AN ABSTRACT OF THE THESIS OF

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Title: Diet of the Mudpuppy (*Necturus maculosus*) in Eastern Kansas

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Abstract approved: ____________________

The Mudpuppy (*Necturus maculosus*) is a rarely seen and poorly understood permanently aquatic salamander of the eastern United States. Little has been published on its habits within extensive portions of its range, especially within the Missouri and Arkansas river drainages, where better knowledge of its natural history is needed to assess its status and inform conservation efforts. I investigated trophic relationships of the Mudpuppy in those drainages by examining its diet using samples from 195 individuals captured in the Marais des Cygnes, Neosho, Cottonwood, Elk, and Verdigris rivers and at Melvern and Pomona lakes, all in Kansas. I extracted the stomach contents of each individual with a non-lethal flushing protocol to describe dietary differences in abundance, frequency of occurrence, volume, and taxonomic diversity of prey items according to habitat, season, Mudpuppy sex, and Mudpuppy size. I estimated the trophic position of the Mudpuppy based on identities, volumes, and trophic levels of its prey, and found it to be a top-level predator with a wide-breadth foraging niche in both rivers and lakes. Individuals fed intensively on insects—the largest number of prey items were mayfly nymphs (Ephemeroptera)—but volumetrically their diets were mainly fishes, especially sunfishes (*Lepomis* spp.) and Gizzard Shad (*Dorosoma cepedianum*). Fishes were recovered from the great majority of individuals, and insects from most, whereas frequencies of occurrence of other prey types were considerably lower. Mudpuppies from rivers, as compared to lakes, consumed a significantly larger number but not volume of fishes and, in both respects, more amphibians. No significant differences in diets between seasons (winter versus spring) or sexes were detected. Mudpuppy size was weakly correlated with total prey volume and with volume of fishes in particular. Altogether, these findings differ markedly from previous studies conducted elsewhere, underscoring the need for more studies from throughout the Mudpuppy's range.

Keywords: amphibian, diet composition, diet variation, food habits, salamander, stomach content analysis, trophic position

DIET OF THE MUDPUPPY (*NECTURUS MACULOSUS*)

IN EASTERN KANSAS

A Thesis

Presented to

The Department of Biological Sciences

EMPORIA STATE UNIVERSITY

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

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April 2020

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ACKNOWLEDGMENTS

I thank Alexis Powell and Lynnette Sievert for advice, setup, and writing support. Justin Autz, Michael Mahr, Greg Sievert, and Cursti Sorell have my thanks for spending long arduous hours in the field and lab. I am grateful to David Edds for advice on this project, equipment, assistance with taxonomic identification, and manuscript comments. Thank you, Darren Rebar, for manuscript comments and assistance with statistical analyses; Sam Schneider and Erika Martin, for being patient enough to guide me through R and RStudio; Curtis Schmidt, for granting me access to the collections of stomach contents from the Sternberg Museum of Natural History; and Roger Ferguson, for creating the squeezebox used to contain uncontrollable Mudpuppies. I am indebted to Jamie & Eric Ratzloff (Melvern Lake Marina), Doug & Donna Hornbeck (Melvern Lake Marina), and Bill & Shelley Hodgson (Lighthouse Bay Marina) for allowing me to keep traps at their marinas through these years; without them, I would not have collected so many Mudpuppy samples. I am also grateful to the landowners who granted me access. I express my sincere gratitude to Gabe Yonts, who always told me I was capable of great things and provided unwavering support throughout our 14 years together, especially these past 2.5 years. This research was conducted in accordance with collecting permits (SC-027-2018, SC-030-2019, SC-045-2020) from the Kansas Department of Wildlife, Parks and Tourism (KDWPT) and IACUC approval from Emporia State University (ESU-IACUC-18-004, ESU-IACUC-19-003). Funding and equipment were provided by the KDWPT, with help from Daren Riedle, and through scholarships (Graduate Student Research Scholarship, Scholars Circle Funding, Thesis Support Award, Newbold Graduate Scholarship, Katherine Smalley Graduate Scholarship, Robert F. Clarke Memorial Biology Scholarship, New Graduate Student Scholarship) and the Department of Biological Sciences at Emporia State University.

PREFACE

This thesis was prepared following the manuscript submission guidelines of *Copeia*.

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1 INTRODUCTION

The Mudpuppy (*Necturus maculosus*) is a permanently aquatic salamander that occurs in the eastern United States (Matson, 2005). It is the only fully aquatic amphibian species in Kansas and one of only three species of salamanders that are widespread in the state (Collins et al., 2010). The species is rarely encountered because it is nocturnal, with individuals seeking refuge during the day (Collins et al., 2010). Two subspecies occur in Kansas: the Common Mudpuppy (*N. m. maculosus*), which is found in portions of the Missouri River drainage, and the Red River Mudpuppy (*N. m. louisianensis*), which frequents parts of the Arkansas River drainage (Collins et al., 2010). These taxa are regarded as full species by some authorities (e.g. Frost, 2018). Herein, references to the Mudpuppy (*N. maculosus*) will refer to both subspecies, following Highton et al. (2017), unless otherwise stated.

The Common Mudpuppy is classified as threatened in Illinois and Iowa (Mankowski, 2010; Matson, 2005); a Species of Special Concern in Indiana, Minnesota, and North Carolina (Matson, 2005; Minnesota Department of Natural Resources, 2013; North Carolina Wildlife Resources Commission, 2015); a Species of Greatest Conservation Need in Michigan, Tennessee, and Vermont (Derosier et al. 2015; Tennessee State Wildlife Action Plan Team, 2015; Vermont Wildlife Action Plan Team, 2015); and endangered/extirpated in Maryland (Matson, 2005). The Red River Mudpuppy is classified as a Species of Greatest Conservation Need in Louisiana (Holcomb et al., 2015). Potential reasons for decline include pollution, habitat degradation, invasive species, and possibly climate change (Matson, 2005; Sievert and Sievert, 2011; Beattie et al., 2017). Little has been published on the natural history and status of either subspecies in Kansas, but the Kansas State Wildlife Action Plan lists the Common Mudpuppy as a Species of Greatest Conservation Need (Rohweder, 2015).

One means of delving into the natural history of an organism, especially its ecological relationships, is analysis of its diet. Such studies shed light on interactions with other organisms and the species' position in the food web (Solé and Rödder, 2010; Whiles and Altig, 2010), which can inform studies of how the ecosystem might be altered in its absence (Vander Zanden et al., 1997; Whiles et al., 2006; Gillespie, 2013). For example, as predators, sometimes even top-level predators, salamanders can influence abundances of other species and thereby shape community structure (Davic and Welch, 2004; Conor Keitzer and Goforth, 2013). How the Mudpuppy interacts with other organisms within its ecosystem, and quantitative description of its diet, has not been investigated in southern portions of its range, including Kansas.

The diet of the Common Mudpuppy has been studied in some northern states, including Minnesota (Cochran and Borash, 2014), Wisconsin (Eycleshymer, 1906; Pearse, 1921; Cochran and Lyons, 1985; Cochran, 1991), Illinois (Beattie et al., 2017), Michigan (Lagler and Goellner, 1941; Gibbons and Nelson, 1968; Cochran, 1991), and New York (Hamilton, 1932), and results suggest a generalist diet composed of fishes, crayfishes, frogs, worms, insect larvae, leeches, earthworms, and zebra mussels (*Dreissena polymorpha*; Harris, 1959). Studies in New York (Hamilton, 1932) and Michigan (Lagler and Goellner, 1941) discovered that insects constituted 30–49% of total diet volume, crustaceans 14–33%, and fishes 13%. In Illinois, fishes composed up to 50% of total volume, followed by crustaceans at ~29%, and insects at ~18% (Beattie et al. 2017). No quantitative studies of the diet of the Red River Mudpuppy have been conducted, but Cagle (1954) noted finding crayfishes, fishes, and dragonfly nymphs in stomach samples. Kansas encompasses the western extent of the Common Mudpuppy's range and the northern extent of the Red River Mudpuppy's range, so the diet ecologies of both subspecies could differ from what is typical elsewhere.

The goal of my study was to examine trophic relationships of the Mudpuppy within Kansas waterways through analysis of its diet. Specifically, I described the composition of its diet quantitatively and tested for differences in diet according to habitat, season, sex, and size. Furthermore, I estimated the species' trophic position from the identities, volumes, and trophic positions of its prey (Vander Zanden et al., 1997; Fry et al., 1999). Because Mudpuppies have been documented elsewhere to be generalist predators, I hypothesized that diet would differ (1) between habitats (lake vs. river) due to differences in the species composition of potential prey; (2) seasonally, due to fluctuations in prey abundance; (3) between sexes, reflecting different foraging opportunities related to their reproductive roles (e.g. as males travel in search of mates, or as females lay and guard eggs; Matson 2005; Vitt and Caldwell, 2014; Chellman et al., 2017); and (4) allometrically, because of increasing gape size as Mudpuppies grow.

2 MATERIALS AND METHODS

Trapping protocol.— Cylindrical wire mesh traps (419 mm L × 229 mm W, 6-mm mesh size; Gee-minnow trap, Memphis Net and Twine, Memphis, TN), with the conical mouth at each end of each trap widened to an oval aperture of ~60 × 30 mm (Heyer et al., 1994; Dodd, 2010; Beattie et al., 2017), were baited with either chicken liver, cheese, or shrimp placed in cloth mesh bags, or were unbaited. Traps were set in waterways—including most major rivers and Pomona and Melvern lakes—of the eastern third of Kansas. Fieldwork was conducted January 2018–April 2019. Measurements taken of each capture included mass (0.1 g) using an electronic balance (Scout Pro SP-6000, Ohaus, Parsippany, NJ), and snout-vent (0.1 mm) and total lengths (mm; TL) using a ruler and modified squeeze box (Burgmeier et al., 2010). The date of capture, location, deformities, and sex of each individual were recorded (Beattie et al., 2017) and each was photographed.

