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✦　SUMMARY

Introduced American Bullfrogs (*Lithobates catesbeianus*) have been present in Grand Teton National Park since approximately the 1950s, but little is known about their distribution and potential impacts. In this study, we surveyed the current bullfrog distribution and spatial overlap with sympatric native amphibians in the park, and characterized post-metamorphic bullfrog diets from July – September 2015. Despite surveys in multiple large rivers and floodplain habitats, we only documented bullfrogs in a geothermal pond and 5 km of stream channel immediately downstream of this pond. In these waters, bullfrogs overlapped with native amphibians at the downstream end of their distribution, and we did not document native amphibians in bullfrog stomach contents. Larger bullfrogs (SVL ≥ 96 mm) primarily consumed native rodents (especially meadow voles, *Microtus pennsylvanicus*), while smaller bullfrogs frequently consumed native invertebrates and less frequently consumed non-native invertebrates and fish. Taken together, these data indicate that the distribution and implications of the bullfrog invasion in Grand Teton National Park are currently localized to a small area, so these bullfrogs should therefore be vulnerable to eradication.

✦　INTRODUCTION

Introduced American Bullfrogs (*Lithobates catesbeianus*; hereafter, bullfrog) are suspected in the decline of native amphibian populations through predation, depletion of food resources and disease spread (Kiesecker and Semlitsch 2003, Kupferberg 1997, Miaud et al. 2016). Bullfrogs can also have large food web impacts because they are generalist predators. Documented bullfrog prey include invertebrates, reptiles, amphibians, fish, birds, bats, and small mammals (Kiesecker and Semlitsch 2003, Pearl et al. 2004, Wu et al. 2005). Once established, bullfrogs are difficult to eradicate because they can persist at low densities, have high fecundity and negative density dependence, and can disperse through water or overland (Doubledee et al. 2003, Govindarajulu et al. 2005, Adams and Pearl 2007, Peterson et al. 2013).

Bullfrogs are now distributed around much of the US and southern Canada, though their native range is eastern North America (Bury and Whelan 1984). They often occur in temperate and warm permanent water bodies, but their large native and introduced ranges indicate a wide environmental tolerance. Original introductions to western North America occurred more than 100 years ago, when bullfrogs were cultivated for human consumption and escaped from captivity (Jennings and Hayes 1985). More recent introductions can be traced to aquarium dumping, pest (mosquito) control, fishing bait, and hunting (Jennings and Hayes 1985, Boersma et al. 2006, Adams and Pearl 2007). Bullfrogs are now present in western national parks, including Yosemite in California (Drost and Fellers 1996), Big Bend in Texas (Dayton and Skiles 2007), and Grand Teton in Wyoming (Patla and Peterson 2004), which function as important havens for native species. Because invasive species' impacts can be permanent and irreversible (Vander Zander and Olden 2008), they threaten the National Park Service mission to manage park resources as "unimpaired for the enjoyment of future generations".

Here, we report the distribution of bullfrogs, their overlap with one of the native amphibians, and

stomach contents of post-metamorphic bullfrogs in Grand Teton National Park. Our goals are to define the spatial extent of the invasion of this non-native species, identify which prey taxa in Grand Teton National Park may be vulnerable to the consumptive effects of bullfrogs as predators, and describe the relative contribution of native and non-native prey to its diet. Knowledge about the distribution and potential effects of bullfrogs is needed to prioritize control efforts for them relative to other looming conservation issues faced by national parks.

Bullfrogs were first documented in the 1950s in Kelly Warm Spring (hereafter, KWS), a geothermal pond near the Park's southeastern border (Figure 1; Patla and Peterson 2004). Bullfrogs are now established in KWS and in Savage Ditch (hereafter, SD), the irrigation canal that drains KWS (Figure 1). Bullfrogs have also been reported in waters on the park's southern boundary (Lake Creek irrigation canal), but these reports have not been confirmed (personal communication, K. Mellander, Grand Teton National Park). Because KWS and SD are hydrologically connected and adjacent to other freshwater habitats (e.g., the Snake River and Gros Ventre River [Figure 1]), there is potential for bullfrog spread into these waters which also provide habitat for the park's four native amphibians: Columbia spotted frog (*Rana luteiventris*), western tiger salamander (*Ambystoma mavortium*), western toad (*Anaxyrus boreas*), and boreal chorus frog (*Pseudacris maculata*) (Ray et al. 2014). Bullfrog overlap with these native amphibians would be of concern since bullfrogs have been implicated as a factor in native amphibian declines throughout the West (Hayes and Jennings 1986, Kiesecker et al. 2001, Pearl et al. 2004).

✦ METHODS

Study area

We conducted this study in valley bottom habitats within the southern section of Grand Teton National Park (Figure 1). This area is atypical bullfrog habitat because it is high elevation (~2000 m) and has long, cold winters with 440 (±129 SD) cm of snow annually (NCDC COOP Station 486428). Summer air temperatures are cool (5 – 27 °C), with occasional drops to below freezing. The Snake River flows north to south through the western portion of this valley, while the Gros Ventre River flows northeast to southwest along the park's southern border.

