly tiger salamanders ([Klaver et al., 2013](#)). For this reason, reviews of historic fishery survey records in GTNP, YNP (see [Jones et al., 1981](#) as an example) and across the GYE, should be completed to better understand the historical distribution of native fish and salamanders. In addition, inventories of amphibians can be a useful addition into future fisheries work plans; these inventories can be used to inform and time management actions and serve as baseline information to quantify responses of amphibians to implemented projects ([Skaar et al., 2017](#)). For amphibian conservation

purposes, permanent ponds and wetlands in the two parks that contain introduced fish could be targeted for fish removal, a strategy which will help restore the resilience of wetland ecosystems in the face of climate change (Ryan et al., 2014).

Our ongoing monitoring work has also helped identify amphibian hotspots (i.e., multi-species breeding locations; Ray et al., 2014), locations where rare species (e.g., Western Toads) have a history of breeding, “source sites” where large and successful breeding populations disproportionately contribute to the persistence of amphibians on the landscape, and locations where disease outbreaks are common (Patla et al., 2016, Patla and Peterson, this issue). When this information is combined with sensitivity information generated through field-based and remotely-sensed monitoring of wetland hydroperiods and climate forecasts, we can prioritize protection of sites most vulnerable to change and actions at sites where disease mitigation measures could be employed.

8. Scaling Up: A case for regional coordination

Parks and protected area networks are not sufficient for protecting habitats or species present in a region. In this issue, we echo recommendations by Hansen and Phillips (2018) for coordinated monitoring, assessment, and management of natural resources and argue that scaling monitoring from the national parks to the boundaries of the larger GYE would provide greater conservation benefits to amphibians and other species dependent on wetlands (e.g., trumpeter swans [*Cygnus buccinator*], moose [*Alces alces*], bats, and passerines; Levandowski et al., 2021). In the GYE, approximately two-thirds of the lands are managed by federal agencies and the remainder are managed by states, Native American tribes, and private citizens. Therefore, monitoring and informed management at ecologically relevant scales must also reflect multi-agency partnerships and significant and regular outreach to stakeholders and the public (Hansen and Phillips, 2018). Regional coordination does not preclude efforts to identify local stressors (Grant et al., 2016) to benefit or reverse declines of an individual amphibian population. Instead, it implies relying on regional knowledge, sharing resources, and leveraging stakeholder funds in ways that can address personnel needs of annual fieldwork and support targeted conservation action. Coordination among stakeholders can also advance regional conservation campaigns (e.g., wader decontamination stations for anglers could be made available at all aquatic invasive species check-stations, boat launches, and visitor centers) that benefit native species writ large.

Land management agencies and researchers across the GYE have individually and sporadically tracked disease-related mortality events and determined that disease agents are widespread (Muths et al., 2008, Murphy et al., 2009, Patla et al., 2016, Muths et al., this issue). Moreover, the long-term effects of isolated mortality events remain unclear and inferences drawn from such events and disease presence is limited to locations of intensive study. For example, Patla and Peterson (this issue) report declines and disease presence at a long-term Columbia Spotted Frog monitoring site in YNP, and Pilliod et al. (2010a, b) report a slow decline in Western Toads at an intensively studied location near GTNP. Despite the widespread prevalence of pathogens (Muths et al., this issue), we believe that much can still be learned about disease occurrence, dynamics, and environmental factors affecting the virulence. Standardized protocols to report abnormal and dead amphibians, collect specimens for pathology exams, and share information from field projects across the GYE can assist in understanding whether parts of the GYE or certain habitats are at higher risk of disease-related mortality and whether some species or populations are experiencing higher levels of mortality. Coordination among stakeholders working with amphibians can provide a better understanding of the key factors driving disease dynamics and advance the development and implementation of disease mitigation strategies rather than simply cataloging die-offs (Bienentreu and Lesbarrères, 2020).

Expansive and sustained long-term monitoring efforts require interdisciplinary teams to carry out complex, coordinated analyses and research (Lindenmayer and Likens, 2018). In GTNP and YNP, the monitoring program originally conceived by scientists from Idaho State University, the USGS, and the NPS was built on experiences and knowledge gained within and beyond park boundaries. Monitoring activities linked to other national park units (e.g., Glacier and Rocky Mountain national parks; Corn et al., 2005, Hossack et al., 2015) provided guidance and protocols to support the launching of similar regional amphibian monitoring activities on nearby federal lands managed by the US Forest Service (Estes-Zumpf et al., 2022). Currently, shared protocols and field forms, co-managed training activities, and combined data management activities are helping to move student-led monitoring activities on the neighboring Custer-Gallatin National Forest from experiential learning activities to participatory monitoring of sentinel wetland sites outside of park boundaries.