Stomach flushing technique.—To examine Mudpuppy diet, I used a non-lethal stomach flushing procedure that involved gentle handling but not anesthetizing each individual (Legler, 1977; Caputo and Vogt, 2008; Solé and Rödder, 2010). This technique is as effective as stomach dissection and does not cause ill effects (Leclerc and Courtois, 1993; Solé et al., 2005). Each Mudpuppy was positioned with its head over a 0.5-µm-mesh sieve. Soft tubing (4-mm outside diameter) was inserted into its mouth, down the esophagus, and into the stomach. A 60-ml syringe filled with water was connected to the tube, then the plunger was depressed to flush the stomach contents out of the mouth and onto the sieve. This process was continued until no more contents were expelled, followed by one more syringe flush to ensure the stomach was empty. Stomach contents were preserved in 70% ethanol (Solé et al., 2005).

Stomach contents analysis.—Preserved stomach contents were examined with a dissecting microscope. Prey items were identified with the aid of keys (Huggins et al., 1985; Voshell, 2002; De Iuliis and Pulera, 2012; Kansas Fishes Committee, 2014) to the lowest practical taxonomic group. Fish scales were identified to family utilizing a key in Daniels (1996), then, based on the geographic origin of the sample, I used known ranges of Kansas fishes to assign them to the genus or species within that family expected at that locality (Kansas Fishes Committee, 2014).

Although some individuals were recaptured (N =24), following other studies (Beattie et al., 2017), each stomach contents sample was treated as independent because the flushing protocol insured that previously described food items were removed and because of the extended time ($\bar{x}$ = 13 weeks) between capture and recapture. Empty stomach samples were excluded from all analyses. Inorganic debris and vegetation data were excluded from analysis on the assumption that they were incidentally ingested as a consequence of the suction feeding mechanism of aquatic salamanders and because these materials are not expected to contribute to nutrition since no evidence exists to suggest that Mudpuppies have symbiotic gut biota to break down cellulose (Whiles and Altig, 2010).

The Sternberg Museum of Natural History (Fort Hays State University, Fort Hays, KS) contributed stomach contents from Red River Mudpuppies captured in the Neosho River on 22 February 2003 in Allen and Woodson Counties. These samples consisted of materials that the Mudpuppies regurgitated during transport (a common occurrence, pers. obs.). Because captures were grouped by county for transport, the regurgitate found in each vessel could not be attributed to a particular individual and might have been contributed by as many as all three in each container. Consequently, my use of data from these samples was limited mainly to their unproblematic inclusion in calculations based on pooled prey item diversity, abundance, or volume. However, I also calculated frequencies of occurrence by counting each of the two pooled samples as a single occurrence (i.e. by assuming, for the sake of analysis, that the regurgitate in each container was contributed by only one individual).

Prey item abundance.— Prey items were counted to estimate their abundance and to describe feeding intensity (Bhimachar and George, 1952) on each prey type. Each whole prey individual counted as a single item, regardless of its size. A minimum number method was used for counting larger prey items if they were degraded; for example, one crayfish claw was counted as one crayfish, fish scales or flesh equaled one fish, and three frog legs equaled two frogs (Beattie et al., 2017). Fragmented invertebrates were counted according to the number of unambiguously unrelated body parts (e.g. two head capsules and one complete thorax equaled two individuals total; Whiles and Altig, 2010).

Prey frequency of occurrence.—Frequency of occurrence was calculated by taking the number of stomachs containing a particular prey type and dividing by the total number of stomachs containing at least one prey item of any type, then multiplying by 100 (Edds et al., 2002; Caputo and Vogt, 2008; Crovetto et al., 2012; Beattie et al., 2017). This metric represents the percentage of Mudpuppies consuming that prey type. Frequency of occurrence of each prey type was calculated for the study overall as well as separately by habitat, season, and sex.

Prey volume.—Volumes of individual prey items in each stomach contents sample were measured or estimated, and were summed for each individual Mudpuppy to generate estimates of meal size [Combined volume likely overestimated meal size; adjustments could be made if studies of digestion rates and passage times in *Necturus* were available].

Volumes of larger prey items, such as crayfish, fishes, frogs, and annelids, were measured using a graduated cylinder by adding water until the prey item was submerged, then subtracting the volume of water added from the final volume (Magnusson et al., 2003; Caputo and Vogt, 2008; Solé and Rödder, 2010; Beattie et al., 2017). Volumes were estimated for smaller prey items (insects, cladocerans, isopods, copepods, mollusks, and arachnids) using the following ellipsoid formula:

$$V = \frac{4\pi}{3}\frac{L}{2}\left(\frac{W}{2}\right)^2$$

where V is volume, W is width, and L is length (ignoring appendages for measurements; Colli and Zamboni, 1999; Magnusson et al., 2003; Maneyro et al., 2004; Solé and Rödder, 2010; Beattie et al., 2017). Length and width (mm) measurements were taken as maximum distances obtained from photographs of prey items lying on their ventral (insects, copepods, isopods) or lateral (fishes, cladocerans) surfaces, along with a size standard, as measured in ImageJ (Schneider et al., 2012).

For all types of degraded prey, fragments or partially digested remnants (e.g. fish vertebral columns) were size-matched to several whole specimens obtained in this study or from the Schmidt Museum of Natural History (Emporia State University, Emporia, KS), the mean volumes of which were used as estimates of the volumes of the prey items from which the fragments originated (Sebastiano et al., 2012). For a small number of severely degraded prey items (scales, legs, claws), Mudpuppy gape-size limitations were considered when estimating volumes of the largest prey types—fishes, amphibians, and crayfish. In these cases (18% of all samples), volume estimates were obtained by using the mean sizes of whole prey of these types found within similar-sized Mudpuppies (± 3 cm TL) from the same habitat.

Prey diversity.—Shannon diversity (H') and equitability (E_H) of all prey items pooled, and taxonomic richness (s) of all prey pooled and of the contents of individual stomachs, were used to investigate potential differences in diet diversity at the ordinal level according to habitat, season, Mudpuppy sex, and Mudpuppy size. Because a generalist predator is expected to incorporate rare prey types in its diet, the Shannon index was chosen in preference to Simpson's diversity index because it is more reflective of taxonomic richness (Gadsen and Palacios-Orona, 1997**;** Maneyro et al., 2004). Shannon diversity was calculated as

$$H' = -\sum \mathrm{p_i} \ln \mathrm{p_i}$$

where $\mathrm{p_i}$ is the proportional abundance of each taxon (i.e. the number of individuals of a taxon divided by the total number of prey items for all taxa; Shannon, 1948). Equitability was calculated as

$$E_H = H'/H'_{max}$$

where H' is the diversity index and H'_{max} is calculated as ln(s), where s is taxonomic richness, which in this study was the number of prey orders present.

Trophic position.— Using published estimated trophic levels of prey items, I estimated the trophic level of each individual lake Mudpuppy sample and of the pooled lake samples using the following formula:

$$T_a = \sum (V_i T_i) + 1$$

where T_a is the trophic level, V_i is the volume of a prey item and T_i is the trophic level of that prey item (Vander Zanden and Rasmussen, 1996; Cortés, 1999; Fry et al., 1999). Estimates of the trophic levels of individual samples were used to test for differences in trophic level according to Mudpuppy size (TL), whereas the estimate based on pooled samples was used for comparisons to other organisms since those estimates, obtained from published studies, were calculated from pooled samples (Vander Zanden et al., 1997; Fry et al., 1999).

Statistical analyses.—Prey items were grouped for tests of dietary difference according to habitat, season, Mudpuppy sex, and Mudpuppy size using the following taxonomic groupings: fishes, amphibians, crustaceans, arachnids, insects, unidentified arthropods, mollusks, and annelids. Due to low sample sizes of Mudpuppies from rivers, analyses comparing seasons, sexes, and sizes were conducted using only lake samples. Amphibian, annelid, and arachnid prey were excluded from these analyses due to low sample sizes ($n \leq 3$). Seasonal analyses compared only winter (December, January, February) to spring (March, April, May) due to low rates of captures for summer ($N = 2$) and fall ($N = 14$).

Parametric test assumptions were violated (right-skewed distributions, unequal variances between samples) for prey abundance, frequency of occurrence, and volume data; therefore, non-parametric tests were employed. Kruskal-Wallis (KW) tests were used to test for significant differences in abundances of each prey group, volumes of each prey group, frequencies of occurrence of prey groups, total prey number in individual Mudpuppies, and total prey volume (meal size) in individual Mudpuppies according to habitat, season, and sex. I also used KW tests to compare trophic levels of individual Mudpuppies according to season and sex. Spearman's rank correlation was used to test for relationships between Mudpuppy size and the following metrics based on the stomach contents of individual mudpuppies: numbers of items of each prey group, volumes of each prey group, total prey number, total prey volume (i.e. meal size), and trophic level of individual Mudpuppies.

Bonferroni corrections (α/number of tests) were applied to reduce type 1 error rates. Differences were considered statistically significant for tests involving five prey group variables (in analyses of differences according to habitat and size) at $P \leq 0.05/5 = 0.010$. Differences were considered statistically significant involving four prey groups (in analyses of season, sex, size) at $P \leq 0.05/4 = 0.013$. In addition, effect sizes were calculated from KW tests using epsilon-squared, where the coefficient is standardized between 0 (no relationship) and 1 (perfect relationship; Tomczak and Tomczak, 2014).