We focused our diet study in the KWS complex, an approximately 60 × 90 m geothermal pond located on the eastern perimeter of Grand Teton

National Park (12N 530948, 483189 UTM; elevation 1989 m). This pond is heavily visited and park-goers have released multiple non-native aquarium species that have successfully established. These include goldfish (*Carrasius auratus*), convict cichlids (*Archocentrus nigrofasciatus*), swordtails (*Xiphophorus hellerii*), guppies (*Poecilia reticulata*), tadpole madtoms (*Noturus gyrinus*) and red-rimmed melania snails (*Melanoides tuberculata*). The KWS complex is less than 1 km overland from the Gros Ventre River, and is hydrologically connected to Ditch Creek, which flows into the Snake River less than 10 km away (Figure 1).

Riparian vegetation along the KWS shoreline consists of willows, grasses, and shrubs with little overhanging canopy cover. A small portion (~15 m) of the perimeter is bare due to human and wildlife trampling of vegetation. From July through September 2015, dense mats of floating algae covered approximately half of the water's surface. During this same season, water temperatures ranged from 20-30° C depending on distance away from the geothermal inputs. Soft-bottomed substrate (e.g., mud and silt) dominated the habitat, though gravel and small cobbles occurred near the geothermal inputs. Maximum pond depth was 1.3 m, but 60% of the pond was less than 0.5 m.

Savage Ditch drains KWS and flows west/northwest along the valley floor and was built to supply irrigation to local hayfields and pastures prior to park designation (Marlow and Anderson 2011). Riparian vegetation bordering the ditch is dominated by sagebrush (*Artemisia tridentata*), with no overhanging canopy cover. From July through September 2015, water temperatures ranged from 17-28° C. Substrate varied from soft-bottomed mud to cobble embedded in silt. Water depths (n = 105 point measurements) ranged from 0.1 – 0.6 m across our surveyed area.

Field sampling

Bullfrog Distribution -- We used daytime visual and dip-net surveys (Thomas et al. 1997) to describe the bullfrog distribution in Grand Teton National Park during three time periods: 14–16 August 2014, 7 July 2015, and 17–22 August 2015. For surveys, we walked along the water's edge, visually scanned the water and shore, and made dip-net sweeps once every three steps to determine the presence of egg, larval, metamorphic, and post-metamorphic bullfrogs and native amphibians between 08:00 and 20:00 hours (Sepulveda et al. 2015a). For August 2015 surveys, we used a dual-observer approach to estimate
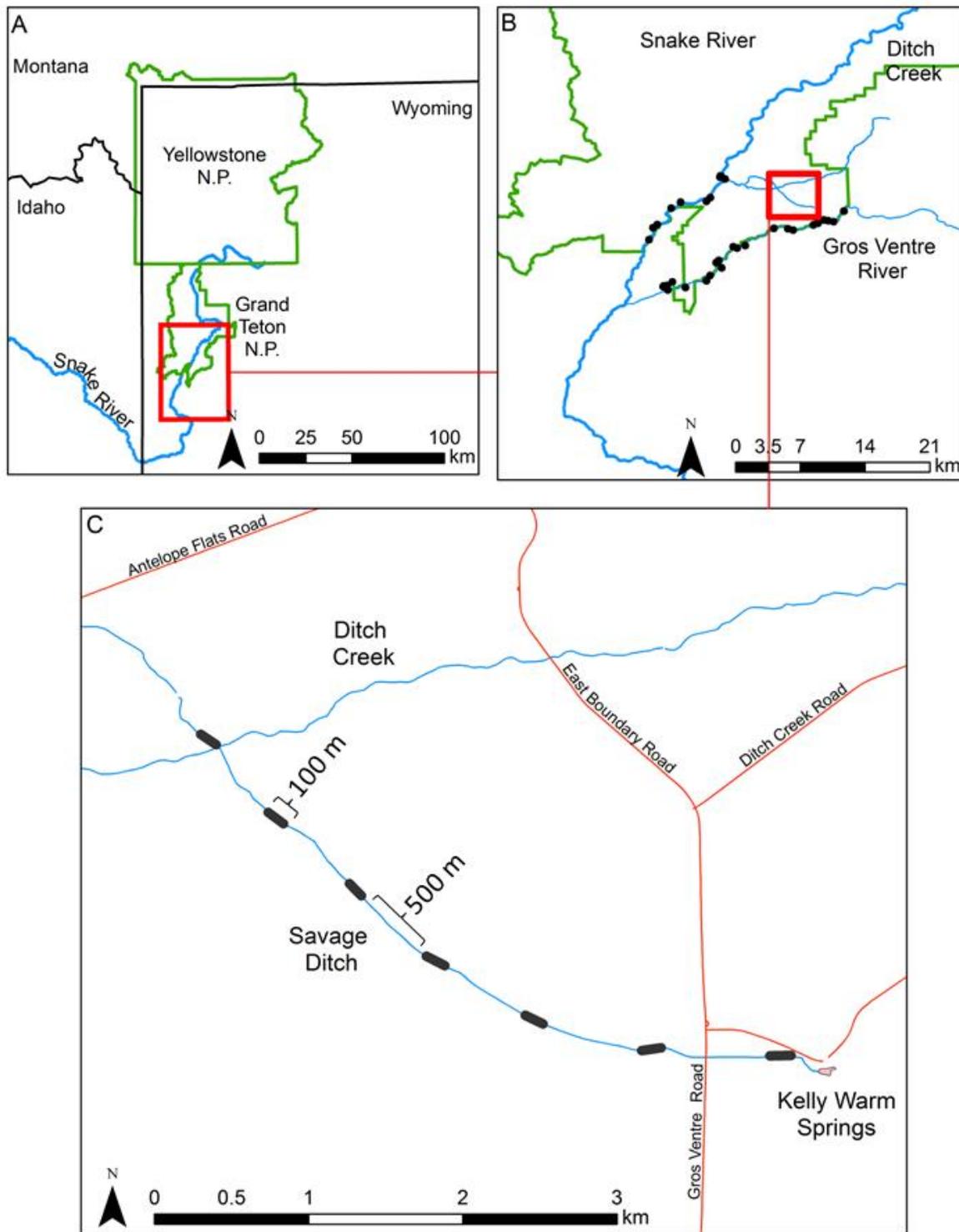
Figure 1. Location of American Bullfrog survey sites in Kelly Warm Spring, Savage Ditch, the Gros Ventre River, and the Snake River in and near Grand Teton National Park, WY (A). Filled circles in panel B are locations of surveys for bullfrogs. Thick black lines in panel C show reach locations and lengths for bullfrog abundance and diet studies in Savage Ditch.