Long-term monitoring efforts also require sustainable and diverse funding sources (Lindenmayer and Likens, 2018) and an understanding that personnel costs increase over years. Adjustments (i.e., adaptive monitoring) to, and expansion of monitoring require increased levels of support. Complementary, intensive studies geared to management-relevant questions are needed to inform science-based decisions and support conservation. Idaho State University, the NPS, and the USGS ARMI helped conceive and were also early financial supporters of this program. The NPS's Vital Signs Monitoring Program continues as the leading supporter of the program while other support has declined due, largely, to flat-funding. Diversification of funding is essential to continue and expand the GYE's long-term amphibian monitoring program. Field et al. (2007) noted that long-term monitoring requires sustained commitment from multiple parties and commitments for a decade or more. While agencies like the NPS will continue to offer vital support in the form of funding and personnel, funding for monitoring and conservation has proven difficult to secure and public sources show limited potential for growth (Rodewald et al., 2020). As a result, funding shortfalls for long-term ecological monitoring are all too common (Birkhead, 2014). Consequently, university partnerships, private conservation foundations, community science programs (Estes-Zumpf et al., 2022) and crowd-sourced data (e.g., iNaturalist Greater Yellowstone Amphibian and Reptile Project), along with traditional granting institutions (e.g., U.S. Environmental Protection Agency), are increasingly important parts of a robust long-term monitoring program.

Finally, conservation exists at the social-ecological interface and, as a result, the public plays an increasingly important role in the support of ecological monitoring and conservation of wildlife (Knight et al., 2019). As practitioners of ecological monitoring our sustainability depends, in part, on our ability to contextualize the benefits of monitoring and biodiversity conservation for all people (Woodhams, 2009). Some national parks have interpretation materials that highlight threats to amphibian habitats and species (Halstead et al., this issue). In GTNP, signs announcing the short-term closure of a picnic area to vehicles (Fig. 10) for the protection of Western Toads helped to educate visitors and park staff about this species of conservation concern. The NPS is also partnering with the Grizzly and Wolf Discovery Center in West Yellowstone, Montana (USA) to produce education materials on YNP's native amphibians that can be displayed in their newly constructed Riparian Exhibit (<https://www.grizzlydiscoveryctr.org/>). These efforts along with direct public outreach in popular press, public talks, collaboration with local artists, and delivery of content for newspaper articles and podcasts, represent attempts to reach beyond the scientific community and describe the broader benefits of amphibian monitoring and ecological indication in GTNP and YNP and across the GYE. In the case of art, engaging the public first requires engaging and welcoming artists into the work that we do. The images, paintings, graphics, and music that artists create (Monroe et al., 2009) offer an entry point into the natural history and ecology of GYE amphibians (see Fig. 11). Successful outreach efforts help us reach new audiences, leave lasting

OPEN TO FOOT TRAVEL

CLOSED TO VEHICLES

Boreal Toad Migration in Progress



Hundreds of juvenile boreal toads are currently inhabiting areas within and surrounding Lakeview Picnic Area as they prepare for winter. Due to the high number of boreal toads being killed on the road, park managers have closed Lakeview Picnic Area to vehicle traffic.

Boreal toads are the only toad species found in Grand Teton National Park. While adult boreal toads can range up to 4 inches (10 centimeters) in length, the juveniles in the area are currently less than 0.80 inches (20 millimeters) in length.

Although historically common in the area, biologists believe boreal toad populations may be in decline throughout the Greater Yellowstone Ecosystem.

As you enjoy the Grand Tetons from Lakeview Picnic Area, please watch your step and leave the juvenile toads to their journey. Thanks for your cooperation.

Fig. 10. Grand Teton National Park closed off a picnic area to protect recently transformed Western Toad metamorphs in August 2015. The sign described the rationale for the closure but was also used to educate visitors on the natural history and ecological status of this species.

impressions, and inspire people in ways that support conservation action.

9. Conclusions

The reflections above characterize how the amphibian and wetland vital sign monitoring program in GTNP and YNP has met our primary objective of estimating occupancy of catchments and sites for four widespread species. The sparseness of observations for the rarest species (e.g., Western Toads) and the clustered nature of Western Tiger Salamanders, however, has complicated our ability to model their breeding associations with covariates and characterize long-term trends across both parks. Our annual monitoring has iteratively updated our understanding of the filling and drying dynamics of wetlands through space and time (Objective 2) and supported analyses that identify the drivers of wetland change. Due to limitations in funding, we have been unable to fully implement fieldwork associated with Objective 3 that called for revisits to known toad breeding sites that fall outside of our long-term monitoring catchments. Still, our program has grown and adapted to accommodate technologies, improved scientific understanding, and shifts in management priorities since the program's formal launching in 2006.

While core field-based data are still collected, complementary, short-term studies have added dimension to our understanding of methodological advancements in monitoring. Longer-term, programmatic decisions to focus on the most wetland-rich catchments and formal incorporation of climate data have reshaped the amphibian and wetland monitoring work described in our original protocol. This adaptive approach has allowed us to communicate findings that reach beyond the

