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Size Doesn't Matter: Body Size Is Not Linked to Diet Specialization in Garter Snakes (Squamata: Natricidae: *Thamnophis*)

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Abstract

Well-documented natural history allows for thorough study of a species' ecology and evolution. However, inadequate natural history data hamper such studies for many species. For example, diet plays a major role in the evolution of species and traits, but thorough quantitative dietary information is often lacking for many groups. Garter snakes (*Thamnophis*) have been used as model organisms for numerous studies, including many focused on feeding ecology and evolution, but these studies lack a thorough compilation of dietary records. To fill the substantial natural history gap, we amassed nearly 10,000 dietary records for 32 of 35 *Thamnophis* species, from more than 150 sources, and classified each species' dietary repertoire. We categorized 15 of 32 species as generalist predators and 17 of 32 species as specialist predators of varying prey groups, presenting novel dietary classifications for 15 species. Additionally, we investigated the hypothesis that generalist predators have larger body size, a pattern shown in other snake communities and lineages. However, we found no significant relationship between body size and dietary specialization in the genus. Our findings add to the knowledge of natural history, ecology, and evolution of *Thamnophis* and provide access to the largest dietary record repository for the genus to date.

Natural history data and observations form the foundation of modern ecological and evolutionary theories, ideas, and questions (Greene, 2005). Specifically, quantitative dietary data are critical for determining the trophic level, niche space, and behavior of a species, thus revealing its role in ecosystems (Greene & Jaksić, 1983; Thompson et al., 2007). However, published natural history records, such as dietary records, are scant or absent for many species, leading to generalized and often inaccurate portrayals of their ecology (M. C. Grundler, 2020; Maritz, Hofmann, et al., 2021; Maritz, Rawoot, et al., 2021; van den Burg, 2020). Problematic generalizations about diet may lead to incorrect conclusions when investigating ecological and evolutionary questions, highlighting the importance of detailed natural history data collection (Maritz, Rawoot, et al., 2021). Furthermore, even species with well-described natural histories often have records published in many different locations and, typically, there is no centralized database that facilitates efficient access to these records (Maritz, Hofmann, et al., 2021). Researchers are beginning to address this problem by building centralized databases such as CarniDIET (carnivore diets; Middleton et al., 2021), SquamataBase (snake diets; M. C. Grundler, 2020), and a generalized database for many organisms and their interactions (GloBI; Poelen et al., 2014). However, these centralized databases often fall short of being comprehensive with respect to published data. SquamataBase (M. C. Grundler, 2020), for example, contains records for fewer than 35% of currently described snake species (1,227 of 4,038; Uetz et al., 2023).

Snakes are an ideal group of organisms with which to study predator–prey interactions and their effects on ecology and evolution. With their unique morphologies and behaviors closely linked to diet acquisition, dietary studies of snakes further our understanding of numerous ecological and evolutionary trends (Durso et al., 2022; Glaudas et al., 2019; Mori & Vincent, 2008). A genus commonly used for ecological and evolutionary studies is garter snakes (*Thamnophis*), a diverse group found throughout North America (Hallas et al., 2022; Rossman et al., 1996). Thanks in part to variable behavior, habitat, morphology, and diet (Rossman et al., 1996), garter snakes are used to test a variety of hypotheses, including those about mating systems and coevolution of toxins/toxin resistance between predator and prey (e.g., Blais et al., 2023; Brodie & Brodie, 1999; Mason & Crews, 1985; Nelson et al., 1987; Reimche et al., 2020; Williams et al., 2004).

The diet of some *Thamnophis* species has been well-documented and linked to the evolution of dental morphology (Britt et al., 2009), head shape (Hallas et al., 2022; Hampton, 2013), energetic constraints (Britt et al., 2006), ontogenetic shifts (Ford & Hampton, 2009), and niche partition-

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ing (Carpenter, 1952). Nonetheless, many species from this genus and aspects of their evolution, such as body size, remain understudied.

Body size has a direct impact on an organism's ecology and behavior (Shine, 1991; Shine et al., 1998). Within snakes, larger body size has been linked to a broader diet in lineages at the snake community level in the Afro-Asian region (Barends & Maritz, 2022) and at finer scales within the genus *Bothrops* (Martins et al., 2002). Intraspecific dietary shifts, plausibly connected to differences in body size, have also been documented in pythons, colubrids, and vipers, with shifts in diet linked to both ontogenetic changes and sexual dimorphism (Hampton, 2018; Lord et al., 2023; Reading & Jofré, 2013; Shine et al., 1998; Vincent et al., 2004). It has been hypothesized that larger body size allows for capture and processing of prey items of multiple size classes, while smaller-bodied predators are limited to select prey items of smaller body size (Shine, 1991). However, the body size of pythons has been shown to predict prey preference rather than dietary breadth, suggesting that body size can impact multiple characteristics of diet (Barends & Naik, 2023).

