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Extreme Starvation Impacts Organ Size and Water Content but Not Bone Integrity in Rattlesnakes

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Abstract: Ambush-hunting snakes have long been of interest in the biology of fasting and starvation, as they are adapted to withstand long durations without eating. Ethical experimental constraints have limited our understanding of their limits in these abilities. The confiscation of over 50 Western Rattlesnakes (*Crotalus oreganus*) by the California Department of Fish and Wildlife from an animal hoarder who had neglected them allowed us to examine the carcasses for effects of extreme starvation. Some of these snakes were extremely starved, being one-third to one-half of the weight of wild snakes of the same length. We used dissection to determine the effects of starvation on the mass of hearts, livers, kidneys, gallbladders, testes, and fat bodies. We desiccated hearts, livers, and kidneys to investigate tissue water content in those organs. We used nanoindentation and photo analysis of bone cross sections to assess whether starvation had any impact on bone integrity. We demonstrated that all measured visceral organs shrank dramatically in response to starvation, with the exception of the gallbladder, which showed the opposite response. We also found that female rattlesnakes tended to have larger livers and gallbladders than males. The tissue water content of the liver and kidneys increased with the extent of starvation, and that of the heart appeared to be unaffected. We found no evidence for changes in rattlesnake bone integrity in response to starvation, but more testing is needed. These results provide insight into how one of the most fasting-adapted species of vertebrate responds to extreme starvation.

Key words: Bone properties; Fasting; Fasting-adapted; Reptile; Starvation physiology

Nutritional stress and dehydration have numerous negative effects on an animal's physiology. Among these are reduced growth rates, reduced reproduction, increased susceptibility to disease, and ultimately, increased mortality (Brahma and Patnaik 1980; Houlihan et al. 1998; Bourgeon and Raclot 2006; Bourgeon et al. 2010; Holden et al. 2019). These effects may become increasingly prevalent for wildlife populations as climate change is projected to increase the frequency and severity of droughts in some regions, reducing the availability and stability of food and water resources (Kundzewicz et al. 2008; Sperry and Weatherhead 2008; Ujvari et al. 2016; Zhao et al. 2020). Animal taxa vary tremendously in their capacity to cope with nutritional stress and dehydration, and investigating taxa with high capacity for fasting and starvation will improve our understanding of these processes. Among vertebrates, ectotherms are able to withstand longer periods without access to food and water than endotherms (McCue 2007a). This is primarily due to their comparatively low metabolic rates (Nagy et al. 1999; Hervant et al. 2001). Ambush-hunting snakes such as pythons and vipers are particularly well-adapted for fasting and have evolved the physiology required to withstand months or even years without feeding (Klauber 1997; Secor and Diamond 2000; Wang et al. 2006; Crowell et al. 2021; Alexander 2025).

Despite our understanding of the progression of events when an animal does not eat, there are no unified definitions of the terms "fasting" and "starvation" (Secor and Carey 2016). Although there have been metrics proposed to demarcate the transition between fasting and starving, such as shifts from lipid catabolism to protein catabolism and increased rates of mass loss in later stages of fasting, these terms have mostly been assessed as they relate to frequently feeding endotherms (Cherel et al. 1988; Castellini and Rea 1992). While these transitions occur more quickly and are easier to delineate in endotherms, the feeding habits of ectotherms vary more widely, and their voluntary nonfeeding intervals can be much longer (McCue 2007a; Secor and Carey 2016). Because snakes often fast after eating large meals, during ecdysis cycles, and during gestation, McCue (2007a) proposed adjusted definitions for fasting and starving in snakes in which voluntarily nonfeeding snakes are in a state of fasting, and those that are nonfeeding as a result of food unavailability are in a state of starvation (Madsen and Shine 1993; Greene 1997; King and Turmo 1997; Kern 2007). We adopt these definitions herein.

While the physiology of feeding, fasting, and starvation has been investigated in snakes—demonstrating their capacity for upregulation and downregulation of metabolism, organ size, and function (Secor et al. 1994; Secor and Diamond 1995; Starck and Beese 2002; McCue 2007b)—the upper bounds of their ability to withstand extended intervals without food have remained untested. Most studies on fasting or starvation in snakes use periods of anorexia of 6 mo or less (McCue 2007a), largely due to ethical guidelines on animal use in experiments that limit intervals of starvation. However, a period of 6 mo falls well within the interval of normal fasting that wild snakes routinely endure (Klauber 1997), suggesting that such laboratory studies are unable to induce severe starvation. These ethical issues have prevented the study of extreme starvation events in snakes.

Because bones are rich in minerals and proteins, bone integrity may also be impacted by starvation (Robey 1989).