The Hutcheson *t*-test (Hutcheson, 1970) was used to evaluate the significance of differences in ordinal-level Shannon diversity between pooled samples according to habitat, season, and Mudpuppy sex. Some individual samples contained only one prey order, causing Shannon diversity to equal zero; therefore, ordinal-level taxonomic richness (s) was preferred for Kruskal-Wallis tests of differences in taxonomic variety among individuals between habitats, seasons, and sexes. The ordinal-level taxonomic richness of prey according to Mudpuppy size (TL) was investigated using Spearman's correlation. I generated species accumulation curves to evaluate the success of sampling all the prey items within each habitat (Kovács and Török, 1997; Maneyro et al., 2004). Data analyses were run in SPSS 24 (IBM Corp., 2016), excepting species accumulation curves, which were coded in RStudio (RStudio Team, 2015) using the vegan package (Oksanen et al., 2007) in R (R Development Core Team, 2018).

3 RESULTS

Diet of Mudpuppies in Kansas.—A total of 189 Mudpuppies were captured, of which 182 came from within the Missouri River drainage (6 from the Marais des Cygnes River and Long Creek and 176, including 24 recaptures, from Pomona and Melvern lakes) and 7 came from within the Arkansas River drainage from the Neosho, Cottonwood, Verdigris, and Elk rivers (see Appendix). A total of 151 (80%) of the Mudpuppies captured—13 from rivers and 138 from lakes—contained at least one identifiable prey item (33 lake samples were empty, and five lake samples contained only heavily digested animal material, so were excluded from analyses). Thirty-one samples contained some unidentified organic material (including vegetation, heavily digested animals) or inorganic objects (e.g. rocks, mud), of which five contained fishing line and four contained expanded polystyrene pellets. Six samples contained roundworms, with one river individual containing 14; these were assumed to be parasitic and not prey items. Additionally, a single incidence of cannibalism was observed—a 123 mm TL Mudpuppy was found in the stomach of a 219 mm TL lake Mudpuppy.

I identified 862 prey items (91 from river samples, 771 from lakes) flushed from Mudpuppies trapped for this project as well as 44 prey items in the two pooled river samples (derived from up to six Mudpuppies from rivers) contributed by the Sternberg Museum of Natural History. Taxonomic groupings used in most analyses, and examples of prey diversity from each, include the following: fishes (*Lepomis macrochirus*, *Percina caprodes*, *Notorus placidus*, *Notropis stramineus*), amphibians (adult *Acris blanchardi*, adult *Lithobates* sp, *Lithobates catesbeianus* tadpoles, juvenile *Necturus maculosus*), crustaceans (*Procambarus* sp., Palaemonidae, Cladocera, Copepoda), arachnids (trombidiform), insects (Trichopteran and Dipteran larvae, Ephemeroptera and Odonata nymphs, Megalopteran larvae), mollusks

(*Dreissena polymorpha*, Physidae), and annelids (Lumbricidae, arhynchobdellid). Altogether, at least 23 orders, including at least 29 families were represented (Table 1).

The most consumed prey type, by numbers, was insects (especially mayfly nymphs; Ephemeroptera) and, by volume, was fishes (especially Centrarchidae—with Clupeidae a close second; Table 1). The great majority of Mudpuppies (87%) consumed fishes, 55% consumed insects, 27% ate mollusks, 20% ate crustaceans, 5% ate amphibians, and 1% had annelid prey in their stomachs. Mudpuppy stomachs contained 5.9 ± 7.76 prey items ($\bar{x}$ ± SD; range = 1–43) and a total prey volume of 2,552 ± 2,386 mm^3 ($\bar{x}$ ± SD; range = 0.23–13,135 mm^3) per individual. Overall ordinal-level taxonomic richness per stomach was 2.5 ± 1.60 ($\bar{x}$ ± SD). Prey items from the seven Red River Mudpuppies captured, together with the two pooled river samples from the Sternberg Museum of Natural History, were included in these totals but are also described separately herein to provide the first quantitative description of the diet of that subspecies; those samples contained 14 orders, including at least 17 families (Table 2). Accumulation curves of ordinal-level taxonomic richness did not plateau—suggesting that these samples did not exhaustively represent all prey available in the environment (Fig. 1)—but did show substantial leveling.

Mudpuppies in rivers fed most intensively on insects (40% of all prey items), followed closely by fishes (39%), and then mollusks (10%), amphibians (7%), crustaceans (3%), and annelids (1%; Fig. 2). The number of prey items consumed by river Mudpuppies was 8.9 ± 7.50 ($\bar{x}$ ± SD) per individual. Fishes were volumetrically the main constituent (63%) of river Mudpuppy diet followed by amphibians (20%), insects (11%), mollusks (4%), crustaceans (1%), and annelids (1%). The total volume of prey was 4,261 ± 4,380 mm^3 ($\bar{x}$ ± SD) per individual. Among river Mudpuppies, 93% of samples contained fishes, 60% included insects, 27% had amphibians, 27% had crustaceans, 27% had mollusks, and 7% had annelids (Fig. 4). The ordinal-level taxonomic richness of prey was 3.7 ± 2.25 ($\bar{x}$ ± SD) for individual Mudpuppies in rivers.

Feeding intensity of Mudpuppies in lakes was highest for insects (60% of all prey items), followed by fishes (24%), crustaceans (8%), mollusks (6%), arachnids (1%), unidentified arthropods (1%), and amphibians (0.3%; Fig. 2). The number of prey items consumed was 5.6 ± 7.70 ($\bar{x}$ ± SD) per individual. Volumetrically, fishes composed 81% of the total diet, followed by crustaceans (7%), insects (6%), mollusks (4%), and amphibians (2%; Fig. 3). Total prey volume (meal size) was 2353 ± 1997 mm^3 ($\bar{x}$ ± SD) per individual. Additionally, 86% of lake Mudpuppies consumed fishes, 54% ate insects, 27% ate mollusks, 19% ate crustaceans, 2% ate amphibians, 1% ate annelids, and 0.01% ate arachnids (Fig. 4). The ordinal-level taxonomic richness of prey was 2.4 ± 1.46 ($\bar{x}$ ± SD) for individual Mudpuppies in lakes.

Habitat-associated differences in diet.—River Mudpuppies (N = 13 captures plus 2 pooled samples), as compared to lake Mudpuppies (N = 138), consumed significantly more total prey items (KW: H = 6.0, df = 1, $P = 0.01$) on average, including numerically more fish (KW: H = 6.56, df = 1, $P = 0.01$) and amphibian (KW: H = 19.27, df = 1, $P < 0.01$) prey, with weak ($\varepsilon^2 = 0.04$) and moderate ($\varepsilon^2 = 0.12$) differences respectively (Fig. 2); this difference was not significant (all $P \geq 0.33$) for insects, crustaceans, and mollusks (KW: H = 0.94, 0.40, and 0.19, respectively; all df = 1). A moderately higher volume of amphibian prey was found in river samples compared to lake samples (KW: H = 18.90, df = 1, $P < 0.01$, $\varepsilon^2 = 0.12$; Fig. 3), whereas fishes, insect, crustacean, and mollusk volumes did not differ significantly (KW: H = 0.38, 1.64, 0.22, 0.18; all df = 1, all $P \geq 0.20$), nor did total prey volume (KW: H = 1.3, df= 1, $P = 0.26$). Among river Mudpuppies, 27% had amphibian prey in their stomach compared to 2% of lake Mudpuppies, a difference that was significant (KW: H = 18.62, df = 1, $P < 0.01$, $\varepsilon^2 = 0.12$; Fig.

3), whereas frequencies of occurrence of fishes, insect, crustacean, and mollusk prey did not differ significantly (KW: H = 0.78, 0.20, 0.54, 0.01; all df = 1, all $P \geq 0.38$). Diet diversity was significantly higher ($t = 4.05$, df = 251, $P < 0.01$; Table 3) in river ($H' = 2.23$, $E_H = 0.85$) versus lake samples ($H' = 1.91$, $E_H = 0.67$). Collectively, the ordinal-level taxonomic richness of the diet of lake Mudpuppies (s = 18) was higher than that of river Mudpuppies (s = 14); however, the ordinal-level taxonomic richness of the stomach contents of the average river Mudpuppy was moderately higher as compared to an average individual lake Mudpuppy ($\bar{x} = 3.7$ versus 2.4 ; KW: H = 6.28, df = 1, $P = 0.01$, $\varepsilon^2 = 0.041$).

Seasonal differences in diet.—Numbers of consumed fishes, insects, crustaceans, and mollusks did not differ significantly according to season (KW: H = 0.37, 1.53, 0.26, 0.86; all df = 1, all $P \geq 0.22$), nor did their volumes (KW: H = 0.54, 0.87, 0.17, 0.94; df = 1, all $P \geq 0.33$) or their frequencies of occurrence (KW: H = 5.61, 3.75, 0.64, 0.83; all df = 1, all $P \geq 0.13$). Diversity was similar ($t = 0.43$, df = 669, $P = 0.68$; Table 3) in spring ($H' = 1.81$, $E_H = 0.67$) versus winter ($H' = 1.84$, $E_H = 0.70$). Pooled ordinal-level taxonomic richness of the diet was higher in spring (s = 15) than in winter (s = 14), but ordinal-level taxonomic richness of individual samples did not differ significantly between seasons (KW: H = 1.39, df = 1, $P = 0.24$). Mudpuppy diet in other seasons (not included in statistical analyses) was not qualitatively different—of the two Mudpuppies captured in summer 2018 (July, August), one yielded a centrarchid fish and the other had an empty stomach, whereas of the 14 Mudpuppies captured in fall 2018 (November), eight stomachs yielded a total of 6 centrarchids, 1 crayfish, 3 mayfly nymphs, 1 caddisfly larva, 4 snails, and 1 adult dipteran; two stomachs contained unidentifiable animal material, and the remaining four stomachs were empty.

