Ichthyology & Herpetology 109, No. 3, 2021, 685–690

What the Dead Tell Us about the Living: Using Roadkill to Analyze the Diet and Endoparasite Prevalence in Two Bahamian Snakes

Sebastian Hoefer[1], Sophie Mills[1], Theodora Pinou[2], and Nathan J. Robinson[1,3]

There is very little information of the foraging ecology and parasite infections of many snake species. Here, we used opportunistically collected roadkill to assess diet and parasite prevalence in two snake species in The Bahamas, the Bahamian Racer (*Cubophis vudii vudii*) and the Bahamian Boa (*Chilabothrus strigilatus strigilatus*). Over eight months, we conducted up to four daily routine road surveys along a 10 km stretch of highway, as well as opportunistic surveys elsewhere on the island of Eleuthera. Overall, we collected 270 roadkilled snakes of which less than half (39%) were intact and suitable for analyses. Lizards were the most prevalent prey items, although we also found rodents and other snakes. We report on new prey items for the Bahamian Racer, including two snakes and a case of oophagy. Endoparasites, which appeared to be all nematodes, were present only in Bahamian Racers, with 74% of all individuals infected. Parasite infection rates and loads were higher in females than in males. We show that using roadkilled snakes is an effective method for studying the diet and endoparasite prevalence in snakes on a Bahamian island.

KNOWLEDGE of an animal's diet can provide insights into foraging behavior (Sutton et al., 2015), ontogenetic shifts in prey preference (Mushinsky et al., 1982), morphological and physiological adaptations (Mori and Vincent, 2008; Brecko et al., 2011), and trophic structure (Miller et al., 2010). Identifying prey preferences can also play a central role in understanding predator–prey dynamics, and how they can be managed to achieve conservation goals, if, for example, the prey is specialized and vulnerable to population decline (Terraube et al., 2011).

There are several ways to investigate a snake's diet. These range from directly evaluating visible animal parts inside the stomach and fecal matter (Luiselli et al., 2007; Reading and Jofré, 2013) to analyzing prey remnants at a molecular level via stable isotopes (Willson et al., 2010) and genetic screening (Brown et al., 2014); these methods can be conducted on living or dead snakes. One of the most common ways to assess diet in snakes is to palpate them to promote regurgitation or defecation, with the expelled matter subsequently being examined for consumed prey items (Carbajal-Márquez et al., 2020). However, regurgitated matter will likely consist only of recently consumed prey, and fecal matter is limited to evidence of already digested animal parts. Thus, neither provides a full picture of an animal's diet. Conducting stomach content analyses on dead individuals is a viable alternative method which eliminates the stress and food deprivation associated with methods using live animals. Preserved museum specimens and roadkilled snakes are frequently used to investigate prey composition (Luiselli et al., 2001). Examining roadkilled snakes can also provide insights into endoparasites that may occupy the stomach (Goldberg et al., 1991; Kavetska et al., 2012). Roadkilled specimens are often easier to encounter than live individuals but may be too damaged to analyze. This risk can be reduced with regular surveys to counteract exposure of roadkill to traffic and damaging weather.

