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Prey Availability and Foraging Events of the Northern Mexican Gartersnake (*Thamnophis eques megalops*) in North-central Arizona

The Northern Mexican Gartersnake (*Thamnophis eques megalops*) is a generalist mesopredator and wetland and riparian obligate distributed in Arizona, New Mexico, and northern Mexico (Degenhardt et al. 1996; Rossman et al. 1996; Brennan and Holycross 2006). Extensive population declines have been documented throughout the range of the species in the United States with potential drivers including the introduction of nonnative predatory species, loss of native prey, and habitat loss. Based on these declines, the U.S. Fish and Wildlife Service (USFWS) listed *T. e. megalops* as federally threatened under the Endangered Species Act on July 8, 2014 (USFWS 2014) with viable populations occurring in north-central, western, and southern Arizona.

The USFWS identified "harmful nonnative species" including the American Bullfrog (*Lithobates catesbeianus*), spiny-rayed predatory fish in the families Centrarchidae and Ictaluridae, and the crayfish *Orconectes virilis* and *Procambarus clarkii* as the leading threat to the survival of *T. e. megalops* throughout its range in the United States (USFWS 2014). Confirmed depredation events on neonates and adults by *L. catesbeianus* and Largemouth Bass (*Micropterus salmoides*) have been documented in previous studies (Rosen and Schwalbe 1995; Young and Boyarski 2013). In addition, potential negative interactions with nonnative species include competition for native prey species (Rosen and Schwalbe 2002; Holycross et al. 2006) and injury or mortality when snakes prey on centrarchid and ictalurid fish and swallow spines (USFWS 2014; Boyarski et al. 2015). Based on these perceived threats, two of the primary constituent elements (PCEs) deemed essential to the conservation of *T. e. megalops* in the proposed rule for designation of critical habitat are: 1) a prey base consisting of viable populations of native amphibian and native fish species; and 2) the absence or occurrence of nonnative aquatic predatory species at "low enough levels such that recruitment of northern Mexican gartersnakes and maintenance of viable native fish or soft-rayed, nonnative fish populations (prey) is still occurring" (USFWS 2013).

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While an appropriate aquatic prey base is considered a significant factor in *T. e. megalops* recovery and long-term survival, dietary descriptions are limited to relatively few studies and records in Arizona and northern Mexico (García and Drummond 1988; d'Orgeix et al. 2013; T. Cotten, T. Sprague, pers. comm.). The species is thought to rely primarily on native, small-bodied prey including annelids, leopard frog (*Lithobates* sp.) adults and tadpoles, Mexican Spadefoot (*Spea multiplicata*) adults, Woodhouse's Toad (*Anaxyrus woodhousii*) juveniles and tadpoles, and Western Tiger Salamander (*Ambystoma mavortium*) larvae (USFWS 2014). However, nonnative aquatic vertebrates have also been identified as potential food sources, including *L. catesbeianus* juveniles and tadpoles, soft-rayed fish including the Western Mosquitofish (*Gambusia affinis*) and the Red Shiner (*Cyprinella lutrensis*) (S. Lashway, T. Sprague, pers. comm.), and Goldfish (*Carassius auratus*), a nonnative spiny-rayed cyprinid fish (García and Drummond 1988).

Building on previous dietary accounts, we investigated potential prey availability and confirmed prey use for *T. e. megalops*, as part of a larger study to determine population demography, habitat use, and spatial behavior for the species along the upper-middle Verde River in north-central Arizona (Emmons and Nowak 2016). Here, we present additional prey records that provide a greater understanding of *T. e. megalops* diets, with implications for critical habitat elements deemed essential for the survival of this federally threatened species in the United States.

Methods.— Study sites were located along the upper-middle Verde River (Yavapai County, Arizona) and featured relatively wild, undeveloped riparian corridors along the perennial Verde River, which is listed as one of five remaining United States localities that contain potentially viable populations of the species in question (USFWS 2014). One of the sites also contained artificial lagoons fed by diversions from the main stem river. Due to the vulnerable status of *T. e. megalops* we have withheld specific site name information to protect snakes at the study locations. We pooled data from sites because there is potential genetic and reproductive connectivity between subpopulations of gartersnakes (D. Wood, pers. comm.), they share a similar assemblage of potential aquatic prey species, and they are included in the same sub-basin unit as described in the designation of critical habitat proposed rule (USFWS 2013).