Sex-associated differences in diet.—Numbers of consumed fishes, insects, crustaceans, and mollusks did not differ significantly according to sex (KW: H = 0.01, 0.65, 0.06, 1.32; all df = 1, all $P \geq 0.25$), nor did their volumes (KW: H = 1.14, 0.97, 0.25, 1.58; all df = 1, all $P \geq 0.21$) or their frequencies of occurrence (KW: H = 0.17, 0.01, 0.05, 1.98; all df = 1, all $P \geq 0.16$). Diversity and equitability of the diet of females (H' = 1.89, E_H = 0.70) were similar to those of male Mudpuppies (H' = 1.81, E_H = 0.68), as the differences were not significant (t = 1.07, df = 754, P = 0.28; Table 3). Ordinal-level taxonomic richness of the pooled diet samples from males (s = 15) was higher than from females (s = 14), but ordinal-level taxonomic richness of individual samples did not differ significantly by sex (KW: H = 0.038, df = 1, P = 0.85).

Size-correlated differences in diet.—No significant relationships were found between Mudpuppy size and numbers of consumed fishes (r_s = 0.08, P = 0.33), insects (r_s = - 0.15, P = 0.07), crustaceans (r_s = - 0.16, P = 0.06), mollusks (r_s = - 0.16, P = 0.07), or total prey items (r_s = - 0.15, P = 0.74). Mudpuppy size was weakly positively correlated with fish volume (r_s = 0.29, P = 0.01) and total volume (r_s = 0.26, P = 0.01) but not with crustacean volume (r_s = 0.19, P = 0.03), mollusk volume (r_s = - 0.16, P = 0.06; Table 4), or the ordinal-level taxonomic richness of the stomach contents of individual Mudpuppies (r_s = -0.08, P = 0.36).

Trophic position of the Mudpuppy.—The trophic level of the lake population was 3.88 ± 0.53 ($\bar{x}$ ± SD), using all samples pooled, and 3.92 ± 0.33 ($\bar{x}$ ± SD) when calculated by averaging the values obtained for individuals. These values place Mudpuppies at a level similar to that of heavily piscivorous carnivorous fishes (Table 5). No differences in trophic level were found between sexes (KW: H = 0.71, df = 1, P = 0.40) or seasons (KW: H = 2.04, df = 1, P = 0.57). Comparison of Mudpuppy size (TL) to individually calculated trophic level revealed no significant relationship (r_s = - 0.05, P = 0.59).

4 DISCUSSION

I found the Mudpuppy to be a top-level predator in lakes with a wide-breadth foraging niche in both rivers and lakes. This study provides the first look at Mudpuppy foraging ecology in the Missouri and Arkansas river drainage and in Kansas in particular. I was not successful in trapping enough Red River Mudpuppies (N = 7) to test for potential differences between the subspecies. However, as the second-largest study of Mudpuppy diet in terms of the number of individuals examined (compared to Eycleshymer, 1906; Pearse, 1921; Hamilton, 1932; Lagler and Goellner, 1941; Harris, 1959; Gibbons and Nelson, 1968; Cochran and Lyons, 1985; Cochran, 1991; Cochran and Borash, 2014; Beattie et al., 2017), my results contribute to general knowledge of the natural history of both subspecies.

Mudpuppies fed most intensively on insects, especially mayfly nymphs (Ephemeroptera), but volumetrically their meals consisted mainly of fishes, particularly sunfishes (Centrarchidae) and Gizzard Shad (*Dorosoma cepedianum*, Clupeidae). The importance of those prey groups was underscored by the fact that the great majority of Mudpuppies (87%) consumed fishes, and 55% consumed insects. The higher proportions and frequencies of occurrence of these prey may reflect their greater availability or that Mudpuppies foraged for them selectively. Studies of prey availability would be needed to judge the relative importance of these explanations. Given the similarities of river to lake samples in terms of species composition and that taxonomic richness accumulation seemed to be leveling off, my results suggest that I captured most of the organismal diversity exploited by the Mudpuppy in my study area. Because the species appears to be a generalist, additional sampling would be expected to increase these measures of dietary diversity (Kovács and Török, 1997; Maneyro et al., 2004).

Differences in diet composition between habitats suggest that Mudpuppies are opportunists and exploit different types of prey according to their availability. In support of that contention, the stomach contents of individual river Mudpuppies were taxonomically more diverse than those of lake Mudpuppies and, overall, river Mudpuppies made greater use of amphibians as prey. On the other hand, although numbers of consumed fishes were higher in rivers, fish prey volume did not differ between habitats, suggesting that the Mudpuppies might have adjusted their feeding intensity to compensate for differences in the size of available fishes to maintain a similar contribution of fishes to total meal size.

For the most part, the diets of Mudpuppies did not differ significantly by season, sex, or size. I did not detect seasonal differences in diet, but I was only able to test between winter and spring due to sample size limitations. To more thoroughly investigate seasonal effects, more samples during summer and fall would be needed. However, obtaining them would be difficult because Mudpuppies are notoriously difficult to capture when water temperatures exceed 15°C, possibly due to seeking refuge in deeper, cooler areas (Pearse, 1921; Gibbons and Nelson, 1968; Bart and Holzenthal, 1985). I predicted that diet would differ by sex because of their different reproductive roles—females produce and guard eggs, whereas males travel more (Matson, 2005; Vitt and Caldwell, 2014; Chellman et al., 2017). However, I found no such differences, perhaps because Mudpuppies feed opportunistically and because both sexes utilize similar microhabitats with similar prey availability. Even if Mudpuppies do feed selectively, the energetic demands of their differing roles in reproduction might be similar, so foraging strategies might not differ by sex. Only two relationships between Mudpuppy size and diet characteristics—fish volume and total volume—were significant, but those correlations were weak, perhaps because my trapping effort yielded only larger Mudpuppies, so I could only test for size-related dietary differences within the relatively narrow range of adult sizes (McDaniel et al., 2009).

My research allows insight into the predatory importance of the Mudpuppy and suggests that it is positioned to potentially influence the community structure of aquatic ecosystems through top-down mechanisms. The trophic level of the Mudpuppy was that of a top-level predator, similar to heavily piscivorous carnivorous fishes (Table 6). I did not measure the trophic level of other members of the food-web, unlike other studies (Vander Zanden and Rasmussen, 1996; Fry et al., 1999), so their precise trophic positions may differ locally from published values (as listed in Table 6). Regardless, given the high proportion of fish prey in its diet, the Mudpuppy is certainly a top-level consumer and is, based on the fresh appearances of most prey items, likely a top-level predator (rather than scavenger) in the lakes. Studies of its relative abundance or biomass relative to its prey and to carnivorous fishes, and studies of the activity level of the Mudpuppy during winter, relative to other predators, are needed to better understand its influence on the ecosystem.

Previous studies of the dietary habits of the Mudpuppy have been restricted to eastern and northern parts of its range (Eycleshymer, 1906; Pearse, 1921; Hamilton, 1932; Lagler and Goellner, 1941; Harris, 1959; Gibbons and Nelson, 1968; Cochran and Lyons, 1985; Cochran, 1991; Cochran and Borash, 2014; Beattie et al., 2017). These studies utilized similar methods (stomach flushing or dissection) with similar biases relating to prey passage and degradation rates (Hyslop, 1980; Pierce and Boyle, 1991), so they should be directly comparable to one another and my own. Their results differ markedly in several respects from one another and my own, which suggests that Mudpuppy diet varies across its range and between habitats. For example, I found that lake Mudpuppies in Kansas consumed a higher percentage of fishes by volume as compared to studies of lake populations in New York, Michigan, and Illinois (Hamilton, 1932; Lagler and Goellner, 1941; Beattie et al., 2017). I also found that volumetric contributions of insects, crustaceans, and annelids were much lower in Kansas than in New York, Michigan, and Illinois, whereas proportional volumes of amphibian and mollusk were similar to those found in other studies. Regional differences in diet are consistent with *Necturus* spp. being opportunistic predators that exhibit dietary differences reflective of local prey availability. Because stomach content analyses have known biases relating to prey degradation, future studies should consider stable isotope analysis (Layman et al., 2012; Gillespie, 2013; Trice et al., 2015) of Mudpuppy tissues or using other means (e.g. metabarcoding of scat; Aiverlo et al., 2018; Sullins et al., 2018) to ensure that all prey items (soft- and hard-bodied) are detected.

The Mudpuppy may be an important generalist predator in its aquatic food web. Knowing its trophic position and relative impact within its food web could help understand the impacts of ecological disturbances (pollution, habitat destruction, invasive species) that affect its populations. Human disturbances can have especially deleterious impacts on higher trophic levels (Newbold et al., 2020), which is particularly concerning for top-level predators from a conservation standpoint because they can have top-down effects on ecosystems. We need to understand impacts of amphibians on ecosystems, especially given that they are experiencing global declines (Blaustein et al., 1994; Houlahan et al., 2000; Davic and Welch, 2004; Whiles et al., 2006; Conor Keitzer and Goforth, 2013). More inventory and monitoring work need to be conducted to determine whether the Mudpuppy is part of the global amphibian decline. Some states indicate that it is declining and listing it as extirpated, threatened, or a Species of Special Concern. This study provides valuable baseline data on the Mudpuppy in the Missouri and Arkansas river drainages, and it should inform conservation and management of this Species of Special Concern in Kansas waterways. Its findings differ markedly from studies conducted elsewhere, underscoring the need for more studies from throughout the Mudpuppy's range.