The island of Eleuthera in The Bahamas is home to four species of snakes (Powell and Henderson, 2012): the Bahamian Racer (*Cubophis vudii vudii*), Bahamian Boa (*Chilabothrus strigilatus strigilatus*), Northern Bahamas Trope (*Tropidophis curtus barbouri*), and Cuban Brown Blindsnake (*Typhlops lumbricalis*). Knowledge of the species' diet is limited and, if present, over 15 years old. One study investigated the dietary composition of West Indian racers (Henderson and Sajdak, 1996), but currently no information exists on the diet of *T. c. barbouri* or *C. s. strigilatus,* with only a single record for the diet of *T. lumbricalis* (Vogel, 1965). Henderson et al. (1987) investigated the diet of the closely related *Chilabothrus striatus* from Hispaniola and found that these snakes consumed lizards (*Anolis* spp.), birds (*Dulus dominicus, Quiscalus niger,* and *Coereba flaveola*), and mammals (*Mus musculus* and *Rattus rattus*). These large-bodied boas also fed on bats and amphibians (Henderson and Powell, 2009). Henderson and Sajdak (1996) investigated the diet of the genus *Cubophis* (formerly known as *Alsophis*) and found these snakes to be highly opportunistic and euryphagous. Although *Anolis* spp. seem to constitute a significant proportion of the snakes' diets, racers have been found to consume a broad range of other vertebrates, including frogs (*Eleutherodactylus planirostris* and *Osteopilus septentrionalis*), lizards (*Sphaerodactylus* spp. and *Pholidoscelis auberi*), snakes (*Cubophis vudii vudii*), mammals (*Mus musculus*), and birds (*Mimus polyglottos*; Hoefer et al., 2020). Furthermore, Henderson and Sajdak (1996) found *C. v. vudii* exhibit an ontogenetic shift in diet, ingesting larger prey as the snakes increased in length. To our knowledge, no information exists on endoparasite prevalence in any Bahamian snake. Of particular interest are helminths, which have been previously reported in high abundances in many species of snakes (Fantham and Porter, 1950, 1954; Detterline et al., 1984; Goldberg and Bursey, 2002). High parasite loads may negatively affect host fitness. For example, parasite load has been correlated with a decrease in the expression of traits for sexual selection (Zuk et al., 1990) and can even alter the hosts' behavior (Dobson, 1988). In some cases, endoparasites may be responsible for a decrease in an animal's motivation

[1] Cape Eleuthera Institute, The Cape Eleuthera Island School, Cape Eleuthera, Eleuthera, The Bahamas; Email: (SH) sebastianhoefer@outlook.com. Send reprint requests to SH.
[2] Department of Biology, Western Connecticut State University, Connecticut.
[3] Fundación Oceanogràfic, Oceanogràfic De Valencia, Valencia, Spain.
Submitted: 13 October 2020. Accepted: 22 February 2021. Associate Editor: M. J. Lannoo.
 DOI: 10.1643/h2020141 Published online: 13 August 2021