We recorded total numbers of potential prey captured in self-baiting Gee™ minnow traps (e.g., Nowak and Santana-Bendix 2002; Holycross et al. 2006). We defined potential prey as invertebrates and vertebrates identified in previous diet studies for *T. e. megalops* and similar aquatic gartersnake species, including spiny-rayed fish. Furthermore, we categorized all *L. catesbeianus* and *A. woodhousii* (the two potential anuran species present at the study sites) by age class to maintain consistency with the USFWS final listing rule, where juveniles and tadpoles, but not subadults or adults, of both species were identified as potential prey (USFWS 2014). We used the following categories: adult (≥ 135 mm), subadult (< 135 mm and ≥ 80 mm), juvenile (< 80 mm), and tadpole for *L. catesbeianus*; and adult (≥ 60 mm), juvenile (< 60 mm), and tadpole for *A. woodhousii*, based on previous studies conducted in Arizona (Sullivan 1983; T. Jones, pers. comm.). Survey effort was measured in trap-hours (the number of traps multiplied by the number of hours traps were open) and calculated for each sampling trip from the median time of the first day when traps were set and opened to the last day when traps were closed and removed. We determined relative prey availability by calculating the mean number (± 1 SE) of each species captured per trap-hour per sampling trip, to standardize survey effort and account for differences in duration and intensity between trips. Minnow traps were checked and emptied at least once per day in 2012–2013, and two times per day in 2014. All potential prey were removed on a daily basis (2012 and May–August 2013–2014) or every other day (September–November 2013–2014) to prevent mortality during trapping sessions.

We recorded prey to species when possible that were in the process of being consumed or regurgitated by *T. e. megalops* captured in Gee™ minnow traps and through opportunistic encounters, including while tracking radio-telemetered snakes (Nowak 2006; Boyarski et al. 2015; Emmons and Nowak 2016). We did not induce regurgitation through palpation, as previous studies suggest the method results in short-term negative impacts on snakes through increased hormonal stress levels, and potential long-term impacts via injury or mortality through hemorrhaging (Schuett et al. 2002; Fauvel et al. 2012). This precaution seemed particularly prudent given the conservation status of *T. e. megalops*, and the possibility for spiny-rayed fish as prey items.

Gartersnakes were uniquely marked using heat cautery brands and passive integrated transponder (PIT) tags (Fagerstone and Johns 1987; Jemison et al. 1995; Winne et al. 2006) to identify the number of individual snakes with respect to the number of prey use events observed. We recorded measurements for captured *T. e. megalops* and confirmed prey, including gartersnake snout–vent (SVL) length, mass, and sex, total length (snout to tail tip) for fish and tadpoles, snout–urostyle length (SUL) for metamorphosed frogs and toads, and mass for snakes and prey species when possible. Anurans were identified to age class using the same categories as used in trap surveys. We also calculated prey-snake ratios for length and mass and calculated ratios (mean ± 1 SE) for length and mass, when measurements were available for prey items. Telemetered snakes in the process of consuming prey items contained surgically implanted internal radio transmitters; surgical procedures and care followed those of Hardy and Greene (1999), as modified in Nowak (2006) and Boyarski et al. (2015).