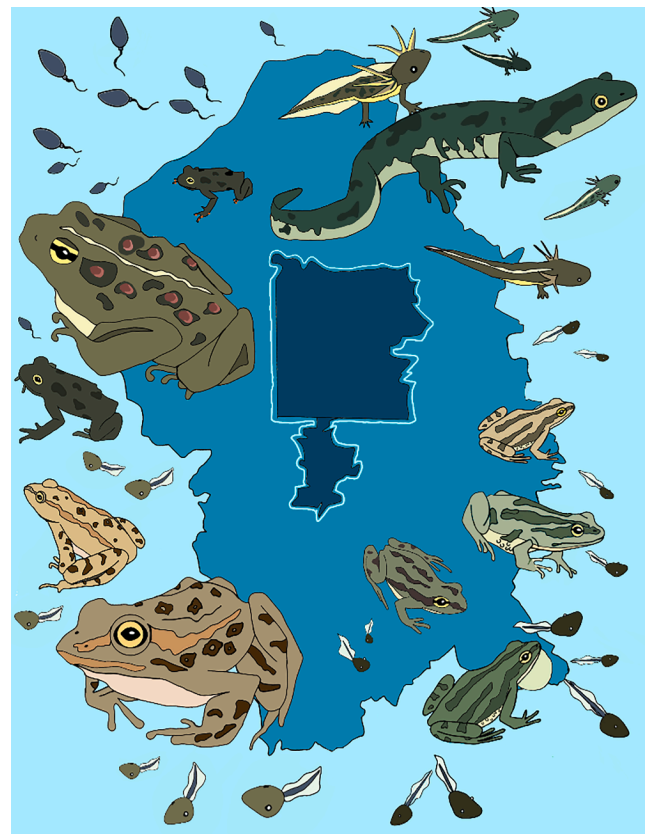


Fig. 11. Artistic summary of the widespread amphibian species and life stages present in Grand Teton and Yellowstone national parks. The artist of this graphic spent the summer as a field crew member conducting amphibian monitoring and developed this digital summary after her experience. Artwork by G. Thompson.

initial goal of characterizing long-term trends of amphibian and wetland indicators in two national parks. For example, our dataset has been used to characterize variations in indicator sensitivity to environmental drivers among species and across landscapes. More broadly, our approach has contributed to understanding important associations between beaver and biodiversity, insights on rare species monitoring, the value of collaborative, multi-agency partnerships in ecological monitoring, and the benefits of combining monitoring data with climate projections to support ecological forecasting. Sustaining this monitoring program for the next 15 years will require a diverse funding portfolio, programmatic champions, and continued reflection on our work. We have outlined advances in our understanding that are directly linked to the long-term monitoring of amphibians in GTNP and YNP, but the most promise lies ahead. As information from our program accumulates, it will allow land managers of the GYE to address tomorrow's conservation challenges—perhaps even those that we have not yet imagined.

CRediT authorship contribution statement

Andrew M. Ray: Conceptualization, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Blake R. Hossack:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **William R. Gould:** Writing – original draft, Writing – review & editing. **Debra A. Patla:** Writing – review & editing. **Stephen F. Spear:** Writing – original draft, Writing – review & editing. **Robert W. Klaver:** Writing – review & editing. **Paul E. Bartelt:** Writing – review & editing. **David P. Thoma:** Writing – review & editing. **Kristin L. Legg:** Writing – review & editing. **Rob Daley:** Visualization, Data curation. **P. Stephen Corn:** Writing –

review & editing. **Charles R. Peterson:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We recognize our gratitude to Rob Bennetts for his essential role in the creation of the amphibian monitoring protocol in Grand Teton and Yellowstone national parks. Without Rob's leadership this work would have not been possible. We acknowledge the efforts of current and past field crews who collectively produced the ground-based data that supported these analyses and reflections. Northern Rockies Conservation Cooperative has been an important partner for implementing annual monitoring work. Funding for this effort was provided by the National Park Service's Greater Yellowstone Network and the U.S. Geological Survey's Amphibian Research and Monitoring Initiative (ARMI). We thank Jana Cram for assistance with visualizations and comments on an earlier version of this manuscript and Gabbie Thompson for sharing her artwork for this manuscript. Any use of trade, product, or firm names is descriptive and does not imply endorsement by the U.S. Government. This manuscript is ARMI product no. 827.