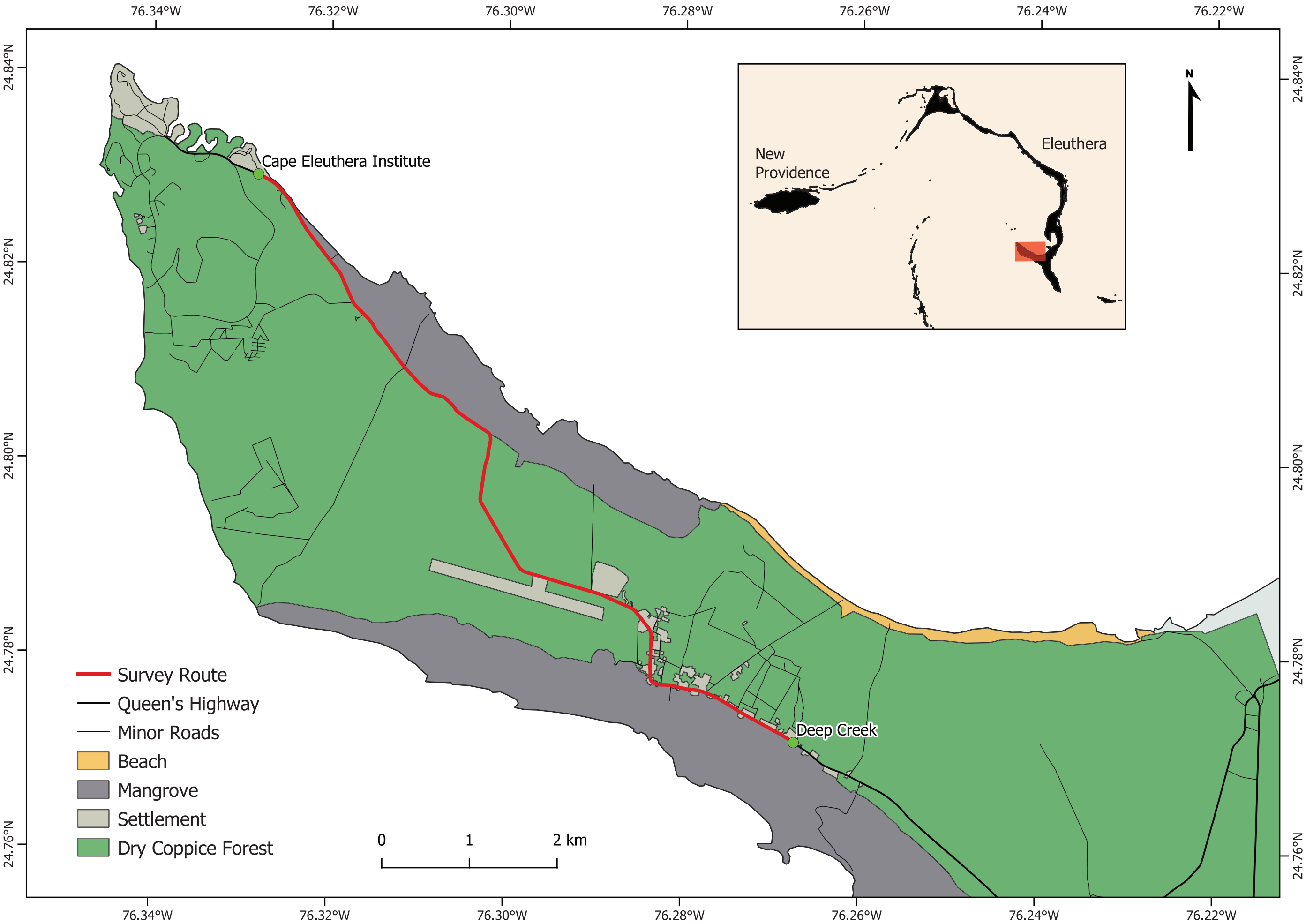

Fig. 1. Overview of the study site including the survey area and the different habitat types found along the survey stretch. The red box in the inset map represents the extent of the main map.

to obtain food (Lõhmus et al., 2012). Thus, it is vital to get an understanding of parasite infections in Bahamian snakes.

We collected roadkill snakes (including the Bahamian Racer, Bahamian Boa, Northern Bahamas Trope, and Cuban Brown Blindsnake) on the island of Eleuthera to assess their diet and parasite prevalence. Our ancillary goal was to also determine whether frequent surveys enabled the collection of a greater number of intact roadkill which were suitable for analyses.

MATERIALS AND METHODS

Study area.—Eleuthera (457 km^2, maximum elevation of 60 m asl) is a 120 km long and, in places, <1 km wide island located in the eastern part of the Great Bahama Bank. We established a survey route (Fig. 1) in the southern half of Eleuthera on a 10 km stretch of the Queen's Highway between the Cape Eleuthera Institute (CEI; 24.829275, –76.328242) and the Deep Creek settlement (DC; 24.771253, –76.267306). We assigned four different habitat types along the survey stretch: settlement, beach with Australian pines, mangroves with tidal creeks, and dry coppice forest.

Sampling method and processing.—From 19 August 2019 to 16 March 2020, we conducted up to four daily surveys via car or bicycle between CEI and DC and collected all roadkilled snakes. Surveys were primarily conducted at 0700 and 1600 h, with fewer opportunistic surveys at other times of the day. In total, we conducted 460 surveys over 211 consecutive days. We also collected roadkill found during opportunistic expeditions to other parts of Eleuthera. We recorded location and time using the Epicollect5 application (Aanensen et al., 2014). All spatial information was collected in WGS84 with an accuracy of <10 m. After collection, samples were either dissected immediately or stored at –20°C for later dissection. We measured snout–vent length (SVL) and total length (TTL) to the nearest mm using a flexible measuring tape and weighed the carcasses to the nearest g using a weighing scale (DAPHA DWS Weighing Scale). We determined the sex of each snake via presence of hemipenes for males and absence for females. We used morphological characteristics to identify prey items during direct assessments. Due to the strong deterioration of many food items, we did not attempt to record prey mass. Endoparasites were visually identified by Stephen R. Goldberg from photographs.