detection probability in a single visit, where two independent surveys were conducted at each site by two trained observers on a single visit (Gould et al. 2012). Safety concerns (e.g., wildlife) necessitated surveying during daylight hours. Diurnal surveys are effective at detecting eggs, tadpoles, and recent metamorphs (e.g., Gould et al. 2012, Sepulveda et al. 2015a), but nocturnal surveys can be more effective for detecting post-metamorphic ranid frogs (Fellers and Kleeman 2006).

During all three time periods, we surveyed (1) the entire perimeter of KWS, (2) the entire length of SD from its source to the Antelope Flats Road, (3) 1 km upstream and downstream of the Ditch Creek confluence with SD, and (4) backwaters of the Gros Ventre River proximate to KWS (Figure 1). In August 2015, we added surveys of randomly selected backwater and side channel habitats of the Gros Ventre River and Snake River (Figure 1). The park border delineated the upstream and downstream boundary for the Gros Ventre River survey. In the Snake River, the upstream boundary was 5 km upstream of the Ditch Creek mouth and the downstream boundary was the park border. We based the Snake River upstream boundary on the assumption that Ditch Creek is the likely movement corridor for bullfrogs. Within this study frame, we used the National Wetlands Inventory layer and aerial imagery to identify lacustrine, palustrine, and riverine wetland habitat types associated with each river (Cowardin et al. 1979, USDI Fish and Wildlife Service 2012). We then used a random tessellation approach to select 25 sites in each river (e.g. Sepulveda et al. 2015a).

Bullfrog Diet -- We observed bullfrogs in KWS and SD in August 2014 and July 2015 surveys, so we collected post-metamorphic bullfrogs (i.e., individuals with four legs and no tail) in these two habitats. To capture bullfrogs for diet analyses, we used a Smith-Root LR-24 backpack electrofisher (250–300 V, pulsed DC; Smith-Root; Vancouver, WA) to shock bullfrogs around the shore of KWS and in seven reaches in SD; reaches were 100 m long and separated by 500 m (Figure 1). We located our SD sampling reaches starting at the most downstream point where we had previously observed bullfrogs (100 m downstream of where SD intersects Ditch Creek; UTM 12 T 528040, 4834000 N). For KWS, we focused electrofishing efforts within 2 m of the shore. For SD reaches, we sampled in an upstream direction and focused electrofishing efforts within 2 m of each bank. Within KWS and each reach, we sampled for post-metamorphic bullfrogs within three discrete time periods: 14-16 July, 20-21 August, and 29 September – 1 October 2015. Temporal sampling allowed us to

make inferences about seasonal differences in diet. Due to safety concerns, all electrofishing occurred during daylight hours.

We measured bullfrog snout-vent-length (SVL; mm) with calipers and we recorded their wet weight (g) with a handheld spring scale. We did not attempt to distinguish between juveniles and adults, as this can be difficult without dissection and size alone is not a consistent predictor. In July and August, we used gastric lavage to sample stomach contents from a random subset of up to 15 post-metamorphic bullfrogs in each reach and in KWS. The random subset was selected in proportion to the observed size distribution of all post-metamorphic bullfrogs captured in each reach and KWS. Because the number of stomachs that could be analyzed was constrained by resources, these steps helped to ensure spatial representation of bullfrog diets across a gradient of bullfrog SVLs. For any bullfrogs that died during capture or handling, we excised stomachs to verify that gastric lavage removed all stomach contents. We released bullfrogs near the middle of their respective reaches. In September 2015, we sacrificed all bullfrogs and removed a representative subset of their stomachs. All stomachs and stomach contents were stored in ethanol until analyses by Rhithron Associates (Missoula, Montana), who identified prey items to the lowest possible taxonomic unit and measured blotted wet weights.