References

- Adams, M.J., Miller, D.A.W., Muths, E., Corn, P.S., Grant, E.H.C., Bailey, L.L., Fellers, G.M., Fisher, R.N., Sadinski, W.J., Waddle, H., Walls, S.C., Chen, H.Y.H., 2013. Trends in amphibian occupancy in the United States. *PLoS ONE* 8 (5), e64347.
- Andrews, K.R., Good, J.M., Miller, M.R., Luikart, G., Hohenlohe, P.A., 2016. Harnessing the power of RADseq for ecological and evolutionary genomics. *Nat. Rev. Genet.* 17 (2), 81–92.
- Bardeci, M.J., 1991. Wetlands and climate change: a speculative review. *Can. Water Resour. J.* 16 (1), 9–22.
- Bartelt, P.E., Gallant, A.L., Klaver, R.W., Wright, C.K., Patla, D.A., Peterson, C.R., 2011. Predicting breeding habitat for amphibians: a spatiotemporal analysis across Yellowstone National Park. *Ecol. Appl.* 21 (7), 2530–2547.
- Bartelt, P.E., Thornton, P.E., Klaver, R.W., Modelling physiological costs to assess impacts of climate change on amphibians in Yellowstone National Park. *Ecol. Indic.*, this issue.
- Bennetts, R., Corn, P.S., Daley, R., Gould, W.R., Jean, C., Patla, D.A., Peterson, C.R., Ray, A., 2013. Cooperative amphibian monitoring protocol for the Greater Yellowstone Network: Narrative, version 1.0. Natural Resource Report NPS/GRYN/NRR-2013/654. National Park Service, Fort Collins, Colorado, USA.
- Bienentreu, J.-F., Lesbarrères, D., 2020. Amphibian disease ecology: are we just scratching the surface? *Herpetologica* 76 (2), 153. <https://doi.org/10.1655/0018-0831-76.2.15310.1655/0018-0831-76.2.153.s1>.
- Birkhead, T., 2014. Stormy outlook for long-term ecology studies. *Nature* 514 (7523), 405.
- Blaustein, A.R., Wake, D.B., 1990. Declining amphibian populations: a global phenomenon? *Trends Ecol. Evol.* 5 (7), 203–204.
- Brice, E.M., Halabisky, M., Ray, A.M., Making the leap from ponds to landscapes: integrating field-based monitoring of amphibians and wetlands with satellite observations. *Ecol. Indic.*, this issue.
- Carey, C., Alexander, M.A., 2003. Climate change and amphibian declines: is there a link? *Divers. Distrib.* 9 (2), 111–121.
- Carpenter, C.C., 1953. An ecological survey of the herpetofauna of the Grand Teton—Jackson Hole area of Wyoming. *Copeia* 1953 (3), 170. <https://doi.org/10.2307/1439925>.
- Cayuela, H., Besnard, A., Bonnaire, E., Perret, H., Rivoalen, J., Miaud, C., Joly, P., 2014. To breed or not to breed: past reproductive status and environmental cues drive current breeding decisions in a long-lived amphibian. *Oecologia* 176 (1), 107–116.
- Cayuela, H., Dorant, Y., Forester, B.R., Jeffries, D.L., McCaffery, R.M., Eby, L.A., Hossack, B.R., Gippet, J.M.W., Pilliod, D.S., W.C. Funk. In press. Genomic signatures of thermal adaptation are associated with clinal shifts of life history in a broadly distributed frog. *J. Anim. Ecol.*
- Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A., Lodge, D.M., Pascual, M., Pielke Jr., R., Pizer, W., Pringle, C., Reid, W.V., Rose, K.A., Sala, O., Schlesinger, W.H., Wall, D.H., Wear, D., 2001. Ecological forecasting: an emerging imperative. *Science* 293, 657–660.
- Collins, J.P., Storfer, A., 2003. Global amphibian declines: sorting the hypotheses. *Divers. Distrib.* 9 (2), 89–98.
- Cook, Carly.N., Mascia, Michael.B., Schwartz, Mark.W., Possingham, Hugh.P., Fuller, Richard.A., 2013. Achieving conservation science that bridges the knowledge-action boundary. *Conserv. Biol.* 27 (4), 669–678.
- Corn, P.S., 1994. What we know and don't know about amphibian declines in the west. In: DeBano, L.F., Covington, W.W. (Eds.), *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*. Fort Collins, USDA Forest Service, Rocky Mountain Forest Range Experimental Station, pp. 59–67.
- Corn, P.S., 2005. Climate change and amphibians. *Anim. Biodiv. Conserv.* 28, 59–67.
- Corn, P.S., Hossack, B.R., Muths, E., Patla, D.A., Peterson, C.R., Gallant, A.L., 2005. Status of amphibians on the Continental Divide: surveys on a transect from Montana to Colorado, USA. *Alytes* 22, 85–94.
- Cowardin, L.M., Carter, V., Golet, F.C., LaRoe, E.T., 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Office of Biological Services, Washington, DC, USA.
- Deiner, K., Bik, H.M., Mächler, E., Seymour, M., Lacoursière-Roussel, A., 2017. Environmental DNA metabarcoding: transforming how we survey animal and plant communities. *Mol. Ecol.* 26, 5872–5895.
- Devarajan, K., Morelli, T.L., Tenan, S., 2020. Multi-species occupancy models: review, roadmap, and recommendations. *Ecography* 43 (11), 1612–1624.
- Dietze, M.C., Fox, A., Beck-Johnson, L.M., Betancourt, J.L., Hooten, M.B., Jarnevich, C.S., Keitt, T.H., Kenney, M.A., Laney, C.M., Larsen, L.G., Loescher, H.W., Lunch, C.K., Pijanowski, B.C., Randerson, J.T., Read, E.K., Tredeknick, A.T., Vargas, R., Weathers, K.C., White, E.P., 2018. Iterative near-term ecological forecasting: needs, opportunities, and challenges. *Proc. Natl. Acad. Sci.* 115 (7), 1424–1432.