Results.—We conducted 22 minnow trap trips at the study sites for an estimated 122,738 trap-hours from May 2012 through November 2014 and detected 15,519 total of 12 different potential prey species, all aquatic vertebrates, including 10 nonnative species and two native species (Table 1). *Gambusia affinis* was the most frequently encountered nonnative potential prey species in minnow traps, comprising 37% (N = 5780) of the total captures with an availability rate of 0.046 ± 0.012 individuals/trap-hour (mean ± 1 SE), and Common Carp (*Cyprinus carpio*) was the least frequently encountered nonnative potential prey item, comprising < 0.1% (N = 2) of the total captures with an availability rate of 0.001 ± 0.001 individuals/trap-hour (mean ± 1 SE). *Anaxyrus woodhousii* tadpoles were the most frequently encountered native potential prey item, comprising 5% (N = 804) of the total captures with an availability rate of 0.004 ± 0.002 individuals/trap-hour (mean ± 1 SE), and *A. woodhousii* juveniles were the least frequently encountered native potential prey item, comprising < 0.1% (N = 3) of the total captures with an availability rate of 0.001 ± 0.001 individuals/trap-hour (mean ± 1 SE). No native fish species were represented in our samples, and no adult *L. catesbeianus* were captured in minnow traps. We documented > 94% nonnative aquatic vertebrates throughout our sampling efforts, including > 56% that were considered "harmful" as described in the USFWS final listing rule (USFWS 2014).

We observed 23 foraging events from 22 individual snakes consisting of 16 detections in minnow traps and seven opportunistic encounters during telemetry (Table 2). Prey consisted of four nonnative species and one native species with *L. catesbeianus* being the most frequently documented prey species consumed by *T. e. megalops* (16 of 23 events or 70%), including one adult, one subadult, five juveniles, and nine tadpoles. We documented 87% nonnative aquatic vertebrates used as prey, and > 83% that were considered "harmful" as described in the USFWS final listing rule (USFWS 2014). We collected mass measurements for 15 of the 23 prey, and they represented 1.6–32.4% of the respective gartersnake mass measurements, with a mean prey-snake mass ratio of 12.4% (± 2.6 SE). We collected length measurements for 19 of the 23 prey, and they represented 4.6–30.3% of the respective gartersnake SVL measurements, with a mean prey-snake SVL ratio of 14.9% (± 1.2 SE) (Table 3).

We encountered two telemetered snakes in the process of consuming adult anurans > 100 mm, including one female on 16 July 2014 that subdued and swallowed a relatively large (SUL = 147 mm) *L. catesbeianus* (Fig. 1). The same female on 21 April 2015 regurgitated an adult *A. woodhousii* (SUL = 106 mm; mass was not obtained due to the partially digested state of the prey item) on a subsequent date when the snake was recaptured for transmitter removal; the snake had a mass of 169.5 g and an SVL of 702 mm. A second female on 11 September 2014 was found consuming an adult *A. woodhousii* with an SUL of 122 mm (Fig. 2).

FIG. 1. *Thamnophis eques megalops* consuming adult *Lithobates catesbeianus* at the upper-middle Verde River, Yavapai County, Arizona.

FIG. 2. *Thamnophis eques megalops* consuming adult *Anaxyrus woodhousii* at the upper-middle Verde River, Yavapai County, Arizona.

FIG. 3. *Thamnophis eques megalops* with protruding fish spine from suspected *Ameiurus* sp. at the upper-middle Verde River, Yavapai County, Arizona.

FIG. 4. *Thamnophis eques megalops* with regurgitated *Ameiurus melas* and additional suspected *A. melas* as prey bolus mid-body with protruding spine at the upper-middle Verde River, Yavapai County, Arizona.

We recorded three events where nonnative, spiny-rayed fish were preyed upon by *T. e. megalops*, including *M. salmoides* and Black Bullhead (*Ameiurus melas*), and a suspected *Ameiurus* species. On 27 July 2013 one female snake regurgitated two juvenile *M. salmoides* after removal from a minnow trap. On 28 September 2013 we captured a male gartersnake with a spine from a suspected *Ameiurus* sp. protruding through the skin posterior to the head; the spine was safely removed and appeared to be the only remaining part of a prey item that was swallowed and successfully digested (Fig. 3). A male found opportunistically on 17 June 2014 was in the process of consuming one *A. melas* with a second prey bolus suspected to be the same species, with a pectoral spine protruding through the snake's midbody wall (Fig. 4).