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Although this has not previously been studied in snakes, even modest food restriction in rats results in negative bone impacts as the starving animals draw minerals and proteins from their bones (Banu et al. 2001). The skeleton is a physiologically active organ that undergoes remodeling throughout an animal's life (Hadjidakis and Androulakis 2006). The process of remodeling allows components of old, and possibly damaged, bone to be resorbed, making way for new and repaired bone to take its place (Kostenuik 2021). The material properties of bones, like resistance to deformation, may degrade during fasting due to the animal drawing resources from bones, the lack of new dietary materials for remodeling, or both. The effects of fasting and starvation on bones have primarily been studied in mammalian systems, and material properties have only been investigated in a handful of reptile species (Currey 1990; Kueper et al. 2015; Toyama et al. 2024). It is also possible that, instead of reducing the material properties of their bones, starving snakes might deconstruct their bones layer by layer, as has been suggested in mammals (Banu et al. 2001). It should be noted that these possibilities are not mutually exclusive.

We were able to opportunistically study Western Rattlesnakes (*Crotalus oreganus*) that were confiscated by the California Department of Fish and Wildlife (CDFW) from a non-permitted snake collector who had apparently hoarded the snakes for an extended period. The snakes were severely emaciated, consistent with a state of extreme starvation. This situation provided a large sample of euthanized snakes that had been starved to varying degrees, including extreme examples that appear to have been starved far beyond what has been studied previously (e.g., Secor and Diamond 2000; McCue 2007a). The data obtained from these unfortunate and unique circumstances provide the opportunity to understand how extreme starvation impacts fasting-adapted vertebrates.

We assessed the impacts of starvation on the mass of the heart, liver, kidneys, and gallbladder, which are visceral organs impacted by milder fasting (Secor and Diamond 1995). We also measured the tissue water content and dry mass of the heart, liver, and kidneys to determine whether any decrease in mass is a result of water loss, loss of organic material (e.g., protein), or both. Because the heart, liver, and kidneys are responsive to fasting and feeding in snakes (Secor and Diamond 1995), we hypothesized that these organs shrink further as snakes undergo extreme starvation due to a loss in both organic material (e.g., protein) and water content. As such, we predicted that there would be positive relationships between the mass and water content of the visceral organs and the body condition of the snakes. We hypothesized that starvation also results in costs to reproductive potential. To test this, we measured the testes of the male snakes with the prediction of a positive relationship between testes mass and body condition. Additionally, we measured the fat body mass of each snake to estimate the body condition at which fat reserves were depleted. This also allowed us to assess the amount of additional decrease in body condition that resulted from the catabolism of non-lipid sources like proteins. Lastly, we used nanoindentation and photo processing of rib cross sections to measure the material properties (elastic modulus and hardness) and amount of cortical bone in healthy, moderately starved, and extremely starved rattlesnakes. We expected that healthy snakes would have the highest values for measures of bone integrity, extremely starved snakes would have low values, and moderately starved snakes would be intermediate.

MATERIALS AND METHODS

Study Animals and Limitations

In the fall of 2022, the CDFW confiscated 53 Western Rattlesnakes (*C. oreganus*) from a non-permitted snake relocator based near the San Francisco Bay Area. Most of the snakes were severely emaciated (Fig. 1), and their precise collection locations were unknown. As such, they could not