- Drost, C.A., Fellers, G.M., 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada. *USA. Conserv. Biol.* 10 (2), 414–425.
- Estes Zumpf, W., Addis, B., Marsicek, B., Lee, M., Nelson, Z., Murphy, M., 2022. Improving sustainability of long-term amphibian monitoring: The value of collaboration and community science for indicator species management. *Ecol. Indic.* 134, 108451. <https://doi.org/10.1016/j.ecolind.2021.108451>.
- Fancy, S.G., Gross, J.E., Carter, S.L., 2009. Monitoring the condition of natural resources in US national parks. *Environ. Monit. Assess.* 151 (1–4), 161–174.
- Fediajevaite, J., Priestley, V., Arnold, R., Savolainen, V., 2021. Meta-analysis shows that environmental DNA outperforms traditional surveys, but warrants better reporting standards. *Ecol. Evol.* 11 (9), 4803–4815.
- Ficetola, G.F., Miaud, C., Pompanon, F., Taberlet, P., 2008. Species detection using environmental DNA from water samples. *Biol. Lett.* 4 (4), 423–425.
- Field, S.A., O'Connor, P.J., Tyre, A.J., Possingham, H.P., 2007. Making monitoring meaningful. *Austral Ecol.* 32, 485–491.
- Giorgi, F., Hewitson, B.C., 2001. Regional climate information – evaluation and projections. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge, pp. 583–638.
- Gould, W.R., 2020. Multi-state modeling of salamander breeding occupancy in the Greater Yellowstone Area (2006–2018). Research Completion Report Submitted to the Greater Yellowstone Network. New Mexico State University, Las Cruces, New Mexico, USA.
- Gould, W.R., Patla, D.A., Daley, R., Corn, P.S., Hossack, B.R., Bennetts, R., Peterson, C.R., 2012. Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the Greater Yellowstone Ecosystem. *Wetlands* 32 (2), 379–389.
- Gould, W.R., Ray, A.M., Bailey, L.L., Thoma, D., Daley, R., Legg, K., 2019. Multistate occupancy modeling improves understanding of amphibian breeding dynamics in the Greater Yellowstone Area. *Ecol. Appl.* 29 (1) <https://doi.org/10.1002/eap.2019.29.issue-110.1002/eap.1825>.
- Grant, E.H.C., Miller, D.A.W., Schmidt, B.R., Adams, M.J., Amburgey, S.M., Chamber, T., Cruickshank, S.S., Fisher, R.N., Green, D.M., Hossack, B.R., Johnson, P.T.J., Joseph, M.B., Rittenhouse, T., Ryan, M., Waddle, J.H., Walls, S.C., Bailey, L.L., Fellers, G.M., Gorman, T.A., Ray, A.M., Pilliod, D.S., Price, S.J., Saenz, D., Sadinski, W., Muths, E., 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Sci. Rep.* 6, 25625.
- Grant, E.H.C., Muths, E., Schmidt, B.R., Petrovan, S.O., 2019. Amphibian conservation in the Anthropocene. *Biol. Conserv.* 236, 543–547.
- Green, D.M., 1997. Perspectives on amphibian population declines: defining the problem and searching for answers. *Herpetol. Conserv.* 1, 291–308.
- Halabisky, M., Moskal, L.M., Gillespie, A., Hannam, M., 2016. Reconstructing semi-arid wetland surface water dynamics through spectral mixture analysis of a time series of Landsat satellite images (1984–2011). *Remote Sens. Environ.* 177, 171–183.
- Halstead, B.J., Ray, A.M., Muths, E., Campbell Grant, E.H., Grasso, R., Adams, M.J., Semple Delaney, K., Carlson, J., Hossack, B.R., Looking ahead, guided by the past: the role of U.S. national parks in amphibian research and conservation. *Ecol. Indic.*, this issue.
- Hansen, A.J., Phillips, L., 2018. Trends in vital signs for Greater Yellowstone: application of a Wildland Health Index. *Ecosphere* 9 (8). <https://doi.org/10.1002/ecs2.2018.9.issue-810.1002/ecs2.2380>.
- Hohenlohe, P.A., Funk, W.C., Rajora, O.P., 2021. Population genomics for wildlife conservation and management. *Mol. Ecol.* 30 (1), 62–82.
- Honrado, J.P., Pereira, H.M., Guisan, A., 2016. Fostering integration between biodiversity monitoring and modelling. *J. Appl. Ecol.* 53 (5), 1299–1304.
- Hossack, B.R., Gould, W.R., Patla, D.A., Muths, E., Daley, R., Legg, K., Corn, P.S., 2015. Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. *Biol. Conserv.* 187, 260–269.
- Howell, P.E., Muths, E., Hossack, B.R., Sigafus, B.H., Chandler, R.B., 2018. Increasing connectivity between metapopulation ecology and landscape ecology. *Ecology* 99 (5), 1119–1128.
- Howell, P.E., Hossack, B.R., Muths, E., Sigafus, B.H., Chenevert-Steffler, A., Chandler, R. B., 2020. A statistical forecasting approach to metapopulation viability analysis. *Ecol. Appl.* 30 (2) <https://doi.org/10.1002/eap.v30.210.1002/eap.2038>.
- Huang, S., Young, C., Feng, M., Heidemann, K., Cushing, M., Mushet, D.M., Liu, S., 2011. Demonstration of a conceptual model for using LIDAR to improve estimation of