To address the lack of easily accessible dietary data for *Thamnophis*, we created the largest dietary data repository for the genus to date and used these data to explore the evolution of snake body size and dietary specialization. We reviewed trends in diet across the group, classified species as generalists or specialists, and investigated the relationship between garter snake body mass and dietary ecology by testing the hypothesis that larger-bodied *Thamnophis* species display more generalized feeding behavior than smaller-bodied species.

MATERIALS AND METHODS

Dietary Record Collection.—*Thamnophis* dietary records were collected from primary literature searches and unpublished records. We utilized keyword searches in Google Scholar as well as the R package SquamataBase (M. C. Grundler, 2020) and *Herpetological Review*'s taxonomic index to find peer-reviewed articles and natural history notes. Lastly, unpublished records were gathered through personal communication with researchers focusing on many of the lesser-studied, range-restricted *Thamnophis* species, primarily ones occurring outside of the United States.

We included data only if quantitative counts of prey items were reported, or could be deciphered from the text (e.g., "Four *Dryophytes cinereus* were consumed by *T. sirtalis*" or "Out of 20 prey items found inside *T. sirtalis*, 75% were *Dryophytes cinereus*"), while records that only reported qualitative data or percentages with no sample size were excluded. We also removed duplicate records reported across multiple publications and records reported from captivity, as determined by a review of the source's methods.

For each record, we recorded the predator species and allocated it to a subspecific designation based on geographic location and then paired this with the taxonomic serial number from the Integrated Taxonomic Information System (ITIS). Prey were identified to the lowest possible taxonomic level. For all records with prey identified to species level, we included the generic and specific epithet as published and updated taxonomy as listed in ITIS, along with its taxonomic serial number. Counts of prey items were compiled for a quantifiable measure of these interactions. Additional data such as source of the record, geographic coordinates, general location, predator snout-vent length, sex, and age class were recorded when available. Recent phylogenetic studies suggested *Adelophis foxi* and *Adelophis copei* are congeneric with members of *Thamnophis*; however, due to the contradictory literature and small sample sizes of genetic and dietary work, *Adelophis* were excluded from this study (de Queiroz et al., 2002; Hallas et al., 2022; Nuñez et al., 2023).

Dietary Classification.—All analyses were completed in R (version 4.2.2; R Core Team, 2021) with RStudio (version 1.3.1056; R Studio Team, 2020). In the dataset, prey records were grouped by taxonomic levels (species, genus, family, order, class, and phylum). All analyses were conducted with prey categorized to the class level. For each garter snake species, we calculated the proportion of total prey items for each prey group and, from this, determined the dominant prey group for each species. Following Grundler and Rabosky (2020), we classified species as dietary generalists if the dominant prey group accounted for <70% of diet, or dietary specialists if the dominant prey group accounted for ≥70% of diet records. To ensure dietary threshold percentage did not affect results, species were also classified as dietary generalists or specialists using 50% and 90% dietary thresholds. Additionally, to account for ecological/morphological dietary specialization, prey items were grouped by morphology—Amphibian, Bird, Fish, Invertebrate, Mammal, and Reptile—rather than taxonomic groupings, and generalists and specialists were again determined by 50%, 70%, and 90% dietary thresholds.

Relationship between Snake Mass and Diet.—To investigate the relationship between garter snake mass and dietary ecology, we obtained the calculated maximum log mass measurements (hereafter: "mass") for each *Thamnophis* species listed in Feldman et al. (2016) ($n = 32$; Supplementary Data 1, Table S1). We extracted a time-calibrated *Thamnophis* species tree from Hallas et al. (2022) using the physketch function from the phytools R package (version 1.5-1; Revell, 2012) to test relationships across phylogeny. We filtered predator species based on the presence of diet records in our database, mass data from Feldman et al. (2016), and inclusion in the Hallas et al. (2022) phylogeny, leaving 28 species. We used a t-test (using the t.test function in R) to compare the mean maximum mass of generalist ($n = 13$) and specialist ($n = 15$) groups. To incorporate phylogenetic relatedness, we used the phylosig function in phytools (Revell, 2012) to test for phylogenetic signal of mass by calculating both Blomberg's K (Blomberg et al., 2003) and Pagel's lambda (λ; Pagel, 1993); K and λ values closer to zero reflected little to no phylogenetic signaling (evolution occurs independent of phylogeny), while K and λ values closer to one reflected higher levels of phylogenetic signaling. K-values >1 reflected stronger similarity than expected between closely related species (Hallas et al., 2022; Münkemüller et al., 2012). We hypothesized that garter snakes with larger mass have a more generalist diet, as shown in some other snake lineages (Barends & Maritz, 2022; Martins et al., 2002; Shine et al., 2014). Specifically, we expected garter snake species with a generalist diet to have significantly larger mass than species with a specialist diet, as categorized above. We used the phylANOVA function with 1,000 simulations found in phytools (Garland et al., 1993; Revell, 2012) to conduct a phylogenetic analysis of variance (phylANOVA) to test for differences between the two groups while incorporating the time-calibrated phylogeny. For this case, the evolution of snake mass was simulated on the estimated evolutionary tree of *Thamnophis* under a Brownian motion model of trait evolution. *P*-values for comparisons of snake mass of specialists versus generalists were obtained by comparing the *F* ratio from the observed data with the set of *F* ratios from the 100 data sets generated by the simulation. We then further refined our specialist assignments above on the basis of prey groups: that is, if the diet of a specialist species was comprised of >70% of a single vertebrate prey group, they were considered vertebrate specialists, and if the diet of a specialist species was comprised of >70% of a single invertebrate prey group, they were considered invertebrate specialists. This method was also completed using 50% and 90% dietary thresholds, but results are presented from the 70% threshold, following Grundler and Rabosky (2020). At a finer scale, we expected generalist garter snake species to have the largest mass, invertebrate specialists to have the smallest mass, and vertebrate specialists to have an intermediate mass. The groupings for each species can be found in Supplementary Data 2, Table S2. With these revised categories, we reran the phylANOVA function method outlined above with the addition of post-hoc tests to test for differences in mass between each group. To further investigate relationships between mass and dietary behavior, we ran phylogenetic linear regression analyses comparing body mass to both dietary composition and dietary specialization. From the phylolm package (Ho & Ané, 2014) in R, the phylolm function was used to test for relationships between snake body mass and dietary composition. The phyloglm function was also used to test the predictive power of dietary specialization (as a binomial variable: specialists = 1; generalists = 0) on snake mass. All methods described here were implemented at 50%, 70%, and 90% dietary thresholds on both taxonomic and ecological/morphological prey groupings.