Statistical analysis.—Statistical analyses were conducted in RStudio (Version 1.2.5042; R Core Team, 2020), and figures were produced using the package ggplot2 (Wickham, 2016) and QGIS (Version 3.14.0, QGIS Development Team, 2020; Maps in WGS 84/UTM zone 18N). To determine whether

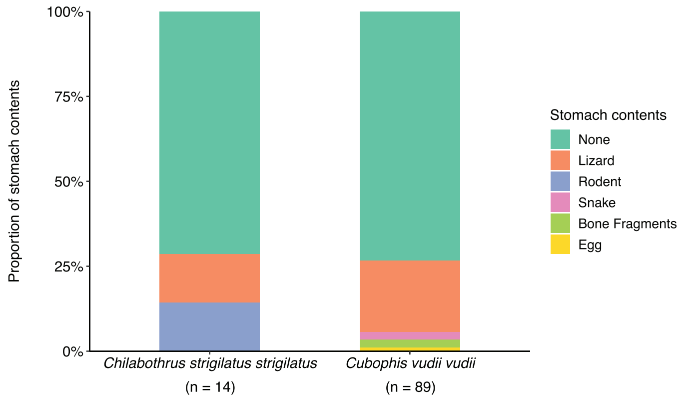

Fig. 2. Proportion of food items found inside stomachs of intact *Chilabothrus strigilatus strigilatus* and *Cubophis vudii vudii*.

prey preference was affected by sex, size, or time of the year, we used non-parametric Kruskal-Wallis tests. To determine if the likelihood of containing prey in the stomach was related to sex, size, or species, we used a generalized linear model (GLM) with prey presence as a binary response variable and sex, SVL, and species as explanatory variables. To test whether endoparasite presence would affect the likelihood of containing prey items, we used a GLM with endoparasite presence as the binary response variable and prey presence/absence as our explanatory variable and controlled for sex differences. To ascertain whether regular surveys enhanced the likelihood of encountering snakes suitable for further analyses compared to opportunistic sampling, we performed another GLM with state of the snake as the binary response variable and survey type as explanatory variable controlled for by SVL and sex of the snakes. We used another GLM to find out if the survey effort, i.e., the number of daily surveys along the survey route, had an impact on the state of the snakes found. For this model, we again used state of the snake as the binary response variable explained by survey effort and controlled for size and sex differences. All four snake species were included in the models assessing the likelihood of encountering snakes suitable for further analyses, but due to low sample sizes for *T. c. barbouri* and *T. lumbricalis*, they were excluded from dietary and endoparasite analyses.

RESULTS

Dietary analysis.—Over the study period, we collected 270 (female = 88, male = 137, NA = 45) roadkilled snakes representing all four species (232 Bahamian Racers, 31 Bahamian Boas, 6 Northern Bahamas Tropes, and 1 Cuban Brown Blindsnake) across Eleuthera. Of all intact and suitable snakes, we found 23 of 88 Bahamian Racers (26%) and 4 of 14 Bahamian Boas (29%) contained evidence of prey items (Fig. 2). We found no effect of sex, size, or species on the likelihood of containing a prey item (GLM, sex = –0.81, SE = 0.50, z-value = –1.60, $P = 0.11$; size < –0.01, SE < 0.01, z-value = –1.62, $P = 0.11$; species = –1.57, SE = 1.01, z-value = –1.55, $P = 0.12$). Both species fed on at least three different groups of vertebrates: lizards, snakes, and rodents. Due to the low sample size of Bahamian Boas containing food items, we excluded them from further dietary analyses. The type of prey did not significantly change with sex ($\chi^2 = 0.47$, df = 2, $P = 0.79$), size ($\chi^2 = 0.11$, df = 2, $P = 0.94$), or time of the year ($\chi^2 = 4.29$, df = 2, $P = 0.12$) in Bahamian Racers. The main prey items consumed by Bahamian Racers were lizards (83%), followed by snakes (9%) and unidentified prey (8%). Lizards were primarily of *Anolis* spp. plus one *Sphaerodactylus notatus*. The snakes preyed upon were identified as *Tropidophis curtus barbouri* and *Typhlops lumbricalis*. Small bone fragments found in two stomachs and a single egg of about one centimeter length found in the same stomach as the *S. notatus* could not be identified (Supplementary Figure S1; see Data Accessibility). Bahamian Boas consumed 50% lizards (*Anolis* spp.) and 50% rodents (*Rattus rattus*), with lizards found only in juvenile snakes and rodents only in adults.