Analyses

For August 2014 and July 2015 surveys, we reported bullfrog and native amphibian occurrence as presence only since we did not estimate survey-specific detection probabilities. No bullfrogs were observed during the August 2015 dual-observer surveys so we did not estimate occupancy probabilities.

Based on observed diets, we *a posteriori* binned bullfrogs into three categories for diet analyses: (1) those with only invertebrates in their stomach contents and (2) those that also had aquatic vertebrates and/or (3) terrestrial vertebrates (Table 1). We assumed that these categories helped standardize comparisons by accounting for ontogenetic constraints, such as gape-width limitations (Werner and Gilliam 1984, Werner et al. 1995). We then used two-way analysis of variance (ANOVA) to test if bullfrog SVL (log-transformed) differed by these three ontogenetic categories, by month, and by the interaction of ontogenetic categories and month. All parametric statistical assumptions could not be satisfied because so few bullfrogs consumed aquatic vertebrates each month, so we confirmed our analyses

Table 1. American Bullfrogs whose stomachs contained only invertebrates and those that also contained aquatic vertebrates and terrestrial vertebrates, their corresponding snout-to-vent lengths (SVL), and number sampled during July, August, and September 2015 in the Kelly Warm Spring complex of Grand Teton National Park, Wyoming.

Diet category	SVL (mm)		Month			
	Mean (± 1SE)	Range	Jul	Aug	Sept	*total*
Invertebrate	64 (2)	21 – 140	18	27	29	74
Aq. vertebrate	72 (6)	50 – 96	3	3	2	8
Ter. vertebrate	120 (6)	96 – 153	2	10	2	14

using Wilcoxon nonparametric comparisons. Parametric and nonparametric results were in concordance, so we only report results of the two-way ANOVA tests.

We additionally used the Amundsen modified-Costello method (1996) to assess the contribution of prey to bullfrog diets within each ontogenetic category. Prey were pooled into taxonomic categories for analysis. We pooled invertebrates by order, fish by species, amphibians by family and small mammals by superfamily (Table 2). Heavily digested items that could not be resolved to a prey category were not included in analyses. We calculated the prey-specific abundance (PSA_i) and the percent occurrence ($\%O_i$) for each prey category (i) as follows:

$$PSA_i = 100 \times \frac{\sum S_i}{\sum S_{ti}}$$
$$\%O_i = 100 \times \frac{J_i}{P}$$

where S_i equals the wet mass of prey i in stomachs, S_{ti} equals the total wet mass of prey in predators that contain prey i. Percent occurrence, O_i, equals the number of bullfrogs (J) containing prey i divided by the number of frogs with food in their stomachs (P). To explore patterns of relative prey category importance for each month, we constructed bivariate plots of PSA_i versus $\%O_i$. When plotted in this fashion, graphical techniques can be used to evaluate relative prey dominance and the degree of homogeneity of the diet (Amundsen et al. 1996, Chipps and Garvey 2007).

✦ **RESULTS**

Bullfrog distribution

In August 2014, we observed all stages of bullfrogs in KWS, including two egg masses. In SD, we observed post-metamorphic bullfrogs up to 1.7 km downstream of KWS and bullfrog larvae up to 5 km downstream. No bullfrogs were observed in surveyed habitats within Ditch Creek or the Gros Ventre River.

In July 2015, we observed all stages of bullfrogs in KWS including one egg mass. In SD, we documented post-metamorphic bullfrogs 3.6 km downstream of KWS and bullfrog larvae 5 km downstream of KWS. We also observed two post-metamorphic bullfrogs in Ditch Creek, ~30 m downstream of the SD crossing. We did not observe bullfrogs in surveyed habitats in the Gros Ventre River. In August 2015, we did not observe any bullfrogs in surveyed habitats in Ditch Creek, the Gros Ventre River, or the Snake River.

The western toad was the only native amphibian species we observed in habitats where bullfrogs occurred. During all survey periods, we documented presence of western toad larvae, metamorphs and post-metamorphs in SD, immediately downstream of the crossing. We also documented presence of toad metamorphs and post-metamorphs in Ditch Creek, immediately downstream of the crossing. We did not observe toads or the other three native amphibian species in other surveyed sites.

Bullfrog diet

We lavaged the stomach contents of 112 bullfrogs across our sampling periods (Table 1). Sixteen bullfrogs had empty stomachs, so we used the remaining 96 individuals for diet analyses. The size distribution of bullfrogs used in diet analyses was comparable to the size distribution of all bullfrogs captured (Figure 2). We dissected stomachs from four bullfrogs in July, three bullfrogs in August and three bullfrogs in September and found gastric lavage successfully removed all visible stomach contents.