Data Availability.—Data gathered for this project, including the raw dietary data used for analyses, mass data, and the time-calibrated tree, can be found at https://github.com/theptin/Thamnophis-GloBI. We formatted diet data for accessibility through the GloBI online database (https://www.globalbioticinteractions.org). The dietary data repository will be continually updated after publication. The most current version is available at https://github.com/theptin/Thamnophis-GloBI/blob/main/GloBI_Thamnophis_Diet_records.csv or through the GloBI online database.

Results

Dietary Record Collection.—The *Thamnophis* diet database includes 32 of the 35 currently recognized species and totals 9,551 prey items from 173 total sources spanning over a century of research (Table 1). Records per species range from 0 to 3,409, with an average of 258.13 and a median of 53 records per species (Table 1). No records were found for *T. exsul*, *T. postremus*, or *T. unilabialis*. *Thamnophis* records were primarily found in journal articles or books (90.63%), while natural history notes and previously unpublished data provided many novel records, but their data made up a relatively small proportion of the database (7.48% and 1.89%, respectively). Most dietary records we collected were published in the last 40 years (73.08%), with the majority of available natural history records and primary publications coming within that period (96.02% and 71.7% respectively).

Thamnophis *Dietary Specialization.*—We analyzed dietary trends for the 32 species for which diet data were available (Fig. 1). All analyses were conducted using a 50%, 70%, and 90% dietary threshold, but all results presented here are from the 70% threshold, following Grundler and Rabosky (2020). We classified 15 species as generalists and 17 species as specialists. We further classified 14 species as vertebrate specialists (twelve amphibian specialists, two fish specialists) and three as invertebrate (Clitellata—earthworm) specialists.

Relationship Between Snake Mass and Dietary Specialization.—Because major conclusions did not change by varying thresholds for classifications, all results presented here are following prey grouping by taxonomic class and dietary classification using a 70% dietary threshold value. Results for all analyses featuring ecological groupings at 50%, 70%, and 90% dietary thresholds (Supplementary Data 3, Figures S1–S6 and Tables S3–S6) and taxonomic groupings at 50% and 90% (Supplementary Data 4, Figures S7–S10 and Tables S7–S8) dietary thresholds of prey taxonomic class to determine specialization can be found in the Supplementary Data. Using the nonphylogenetic t.test, we found no significant variation in mass between the generalist ($\bar{x}_{generalist\ mass} = 2.33$) and specialist ($\bar{x}_{specialist\ mass} = 2.21$) groups ($P = 0.6144$; df = 20.482). We recovered moderate phylogenetic signal for mass across the phylogeny ($\lambda = 0.722$; $K = 0.807$; Fig. 2). Accounting for this phylogenetic signal, we again found body mass to be a poor predictor of dietary group between our generalist and specialist groups (phylANOVA: $F = 0.276$; $P = 0.63$; df =1), including at finer comparisons of vertebrate and invertebrate specialists (phylANOVA: $F = 1.48$; $P = 0.325$; df =1). The post-hoc tests also resulted in no support for differences (Generalist vs. Invertebrate Specialist: pairwise corrected $P = 0.453$; Generalist vs. Vertebrate Specialist: pairwise corrected $P = 0.989$; Invertebrate Specialist vs. Vertebrate Specialist: pairwise corrected $P = 0.453$). We also found no significant relationships between dietary specialization and snake mass using phylogenetic linear regressions (df = 27) (Table 2). The only significant relationships found were a significant positive relationship between snake mass and percent of diet comprised of *Actinopterygii* in our prey taxonomic class grouping (slope = 18.29; $P = 0.028$; df = 27) (Table 3) and of fish in our ecological prey grouping (slope = 18.34; $P = 0.029$; df = 27) (Supplementary Data 3). However, there was no significant relationship between body mass and *Actinopterygii* specialization (slope = 0.745; $P = 0.61$; df = 27) (Table 2) or fish specialization (slope = 0.745; $P = 0.61$; df = 27) (Supplementary Data 3).