Table 1. Endoparasite prevalence and load for female and male *Cubophis vudii vudii* and *Chilabothrus strigilatus strigilatus*.

		Endoparasites			
Species	Sex	Absent	<30	>30	Endoparasite prevalence
C. v. vudii	Female	8	30	11	84%
C. v. vudii	Male	14	18	5	62%
Total		**22**	**48**	**16**	**74%**
C. s. strigilatus	Female	8	0	0	0%
C. s. strigilatus	Male	6	0	0	0%
Total		**14**	**0**	**0**	**0%**

Endoparasite prevalence.—Endoparasites were exclusively nematodes and found only in Bahamian Racers, where they were present in 74% of all individuals. Most snakes were infected with fewer than 30 individual nematodes, although 16 racers hosted more than 30 nematodes per stomach (Table 1). Nematode presence or absence was not correlated with the presence or absence of prey items (GLM, prey presence = 0.17, SE = 0.60, z-value = 0.28, $P = 0\ .78$). We found significantly fewer males (62%) than females (84%) infected with nematodes (GLM, males = –1.12, SE = 0.52, z-value = –2.18, $P = 0.03$), and parasite loads were higher in females than in males.

Suitability for analyses.—The suitability of snakes was negatively affected by physical damage caused from vehicles on the road and natural decay accelerated by unfavorable weather conditions. Of all snakes collected, only 104 (39%)—58 females and 46 males—were suitable for analyses. Divided by species, we collected 14 Bahamian Boas (45%), 88 Bahamian Racers (38%), 2 Northern Bahamas Tropes (33%), and no Cuban Brown Blindsnakes suitable for dietary and endoparasite assessments (Table 2). Significantly more individuals were suitable for further analysis when collected on the survey stretch (46%) compared to the opportunistic collections (33%; GLM, survey = 0.62, SE = 0.30, z-value = 2.08, $P = 0.03$). Male snakes also were significantly less likely to be suitable for stomach content analyses than females (GLM, males = –1.38, SE = 0.31, z-value = –4.49, $P < 0.001$; Fig. 3). We observed no significant improvement in the state of the collected snakes when more than one survey was conducted per day (GLM, 2 daily surveys = –0.24, SE = 0.97, z-value = –0.24, $P = 0.81$; 3 daily surveys = 0.52, SE = 1.09, z-value = 0.48, $P = 0.63$; 4 daily surveys = –0.77, SE = 1.07, z-value = –0.72, $P = 0.47$). In two cases, we found stomachs that were too damaged and thus unsuitable for dietary analysis but recorded parasites. Additionally, parasite prevalence was not recorded for three empty stomachs. Therefore, a slight

Table 2. Number of collected specimens suitable/unsuitable for further analyses overall, and divided by regular (Routine) and opportunistic (Opportunistic) surveys. Damaged = unsuitable, intact = suitable.

			Routine		Opportunistic	
Species	Damaged	Intact	Damaged	Intact	Damaged	Intact
C. s. strigilatus	17	14	3	3	14	11
C. v. vudii	144	88	57	47	87	41
T. c. barbouri	4	2	1	2	3	0
T. lumbricalis	1	0	0	0	1	0
Total	**166**	**104**	**61**	**52**	**105**	**52**

variation in sample sizes exists between dietary analyses and endoparasite prevalence.