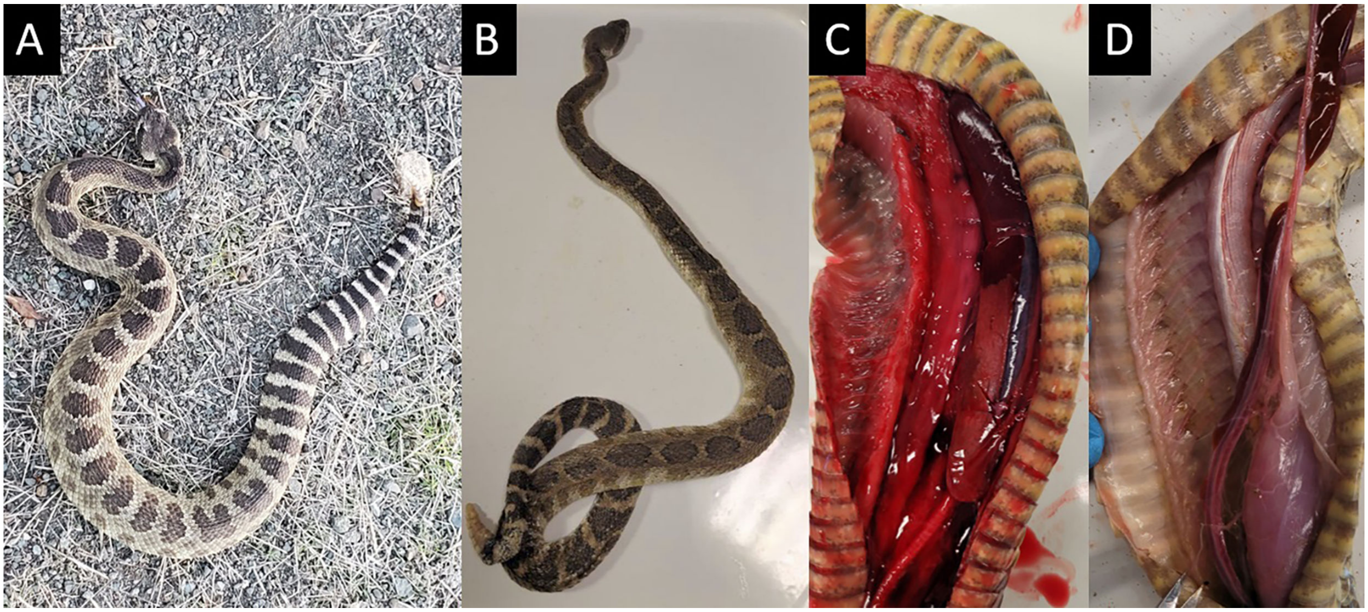

FIG. 1.—Visual comparison of the body condition of Western Rattlesnakes (*C. oreganus*) in a healthy, wild snake (A), a severely starved snake (B), the blood- and fluid-filled body cavity of a modestly starved rattlesnake (C), and the dry body cavity of a severely starved and presumably dehydrated rattlesnake (D). Panels B–D are from snakes that were confiscated from a non-permitted snake collector who had apparently hoarded the snakes for an extended period.

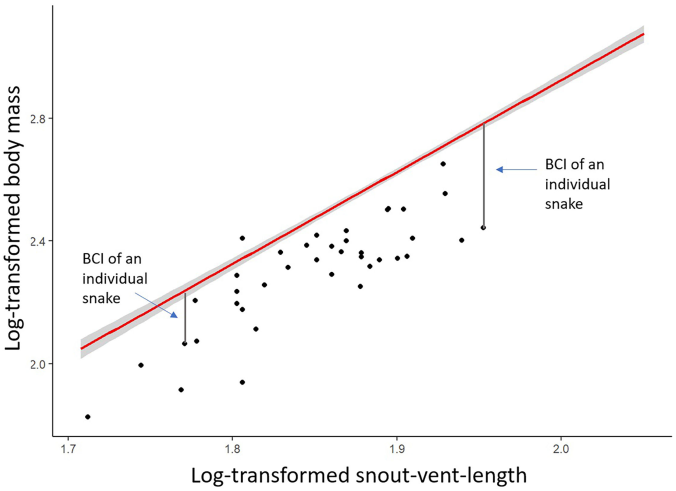

FIG. 2.—The relationship between SVL and body mass in confiscated Western Rattlesnakes (*C. oreganus*; log SVL vs. log mass), relative to a regression line of SVL and body mass generated from 334 wild Western Rattlesnakes. The points represent the log-transformed SVL and body mass of the confiscated rattlesnakes, and the shading represents the 95% confidence interval. Two residuals, representing the BCI, of individual snakes are highlighted. The fact that most of the confiscated snakes fell well below the line shows that they were very low in mass, especially given the logarithmic scale. For example, a 64-cm-long confiscated rattlesnake was about 67% lower in mass than a wild rattlesnake of the same length.

be released and were euthanized and transported to our lab on 5 October 2022 for subsequent study. Among the confiscated snakes, there were three neonates, presumably born in captivity. These were excluded from the study to minimize confounding variables related to life stages and body size. Several adult snakes were either sent back to CDFW for necropsy or set aside for other research purposes, reducing the final number of snakes dissected in this study to 39 (females, *n* = 11; males, *n* = 28).

Several constraints were imposed on our study in tandem. Because we did not know how long the snakes had been starved, we used body condition as a proxy for starvation. Body condition indices describe how body mass is related to body length and are commonly used to assess animal health or body reserves (Naulleau and Bonnet 1996; McCue 2008). We used a dataset of 334 wild *C. oreganus* collected from the species' range in northern California (courtesy of M. Holding) to calculate a baseline body condition index (BCI) for *C. oreganus* by regressing the log-transformed mass against the log-transformed snout–vent length (SVL) as in McCue (2007a). For each confiscated snake, the BCI was calculated as the residual from the baseline regression line (Fig. 2).

In addition to starvation, dehydration also likely contributed to the variables of interest. We infer water limitation based on the extremely dry body cavities observed in the starved snakes (see Fig. 1D). We do not know whether water was withheld from the snakes for the same duration that food was withheld. Because we cannot disentangle starvation and dehydration, discussions in this study of starvation effects should be interpreted as also encompassing hydration effects.

Organ Mass and Water Content

We stored the snake carcasses at –20°C. We thawed the snakes overnight at room temperature and removed the heart (*n* = 39), liver (*n* = 39), kidneys (*n* = 39), gallbladder including its bile (*n* = 33; some were excluded because they were punctured during dissection), testes (*n* = 28), and fat bodies (*n* = 39). Connective tissue, including the pericardia of the hearts, was removed, and arteries and other vessels were severed at the margins of each organ. We weighed all organs from each snake individually to measure their wet mass, except for the kidneys and testes, which we weighed as pairs. We then stored the organs at –20°C until we could desiccate them. We thawed batches of organs at 22°C for approximately 24 h, then desiccated them in a Fisher Scientific IsoTemp drying oven set at 60°C. To ensure the organs were completely desiccated, they were weighed daily until their weight remained constant for two consecutive days.