TABLE 1. Summary of compiled dietary records in the *Thamnophis* diet database by predator species and prey class. *T. exsul*, *T. postremus*, and *T. unilabialis* are absent as they lacked records.

	Prey Type												
Snake Species	**Actinopterygii**	**Amphibia**	**Arachnida**	**Aves**	**Clitellata**	**Diplopoda**	**Gastropoda**	**Hyperoartia**	**Insecta**	**Malacostraca**	**Mammalia**	**Reptilia**	**Total Records**
Thamnophis atratus	69	305	-	-	9	-	5	1	-	-	-	-	389
Thamnophis bogerti	-	4	-	-	1	-	-	-	-	-	-	2	7
Thamnophis brachystoma	-	-	-	-	27	-	-	-	-	-	-	-	27
Thamnophis butleri	-	1	-	-	63	-	-	-	-	-	-	-	64
Thamnophis chrysocephalus	1	21	-	-	-	-	-	-	-	-	-	-	22
Thamnophis conanti	-	-	-	-	2	-	-	-	-	-	-	3	5
Thamnophis couchii	50	38	-	-	-	-	-	-	-	-	-	-	88
Thamnophis cyrtopsis	96	364	-	-	23	-	-	-	-	-	-	1	484
Thamnophis elegans	882	835	-	53	905	-	613	-	-	79	37	5	3409
Thamnophis eques	129	84	-	-	190	-	4	-	-	-	2	1	410
Thamnophis errans	-	2	-	-	7	-	-	-	-	-	1	10	20
Thamnophis fulvus	-	51	-	-	1	-	-	-	1	-	-	-	53
Thamnophis gigas	44	93	-	-	-	-	-	-	-	-	1	-	138
Thamnophis godmani	-	3	-	-	2	-	-	-	-	-	-	10	15
Thamnophis hammondii	5	24	-	-	25	-	-	-	-	-	-	-	54
Thamnophis lineri	-	5	-	-	2	-	-	-	-	-	-	2	9
Thamnophis marcianus	2	74	-	-	11	-	-	-	-	-	-	4	91

	Prey Type											
Thamnophis melanogaster	257	270	-	-	97	-	-	-	-	76	-	-	700
Thamnophis mendax	-	2	-	-	-	-	-	-	-	-	-	-	2
Thamnophis nigronuchalis	1	2	-	-	1	-	-	-	-	-	-	-	4
Thamnophis ordinoides	-	1	-	-	75	-	63	-	-	-	-	-	139
Thamnophis proximus	14	522	-	-	-	-	-	-	2	3	-	4	545
Thamnophis pulchrilatus	-	9	-	-	-	-	-	-	-	-	-	-	9
Thamnophis radix	2	301	-	-	31	-	2	-	-	-	11	1	348
Thamnophis rossmani	2	-	-	-	-	-	-	-	-	-	-	-	2
Thamnophis rufipunctatus	40	-	-	-	-	-	-	-	-	-	-	-	40
Thamnophis saurita	-	156	1	-	-	-	-	-	-	-	-	-	157
Thamnophis scalaris	-	18	-	-	26	-	-	-	-	-	2	21	67
Thamnophis scaliger	-	1	-	-	70	-	-	-	-	-	-	10	81
Thamnophis sirtalis	47	1292	1	31	590	1	7	-	41	4	34	10	2058
Thamnophis sumichrasti	-	13	-	-	-	-	-	-	-	-	-	-	13
Thamnophis validus	28	71	-	-	1	-	1	-	-	-	-	-	101