Discussion.—Based on our survey efforts, nonnative species comprised the majority (> 94%) of potential aquatic vertebrate prey available to *T. e. megalops* at our study sites in north-central Arizona, and native fish species were absent or in such low numbers that they escaped detection. The potential prey availability and confirmed prey use records from minnow traps could be interpreted as biased due to artificial conditions that can concentrate and limit escape of species that snakes may not normally associate with food sources, and underestimation of larger-bodied prey items that were unlikely to access traps due to their terrestrial nature or the confining size of the funnel entrances. However, even when these possible biases are taken into account, our trap sampling efforts still suggest that potential aquatic prey availability is dominated by nonnative aquatic species in the upper-middle Verde River, a locality recognized by the USFWS to contain one of five remaining likely viable populations for *T. e. megalops* in the United States (USFWS 2014). Given that the snake populations at our study sites appear to

Table 1. *Thamnophis eques megalops* potential aquatic prey captured during minnow trap surveys in the upper-middle Verde River, Arizona, 2012–2014. Potential prey species are listed by their standard and scientific names, and anurans are categorized by age class. "Number" refers to total captures per potential prey species throughout the duration of the study, "%" refers to relative proportion of each potential prey species, and "Prey availability" refers to the mean number (± SE) of potential prey species captured per trap-hours per trap survey trip.

Potential Prey Species	Number	%	Prey availability
Nonnative			
Western Mosquitofish, *Gambusia affinis*	5780	37.3	0.046 ± 0.012
Red Shiner, *Cyprinella lutrensis*	121	0.8	0.001 ± 0.001
Green Sunfish, *Lepomis cyanellus*	4072	26.3	0.029 ± 0.011
Bluegill, *Lepomis macrochirus*	248	1.6	0.002 ± 0.001
Smallmouth Bass, *Micropterus dolomieu*	149	1.0	0.001 ± 0.001
Largemouth Bass, *Micropterus salmoides*	630	4.1	0.004 ± 0.002
Yellow Bullhead, *Ameiurus natalis*	7	< 0.1	0.001 ± 0.001
Black Bullhead, *Ameiurus melas*	13	< 0.1	0.001 ± 0.001
Common Carp, *Cyprinus carpio*	2	< 0.1	0.001 ± 0.001
American Bullfrog, *Lithobates catesbeianus* (subad.)	101	< 0.1	0.001 ± 0.001
American Bullfrog, *Lithobates catesbeianus* (juv.)	239	1.5	0.002 ± 0.001
American Bullfrog, *Lithobates catesbeianus* (tad.)	3324	21.4	0.020 ± 0.011
Native			
Woodhouse's Toad, *Anaxyrus woodhousii* (ad.)	20	0.1	0.001 ± 0.001
Woodhouse's Toad, *Anaxyrus woodhousii* (juv.)	3	< 0.1	0.001 ± 0.001
Woodhouse's Toad, *Anaxyrus woodhousii* (tad.)	804	5.2	0.004 ± 0.003
Sonora Mud Turtle, *Kinosternon sonoriense* (hatchling)	6	< 0.1	0.001 ± 0.001
Total	15519		

be persisting, it seems likely that our prey use observations are broadly representative of potential *T. e. megalops* diets within the watershed.

Our study builds on previous dietary accounts that nonnative species are used as prey, including at least three species listed as "harmful" in the final listing rule for *T. e. megalops* (USFWS 2014). To our knowledge, we present the first confirmed records of *T. e. megalops* eating large-bodied (SUL > 100 mm) native and nonnative anurans, and spiny-rayed centrarchid and ictalurid fish. We also present the first species record of an individual that survived after apparently consuming a spiny-rayed fish and a spine punctured the snake's body wall, similar to accounts for other aquatic snake species (Mills 2002; Šukalo 2014; J. Placyk pers. comm.). Diet studies of similar aquatic gartersnake species have also documented prey use of nonnative spiny-rayed fish and anurans, including the Black-necked Gartersnake (*T. cyrtopsis*) eating *L. catesbeianus* (Fleharty 1967); the Two-striped Gartersnake (*T. hammondii*) consuming Redbelly Tilapia (*Tilapia zillii*) and *Xenopus laevus* (Ervin and Fisher 2001; Rodríguez-Robles and Galina-Tessaro 2006); the Eastern Ribbonsnake (*T. saurita*) consuming spiny-rayed cyprinid fish (Bell et al. 2007); the Mexican Black-bellied Gartersnake (*T. melanogaster*) eating *Carassius auratus* (Manjarrez et al. 2013); and the Giant Gartersnake (*T. gigas*) eating *L. catesbeianus* and spiny-rayed centrarchid and ictalurid fish (Ersan 2015). Conversely, previous studies with the Aquatic Gartersnake (*T. atratus*) and the Mountain Gartersnake (*T. elegans elegans*) suggest a reliance on native amphibians as a food source, and negative repercussions on snake populations when native prey sources are removed by introduced predators (Matthews et al. 2002; Preston and Johnson 2012). It is possible that the response to the loss of native prey and the capacity to utilize novel food sources is site-based or intraspecific for different gartersnake species.