Bone Integrity

We selected nine adult *C. oreganus* for bone extraction. Three of the snakes were extremely starved (e.g., BCI below –0.254), three were moderately starved (e.g., BCI between –0.134 and –0.104), and three were "healthy" wild snakes (e.g., BCI between 0.056 and 0.079), from a separate sample of snakes collected as roadkill. Only male snakes were selected to eliminate the possibility that reproductive processes in females might affect their bones, as has been reported in other animals (Speakman 2008; Schmidt and Hood 2014). We harvested 6–12 midbody ribs and associated vertebrae from the left side of each snake at mid-body and froze the samples at –20°C. We subsequently thawed the ribs and vertebrae at 22°C overnight and removed the flesh from the ribs using forceps, then manually separated the ribs from the vertebral column. To dehydrate the ribs, we adapted a procedure described by Mathews and Mehr (1979) by placing them in 70% ethanol for approximately 24 h and then transferred them to 100% ethanol for an additional 24 h. Once dehydrated, we used an IsoMet 1000 precision saw with a diamond wafering blade to cross-section each rib at its midpoint. We then cross-sectioned the proximal half of each rib at its midpoint and moved forward using the distal section resulting from this second cut (Fig. 3A). To ensure that any

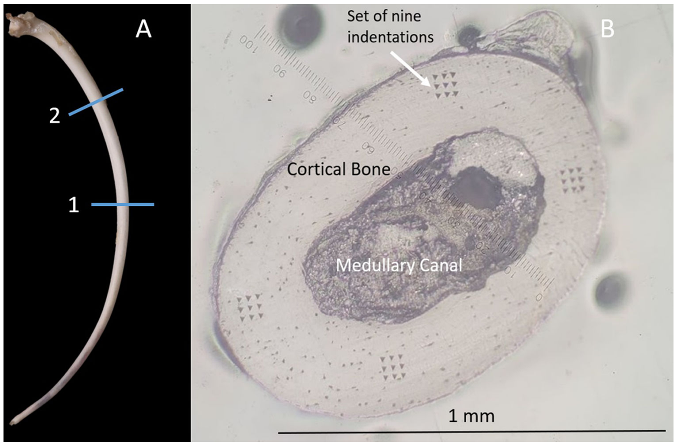

FIG. 3.—Western Rattlesnake (*C. oreganus*) rib and magnified cross section used in nanoindentation. (A) Rib with blue lines showing where the first and second cross sections were made. Nanoindentation was performed on surfaces resulting from cross section 2. (B) Cross section of rib at 200× magnification showing the typical location of the four selected indentation regions. Each dark triangle is an individual indentation.

splintering resulting from sectioning was removed, we visually inspected the sections after using 800 grit sandpaper to sand the ends of each rib for 30 to 60 s.

We then prepared the bone samples for nanoindentation, a method used to collect data on a sample's material properties. For each snake, we cold-mounted six rib sections in a mold to produce an epoxy resin puck (Mathews and Mehr 1979). Within each mold, we inserted bone samples individually into aluminum tubes and secured them with wax to ensure that the rib samples were positioned perpendicular to the plane of the puck. We allowed the pucks to cure overnight before removing them from the molds. We then sanded the face of each puck with 240 grit sandpaper until the cross-section of the bone was exposed (no resin layer covering it), and visually verified at 200× magnification. We subsequently sanded the pucks sequentially with 320, 400, and 600 grit sandpaper. We followed standard metallographic techniques by polishing them sequentially to 0.05 μm using diamond polishing compound applied to microcloth via spray application. These techniques have previously been applied to studies of human bone biopsies (Griffin et al. 2021). Bone tissue quality was assessed by nanoindentation using a Berkovich pyramidal diamond tip (NanoTest 600, Micromaterials, LTD). Four regions were selected for indentation on the cortical bone of each rib cross-section, and nine indentations were made in each region in a 3 × 3 grid arrangement. Typical indentation regions are depicted in Fig. 3B. The ribs were indented with a peak load of 75 μN with load and displacement continuously recorded. This process produced elastic modulus and hardness data from our bone samples. The elastic modulus of a material describes its resistance to nonpermanent (elastic) deformation, and hardness is defined as a material's resistance to permanent (plastic) deformation.

To assess cortical bone area, we manually traced around the entire cross section and around the medullary cavity of each rib bone using the polygon selection method in ImageJ v1.54j (National Institute of Health, Bethesda, MD, USA). Three technical replicates were done using this method for each bone. The average value for the medullary cavity cross-sectional area was then subtracted from that of the entire cross-sectional area of each rib area to obtain the rib's cortical bone area. The cortical bone area values from the six ribs of each snake were then averaged to yield a single value for each individual snake to be used in analyses.