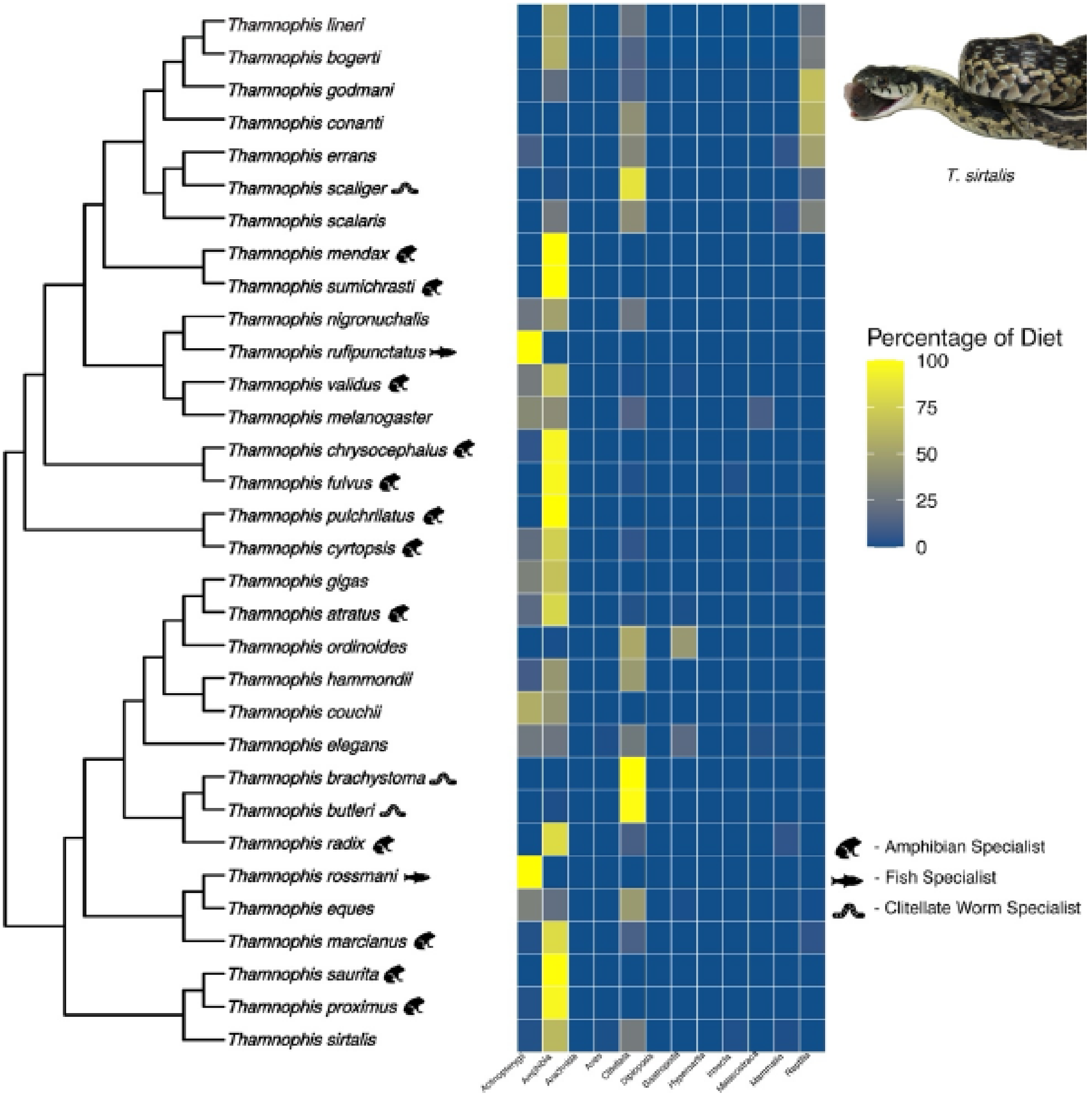
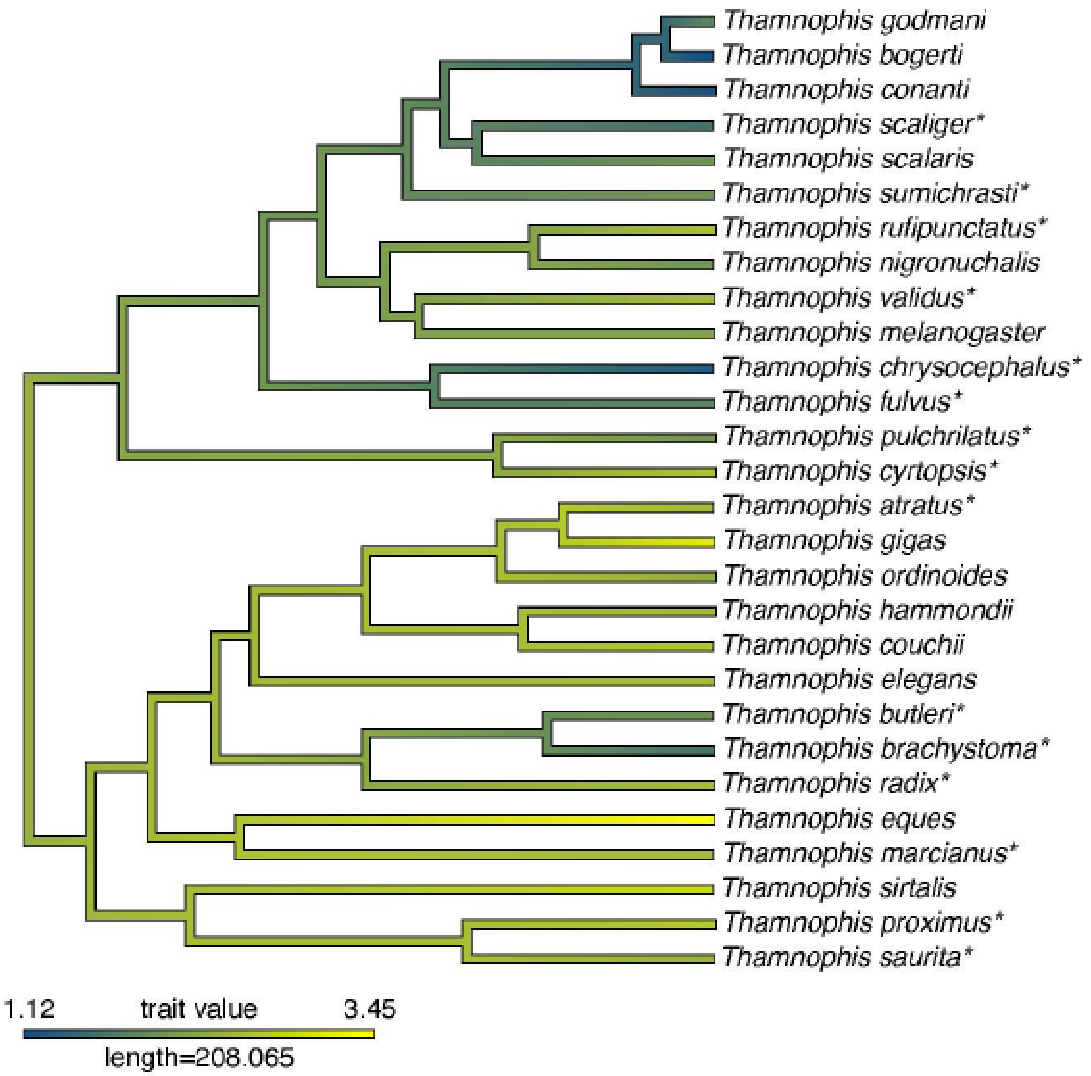