5 LITERATURE CITED

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Table 1. Diet composition of the Mudpuppy (*Necturus maculosus*; N = 153 samples) in eastern Kansas rivers and lakes (Missouri and Arkansas river drainages). Sampling was conducted January 2018–April 2019. Metrics include number of each prey type as a count (N) and percentage (%N), volume of each prey type in mm^3 (V) and its percentage of total volume (%V), and number of Mudpuppies in which each prey type occurred as a count (O) and as frequency of occurrence (%O). Anurans and insects were larvae or nymphs, except where noted.

Prey items	**N**	**%N**	**V**	**%V**	**O**	**%O**
Fishes						
Clupeiformes; Clupeidae; *Dorosoma cepedianum*	53	5.8	133660	34.3	47	30.7
Cypriniformes; Cyprinidae; unid. cyprinid	17	1.9	6270	1.6	9	5.9
Notropis stramineus	1	0.1	600	0.2	1	0.7
Perciformes						
Percidae; *Percina caprodes*	2	0.2	5000	1.3	1	0.7
Centrarchidae; unid. centrarchid	142	15.7	145220	37.2	96	62.7
Micropterus sp.	1	0.1	400	0.1	1	0.7
Lepomis macrochirus	11	1.2	8390	2.2	11	7.2
Siluriformes; Ictaluridae; unid. ictalurid	4	0.4	4200	1.1	4	2.6
Noturus placidus	1	0.1	1300	0.3	1	0.7
Amphibians						
Anura; unid. anuran adult	5	0.6	6000	1.5	3	2.0
Hylidae; *Acris blanchardi* adult	3	0.3	4500	1.2	1	0.7
Ranidae; unid. *Lithobates* sp. adult	1	0.1	2000	0.5	1	0.7
Lithobates catesbeianus	2	0.2	3540	0.9	1	0.7

Caudata; Proteidae; *Necturus maculosus* juvenile	1	0.1	4000	1.0	1	0.7
Crustaceans						
Diplostraca; Cladocera; unid. cladoceran	31	3.4	6.98	< 0.1	2	1.3
Copepoda; unid. copepod [1]	3	0.3	9.54	< 0.1	3	2.0
Decapoda						
Cambaridae; *Procambarus* sp.	29	3.2	22214	5.7	22	14.4
Palaemonidae; unid. palaemonid	3	0.3	600	0.2	3	2.0
Isopoda; unid. isopod	1	0.1	22.6	< 0.1	1	0.7
Arachnids						
Trombidiformes; unid. trombidiform	8	0.9	1.9	< 0.1	1	0.7
Insects						
Coleoptera; Dytiscidae; unid. dytiscid adult	1	0.1	12	< 0.1	1	0.7
Diptera; Chironomidae; unid. chironomid	70	7.7	134	< 0.1	28	18.3
unid. dipteran adult	1	0.1	0.6	< 0.1	1	0.7
Ephemeroptera; Ephemeridae; unid. ephemerid	61	6.7	9983	2.6	17	11.1
Heptageniidae; unid. heptageniid	299	33.0	7412	1.9	46	30.1
Megaloptera; Corydalidae; *Corydalus cornutus*	4	0.4	12	< 0.1	2	1.3
Odonata; Coenagrionidae; unid. coenagrionid	26	2.9	364	0.1	11	7.2
Corduliidae; unid. corduliid	15	1.7	2000	0.5	17	11.1
Gomphidae; unid. gomphid	3	0.3	3884	1.0	1	0.7
Plecoptera; unid. plecopteran	2	0.2	7.9	< 0.1	2	1.3
Trichoptera; Hydropsychidae; unid. hydropsychid	2	0.2	0.03	< 0.1	2	1.3
unid. trichopteran	29	3.2	3141	0.8	14	9.2

[unidentified arthropods]	9	1.0	-		9	5.9
Bivalves						
Myida; Dreissenidae; *Dreissena polymorpha*	21	2.3	5073	1.3	17	11.1
Unionida; unid. unionid	15	1.7	3615	0.9	15	9.8
Gastropods						
Basommatophora; Physidae; unid. physid	27	3.0	5850	1.5	13	8.5
Annelids						
Arhynchobdellida; unid. arhynchobdellid	1	0.1	200	0.1	1	0.7
Haplotaxida; Lumbricidae; unid. lumbricid	1	0.1	600	0.2	1	0.7
Total	906		390224			

[1] For purposes of analyses, Copepoda was treated as an ordinal-level taxon in this study.

Table 2. Diet composition of the Red River Mudpuppy (*Necturus maculosus louisianensis*; N = 9 samples) in eastern Kansas rivers (Arkansas River drainage). Samples include stomach contents of individuals captured January 2018–April 2019 in this study (N = 7) and those contributed by the Sternberg Museum of Natural History (Fort Hays State University, Fort Hays, KS) as pooled samples (N = 2) derived from 6 individuals captured in February 2003. Metrics include number of each prey type as a count (N) and percentage (%N), volume of each prey type in mm^3 (V) and its percentage of total volume (%V), and number of Mudpuppies in which each prey type occurred as a count (O) and as frequency of occurrence (%O). Anurans and insects were larvae or nymphs, except where noted.

Prey items	**N**	**%N**	**V**	**%V**	**O**	**%O**
Fishes						
Cypriniformes; Cyprinidae; unid. cyprinid	12	12.5	4020	8.0	6	66.7
Notropis sp.	1	1.0	600	1.2	1	11.1
Perciformes						
Percidae; *Percina caprodes*	2	2.1	5000	9.9	1	11.1
Centrarchidae; unid. centrarchid	16	16.7	14330	28.5	4	44.4
Micropterus sp.	1	1.0	400	0.8	1	11.1
Lepomis macrochirus	6	6.3	2470	4.9	2	22.2
Siluriformes; Ictaluridae; unid. ictalurid	4	4.2	4200	8.4	3	33.3
Noturus placidus	1	1.0	1300	2.6	1	11.1
Amphibians						
Hylidae; *Acris blanchardi* adult	2	2.1	3000	6.0	1	11.1
Ranidae; unid. *Lithobates* sp. adult	1	1.0	2000	4.0	1	11.1

Lithobates catesbeianus	2	2.1	3540	7.0	1	11.1
Crustaceans						
Decapoda						
Cambaridae; *Procambarus* sp.	1	1.0	100	0.2	1	11.1
Palaemonidae; unid. palaemonid	1	1.0	200	0.4	1	11.1
Insects						
Diptera; Chironomidae; unid. chironomid	1	1.0	3.8	< 0.1	1	11.1
Ephemeroptera; Heptageniidae; unid. heptageniid	5	5.2	82	0.2	3	33.3
Megaloptera; Corydalidae; *Corydalus cornutus*	3	3.1	9.3	< 0.1	1	11.1
Odonata; Gomphidae; unid. gomphid	3	3.1	3884	7.7	1	11.1
Plecoptera; unid. plecopteran	2	2.1	7.9	< 0.1	2	22.2
Trichoptera; Hydropsychidae; unid. hydropsychid	1	1.0	0.02	< 0.1	1	11.1
unid. trichopteran	12	12.5	1434	2.9	3	33.3
[unidentified arthropods]	1	1.0	–		1	11.1
Bivalves						
Myida; Dreissenidae; *Dreissena polymorpha*	1	1.0	241	0.5	1	11.1
Gastropods						
Basommatophora; Physidae; unid. physid	13	13.5	2500	5.0	3	33.3
Annelids						
Haplotaxida; Lumbricidae; unid. lumbricid	1	1.0	600	1.2	1	11.1
Total	96		50274			

Table 3. Shannon diversity (*H′*), equitability (E_H), and ordinal-level taxonomic richness (s) of prey orders composing the diet of the Mudpuppy (*Necturus maculosus*; N = 153 samples) in eastern Kansas rivers and lakes (Missouri and Arkansas river drainages). Sampling was conducted January 2018–April 2019. Other metrics include number of prey items (n) and Hutcheson *t*-tests of significant differences in *H′* according to habitat, season, and sex. Differences according to season and sex were conducted using samples from lakes only.

	Habitat		**Season**		**Sex**	
	Rivers (15 Mudpuppies)	**Lakes** (138 Mudpuppies)	**Spring** (79 Mudpuppies)	**Winter** (51 Mudpuppies)	**Female** (61 Mudpuppies)	**Male** (77 Mudpuppies)
n	135	771	437	314	363	408
H′	**2.23**	**1.91**	1.81	1.84	1.89	1.81
T	**4.05**		0.43		1.07	
df	**251**		669		754	
P	**< 0.01**		0.68		0.28	
E_H	0.85	0.67	0.67	0.70	0.70	0.68
s	14	18	15	14	14	15

Table 4. Relationships between body sizes of Mudpuppies (*Necturus maculosus*) and volumes of prey types composing their diets in eastern Kansas lakes (Missouri River drainage). Sampling was conducted January 2018–April 2019. Metrics include number of stomachs with prey group (N) and Spearman rank correlation coefficients (r_s) between total lengths of Mudpuppies and volumes of prey. Amphibians and annelids were not analyzed due to low sample sizes ($N \leq 3$).