Analyses

Statistical analyses and figures were generated in R (v4.4.0; R Core Team 2024) with significance level set at $\alpha = 0.05$ (data and analyses are presented in Supplemental File S1, available online). We used multiple linear regression (MLR) to test for relationships between organ mass (response variable) and BCI (predictor variable). To control for effects of snake body size and sex, we included SVL and sex as additional covariates in our MLR models. Each organ type was analyzed separately.

The same approach was used to assess the effect of BCI on organ dry mass. However, the models reported for organ dry mass only use SVL and BCI as covariates because sex had no significant effect on the dry mass of the heart, and dried livers and kidneys were measured only from male snakes. Because several snakes had a value of zero for the mass of fat bodies, we log-transformed this variable with an added constant of 1 before using a MLR model to assess its relationship with BCI, with SVL as a covariate. Because most of the linear models above used BCI (derived from SVL and mass) as a main predictor variable and SVL as a covariate to control for the effect of body size on organ mass, we ensured that these two predictors varied independently by testing for collinearity in each model using the performance package (Lüdecke et al. 2021). This test uses variance inflation factor (VIF) as a metric to detect collinearity, and SVL (VIF = 1.45) and BCI (VIF = 1.11) both have low correlation with their covariates in our models.

Because tissue water content is a proportional variable, we used the betareg package to make beta regression models with a logit link to test for relationships between body condition and tissue water content of each type of organ individually (Cribari-Neto and Zeileis 2010).

We constructed individual analysis of covariance (ANCOVA) models to assess whether starvation state (extreme, moderate, or healthy) had an effect on the material properties of snake bones (elastic modulus and hardness) and the amount of cortical bone area, with SVL as a covariate to control for the size of the snakes. Snake sex was not included in these models, as only male snakes were used for tests of bone integrity. With such limited sample sizes in the bone analyses, tests of data and residual distribution assumptions could not appropriately be performed.

RESULTS

Organ Mass

Individual MLR models for heart, liver, kidney, and testes wet mass revealed significant relationships, with organ mass positively related to both SVL and body condition (Table 1; Fig. 4). The MLR model for gallbladder mass also revealed significant relationships with SVL and body condition. While gallbladder mass was significantly positively correlated with SVL, it was negatively correlated with body condition (Table 1; Fig. 4D). Sex also had a significant effect on liver and gallbladder mass, with both organs being larger in females when controlling for body size (SVL) and body condition (Table 1). There was no effect of sex on the mass of the heart or kidneys. The log-transformed mass of fat bodies was also significantly predicted by our overall fat body MLR model ($R^2 = 0.723$, $F = 34.02$, $P < 0.0001$), with significant positive relationships with SVL ($\beta = 0.011$, $P = 0.035$) and body condition ($\beta = 3.860$, $P < 0.0001$; Fig. 5), and females had slightly more fat bodies than males when SVL and body condition were taken into account ($\beta = -0.216$, $P = 0.028$). Nine snakes in our sample had zero fat bodies.

Individual MLR models for heart, liver, and kidney dry mass also showed significant positive relationships between both SVL and body condition and the dry mass of each organ type (Table 2).

Tissue Water Content

We found that body condition did not predict the tissue water content of the heart (pseudo $R^2 = 0.051$, $\beta = -0.455$, $P = 0.176$; Fig. 6A). There was a significant negative relationship between body condition and tissue water content of the liver (pseudo $R^2 = 0.619$, $\beta = -0.823$, $P < 0.0001$;

TABLE 1.—Summary statistics for MLR models that used SVL, sex, and BCI as predictors of organ wet mass in starved Western Rattlesnakes (*C. oreganus*) that were confiscated from a non-permitted snake collector who had apparently hoarded the snakes for an extended period.

Organ	*n*	R^2	*F* statistic$_{(df)}$	*P* value	Explanatory variable	β	*P* value
Heart	39	0.506	$13.97_{(3,35)}$	<0.0001	BCI	2.087	0.0005
					SVL	0.035	<0.0001
					Sex (F)	–0.045	0.739
Liver	39	0.684	$28.47_{(3,35)}$	<0.0001	BCI	18.056	<0.0001
					SVL	0.166	<0.0001
					Sex (F)	–2.696	<0.0001
Kidneys	39	0.640	$23.53_{(3,35)}$	<0.0001	BCI	8.435	<0.0001
					SVL	0.085	<0.0001
					Sex (F)	0.505	0.163
Gallbladder	33	0.613	$17.89_{(3,29)}$	<0.0001	BCI	–3.386	0.005
					SVL	0.083	<0.0001
					Sex (F)	–0.611	0.041
Testes	28	0.647	$25.72_{(2,25)}$	<0.0001	BCI	1.809	<0.0001
					SVL	0.013	0.0001

Fig. 6B), as well as the tissue water content of the kidneys (pseudo $R^2 = 0.488$, $\beta = -1.202$, $P < 0.0001$; Fig. 6C).