DISCUSSION

Dietary analysis.—We found Bahamian Racers to predominantly feed on lizards, particularly *Anolis* spp., with an even greater reliance on this prey type than had previously been reported (Henderson and Sajdak, 1996). It is remarkable that, although lizards made up over 80% of the racer's diet, we found these snakes to be opportunistic generalists with an even broader diet than previously described by Henderson and Sajdak (1996). In addition to documenting oophagy for the first time in any Bahamian snake, we also described two snakes, *T. c. barbouri* and *T. lumbricalis*, as new prey species. These two snakes are considered nocturnal whereas racers are active during the day, further emphasizing the opportunistic nature of the Bahamian Racer.

The diet of Bahamian Boas consisted of anoles and rats. Interestingly, juvenile boas fed exclusively on anoles whereas adults consumed only rats. Even though sample size was very limited, this suggests an ontogenetic shift in the feeding ecology of the Bahamian Boa that would be consistent related *Chilabothrus striatus* from Hispaniola (Henderson et al., 1987).

We found that about three-quarters of all the snakes within both species that had adequate samples contained no food items. The likelihood of containing prey did not differ with size, sex, or across species. It may be that snakes that had successfully captured a prey item retreated into refugia and lowered activity, similar to what has been reported by Siers et al. (2018) for the Brown Treesnake (*Boiga irregularis*). In contrast, snakes that had not fed for some time may have increased activity to search for prey. Subsequently, this increase in foraging activity likely increased the chances for those snakes to cross roads and be killed by vehicles.

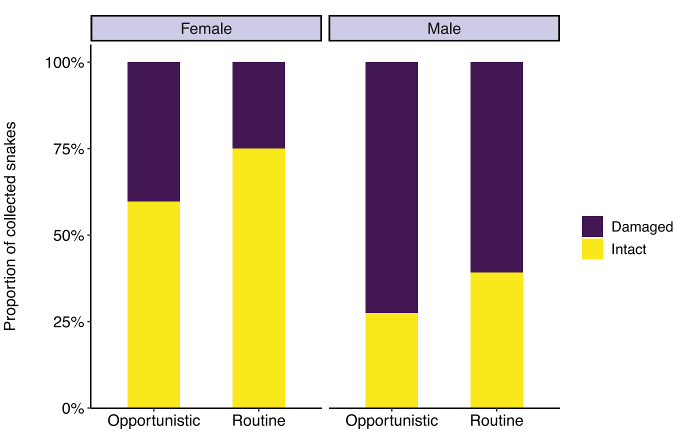

Fig. 3. Proportion of damaged and intact snakes collected via either regular surveys (Routine) or opportunistically (Opportunistic), split up by sex for all species combined. Snakes for which sex could not be determined were removed ($n = 45$).

Endoparasite prevalence.—We recorded nematodes in most of the racers but none of the boas. The higher parasite infection rates for racers compared to boas could be due to differences in activity, movement patterns, and foraging behavior; however, due to the large discrepancy in the number of boas and racers, the absence of nematodes in boas could simply reflect small sample size. Endoparasites have been known to change the host's behavior and can even influence their motivation to obtain food (Lõhmus et al., 2012). However, in our *post hoc* analysis we found no evidence that the presence of nematodes was responsible for the absence of food in the Bahamian Racers. Nematodes were instead randomly found in combination with or without food items. To conclusively answer whether nematode presence affects the snakes' ability or motivation to capture prey, nematodes would need to be introduced to individual racers and their prey-capture rates studied.

The higher parasite infection rates and loads that we found in females contradicts the male bias found in many other vertebrates across various taxa (Zuk and McKean, 1996). The higher parasite load in males is often attributed to differences in testosterone levels that increase reproductive success, but also impair the males' immune systems and affect their ability to successfully fight off parasites. However, Thomas (1965) found male lizards in the genus *Agama* have lower parasite infections than females and postulated that higher body temperatures in males, due to prolonged basking periods, might impede the development of parasites and explain the sex differences in parasite prevalence. Further research focusing on different ecological and physiological aspects, such as activity patterns, basking periods, and testosterone levels, is needed to explain the higher endoparasite infection rates and loads in female Bahamian Racers.