FIG. 1. Dietary profiles across *Thamnophis*. The heatmap displays the percentage of dietary records for each *Thamnophis* species based on prey class. The phylogenetic tree was adapted from Hallas et al. (2022), with additional placement of *T. mendax* following de Queiroz et al. (2002), *T. rossmani* following Conant (2000), and *T. lineri* inferred from Rossman and Burbrink (2005). The heatmap was generated using the *gheatmap* function on the *ggtree* R package (Yu et al., 2017). Photo of *T. sirtalis* consuming earthworm by TCH.

DISCUSSION

The diversity and proportionality of prey types found in garter snake diets is substantial, and our review of this diversity enhances our understanding of *Thamnophis* natural history. Here, we classified 32 *Thamnophis* species as dietary generalists or specialists, enabling the investigation of traits often associated with feeding behaviors, such as body mass. Our study collates the largest dataset of garter snake dietary records to date and is the first quantitative review of garter snake diet across the genus. This data repository provides increased access to *Thamnophis* dietary records from 91% of the currently recognized garter snake species, spanning over a century of research. In contrast to previous investigations of pythons (Barends & Naik, 2023) and pitvipers (Martins et al., 2002), we found no relationship between *Thamnophis* body mass and dietary trends.

Dietary Review.—Our results largely follow previously reported trends throughout the genus, but with new insights, especially for species not found in the United States. With our dataset, we categorized 15 *Thamnophis* species as generalist or specialist, in agreement with Rossman et al. (1996): *T. bogerti, T. couchii, T. elegans, T. eques, T. gigas, T. hammondii, T. melanogaster,* and *T. sirtalis* as generalists, and *T. brachystoma, T. butleri, T. cyrtopsis, T. marcianus, T. proximus, T. rufipunctatus,* and *T. saurita* as specialists. Three species were unclassified as they lacked dietary records (*T. exsul, T. postremus,* and *T. unilabialis)*. Rossman et al. (1996) classified *T. ordinoides* as "a specialist on slugs and earthworms," confirmed by our data; however, we classified *T. ordinoides* as a generalist due to the difference in taxonomic class between earthworms (Clitellata) and slugs (Gastropoda). Our assignment of *T. scaliger* as an earthworm specialist (86.42% of diet records) agrees with



*- Denotes Specialist Predator

FIG. 2. Log body mass of *Thamnophis* species (from Feldman et al., 2016) plotted across the phylogeny. The plot was produced with the *contmap* function from the *phytools* R package (Revell, 2012).

TABLE 2. Results from the phylogenetic linear regression between snake body mass and dietary specialization using prey taxonomic class groupings and a dietary threshold of 70% composition. Actintopterygii, Amphibia, and Clitellata were the only prey groups tested, as they were the only groups with specialist predators.