Seventy-four of the 96 individuals with discernable prey items in their stomachs only consumed invertebrates, while eight individuals also consumed aquatic vertebrates, and 14 individuals also consumed terrestrial vertebrates (Table 1). Diet composition differed significantly by bullfrog SVL ($F_2 = 38.80$, $P < 0.01$). Bullfrogs that consumed terrestrial vertebrates were significantly larger than bullfrogs in the other two ontogenetic categories, while bullfrogs that consumed aquatic invertebrates were not

Table 2. Prey-specific abundance by weight (*PSA_i*) and percent occurrence (*O_i*) of prey in the stomach contents of American Bullfrogs whose stomachs contained only invertebrates (A) and those that also contained aquatic vertebrates (B) and terrestrial vertebrates (C) from the Kelly Warm Spring complex in Grand Teton National Park, Wyoming in July, August and September 2015. Dashed lines indicate values that were less than 1%.

| | | A | | | | | | B | | | | | | C | | | | | |
| | | *PSA_i* | | | *O_i* | | | *PSA_i* | | | *O_i* | | | *PSA_i* | | | *O_i* | | |
		Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep	Jul	Aug	Sep
Inverte-brate	Araneae	6	1	3	50	26	24	3	-	-	67	67	-	-	-	-	-	40	-
	Coleoptera	28	4	12	72	30	45	6	-	2	67	33	50	-	-	-	-	-	-
	Dermaptera	4	-	-	28	7	-	-	-	-	-	-	-	-	-	-	-	10	-
	Diptera	7	34	7	39	44	66	-	6	-	-	100	50	-	-	-	-	10	-
	Hemiptera	2	-	-	28	33	10	1	-	-	33	-	100	-	-	-	-	20	-
	Hymenoptera	11	3	2	39	44	38	-	3	-	33	33	50	-	-	-	-	10	-
	Lepidoptera	5	1	3	6	7	17	18	3	-	67	33	100	-	-	-	-	30	-
	Lymnaeidae	2	-	-	22	-	3	-	-	-	-	-	-	-	-	-	-	10	-
	Odonata	16	48	3	11	19	10	-	-	11	-	33	50	-	-	-	-	-	-
	Orthoptera	4	4	-	6	11	-	-	-	-	-	-	-	-	1	-	-	10	-
	Physidae	7	-	17	6	-	7	-	-	-	33	-	-	-	-	-	-	10	-
	Planorbidae	4	1	44	6	7	34	3	-	12	33	-	50	-	-	-	-	10	-
	Succineidae	5	1	-	22	11	-	-	-	-	-	33	-	-	-	-	-	-	-
	Thiaridae	-	3	10	6	19	21	-	-	-	33	-	-	-	-	-	-	-	-
	Thysanoptera	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
	Other	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	10	-
Fish	N. gyrinus	-	-	-	-	-	-	-	83	-	-	33	-	-	-	-	-	-	-
	X. hellerii	-	-	-	-	-	-	6	-	-	33	33	-	-	-	-	-	-	-
	Other	-	-	-	-	-	-	64	4	24	67	33	50	-	-	-	-	10	-
Amphibian	Ranidae	-	-	-	-	-	-	-	-	51	-	-	50	-	-	-	-	-	-
Mammal	Muroidea	-	-	-	-	-	-	-	-	-	-	-	-	100	98	100	100	100	100

significantly larger than those that only consumed invertebrates (Tukey HSD; Table 1). These relationships did not vary by month ($F_2 = 1.35$, $P = 0.26$).

For the bullfrogs that only consumed invertebrates, the types of consumed invertebrates varied among individuals and sampling periods (Table 2). In July, bullfrog diets had high within individual variation (i.e., low *PSA_i* and high *O_i*; Figure 3). Most individuals consumed a variety of invertebrates, especially adult life stages of beetles (Tenebrionidae), ramshorn snails (Planorbidae), and spiders (Araneae).

In August, bullfrogs demonstrated high between individual variation (i.e., high *PSA_i* and low *O_i*; Figure 3). A few individuals had high *PSA_i* for dragonfly adults (Anisoptera) and hoverfly adults (Syrphidae), but most individuals had low *PSA_i* for multiple orders of invertebrates. In September, bullfrogs displayed a specialist feeding strategy (i.e.,

high *PSA_i* and high *O_i*; Figure 3) on ramshorn and bladder snails (Physidae).

Few bullfrogs consumed aquatic vertebrates each month (Table 1). In July and August, the six sampled bullfrogs specialized on tadpole madtom fish but invertebrates were rare prey items (i.e., low *PSA_i* and low *O_i*; Figure 3). In September, only two sampled bullfrogs consumed aquatic vertebrates. One bullfrog consumed a larval frog in the true frog (Ranidae) family, but this prey item was too heavily digested to further resolve. Given that the only ranids we documented in KWS and SD were bullfrogs, this was likely evidence of cannibalism. The other bullfrog consumed a tadpole madtom fish and dragonfly adult.