Prey type	**N**	**r_s**	**P**
Fishes	118	**0.29**	**0.01**
Insects	75	-0.11	0.19
Crustaceans	26	0.19	0.03
Mollusks	36	-0.16	0.06
All prey types combined	138	**0.26**	**0.01**

Table 5. Trophic position of the Common Mudpuppy (*Necturus m. maculosus*) estimated from its diet in eastern Kansas lakes (Missouri River drainage) and compared to the positions of other taxa with which it may occur. Sampling was conducted January 2018–April 2019.

Organism	**Estimated trophic position**	**Examples**
Carnivorous fishes	4.1	Largemouth Bass [1]
Mudpuppy	**3.9**	**Common Mudpuppy**
Carnivorous fishes	3.7	Yellow Perch [1,3]
	3.5	White Bass [1]
	3.3	sunfish [1]
Omnivorous fishes	2.9	Channel Catfish [1]
	2.6	Gizzard Shad [2]
	2.5	minnow [1]
Decapoda	3	crayfish [1]
Predatory invertebrates	3	dragonfly, hellgrammite, leech [1]
Omnivorous insects	2.5	caddisfly, mayfly, stonefly [1]
Zooplankton	2.5	cladoceran, copepod [1]
Mollusks	2	mussel, snail [1]

[1] Adapted from Vander Zanden et al. (1997)

[2] Adapted from Fry et al. (1999)

[3] Does not occur in Kansas but is common within the overall range of the Common Mudpuppy.

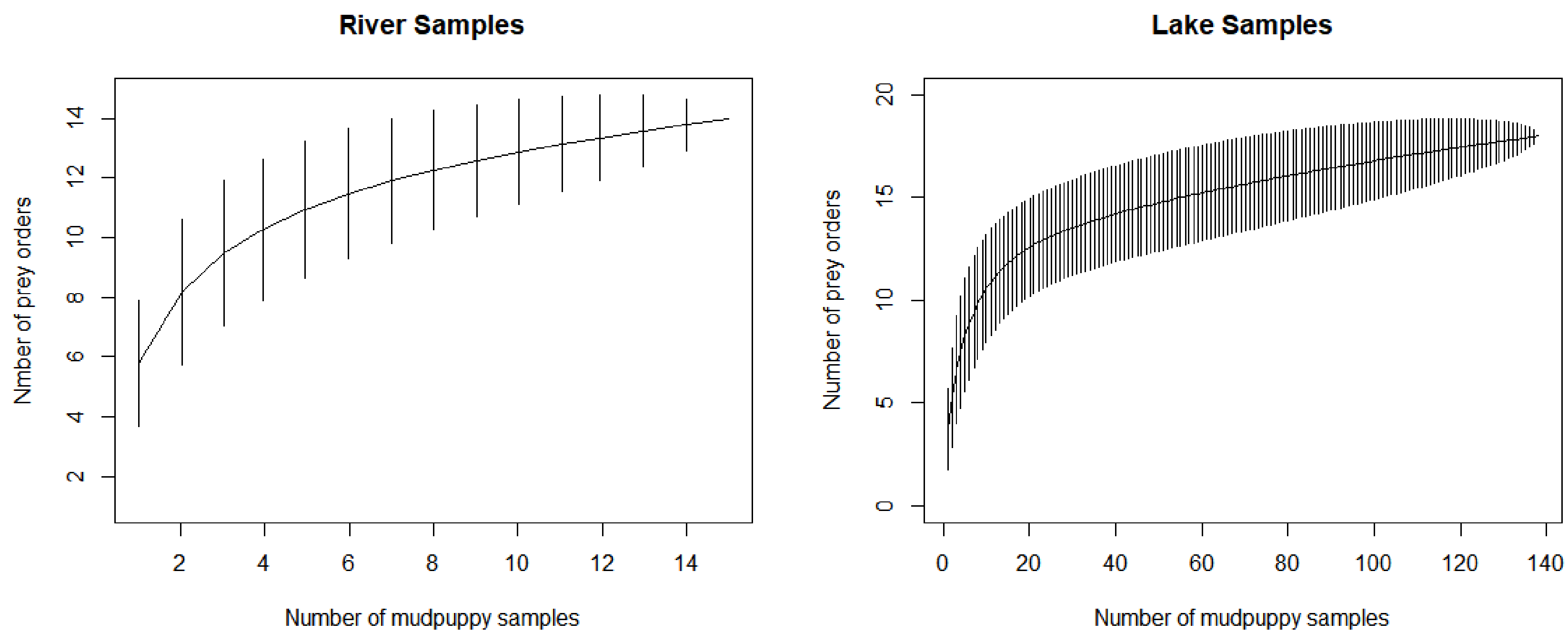

Fig. 1. Accumulation curves of ordinal-level taxonomic richness of the diet of the Mudpuppy (*Necturus maculosus*) based on stomach contents samples from individuals from rivers (N = 15) and lakes (N = 138) in eastern Kansas (Missouri and Arkansas river drainages). Sampling was conducted January 2018–April 2019. Vertical lines represent 95% confidence intervals.

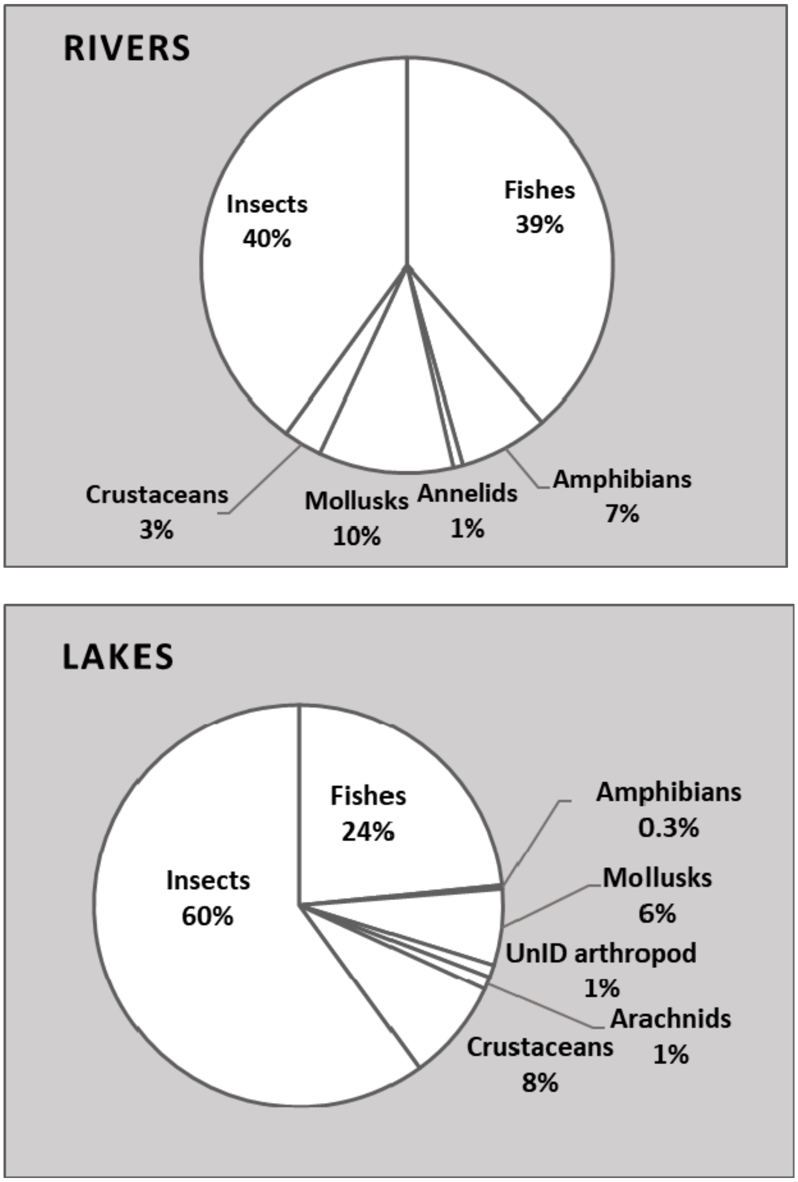

Fig. 2. Abundances of prey types as proportions of the total number of items in the diet of the Mudpuppy (*Necturus maculosus*) in eastern Kansas rivers and lakes (Missouri and Arkansas river drainages). Sampling was conducted January 2018–April 2019. River samples (N = 13 Mudpuppies plus 2 pooled samples derived from 6 individuals) yielded 135 prey items and lake samples (N = 138 Mudpuppies) yielded 771 prey items.