- floodwater mitigation potential of Prairie Pothole Region wetlands. *J. Hydrol.* 405, 417–426.
- Jones, R. D., Gresswell, R.E., Rubrecht, S.M., Bigelow, P.E., Carty, D., 1981. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1980, Yellowstone National Park, Wyoming, USA.
- Kissel, A.M., Halabisky, M., Scherer, R.D., Ryan, M.E., Hansen, E.C., 2020. Expanding wetland hydroperiod data via satellite imagery for ecological applications. *Front. Ecol. Environ.* 18 (8), 432–438.
- Klaver, R.W., Peterson, C.R., Patla, D.A., 2013. Influence of water conductivity on amphibian occupancy in the Greater Yellowstone Ecosystem. *West. N. Am. Nat.* 73 (2), 184–197.
- Knapp, R.A., Matthews, K.R., 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog within protected areas. *Conserv. Biol.* 14, 428–438.
- Knight, A.T., Cook, C.N., Redford, K.H., Biggs, D., Romero, C., Ortega-Argueta, A., Norman, C.D., Parsons, B., Reynolds, M., Eoyang, G., Keene, M., 2019. Improving conservation practice with principles and tools from systems thinking and evaluation. *Sustain. Sci.* 14 (6), 1531–1548.
- Koch, E.D., Peterson, C.R., 1995. Amphibians & reptiles of Yellowstone and Grand Teton National Parks. University of Utah Press, Salt Lake City, Utah, USA.
- Law, A., McLean, F., Willby, N.J., 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biol.* 61 (4), 486–499.
- Law, A., Gaywood, M.J., Jones, K.C., Ramsay, P., Willby, N.J., 2017. Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands. *Sci. Total Environ.* 605–606, 1021–1030.
- Lindenmayer, D.B., Likens, G.E., 2010. The science and application of ecological monitoring. *Biol. Conserv.* 143 (6), 1317–1328.
- Lindenmayer, D.B., Likens, G.E., 2018. Effective ecological monitoring, second ed. Victoria, Australia.
- Levandowski, M.L., Litt, A.R., McKenna, M.F., Burson, S., Legg, K.L., 2021. Multi-method biodiversity assessments from wetlands in Grand Teton National Park. *Ecol. Indic.* 131, 108205. <https://doi.org/10.1016/j.ecolind.2021.108205>.
- MacKenzie, D.I., Nichols, J., Royle, J., Pollock, K., Bailey, L., Hines, J., 2017. Occupancy estimation and modeling, 2nd Edition. Academic Press, Salt Lake City, p. 648.
- MacKenzie, D.I., Nichols, J.D., Seamans, M.E., Gutiérrez, R.J., 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90 (3), 823–835.
- McCaffery, R., Russell, R.E., Hossack, B.R., 2021. Enigmatic near-extirpation in a Boreal Toad metapopulation in northwestern Montana. *J. Wildlife Manage.* 85 (5), 953–963.
- McMenamin, S.K., Hadly, E.A., Wright, C.K., 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proc. Natl. Acad. Sci.* 105 (44), 16988–16993.
- McMenamin, S.K., Hadly, E.A., Nogues-Bravo, D., 2012. Ancient DNA assessment of tiger salamander population in Yellowstone National Park. *PLoS One* 7 (3), e32763.
- Miaud, C., Arnal, V., Poulain, M., Valentini, A., Dejean, T., 2019. eDNA increases the detectability of ranavirus infection in an alpine amphibian population. *Viruses* 11 (6), 526. <https://doi.org/10.3390/v11060526>.
- Monroe, J.B., Baxter, C.V., Olden, J.D., Angermeier, P.L., 2009. Freshwaters in the public eye: understanding the role of images and media in aquatic conservation. *Fisheries* 34, 581–585.
- Murphy, M.A., Evans, J.S., Storfer, A., 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* 91 (1), 252–261.
- Murphy, P., St-Hilaire, S., Bruer, S., Corn, P.S., Peterson, C., 2009. Distribution and pathogenicity of *Batrachochytrium dendrobatidis* in western toads from the Grand Teton area of western Wyoming. *EcoHealth* 6, 109–120.
- Muths, E., Jung, R.E., Bailey, L.L., Adams, M.J., Corn, P.S., Dodd Jr., C.K., Fellers, G.M., Sadinski, W.J., Schwalbe, C.R., Walls, S.C., Fisher, R.N., Gallant, A.L., Battaglin, W. A., Green, D.A., 2005. Amphibian Research and Monitoring Initiative (ARM): a successful start to a national program in the United States. *Appl. Herpetol.* 2, 355–371.
- Muths, E., Pilliod, D.S., Livo, L.J., 2008. Distribution and environmental limitations of an amphibian pathogen in the Rocky Mountains. *USA. Biol. Conserv.* 141 (6), 1484–1492.
- Muths, E., Hossack, B.R., 2019. The role of monitoring and research in the Greater Yellowstone Ecosystem in framing our understanding of the response of amphibians to disease. *Ecol. Indic.*, this issue.
- NatureServe. 2021. NatureServe Explorer [web application]. NatureServe, Arlington, Virginia. Available <https://explorer.natureserve.org/>. (Accessed: December 09, 2021).
- Nunziata, S.O., Weisrock, D.W., 2018. Estimation of contemporary effective population size and population declines using RAD sequence data. *Heredity* 120 (3), 196–207.
- Oja, E.B., Swartz, L.K., Muths, E., Hossack, B.R., 2021. Amphibian population responses to mitigation relative to wetland age and design features. *Ecol. Indic.* 131, 108123. <https://doi.org/10.1016/j.ecolind.2021.108123>.
- Pasquarella, V.J., Holden, C.E., Kaufman, L., Woodcock, C.E., Nagendra, H., He, K., 2016. From imagery to ecology: leveraging time series of all available Landsat observations to map and monitor ecosystem state and dynamics. *Remote Sens. Ecol. Conserv.* 2 (3), 152–170.
- Patla, D.A., Peterson, C.R., 2019. The slow decline of a Columbia Spotted Frog population in Yellowstone National Park: a cautionary tale from a developed zone within a large protected area. *Ecol. Indic.*, this issue.
- Patla, D., St-Hilaire, S., Ray, A., Hossack, B.R., Peterson, C.R., 2016. Amphibian mortality events and ranavirus outbreaks in the Greater Yellowstone Ecosystem. *Herpetol. Rev.* 47, 50–54.
- Patla, D., Ray, A., 2020. Greater Yellowstone Network amphibian and wetland monitoring: status report for 2017 and 2018. Natural Resource Report. NPS/GRYN/NRR—2020/2111. National Park Service, Fort Collins, Colorado, USA.