Bullfrogs that consumed terrestrial vertebrates consumed little else besides small mammals in the superfamily Muroidea in July, August and September. Nine of the 15 Muroidea documented were identified as meadow voles (*Microtus*

pennsylvanicus); the remaining six were too heavily digested to further resolve. For each of these months, PSA_i and O_i were ~ 100% for Muroidea (Figure 3). These bullfrogs also consumed fish and invertebrates, but they were rare prey items.

Native taxa were dominant prey (high PSA_i and O_i values) and constituted the majority of prey items documented in bullfrog stomachs in all months. All 96 bullfrog stomachs contained at least one native prey item, while only 14 of these stomachs contained at least one non-native prey item. Red-rimmed melania snails, tadpole madtoms and swordtail fish were the only nonnative prey we documented in bullfrog diets. Only bullfrogs in the invertebrate and aquatic vertebrate categories consumed red-rimmed melania snails, and PSA_i and O_i values for this prey ranged from 0 – 10% and 6 – 33% (Table 2). Since all documented aquatic vertebrate species in bullfrog diets were non-natives, bullfrogs in the aquatic vertebrate ontogenetic category had much higher PSA_i and O_i values for non-native taxa. Only one bullfrog in the terrestrial vertebrate category consumed a non-native fish, so PSA_i and O_i values of nonnatives were low (Table 2).
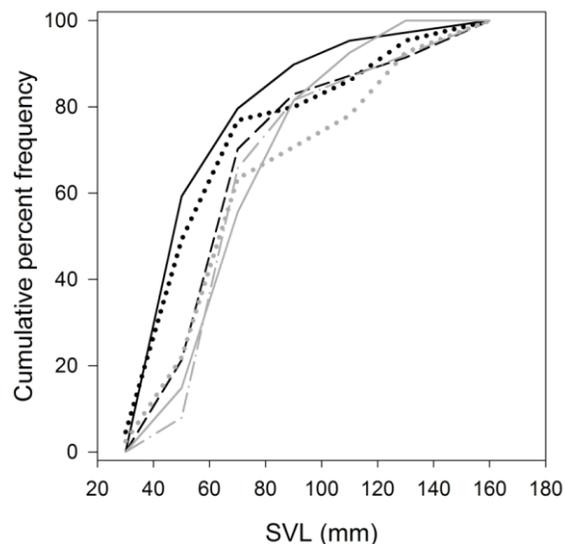

Figure 2. Cumulative percent frequencies of the snout-vent-lengths (SVL; mm) of American Bullfrogs captured in Kelly Warms Spring and Savage Ditch in July (solid lines), August (dotted lines), and September (dashed lines). Black lines describe all captured bullfrogs, while gray lines show the subset used for diet analyses.
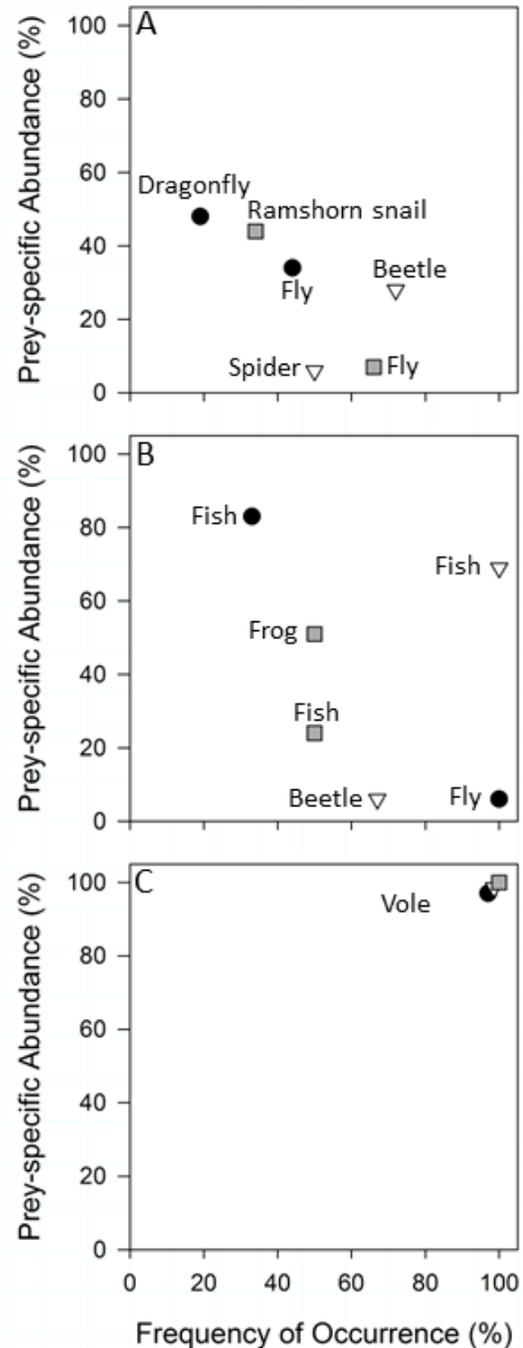

Figure 3. Prey-specific abundance by weight (PSA_i) versus percent occurrence (O_i) for stomach contents of American Bullfrogs that only consumed invertebrates (A) and those that also consumed aquatic vertebrates (B) and terrestrial vertebrates (C) in July (open triangles), August (gray squares), and September (filled circles) 2015. Only the top two taxa that had the largest PSA_i and O_i values are displayed.