For *T. e. megalops*, trapping surveys indicate nonnative species dominate prey availability at two of the other locations that have potentially viable *T. e. megalops* populations in the United States: Page Springs and Bubbling Ponds State Fish Hatcheries associated with Oak Creek in north-central Arizona, and the upper Santa Cruz River in the San Rafael Valley in southern Arizona (S. Lashway, T. Sprague, pers. comm.). There are confirmed observations of snakes regurgitating *G. affinis* and *L. catesbeianus* tadpoles and juveniles during minnow trap surveys and opportunistic encounters at both sites (S. Lashway, T. Sprague, pers. comm.), and one record of a large adult snake captured from a minnow trap with a suspected subadult or adult *L. catesbeianus* as a prey bolus from the Santa Cruz River (S. Lashway, pers. comm.). Additionally, a large adult snake was observed consuming an adult *A. woodhousii* from Bubbling Ponds during an opportunistic encounter, although no measurements were recorded for the snake or prey item (V. Boyarski, pers. comm.). Given the ontogenetic shifts in diet observed by García and Drummond (1988), Lind and Welsh (1994), De Queiroz et al. (2001), and Manjarrez et al. (2013), where *T. e. megalops* and similar aquatic gartersnake species utilize increasingly larger prey as they grow, it is likely that both subadult and adult *L. catesbeianus* and adult *A. woodhousii* may represent seasonally important food sources for larger individuals that inhabit sites populated by native and nonnative larger-bodied anuran species.

These records conflict with the perceptions that the species relies primarily on small-bodied prey, and requires a high abundance of native prey sources and the absence or low abundance of predatory nonnative species to survive (USFWS 2013, 2014). Instead, our prey use records, combined with previous dietary accounts for *T. e. megalops* and other snake species, suggest plasticity in foraging behavior, enabling the use of novel, seasonably available (Ervin and Fisher 2001; Rodríguez-

TABLE 2. *Thamnophis eques megalops* confirmed prey based on field observations from minnow traps and opportunistic encounters in the upper-middle Verde River, Arizona, 2012–2015. Prey species are listed by their standard and scientific names, and anurans are categorized by age class. "Number" refers to total prey use events observed per prey species, "%" refers to the relative proportion of each prey species, and "Method" refers to the type of observation ("minnow trap" or "opportunistic encounter") used for each prey use event.

Prey Species	Number	%	Method
Nonnative			
Western Mosquitofish, *Gambusia affinis*	1	4.4	minnow trap
Largemouth Bass, *Micropterus salmoides*	1	4.4	minnow trap
Black Bullhead, *Ameiurus melas*	1	4.4	opportunistic
Ameiurus sp. (spine)	1	4.4	opportunistic
American Bullfrog, *Lithobates catesbeianus* (ad.)	1	4.4	opportunistic
American Bullfrog, *Lithobates catesbeianus* (subad.)	1	4.4	opportunistic
American Bullfrog, *Lithobates catesbeianus* (juv.)	5	21.6	minnow trap
American Bullfrog, *Lithobates catesbeianus* (tad.)	9	39.0	minnow trap
Native			
Woodhouse's Toad, *Anaxyrus woodhousii* (ad.)	3	13.0	opportunistic
Total	23		