Bone Integrity

We found no effect of starvation state on elastic modulus ($F_{(2,5)} = 0.612$, $P = 0.578$; Fig. 7A), hardness ($F_{(2,5)} = 1.372$, $P = 0.335$; Fig. 7B), or amount of cortical bone area ($F_{(2,5)} = 1.741$, $P = 0.411$). There was no effect of SVL on elastic modulus ($F_{(1,5)} = 0.025$, $P = 0.880$) or hardness ($F_{(1,5)} = 0.034$, $P = 0.861$). There was an effect of SVL on the amount of cortical bone area ($F_{(1,5)} = 7.543$, $P = 0.040$).

DISCUSSION

Previous studies that have investigated the physiological responses of fasting and refeeding in snakes only withheld food for a couple of weeks to about a month (Secor and Diamond 1995; Secor et al. 2012). Studies specifically on starvation effects in snakes have focused on animals starved for up to 6 mo (McCue 2007a,b, 2008). The level of emaciation of snakes in our study is consistent with what is expected for animals starved for over a year (Leite et al. 2014; Crowell et al. 2021). Our study is among the first to assess the impact of starvation that is more severe than what is regularly endured in natural settings in snakes (Greene and Hardy 1989).

In this study, we aimed to determine the effects of extreme starvation on organ size, organ water content, and bone integrity. Our results support the hypothesis that visceral organs, with the exception of the gallbladder, continue to decrease in mass as snakes starve. In testing our hypothesis that organs would have lower water content in more starved snakes due to malnutrition, we found that this is not the case. Our hypothesis that snake bones decrease in structural integrity in response to starvation was also not supported. We found no relationships between body condition and the material properties of snake bones, though the sample size was admittedly small.

We found that as body condition decreases, the wet mass of the rattlesnake heart, liver, and kidneys also decreases. In severely starved snakes (<50% body mass of wild individuals of the same length; see Fig. 1A), this was dramatic, with organs extremely shrunken upon visual inspection, and in some cases very little blood or other moisture visible in the carcass (see Fig. 1D). This is in accordance with previous work that demonstrated that the mass of the heart, liver, and kidneys in Burmese Pythons (*Python bivittatus*) responds positively to feeding and subsequently decreases in mass as digestion progresses and ceases (Secor and Diamond 1995). The heart is plastic in response to feeding status in snakes because it must accommodate a broad range of fluctuations in metabolic demands associated with the digestion of large, infrequent meals (Secor et al. 1994; Secor and Diamond 1995, 2000). However, it should be noted that not all studies looking at the size of the heart in snakes have found flexibility in response to digestive state (Enok et al. 2013; Wang and Rindom 2021). Similar to the heart, the liver showed flexibility in size as its functions in filtering blood and processing lipids vary depending on feeding state (Secor et al. 1994; Starck and Beese 2002).

The kidneys' plasticity observed here is notable, as the size of these organs tends to be particularly static in other animals (Jordan 1953; Secor and Carey 2016). With the cessation of feeding and digestion, a reduced rate in the production of nitrogenous waste entering circulation in the blood naturally follows. Thus, as fasting progresses, the kidneys' function of filtering waste products from the blood is needed to a lesser extent, and it becomes more advantageous to maintain the organs at a reduced size (Secor and Diamond 2000). We demonstrated that, similar to the aforementioned organs, kidney size reduction continues with the extent of starvation. In addition to filtering blood, the kidneys are also responsible for regulating blood pressure and other aspects of fluid balance in the body, such as resorption of water and salts (Wadei and Textor 2012). A potential demand-related reduction in size, in regard to this function of the kidneys, is also congruent with our inference of water deprivation in these snakes (based on our observations of extremely dry body cavities in highly starved individuals; see Fig. 1D), but more detailed study is needed. Given this context of kidney size plasticity, we expected the relationship between decreasing organ mass and body condition to continue as starvation progressed, but it has not been previously quantified in samples of snakes that include extremely starved individuals. The point at which organ shrinkage decouples from energetic demand and becomes a function of protein catabolism remains unknown.

In contrast to the other measured organs, we detected a negative relationship between body condition and the wet mass of the gallbladder. Secor and Diamond (1995) also demonstrated that the gallbladder of snakes increases in mass while the other organs decrease as fasting commences, due