	Results				
Dietary Group	**AIC**	**Log likelihood**	**Alpha**	**Slope**	**P-value**
Actinopterygii	14.77	-4.39	0.12	0.74	0.61
Amphibia	41.18	-17.59	0.01	>-0.01	0.99
Clitellata	20.73	-7.37	0.01	-1.73	0.13

Reguera et al. (2011). Importantly, we assigned novel classifications for 15 species. Rossman et al. (1996) classified *T. atratus*, *T. radix*, and *T. validus* as generalist species; however, we considered them all amphibian specialists, as amphibians comprised 78.41%, 86.49%, and 70.30% of their diets, respectively. Manjarrez et al. (2007) identified *T. scalaris* as a specialist because 81% of their diet was comprised of earthworms; however, including more diet records led to an assignment as a generalist, with Clitellata comprising only 38.81% of dietary records. Due to similar ecologies and morphologies of prey items, we ran additional analyses grouping prey into six broader categories—Amphibian, Bird, Fish, Invertebrate, Mammal, Reptile—to reduce the effect of arbitrary taxonomic rankings.

TABLE 3. Results from the phylogenetic linear regression between snake body mass and dietary composition using prey taxonomic class grouping.

	Results						
Dietary Group	**AIC**	**Log likelihood**	**Sigma^2**	**Slope**	**P-value**	**R-squared**	**Adj. R-squared**
Actinopterygii	256.8	-125.4	1.841	18.286	0.0278*	0.172	0.141
Amphibia	289.2	-141.2	5.870	-7.7061	0.586	0.012	-0.027
Arachnida	-285.7	145.9	<0.001	-1.73E-04	0.724	0.005	-0.033
Aves	22.9	-8.4	<0.001	0.0578	0.635	0.009	-0.029
Clitellata	270.1	-132.1	2.966	-19.2297	0.064	0.125	0.091
Diplopoda	-460	233	<0.001	1.37E-05	0.533	0.015	-0.023
Gastropoda	214.5	-104.2	0.406	-2.6794	0.473	0.020	-0.018
Hyperoartia	-340.1	173.1	<0.001	-1.35E-04	0.470	0.020	-0.017
Insecta	41.3	-17.6	<0.001	0.0832	0.623	0.009	-0.028
Malacostraca	128.3	-61.1	<0.001	0.0199	0.980	<0.001	-0.038
Mammalia	89.6	-41.8	<0.001	0.5358	0.188	0.066	0.030
Reptilia	249.1	-121.6	1.401	10.5284	0.136	0.083	0.048

* - indicates a significant p-value below 0.05 .

Thamnophis ordinoides was the only species reclassified—from generalist to specialist in agreement with Rossman et al. (1996)—under these new groupings. This reclassification did not significantly affect results in the body mass and dietary behavior analyses (Supplementary Data 3). We found no publications quantifying dietary preferences of the generalists *T. conanti, T. errans, T. godmani, T. lineri, T. nigronuchalis,* or the specialists *T. chrysocephalus, T. fulvus, T. mendax, T. pulchrilatus, T. rossmani,* and *T. sumichrasti*. All data for these species were gathered through natural history notes or through previously unpublished data and our categorizations are the first attempt at a comprehensive quantitative description of their diet classification. However, we note their diets are in need of further exploration. This dataset represents a starting point for further investigation into relationships between feeding ecology and other life history traits, such as sexual size dimorphism, ontogenetic shifts, competition, toxin resistance, and habitat, all of which could potentially influence dietary specialization and some of which have been investigated in select lineages within the genus *Thamnophis* (Brodie & Brodie, 1999; Ford & Hampton, 2009; Hampton, 2018).

Effect of Snake Mass on Dietary Trends.—Recent work has shown that larger body size allows for capturing and processing of prey across broader size ranges and has been linked to a more generalized diet and prey preference (Barends & Maritz, 2022; Barends & Naik, 2023; Lord et al., 2023). However, our results for the genus *Thamnophis* show there are no significant differences in the mass of species classified as dietary generalists or dietary specialists regardless of threshold, including when considering finer scales of dietary classification.

Nonetheless, while often correlated, body size is not the only characteristic associated with dietary breadth. As gape-limited predators, snake feeding is also constrained by maximum opening of the mouth (Moon et al., 2019), and characteristics such as head and snout length and snout width have been linked to dietary trends in multiple snake lineages (e.g., Fabre et al., 2016; Gripshover et al., 2023; Klaczko et al., 2016), including *Thamnophis* (Hallas et al., 2022). Ecological and behavioral characteristics have also been linked to feeding trends. Habitat choice potentially plays a role in evolution of body size both inter- and intraspecifically (Huey, 1991; Hyslop et al., 2014), with the result that habitat variation drives body size evolution rather than dietary behavior. Feeding mode is correlated with both feeding behavior and body size, with ambush-hunting snakes often possessing larger body size and a wider dietary breadth, whereas actively foraging snakes are often slenderer and feed on a smaller range of prey items (Glaudas et al., 2019). Garter snakes are primarily active foragers (Rossman et al., 1996), so it is plausible a slenderer body type is more suitable for this feeding behavior regardless of dietary classification, leading to generalist species that are not as large as might be expected. To our knowledge, ours is the first analysis of its kind to explicitly focus on a single genus of active foraging snakes. Additionally, feeding behavior throughout the genus may not be conducive to a specialized body size. While invertebrate specialists are often smaller in body size than other groups (Vitt & Vangilder, 1983), the varying sizes of prey items, such as fish and amphibians, consumed by other specialist garter snake species may lead to inconsistencies in body size evolution throughout the genus. Additionally, slightly larger body sizes of our species classified as generalists could be due to occasional consumption of other, larger prey items such as birds and mammals (Greene & Wiseman, 2023) rather than true dietary generalization, aligning with trends found in pythons (Barends & Naik, 2023). Given the multiple potential selective pressures and lack of relationship between body size and feeding, it is likely *Thamnophis* has adaptive characteristics other than body size to increase efficiency in prey capture and handling, with body size evolution driven by other, potentially confounding, forces. Further exploration is needed throughout this genus to understand more fully the evolutionary relationship between dietary and ecological variables.