TABLE 3. Confirmed prey use event measurements for prey and *Thamnophis eques megalops* in the upper-middle Verde River, Arizona, 2012–2015. Prey species are listed by their scientific names, and anurans are categorized by age class. "Prey mass" and "Snake mass" are measured in grams (when available), and "Prey-snake mass ratio" refers to the percentage of snake mass represented by the prey item. "Prey length" and "Snake SVL" are measured in millimeters (when available), and TL = total length, SUL = snout–urostyle length, and SVL = snout–vent length. "Prey-snake length ratio" refers to the percentage of snake length represented by the prey item.

Prey Species	Prey mass (g)	Snake mass (g)	Prey-snake mass ratio (%)	Prey length (mm)	Snake SVL (mm)	Prey-snake length ratio (%)
Nonnative						
Gambusia affinis	1.3	82.0	1.6	25 (TL)	540	4.6
Micropterus salmoides	1.5	67.0	2.2	64 (TL)	512	12.5
Ameiurus melas	7.4	58.7	12.6	90 (TL)	484	18.6
Ameiurus sp. (spine)	unknown	43.1	unknown	unknown	463	unknown
Lithobates catesbeianus (tad.)	1.3	28.5	4.6	60 (TL)	369	16.3
	0.5	23.1	2.2	40 (TL)	385	10.4
	0.8	29.5	2.7	53 (TL)	381	13.9
	1.2	28.3	4.2	65 (TL)	355	18.3
	4.4	26.0	16.9	86 (TL)	376	22.9
	13.6	42.0	32.4	135 (TL)	445	30.3
	unknown	6.0	unknown	unknown	229	unknown
	unknown	38.0	unknown	unknown	470	unknown
	2.3	79.0	2.9	60 (TL)	540	11.1
Lithobates catesbeianus (juv.)	8.3	55.5	15.0	49 (SUL)	455	10.8
	13.5	69.0	19.6	56 (SUL)	506	11.1
	18.1	76.5	23.7	74 (SUL)	535	13.8
	22.8	92.5	24.6	75 (SUL)	584	12.8
	unknown	46.0	unknown	75 (SUL)	520	14.4
Lithobates catesbeianus (subad.)	45.1	217.0	20.8	94 (SUL)	697	13.5
Lithobates catesbeianus (ad.)	unknown	169.5	unknown	147 (SUL)	702	20.9
Native						
Anaxyrus woodhousii (ad.)	unknown	185.0	unknown	71 (SUL)	705	10.1
	unknown	262.0	unknown	106 (SUL)	727	14.6
	unknown	236.0	unknown	122 (SUL)	725	16.8
Mean prey-snake ratios			12.4 ± 2.6			14.9 ± 1.2

Robles and Galina-Tessaro 2006; d'Orgeix et al. 2013), and in some cases, nonnative prey. Indeed, nonnative prey have allowed population-level benefits including increased size of adults and number of offspring of Lake Erie Watersnakes (*Nerodia sipedon insularum*; King et al. 2006, 2008), and the continued abundance of introduced Brown Treesnakes (*Boiga irregularis*) in Guam following the decline or extirpation of native vertebrate prey (Rodda and Savidge 2007; Siers 2015). Our findings suggest that adult *T. e. megalops* will utilize relatively large-bodied native and nonnative prey items, and in certain watersheds where native aquatic prey species are much-reduced or even extirpated, the species may be able to maintain viable populations by shifting to a diet comprised primarily of nonnative prey, even those considered "harmful" in USFWS listing documents. We encourage continued investigations into prey use, including ontogenetic dietary shifts, prey use in ephemeral watersheds, and the potential impacts on gartersnakes swallowing spiny-rayed fish, to inform management and recovery efforts for this threatened species. We also recommend a revision of the primary constituent elements for the USFWS critical habitat designation final rule to reflect a wider variety of native and nonnative prey sources that contribute to the long-term survival of *T. e. megalops* populations in the United States.

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