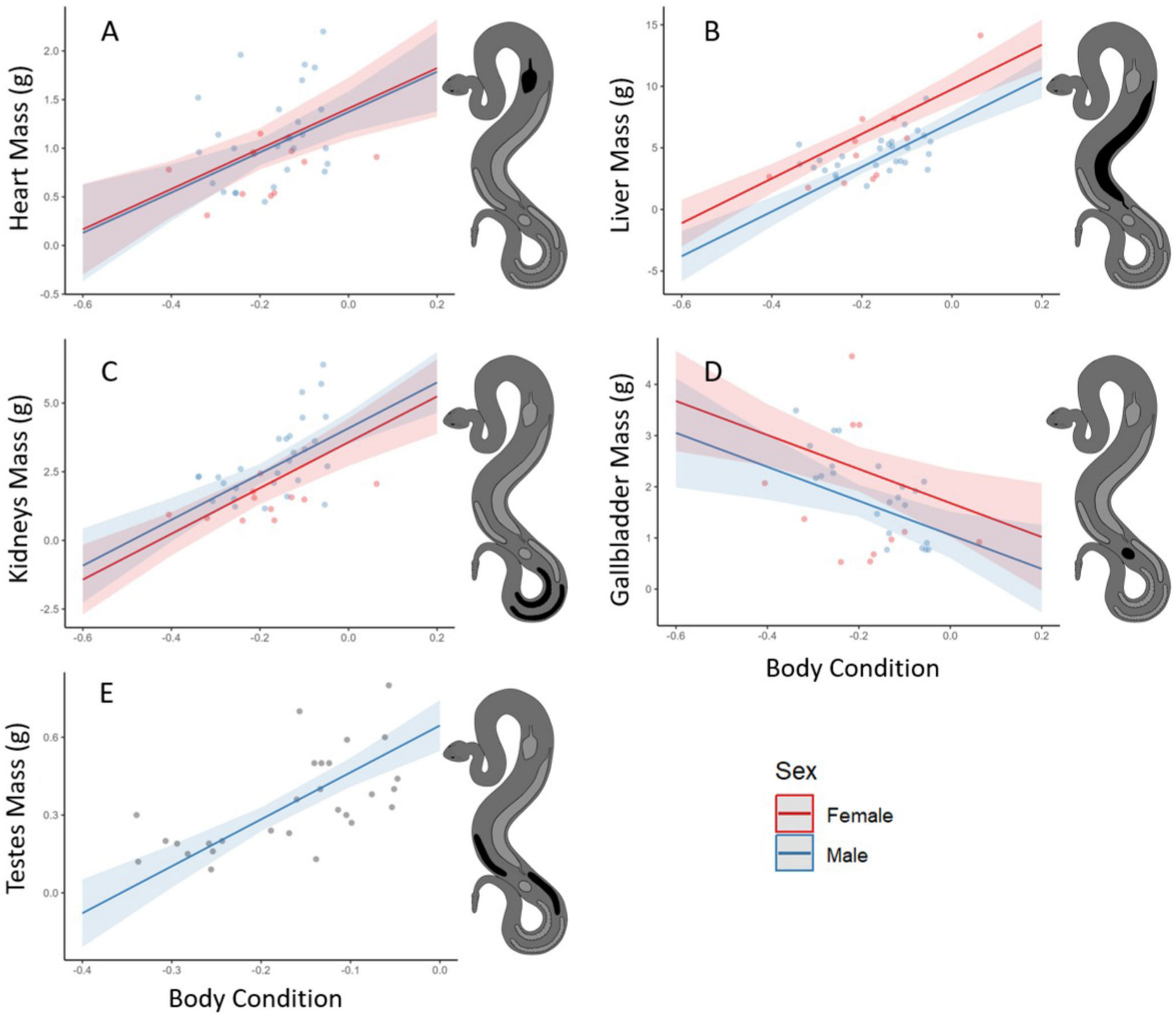

FIG. 4.—Relationships between organ wet mass and BCI of confiscated Western Rattlesnakes (*C. oreganus*) as predicted by MLR. Lines represent relationships between these variables when snake size (SVL) and sex are adjusted for in each MLR model, and the shading around the lines represents 95% confidence intervals. Points represent raw data values between organ mass and BCI. For the heart (A), liver (B), kidneys (C), and testes (E), lower body condition (indicating a more severely starved snake) corresponds to lower organ mass. The opposite relationship is seen in the gallbladder (D).

to the gallbladder refilling with bile following the absorptive state. We found that the gallbladder's size continues to increase as rattlesnakes become more and more starved. The release of bile from the gallbladder is associated with feeding and is connected to both neural and hormonal triggers (Furukawa and Okada 1991; Housset et al. 2016). Our result, showing that the gallbladder continues to increase in size as the severity of starvation increases, may suggest that these mechanisms for emptying the gallbladder are not triggered in the absence of feeding in this species, and accumulation of bile is not alleviated. Inflammation of the gallbladder is also possible because retention of bile acids for extended amounts of time can lead to lipid peroxidation, causing detrimental effects on gallbladder health (Pandey and Shukla 2000). These are a few potential mechanisms underlying the observed pattern, and more targeted studies should be conducted if the opportunity arises.