Suitability for further analyses.—As expected, we collected significantly more intact snakes during regular snake surveys than opportunistically. By conducting daily surveys, we likely decreased the time dead snakes would be exposed to damaging environmental factors. That said, an increase in the number of daily snake surveys along the survey stretch did not increase the number of intact snakes found, suggesting that multiple surveys might not be necessary if at least one daily survey is conducted. The state of the snakes found should be highly dependent on traffic volume and weather conditions, and, in some instances, only a short time exposed to extreme conditions might be enough to dramatically deteriorate specimens.

Overall, females were twice as likely to be intact and not damaged compared to males. Both sexes are morphologically similar, and even after controlling for size and species in our models we found significant sex effects. It is possible that females and males are active at different times and thus differ in their environmental exposure after being killed on the road. Further research is needed to investigate a difference in the activity patterns of females and males to help answer whether the sex differences in suitability have a behavioral origin.

DATA ACCESSIBILITY

All datasets and code used for the analyses in this study are available online (Open Science Framework, https://osf.io/e8jpt/). Supplemental material is available at https://www.ichthyologyandherpetology.org/h2020141.

ACKNOWLEDGMENTS

We would like to thank The Cape Eleuthera Island School for providing the resources to conduct research in The Bahamas and Stephen Goldberg for identifying endoparasites. We also thank the various interns and staff, as well as the ever enthusiastic Zev, Kai, Cove, Heidi, and Josh Holloway for helping with snake dissections and data collection. Research was conducted under the Cape Eleuthera Institute research permit number MAMR/FIS/2/12A/17/17B.

LITERATURE CITED

Aanensen, D. M., D. M. Huntley, M. Menegazzo, C. I. Powell, and B. G. Spratt. 2014. EpiCollect+: linking smartphones to web applications for complex data collection projects. F1000Research 3:199.

Brecko, J., B. Vervust, A. Herrel, and R. V. Damme. 2011. Head morphology and diet in the Dice Snake (*Natrix tessellata*). Mertensiella 18:20–29.

Brown, D. S., K. L. Ebenezer, and W. O. C. Symondson. 2014. Molecular analysis of the diets of snakes: changes in prey exploitation during development of the rare Smooth Snake *Coronella austriaca*. Molecular Ecology 23:3734–3743.

Carbajal-Márquez, R. A., J. R. Cedeño-Vázquez, D. González-Solís, and M. Martins. 2020. Diet and feeding ecology of *Crotalus tzabcan* (Serpentes: Viperidae). South American Journal of Herpetology 15:9–19.

Detterline, J. L., J. S. Jacob, and W. E. Wilhelm. 1984. A comparison of helminth endoparasites in the Cottonmouth (*Agkistrodon piscivorus*) and three species of Water Snakes (*Nerodia*). Transactions of the American Microscopical Society 103:137–143.

Dobson, A. P. 1988. The population biology of parasite-induced changes in host behavior. The Quarterly Review of Biology 63:139–165.

Fantham, H. B., and A. Porter. 1950. The endoparasites of certain South African snakes, together with some remarks on their structure and effects on their hosts. Proceedings of the Zoological Society of London 120:599–647.

Fantham, H. B., and A. Porter. 1954. The endoparasites of some North American snakes and their effects on the Ophidia. Proceedings of the Zoological Society of London 123:867–898.

Goldberg, S. R., and C. R. Bursey. 2002. Gastrointestinal helminths of the Blackneck Garter Snake, *Thamnophis cyrtopsis* (Colubridae). Western North American Naturalist 62:243–245.

Goldberg, S. R., C. R. Bursey, and A. L. Aquino-Shuster. 1991. Gastric nematodes of the Paraguayan Caiman, *Caiman yacare* (Alligatoridae). The Journal of Parasitology 1009–1011.

Henderson, R. W., J. A. Ottenwalder, T. A. Noeske-Hallin, and A. Schwarz. 1987. On the diet of the boa *Epicrates striatus* on Hispaniola, with notes on *E. fordi* and *E. gracilis*. Amphibia-Reptilia 8:251–258.

Henderson, R. W., and R. Powell. 2009. Natural History of West Indian Reptiles and Amphibians. University Press of Florida, Gainesville, Florida.