✦ **DISCUSSION**

U.S. national parks form a cornerstone of biodiversity conservation because they provide well-connected landscapes and vital habitats that have relatively low anthropogenic disturbances. However, the introduction and establishment of invasive species can limit the ability of national parks to be safe havens for native species (Koel et al. 2005, Dorcas et al. 2012). In Grand Teton National Park, we documented the distribution and diets of invasive bullfrogs. Despite unconfirmed reports of bullfrogs near the park's southern boundary, we only observed bullfrogs in waters connected to KWS. In this warm spring complex, bullfrogs only overlapped with a native amphibian (western toad) at the downstream extent of the bullfrog distribution and we did not document bullfrog consumption of this native amphibian. Rather, larger bullfrogs (SVL ≥ 96 mm) primarily consumed native rodents, while smaller bullfrogs frequently consumed native invertebrates and less frequently consumed non-native invertebrates and fish. Taken together, these data suggest that the bullfrog distribution appears to be localized at present, so their effects are also likely to be localized but largely concentrated on native taxa. Abundance data on bullfrogs and their prey are necessary for placing bullfrog consumption patterns into context relative to other mortality sources on these prey items and to determine if bullfrog predation is limited to these native taxa.

Our survey results suggest that bullfrog range expansion, and therefore consumptive impacts, are limited in Grand Teton National Park. Bullfrogs were introduced to KWS in the 1950s (Patla and Peterson 2004), but they appear to have only extended their range ~5 km downstream to SD and an adjacent habitat in Ditch Creek in the past 60 years. We documented evidence of bullfrog reproduction (e.g., larvae as small as Gosner stages 23-25) throughout this 5 km section in SD, but not in Ditch Creek. We do not know if the larvae originated in SD (indicating local establishment) or if they dispersed from upstream. Regardless, this limited spread contrasts with the much broader spread of bullfrogs in other invaded waters. For example, bullfrogs in the Yellowstone River in southcentral Montana spread roughly ten times this distance in three years (Sepulveda et al. 2015a) and molecular evidence suggests that this spread was natural and not aided by human secondary translocations (Kamath et al. 2016). In southwest France, bullfrogs have spread to over 2,000 km^2 since their introduction in the 1960s but this spread was likely facilitated by secondary translocations (Ficetola et al. 2007a). The Snake and Gros Ventre Rivers are ~8 km and 1 km, respectively, from KWS– overland distances that bullfrogs in other systems have moved without the aid of human secondary translocations (e.g., 10 km overland in a week in southern Arizona [Suhre 2010] and 1.2 km between June and July in Missouri [Willis et al. 1956]). Despite their proximity, we did not observe bullfrogs in lentic or slower-moving waters associated with the Snake or Gros Ventre rivers. Barriers to bullfrog spread in Grand Teton National Park likely exist since bullfrogs have been present in the KWS complex since the 1950s but have not been documented in neighboring waters.

We suspect habitat suitability is a barrier to bullfrog spread in Snake River habitats. Surveyed sites in August 2015 were spring-influenced and had cold water temperatures < 10° C, which are not conducive to bullfrog rearing or growth (Lillywhite 1970, Viparina and Just 1975). However, summer water temperatures in the Gros Ventre River were much warmer (> 20° C) and comparable to KWS and SD, suggesting that these habitats could have at least seasonal suitability; we have no data on their suitability as overwintering habitat. Post-metamorphic bullfrogs in their native range and in other areas of their introduced range are known to seasonally use habitats, even if they are not conducive to breeding or overwintering (Gahl et al. 2009, Peterson et al. 2013). Thus, factors other than temperature may limit bullfrog spread to these thermally-suitable habitats. Factors that may limit overland dispersal and spread include cold nighttime temperatures and low humidity associated with the high-elevation (~2,000 m) of KWS and SD. Nevertheless, further detection surveys using more sensitive methods, like environmental DNA (e.g., Ficetola et al. 2008), are warranted to confirm bullfrog absence given the proximity of these habitats to KWS, the low capture probabilities documented in SD and KWS (*unpublished data*), and the high and consistent source of bullfrog propagules in KWS and SD.