Dietary Data Repository.—Our diet database is not the first large-scale ecological interaction data repository assembled, but it works to further address the need for centralized, publicly available repositories. Our database improves upon the *Thamnophis* records of the only large-scale snake diet repository, Squamatabase (M. C. Grundler, 2020), increasing the total number of prey items to 9,551 (from 1,381) and species coverage to 32 (from 25). For a more detailed look at ecological interactions, we must continue expanding these databases at the genus and species level (Maritz, Hofmann, et al., 2021). Incorporation of these data in public databases, such as GloBI (Poelen et al., 2014), will ensure accessibility and preservation of these records for generations to come. In addition to providing data for novel research, these databases can play a critical role in effective management of declining populations. Dietary analyses are crucial in management plans and recovery of a variety of vertebrate taxa (Cade & Temple, 1995; Castle et al., 2020; Gillespie, 2013). According to the IUCN Red List (2023), *T. gigas* and *T. scaliger* are listed as "vulnerable" with decreasing populations, and *T. melanogaster* and *T. mendax* are listed as "endangered" with decreasing populations. Additionally, *T. nigronuchalis* and *T. rossmani* are "Data Deficient." *Thamnophis butleri, T. hammondii,* and populations referred to as the subspecies *T. sirtalis tetrataenia* have varying levels of protections at the U.S. state level. The data we have compiled here could provide valuable insights into diets of these species and allow for increased understanding of their natural history and ecology.

Limitations.—While this diet database is the largest for the genus *Thamnophis* to date, we acknowledge its limitations. Efforts were made to gather records from all available publications while ensuring records published multiple times were only included once in the dataset; however, it is probable records were unintentionally omitted. Additionally, some *Thamnophis* species have diet records limited in number and coverage of species' distribution, which can introduce bias in results due to small sample size and we anticipate classification as specialists or generalists may change as more data is obtained. We chose to proceed with these methods to maximize sample size and coverage across the genus. Species classified as generalist predators in our prey taxonomic class grouping with our methodology at the 70% dietary threshold have a mean of 474.87 dietary records (± 95% C.I. = 491.14) while the species classified as specialists have a mean of 142.82 records (± 95% C.I. = 85.42). However, the generalist mean is skewed by the large number of dietary records found for *T. sirtalis* and *T. elegans*—2,058 and 3,409 respectively. When *T. sirtalis* and *T. elegans* are removed, the mean of prey records for generalist species drops to 127.38 (± 95% C.I. = 103.45). Additionally, lack of available metadata, such as species-specific identification for prey, location, date, snake and prey body size and mass, and other characteristics, further limit our ability to test for ontogenetic and seasonal shifts, intraspecific variation, and niche partitioning. Within garter snakes, seasonal changes in dietary behavior due to prey availability are documented in *Thamnophis radix* (Tuttle & Gregory, 2009) and ontogenetic and sex differences in body size are documented in *Thamnophis proximus*, potentially affecting dietary behavior (Ford & Hampton, 2009). However, these trends are hidden at a larger scale without adequately recorded metadata. As availability and accessibility of natural history information improves, large-scale meta-analyses such as this one can better interrogate ecological and evolutionary trends and serve as valuable foundations for additional studies. Thus, we encourage all researchers to collect and report as much standardized information as possible when publishing diet information, as suggested by Maritz et al. (2021).

Conclusion.—While descriptions of the ecology of *Thamnophis* species are common, large-scale, quantitative reviews of specific natural history traits are rare (Rossman et al., 1996). Here, we created a diet database of almost 10,000 records for the genus, presented novel descriptions of diet for 15 species, and reviewed large-scale trends across the group. We did not find a significant relationship between body mass and dietary behavior in the genus, suggesting garter snakes have adapted other characteristics to increase feeding efficiency and prey handling. Our findings highlight the importance of large-scale databases, such as this one, to allow for accurate representation of a species' ecology, and permit increased efficiency of analyses of ecological interactions.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online alongside the manuscript.

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SUPPLEMENTARY MATERIALS

Supplementary Data 1

Download: https://jherpetol.scholasticahq.com/article/118880-size-doesn-t-matter-body-size-is-not-linked-to-diet-specialization-in-garter-snakes-squamata-natricidae-_thamnophis_/attachment/230713.docx?auth_token=XpHKIMS1X2_VwWCRIQsS

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