- Petranka, J.W., Smith, C.K., Floyd Scott, A., 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. *Ecol. Appl.* 14 (4), 1065–1078.
- Pilliod, D.S., Hossack, B.R., Bahl, P.F., Bull, E.L., Corn, P.S., Hokit, G., Maxell, B.A., Munger, J.C., Murphy, P., Wyrick, A., 2010a. Nonnative salmonids affect amphibian occupancy at multiple spatial scales. *Divers. Distrib.* 16, 959–974.
- Pilliod, D.S., Muths, E., Scherer, R.D., Bartelt, P.E., Corn, P.S., Hossack, B.R., Lambert, B. A., McCaffery, R., Gaughan, C., 2010b. Effects of amphibian chytrid fungus on individual survival probability in wild western toads. *Conserv. Biol.* 24, 1259–1267.
- Ray, A.M., Gould, W., Hossack, B., Sepulveda, A., Thoma, D., Patla, D., Daley, R., Al-Chokachy, R., 2016. Influence of climate drivers on extinction and colonization rates of wetland-dependent species. *Ecosphere* 7, e01409.
- Ray, A.M., Sepulveda, A.J., Irvine, K.M., Wilmoth, S.K.C., Thoma, D.P., Patla, D.A., 2019. Wetland drying linked to variations in snowmelt runoff across Grand Teton and Yellowstone national parks. *Sci. Total Environ.* 666, 1188–1197.
- Ray, A.M., Sepulveda, A.J., Hossack, B., Patla, D., Legg, K., 2014. Using monitoring data to map amphibian hotspots and describe wetland vulnerability in Yellowstone and Grand Teton national parks. *Park Sci.* 31, 112–119.
- Rodewald, A.D., Arcese, P., Sarra, J., Tobin-de la Puente, J., Sayer, J., Hawkins, F., Martin, T., Guy, B., Wachowicz, K., 2020. Innovative finance for conservation: roles for ecologists and practitioners. Ecological Society of America, Issues in Ecology Report No. 22.
- Rodhouse, T.J., Sergeant, C.J., Schweiger, E.W., 2016. Ecological monitoring and evidence-based decision-making in America's National Parks: highlights of the special feature. *Ecosphere* 7 (11). <https://doi.org/10.1002/ecs2.2016.7.issue-1110.1002/ecs2.1608>.
- Rossman, S., Yackulic, C.B., Saunders, S.P., Reid, J., Davis, R., Zipkin, E.F., 2016. Dynamic N-occupancy models: estimating demographic rates and local abundance from detection-nondetection data. *Ecology* 97 (12), 3300–3307.
- Ryan, M.E., Palen, W.J., Adams, M.J., Rochefort, R.M., 2014. Amphibians in the climate vise: loss and restoration of resilience of montane wetland ecosystems in the western U.S. *Front. Ecol. Environ.* 12 (4), 232–240.
- Sall, I., Jarchow, C.J., Sigafus, B.H., Eby, L.A., Forzley, M.J., Hossack, B.R., He, K., Zlinszky, A., 2021. Estimating inundation of small waterbodies with sub-pixel analysis of Landsat imagery: long-term trends in surface water area and evaluation of common drought indices. *Remote Sens. Ecol. Conserv.* 7 (1), 109–124.
- Schneider, D., Treanor, J.J., Richards, J., Wood, J., Lee, E., Waag, A., 2015. Plains spadefoot, *Spea bombifrons*, confirmed in Yellowstone National Park. *NW Nat.* 96 (3), 227–229.
- Schwartz, M., Luikart, G., Waples, R., 2007. Genetic monitoring as a promising tool for conservation and management. *Trends Ecol. Evol.* 22 (1), 25–33.
- Sepulveda, A.J., Tercek, M.T., Al-Chokachy, R., Ray, A.M., Thoma, D.P., Hossack, B.R., Pederson, G.T., Rodman, A.W., Olliff, T., Añel, J.A., 2015. The shifting climate portfolio of the Greater Yellowstone Area. *PLoS ONE* 10 (12), e0145060.
- Sergeant, C.J., Moynahan, B.J., Johnson, W.F., 2012. Practical advice for implementing long-term ecosystem monitoring. *J. Appl. Ecol.* 49, 969–973.
- Shive, J.P., Pilliod, D.S., Peterson, C.R., 2010. Hyperspectral analysis of Columbia Spotted Frog habitat. *J. Wildlife Manage.* 74, 1387–1394.
- Sieber, N., Hartikainen, H., Vorburger, C., 2020. Validation of an eDNA-based method for the detection of wildlife pathogens in water. *Dis. Aquat. Organ.* 141, 171–184.
- Skaar, D.R., Arnold, J.L., Koel, T.M., Ruhl, M.E., Skorupski, J.A., Treanor, H.B., 2017. Effects of Roteone on amphibians and macroinvertebrates in Yellowstone. *Yellowstone Sci.* 25, 28–34.
- Smith, M.M., Goldberg, C.S., 2020. Occupancy in dynamic systems: accounting for multiple scales and false positives using eDNA to inform monitoring. *Ecography* 43, 376–386.
- Smith, D.W., Tyers, D.B., 2012. The history and current status and distribution of beavers in Yellowstone National Park. *Northwest Sci.* 86, 276–288.
- Spear, Stephen F., Peterson, Charles R., Matocq, Marjorie D., Storfer, Andrew, 2005. Landscape genetics of the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). *Mol. Ecol.* 14 (8), 2553–2564.
- Storfer, A., Murphy, M.A., Evans, J.S., Goldberg, C.S., Robinson, S., Spear, S.F., Dezzani, R., Delmelle, E., Vierling, L., Waits, L.P., 2006. Putting the “landscape” in the landscape genetics. *Heredity* 98, 128–142.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306 (5702), 1783–1786.
- Swartz, L.K., Hossack, B.R., Muths, E., Newell, R.L., Lowe, W.H., 2019. Aquatic macroinvertebrate community responses to wetland mitigation in the Greater Yellowstone Ecosystem. *Freshw. Biol.* 64 (5), 942–953.
- Tercek, M., 2019. Nowcasting & forecasting fire severity in Yellowstone. *Yellowstone Sci.* 27, 27–33.
- Tercek, M., Rodman, A., Añel, J.A., 2016. Forecasts of 21st century snowpack and implications for snowmobile and snowcoach use in Yellowstone National Park. *PLoS ONE* 11 (7), e0159218.
- Tercek, M.T., Gray, S.T., Nicholson, C.M., 2012. Climate zone delineation: evaluating approaches for use in natural resource management. *Environ. Manage.* 49 (5), 1076–1091.
- Tercek, M.T., Rodman, A., Woolfolk, S., Wilson, Z., Thoma, D., Gross, J., 2021a. Correctly applying lapse rates in ecological studies: comparing temperature observations and gridded data in Yellowstone. *Ecosphere* 12 (3). <https://doi.org/10.1002/ecs2.v12.310.1002/ecs2.3451>.