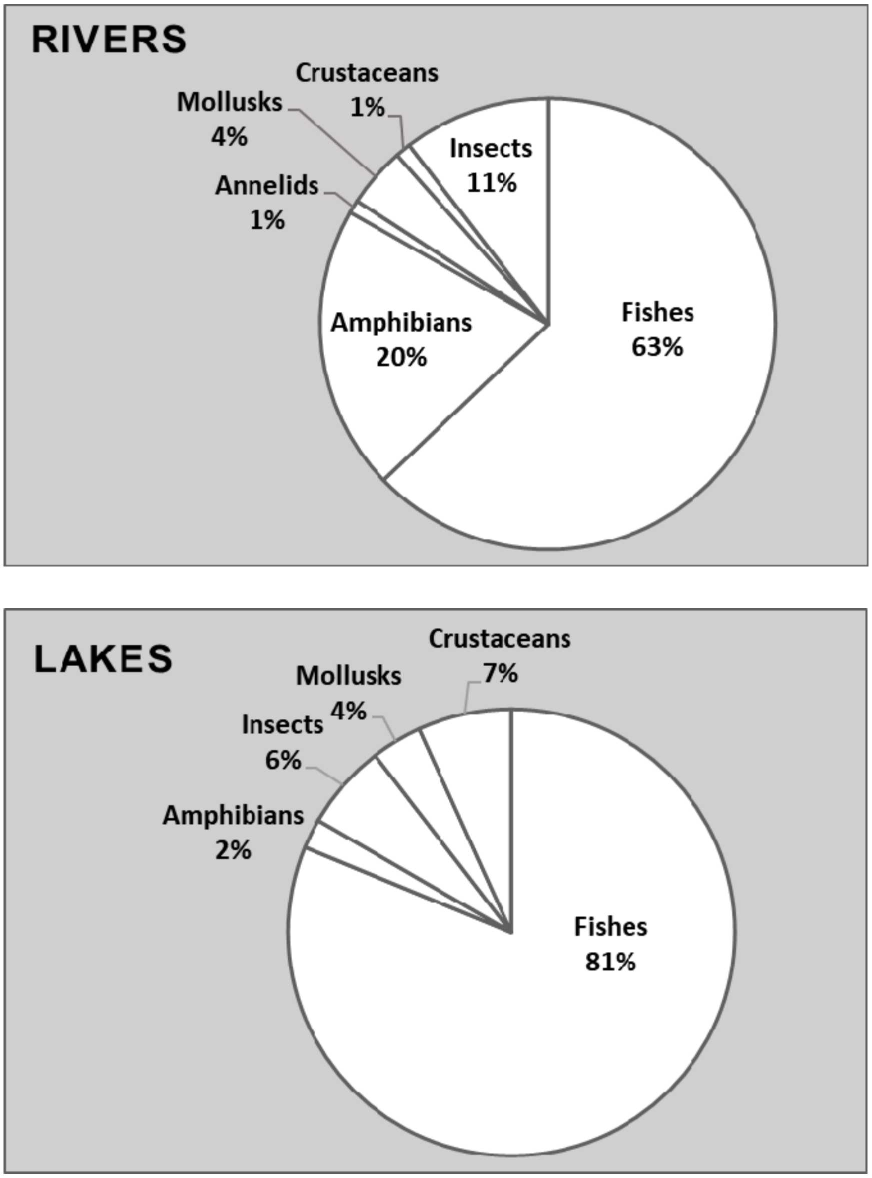

Fig. 3. Volumes of prey types as proportions of the total volume of items in the diet of the Mudpuppy (*Necturus maculosus*) in eastern Kansas rivers and lakes (Missouri and Arkansas river drainages). Sampling was conducted January 2018–April 2019. River samples (N = 13 Mudpuppies plus 2 pooled samples derived from 6 individuals) totaled 63,914 mm^3 and lake samples (N = 138 Mudpuppies) totaled 326,309 mm^3.

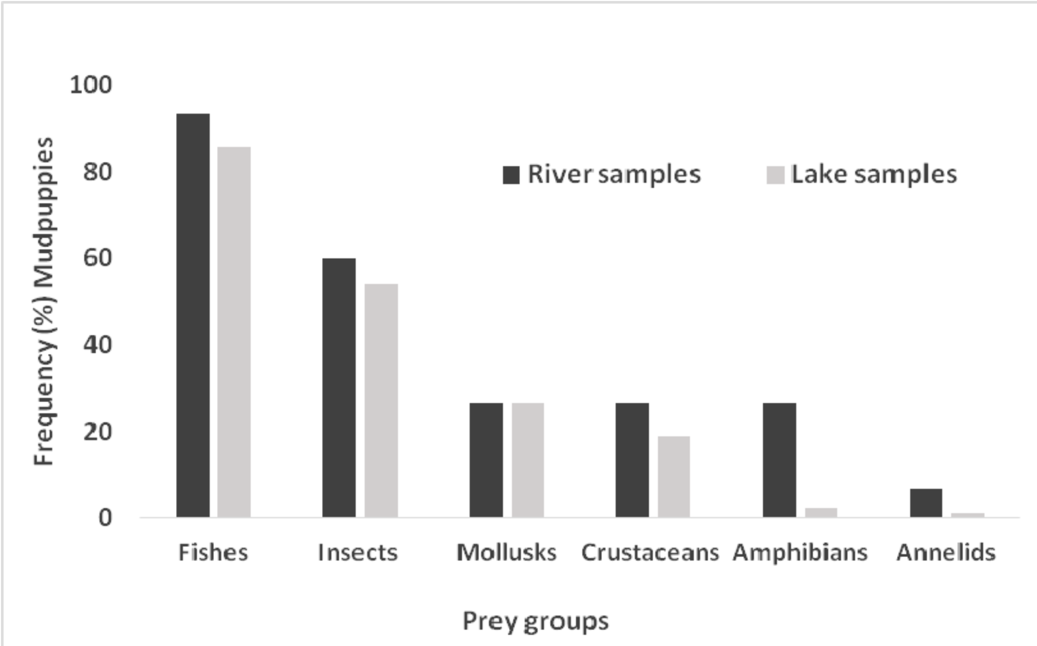

Fig. 4. Frequencies of occurrence of prey types among stomachs of the Mudpuppy (*Necturus maculosus*) in eastern Kansas rivers and lakes (Missouri and Arkansas river drainages). Sampling was conducted January 2018–April 2019. River samples included stomach contents from 13 Mudpuppies plus 2 pooled samples derived from 6 individuals, whereas lake samples totaled 138 Mudpuppies.

APPENDIX

Appendix. Locations and dates of capture of Mudpuppies, including *Necturus m. maculosus* (Missouri River drainage) and *N. m. louisianensis* (Arkansas River drainage), used for study of the species' diet in eastern Kansas. Two pooled samples, each derived from up to three individuals, were provided by the Sternberg Museum of Natural History (Fort Hays State University, Fort Hays, KS).

Drainage	**Waterbody**	**Habitat Type**	**County**	**Date**	**MU-ID**
Arkansas	Cottonwood River	River	Chase	11/27/2018	18-109-001
Arkansas	Elk River	River	Elk	1/17/2019	19-235-001
Arkansas	Neosho River	River	Allen	2/22/2003	Sternberg MNH
Arkansas	Neosho River	River	Woodson	2/22/2003	Sternberg MNH
Arkansas	Neosho River	River	Lyon	1/21/2018	18-049-002
Arkansas	Neosho River	River	Lyon	1/21/2018	18-049-003
Arkansas	Neosho River	River	Lyon	3/4/2018	18-002-001
Arkansas	Verdigris River	River	Greenwood	12/10/2018	18-117-01
Arkansas	Verdigris River	River	Greenwood	12/10/2018	18-118-01
Missouri	Long Creek	River	Osage	3/26/2019	19-004-001
Missouri	Marais des Cygnes River	River	Franklin	1/29/2018	18-030-003
Missouri	Marais des Cygnes River	River	Franklin	2/18/2018	18-072-001
Missouri	Marais des Cygnes River	River	Franklin	2/18/2018	18-081-001
Missouri	Marais des Cygnes River	River	Osage	3/11/2018	18-089-001
Missouri	Marais des Cygnes River	River	Osage	3/11/2018	18-090-001

Missouri	Melvern Lake	Lake	Osage	2/18/2018	18-008-002
Missouri	Melvern Lake	Lake	Osage	2/18/2018	18-008-003
Missouri	Melvern Lake	Lake	Osage	2/27/2018	18-008-004
Missouri	Melvern Lake	Lake	Osage	3/4/2018	18-008-005
Missouri	Melvern Lake	Lake	Osage	3/4/2018	18-008-006
Missouri	Melvern Lake	Lake	Osage	3/4/2018	18-008-007
Missouri	Melvern Lake	Lake	Osage	3/4/2018	18-008-008
Missouri	Melvern Lake	Lake	Osage	3/4/2018	18-008-009
Missouri	Melvern Lake	Lake	Osage	3/13/2018	18-008-010
Missouri	Melvern Lake	Lake	Osage	3/13/2018	18-008-011
Missouri	Melvern Lake	Lake	Osage	3/13/2018	18-008-012
Missouri	Melvern Lake	Lake	Osage	3/24/2018	18-008-013
Missouri	Melvern Lake	Lake	Osage	11/16/2018	18-008-014
Missouri	Melvern Lake	Lake	Osage	11/22/2018	18-008-015
Missouri	Melvern Lake	Lake	Osage	11/22/2018	18-008-016
Missouri	Melvern Lake	Lake	Osage	11/22/2018	18-008-017
Missouri	Melvern Lake	Lake	Osage	11/30/2018	18-008-018
Missouri	Melvern Lake	Lake	Osage	11/30/2018	18-008-019
Missouri	Melvern Lake	Lake	Osage	11/30/2018	18-008-020
Missouri	Melvern Lake	Lake	Osage	12/7/2018	18-008-021
Missouri	Melvern Lake	Lake	Osage	12/7/2018	18-008-022
Missouri	Melvern Lake	Lake	Osage	12/21/2018	18-008-023
Missouri	Melvern Lake	Lake	Osage	12/21/2018	18-008-024

Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-025
Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-026
Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-027
Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-028
Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-029a
Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-030(29b)
Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-031(30)
Missouri	Melvern Lake	Lake	Osage	1/2/2019	19-008-032(31)
Missouri	Melvern Lake	Lake	Osage	1/17/2019	19-008-036
Missouri	Melvern Lake	Lake	Osage	1/17/2019	19-008-037
Missouri	Melvern Lake	Lake	Osage	1/17/2019	19-008-038
Missouri	Melvern Lake	Lake	Osage	1/18/2019	19-008-033(32)
Missouri	Melvern Lake	Lake	Osage	1/24/2019	19-008-039
Missouri	Melvern Lake	Lake	Osage	1/24/2019	19-008-040
Missouri	Melvern Lake	Lake	Osage	1/24/2019	19-008-041
Missouri	Melvern Lake	Lake	Osage	1/24/2019	19-008-042
Missouri	Melvern Lake	Lake	Osage	2/4/2019	19-008-043
Missouri	Melvern Lake	Lake	Osage	2/4/2019	19-008-044
Missouri	Melvern Lake	Lake	Osage	2/4/2019	19-008-045
Missouri	Melvern Lake	Lake	Osage	2/14/2019	19-008-047
Missouri	Melvern Lake	Lake	Osage	2/14/2019	19-008-047a
Missouri	Melvern Lake	Lake	Osage	2/14/2019	19-008-048
Missouri	Melvern Lake	Lake	Osage	3/7/2019	19-008-048

Missouri	Melvern Lake	Lake	Osage	3/7/2019	19-008-049
Missouri	Melvern Lake	Lake	Osage	3/7/2019	19-008-050
Missouri	Melvern Lake	Lake	Osage	3/26/2019	19-008-015
Missouri	Melvern Lake	Lake	Osage	3/26/2019	19-008-051
Missouri	Melvern Lake	Lake	Osage	3/26/2019	19-008-052
Missouri	Melvern Lake	Lake	Osage	3/26/2019	19-008-053
Missouri	Melvern Lake	Lake	Osage	3/26/2019	19-008-054
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-023
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-055
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-056
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-057
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-058
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-059
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-060
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-061
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-062
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-063
Missouri	Melvern Lake	Lake	Osage	4/2/2019	19-008-064
Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-029
Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-065
Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-066
Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-067
Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-068

Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-069
Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-070
Missouri	Melvern Lake	Lake	Osage	4/9/2019	19-008-071
Missouri	Pomona Lake	Lake	Osage	1/29/2018	18-006-010
Missouri	Pomona Lake	Lake	Osage	2/12/2018	18-006-012
Missouri	Pomona Lake	Lake	Osage	2/12/2018	18-006-013
Missouri	Pomona Lake	Lake	Osage	2/12/2018	18-006-014
Missouri	Pomona Lake	Lake	Osage	2/12/2018	18-006-015
Missouri	Pomona Lake	Lake	Osage	2/25/2018	18-006-016
Missouri	Pomona Lake	Lake	Osage	2/27/2018	18-006-017
Missouri	Pomona Lake	Lake	Osage	2/27/2018	18-006-018
Missouri	Pomona Lake	Lake	Osage	2/27/2018	18-006-019
Missouri	Pomona Lake	Lake	Osage	3/4/2018	18-006-020
Missouri	Pomona Lake	Lake	Osage	3/4/2018	18-006-021
Missouri	Pomona Lake	Lake	Osage	3/4/2018	18-006-022
Missouri	Pomona Lake	Lake	Osage	3/4/2018	18-006-023
Missouri	Pomona Lake	Lake	Osage	3/4/2018	18-006-024
Missouri	Pomona Lake	Lake	Osage	3/4/2018	18-006-025
Missouri	Pomona Lake	Lake	Osage	3/4/2018	18-006-026
Missouri	Pomona Lake	Lake	Osage	3/6/2018	18-006-027
Missouri	Pomona Lake	Lake	Osage	3/6/2018	18-006-028
Missouri	Pomona Lake	Lake	Osage	3/13/2018	18-006-029
Missouri	Pomona Lake	Lake	Osage	3/13/2018	18-006-030

Missouri	Pomona Lake	Lake	Osage	3/13/2018	18-006-031
Missouri	Pomona Lake	Lake	Osage	3/13/2018	18-006-032
Missouri	Pomona Lake	Lake	Osage	3/13/2018	18-006-033
Missouri	Pomona Lake	Lake	Osage	3/13/2018	18-006-034
Missouri	Pomona Lake	Lake	Osage	3/13/2018	18-006-035
Missouri	Pomona Lake	Lake	Osage	3/21/2018	18-006-036
Missouri	Pomona Lake	Lake	Osage	3/21/2018	18-006-037
Missouri	Pomona Lake	Lake	Osage	3/28/2018	18-006-038
Missouri	Pomona Lake	Lake	Osage	3/28/2018	18-006-039
Missouri	Pomona Lake	Lake	Osage	3/28/2018	18-006-040
Missouri	Pomona Lake	Lake	Osage	3/28/2018	18-006-041
Missouri	Pomona Lake	Lake	Osage	4/1/2018	18-006-042
Missouri	Pomona Lake	Lake	Osage	7/11/2018	18-006-043
Missouri	Pomona Lake	Lake	Osage	8/15/2018	18-006-044
Missouri	Pomona Lake	Lake	Osage	11/16/2018	18-006-047
Missouri	Pomona Lake	Lake	Osage	11/16/2018	18-006-048
Missouri	Pomona Lake	Lake	Osage	11/16/2018	18-006-049
Missouri	Pomona Lake	Lake	Osage	11/22/2018	18-006-050
Missouri	Pomona Lake	Lake	Osage	11/22/2018	18-006-051
Missouri	Pomona Lake	Lake	Osage	11/22/2018	18-006-052
Missouri	Pomona Lake	Lake	Osage	11/22/2018	18-006-053
Missouri	Pomona Lake	Lake	Osage	12/7/2018	18-006-048
Missouri	Pomona Lake	Lake	Osage	12/7/2018	18-006-054

Missouri	Pomona Lake	Lake	Osage	12/20/2018	18-006-048
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Missouri	Pomona Lake	Lake	Osage	12/21/2018	18-006-055
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Missouri	Pomona Lake	Lake	Osage	12/21/2018	18-006-057
Missouri	Pomona Lake	Lake	Osage	1/2/2019	19-006-058
Missouri	Pomona Lake	Lake	Osage	1/2/2019	19-006-058
Missouri	Pomona Lake	Lake	Osage	1/2/2019	19-006-059
Missouri	Pomona Lake	Lake	Osage	1/2/2019	19-006-059
Missouri	Pomona Lake	Lake	Osage	1/2/2019	19-006-060
Missouri	Pomona Lake	Lake	Osage	1/7/2019	19-006-064
Missouri	Pomona Lake	Lake	Osage	1/8/2019	19-006-061
Missouri	Pomona Lake	Lake	Osage	1/8/2019	19-006-062
Missouri	Pomona Lake	Lake	Osage	1/17/2019	19-006-063
Missouri	Pomona Lake	Lake	Osage	1/17/2019	19-006-065
Missouri	Pomona Lake	Lake	Osage	1/17/2019	19-006-066
Missouri	Pomona Lake	Lake	Osage	1/17/2019	19-006-067
Missouri	Pomona Lake	Lake	Osage	1/17/2019	19-006-068
Missouri	Pomona Lake	Lake	Osage	1/24/2019	19-006-069
Missouri	Pomona Lake	Lake	Osage	1/24/2019	19-006-070

Missouri	Pomona Lake	Lake	Osage	2/4/2019	19-006-048
Missouri	Pomona Lake	Lake	Osage	2/4/2019	19-006-063
Missouri	Pomona Lake	Lake	Osage	2/4/2019	19-006-064
Missouri	Pomona Lake	Lake	Osage	2/4/2019	19-006-071
Missouri	Pomona Lake	Lake	Osage	2/4/2019	19-006-072
Missouri	Pomona Lake	Lake	Osage	2/14/2019	19-006-073
Missouri	Pomona Lake	Lake	Osage	2/25/2019	19-006-074
Missouri	Pomona Lake	Lake	Osage	2/25/2019	19-006-075
Missouri	Pomona Lake	Lake	Osage	2/25/2019	19-006-076
Missouri	Pomona Lake	Lake	Osage	2/25/2019	19-006-078
Missouri	Pomona Lake	Lake	Osage	3/7/2019	19-006-074
Missouri	Pomona Lake	Lake	Osage	3/7/2019	19-006-079
Missouri	Pomona Lake	Lake	Osage	3/7/2019	19-006-080
Missouri	Pomona Lake	Lake	Osage	3/7/2019	19-006-081
Missouri	Pomona Lake	Lake	Osage	3/7/2019	19-006-082
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-026
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-063
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-080
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-083
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-084
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-085
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-086
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-087

Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-088
Missouri	Pomona Lake	Lake	Osage	3/19/2019	19-006-089
Missouri	Pomona Lake	Lake	Osage	3/26/2019	19-006-025
Missouri	Pomona Lake	Lake	Osage	3/26/2019	19-006-055
Missouri	Pomona Lake	Lake	Osage	3/26/2019	19-006-074
Missouri	Pomona Lake	Lake	Osage	3/26/2019	19-006-090
Missouri	Pomona Lake	Lake	Osage	3/26/2019	19-006-091
Missouri	Pomona Lake	Lake	Osage	3/26/2019	19-006-092
Missouri	Pomona Lake	Lake	Osage	4/2/2019	19-006-060
Missouri	Pomona Lake	Lake	Osage	4/2/2019	19-006-093
Missouri	Pomona Lake	Lake	Osage	4/16/2019	19-006-025
Missouri	Pomona Lake	Lake	Osage	4/16/2019	19-006-060
Missouri	Pomona Lake	Lake	Osage	4/16/2019	19-006-094
Missouri	Pomona Lake	Lake	Osage	4/25/2019	19-006-095
Missouri	Pomona Lake	Lake	Osage	4/25/2019	19-006-096

Jennifer Lynn Buchanan
Typed Signature of Author

17 April 2020
Date

Diet of the Mudpuppy (*Necturus maculosus*) in Eastern Kansas
Title of Thesis