We found that bullfrog diet contents were related to bullfrog size. The smallest bullfrogs we sampled (SVL 21 – 49 mm) consumed only invertebrates, while larger bullfrogs (SVL 50 – 95 mm) consumed small fish and tadpoles in addition to invertebrates, and the largest bullfrogs (SVL ≥ 96 mm) primarily consumed voles (the largest prey items we documented). These size-based diet patterns are common in bullfrogs (Werner et al. 1995) and likely reflect ontogenetic shifts in gape-width as small bullfrogs were too small to eat fish, medium bullfrogs were large enough to eat fish but too small to eat voles, and large bullfrogs were big enough to eat voles. In

addition to anatomical constraints, these size-based diet patterns may also reflect different habitat use by large and small bullfrogs, as large bullfrogs were frequently captured along the water's edge while smaller bullfrogs were captured within KWS or SD. Evidence of ontogenetic shifts in bullfrog diets underscores the importance of incorporating size-structure into implications of bullfrog invasions. Specifically, populations dominated by smaller juveniles will have different impacts than populations dominated by larger adults.

Bullfrogs that consumed terrestrial vertebrates consumed little else besides small rodents in the superfamily Muroidea. In fact, PSA_i and O_i were ~ 100% for all three sampling periods (Figure 3), which indicates that this was an energetically important and common resource that larger individuals specialized on. This contrasts with previous research that showed large prey items (such as mice) to have lower occurrence than small prey items (such as invertebrates) (e.g., Bury and Whelan 1984, Hirai 2004, Jancowski and Orchard 2013, Quiroga et al. 2015). For sit-and-wait predators like large bullfrogs, consumption of prey that are large relative to the predator is predicted to maximize energetic potential. In general, preying upon few, large prey rather than many, small prey minimizes the costs associated with predation, including metabolic expenditure and risk of injury or predation (Cooper et al. 2003, Costa 2009, Werner and Gilliam 1984). Given these first principles and our observation that large bullfrogs in KWS and SD consumed little else besides small rodents, it is likely that small rodents were readily available or that large bullfrogs were highly selective for small rodents because the costs associated with predation are large.

Smaller bullfrogs had a more generalized diet, consisting mostly of invertebrates and occasionally fish and tadpoles. The taxonomic identities of invertebrates shifted across seasons, an expected pattern if bullfrogs tracked seasonal pulses in aquatic and terrestrial prey availability. Aquatic invertebrates were important (high PSA_i or O_i) prey items, especially dragonflies in July and August and native and non-native snails in September. Terrestrial invertebrates, like the adult life-stages of the beetle family Tenebrionidae in July, were energetically important and frequent prey items and other terrestrial invertebrates, like spiders and grasshoppers, were rare prey during each sampling period. Frequent consumption of terrestrial prey by larger bullfrogs contradicts the general patterns of other bullfrog diet studies, where aquatic prey constituted a substantial portion of bullfrog diets (Bury and Whelan 1984,

Werner et al. 1995, Wu et al. 2005). Inputs of terrestrial invertebrates into aquatic ecosystems are often associated with closed-canopy riparian zones (e.g., Baxter et al. 2005), however, KWS and SD have minimal canopy cover so a better understanding of how bullfrogs access terrestrial inputs is warranted in this system. Small and large bullfrogs in KWS and SD may be more vulnerable to capture and control efforts if they consume terrestrial prey near the water's edge or on land.

Native prey items were present in every stomach sample we analyzed, while non-native prey occurred in ~ 15% of stomachs. Non-native prey included one putative bullfrog larva, several tadpole madtom and swordtail fishes, and multiple red-rimmed melania snails. Cannibalism is frequent in other introduced, abundant bullfrog populations (Wu et al. 2005, Quiroga et al. 2015), so the single observation of a putative bullfrog larva was unexpected given that we captured at least 225 post-metamorphic bullfrogs and more than 900 larvae during the 2015 sampling season (*unpublished data*). Future studies of native and non-native prey abundance in the KWS/SD complex may help to contextualize these unexpected results.

The bullfrog distribution and consumptive impacts are localized at present to KWS and SD, though changing environmental conditions that increase seasonal and overwintering habitat suitability may allow bullfrogs to expand their range and impacts in this region. Evidence for this scenario is found in the positive relationship between bullfrog occurrence and maximum temperatures observed across their native and nonnative distributions (Ficetola et al. 2007b), rapidly warming air temperatures in this region (Sepulveda et al. 2015b) and our discovery of bullfrogs in habitats along Ditch Creek. However, our lack of bullfrog detections in the Gros Ventre River suggests that factors in addition to temperature and dispersal distance limit bullfrog spread in Grand Teton National Park. Future bullfrog studies in this region should closely track factors in addition to water temperature that are sensitive to climate change and may affect bullfrog spread and establishment in riverine habitats, such as hydroperiods of backwaters, flow magnitude and flow timing (Ray et al. 2016; Al-Chokhachy et al., *in press*).

Managers will need to weigh the impacts of potential bullfrog range expansion against the costs of an eradication effort of the current population. Generally, eradication of invasive species is a difficult endeavor, but can be tractable when an area of infestation is small and contained (Rejmánek and

Pitcairn 2003, Simberloff 2009, Sepulveda et al. 2012). Though the bullfrog population in Grand Teton National Park has been established for ~60 years, our research suggests that this population is currently localized and should therefore be vulnerable to eradication.

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