- Tercek, M.T., Thoma, D., Gross, J.E., Sherrill, K., Kagone, S., Senay, G., Martínez-Yrizar, A., 2021b. Historical changes in plant water use and need in the Continental United States. *PLoS ONE* 16 (9), e0256586.
- Thoma, D.P., Tercek, M.T., Schweiger, E.W., Munson, S.M., Gross, J.E., Olliff, S.T., 2020. Water balance as an indicator of natural resource condition: case studies from Great Sand Dunes National Park and Preserve. *Global Ecol. Conserv.* 24, e01300. <https://doi.org/10.1016/j.gecco.2020.e01300>.
- Thomsen, P.F., Kielgast, J., Iversen, L.L., Møller, P.R., Rasmussen, M., Willerslev, E., Lin, S., 2012. Detection of a diverse marine fish fauna using environmental DNA from seawater samples. *PLoS ONE* 7 (8), e41732.
- Turner, W., 2014. Sensing biodiversity. *Science* 346 (6207), 301–302.
- Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J.J., Holt, R.D., Huth, A., Johst, K., Krug, C.B., Leadley, P.W., Palmer, S.C.F., Pantel, J.H., Schmitz, A., Zollner, P.A., Travis, J.M.J., 2016. Improving the forecast for biodiversity under climate change. *Science* 353 (6304). <https://doi.org/10.1126/science.aad8466>.
- Vilaça, S.T., Grant, S.A., Beaty, L., Brunetti, C.R., Congram, M., Murray, D.L., Wilson, C.C., Kyle, C.J., 2019. Detection of spatiotemporal variation in ranavirus distribution using eDNA. *Environ. DNA* 2 (2), 210–220.
- Wake, D.B., 1991. Declining amphibian populations. *Science* 253 (5022), 860.
- Watts, A.G., Schlichting, P., Billerman, S., Jesmer, B., Micheletti, S., Fortin, M.J., Funk, C., Hapeman, P., Muths, E.L., Murphy, M.A., 2015. How spatio-temporal habitat connectivity affects amphibian genetic structure. *Frontiers in Genetics* 6. <https://doi.org/10.3389/fgene.2015.00275>.
- Welsh, H.H., Ollivier, L.M., 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. *Ecol. Appl.* 8 (4), 1118–1132.
- Woodhams, D.C., 2009. Converting the Religious: Putting Amphibian Conservation in Context. *Bioscience* 59 (6), 463–464.
- Wu, Q., Lane, C.R., Li, X., Zhao, K., Zhou, Y., Clinton, N., DeVries, B., Golden, H.E., Lang, M.W., 2019. Integrating LiDAR data and multi-temporal aerial imagery to map wetland inundation dynamics using Google Earth Engine. *Remote Sens. Environ.* 228, 1–13.
- Zero, V.H., Murphy, M.A., 2016. An amphibian species of concern prefers breeding in active beaver ponds. *Ecosphere* 7 (5). <https://doi.org/10.1002/ecs2.1330>.
- Zero, V.H., Murphy, M.A., 2019. Influence of beaver modification on amphibian occupancy: does the loss of beavers represent an extinction debt in the Greater Yellowstone Ecosystem? *Ecol. Indic.*, this issue.