Henderson, R. W., and R. A. Sajdak. 1996. Diets of West Indian racers (Colubridae: *Alsophis*): composition and biogeographic implications, p. 327–338. *In*: Contributions to West Indian Herpetology: A Tribute to Albert Schwartz. SSAR Contributions to Herpetology Vol. 12, Ithaca, New York.

Hoefer, S., N. J. Robinson, and A. Jones. 2020. *Cubophis vudii vudii* (Bahamian Racer). Diet. Herpetological Review 51:346–347.

Kavetska, K. M., B. Pilarczyk, and K. Królaczyk. 2012. Stomach nematodes of wild ducks (subfamily Anatinae) wintering in the North-Western Poland. Bulletin of the Veterinary Institute in Pulawy 56:27–31.

Lõhmus, M., S. Moalem, and M. Björklund. 2012. Leptin, a tool of parasites? Biology Letters 8:849–852.

Luiselli, L., D. Capizzi, E. Filippi, C. Anibaldi, L. Rugiero, and M. Capula. 2007. Comparative diets of three populations of an aquatic snake (*Natrix tessellata*, Colubridae) from Mediterranean streams with different hydric regimes. Copeia 2007:426–435.

Luiselli, L., J. M. Pleguezuelos, M. Capula, and C. Villafranca. 2001. Geographic variation in the diet composition of a secretive Mediterranean colubrid snake: *Coronella girondica* from Spain and Italy. Italian Journal of Zoology 68:57–60.

Miller, T. W., R. D. Brodeur, G. Rau, and K. Omori. 2010. Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Marine Ecology Progress Series 420:15–26.

Mori, A., and S. E. Vincent. 2008. An integrative approach to specialization: relationships among feeding morphology, mechanics, behaviour, performance and diet in two syntopic snakes. Journal of Zoology 275:47–56.

Mushinsky, H. R., J. J. Hebrard, and D. S. Vodopich. 1982. Ontogeny of water snake foraging ecology. Ecology 63:1624–1629.

Powell, R., and R. W. Henderson. 2012. Island lists of West Indian amphibians and reptiles. Florida Museum of Natural History Bulletin 51:85–166.

QGIS Development Team. 2020. QGIS Geographic Information System. Open Source Geospatial Foundation. https://qgis.org

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reading, C., and G. Jofré. 2013. Diet composition changes correlated with body size in the Smooth Snake, *Coronella austriaca*, inhabiting lowland heath in southern England. Amphibia-Reptilia 34:463–470.

Siers, S. R., A. A. Yackel Adams, and R. N. Reed. 2018. Behavioral differences following ingestion of large meals and consequences for management of a harmful invasive snake: a field experiment. Ecology and Evolution 8:10075–10093.

Sutton, G. J., A. J. Hoskins, and J. P. Y. Arnould. 2015. Benefits of group foraging depend on prey type in a small marine predator, the Little Penguin. PLoS ONE 10: e0144297.

Terraube, J., B. Arroyo, M. Madders, and F. Mougeot. 2011. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. Oikos 120:234–244.

Thomas, J. D. 1965. Studies on some aspects of the ecology of *Mesocoelium mondodi*, a trematode parasite of reptiles and amphibia. Proceedings of the Zoological Society of London 145:471–494.

Vogel, Z. 1965. Herpetologische Beobachtungen auf Kuba (II). Aquarien und Terrarien 12:98–99.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York. https://ggplot2.tidyverse.org

Willson, J. D., C. T. Winne, M. A. Pilgrim, C. S. Romanek, and J. W. Gibbons. 2010. Seasonal variation in terrestrial resource subsidies influences trophic niche width and overlap in two aquatic snake species: a stable isotope approach. Oikos 119:1161–1171.

Zuk, M., and K. A. McKean. 1996. Sex differences in parasite infections: patterns and processes. International Journal for Parasitology 26:1009–1023.

Zuk, M., R. Thornhill, J. D. Ligon and K. Johnson. 1990. Parasites and mate choice in Red Jungle Fowl. Integrative and Comparative Biology 30:235–244.