There was a significant effect of sex on the size of the liver and the gallbladder, with both of these organs being larger in females after body size was accounted for. While previous work has shown that the positioning of various organs can differ according to sex in snakes, we are unaware of any study that reports significant sex differences in the relative size of these organs in snakes (Anderson and Secor 2015). In humans, it has been shown that females have proportionately larger livers than males (Kwo et al. 1998). However, this finding was only discussed in a clinical context having to do with alcohol metabolism, and any potential functional consequences of a sex difference in visceral organ size remain unknown in other animals such as *C. oreganus*. Future studies should

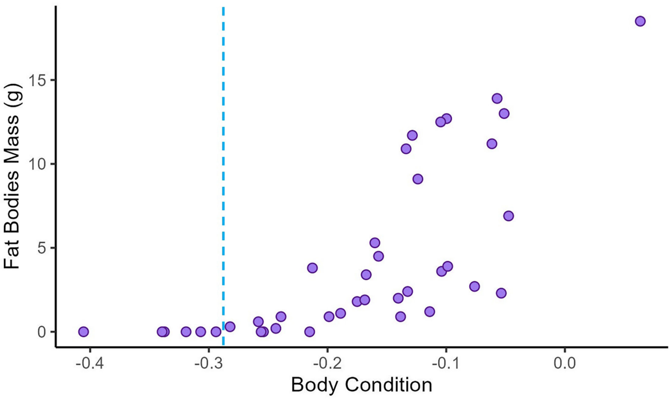

FIG. 5.—Scatterplot showing the mass of fat bodies in relation to the body condition of confiscated Western Rattlesnakes (*C. oreganus*). Individuals below a certain threshold (dashed line) of body condition (BCI ≤ –0.28) had no body fat.

also assess whether the same pattern of difference in organ size is recovered in balanced samples of snakes reared on a controlled feeding regimen.

To investigate potential reproductive costs of starvation in *C. oreganus*, we also measured the mass of the testes of the male snakes. We detected a positive relationship between BCI and the wet mass of the testes weighed as a pair, demonstrating that the testes shrink as snakes become more starved. In contrast, the testes of rats do not decrease in size in response to starvation (Goodman and Ruderman 1980). This disparity may be related to the fact that rats are short-lived mammals that may only experience a single reproductive season; thus, they preserve reproductive potential regardless of feeding state. On the other hand, for slow-living reptiles, the ability to reproduce in a given year may not be as high a priority as being able to utilize the resources contained in their reproductive organs when in the throes of starvation. Future work should pursue this possibility of differential reproductive costs of starvation among animal taxa with contrasting life histories.

We also found positive relationships between body condition and the dry mass of the heart, liver, and kidneys. Therefore, we demonstrated that the dramatic shrinkage of the organs is not merely a result of water loss but of the degradation or breakdown of tissues, cells, or both, as has been shown in the heart, liver, and kidneys of rats in response to prolonged starvation (Addis et al. 1936; Goodman and Ruderman 1980). Future studies should examine the structure of tissues to determine the underlying mechanism leading to the observed difference in tissue dry mass.

We found that tissue water content of the liver and kidneys increased as body condition decreased in this sample of *C. oreganus*. Although this is seemingly in alignment with previous findings that the total body water content of snakes increased with starvation, it is not what we expected to find with our study animals (McCue 2007a). The snakes used by McCue (2007a) had access to water during that study. The extremely dry body cavities of the starved snakes in our sample (see Fig. 1D) suggest that these snakes were likely deprived of water. This observation, in combination with the increased relative water content of organs in starved individuals, suggests that snakes may concentrate body fluids in the liver and kidneys as they starve. We also detected no relationship between body condition and the water content of the heart. This suggests that the heart is not as plastic in response to starvation, requiring more stable levels of water content to maintain functionality. Several studies have described the distribution of body fluids in the African Clawed Frog (*Xenopus laevis*) in response to dehydration (Luu et al. 2021). Hillman (1978) showed that dehydrated *X. laevis* experience decreased plasma volume but maintain higher water content in their skeletal and ventricular muscles than in their body as a whole. Additionally, *X. laevis* experiencing dehydration are able to maintain blood circulation to the brain, while circulation to skeletal muscles is reduced (Hillman and Sommerfeldt 1981). It appears that rattlesnakes may have similar mechanisms allowing them to prioritize intracellular over extracellular hydration and homeostasis.

As expected, we found that fat bodies decreased in mass with the degree of starvation. The fact that females in our study had more fat bodies on average is consistent with previous work that suggested that female snakes store more fat than males because of their higher reproductive demands (Lourdais et al. 2006). Additionally, we found that all snakes in our study with a BCI below –0.28 were entirely lacking in fat bodies. We believe that this has interesting consequences in the context of the "pay before pumping" hypothesis outlined by Secor and Diamond (1995). The hypothesis reasons that for a snake to successfully digest a meal, it must have substantial energy reserves in the form of fat to fuel the large physiological upregulation that increases the size and functionality of the organs involved in digestion. It should be noted that in more recent years, the pay before pumping hypothesis has come under some scrutiny, as several studies on snakes have demonstrated that the energy source for digestion rapidly switches from endogenous stores to energy metabolized from the recently consumed meal, greatly limiting pre-absorptive costs (Starck and Beese 2001; Starck et al. 2004; Waas et al. 2010; McCue et al. 2015). However, some of these authors have noted that these findings aren't mutually exclusive with the pay before pumping hypothesis, and that some amount of starting energy reserves may still be required (Starck et al. 2004; Bury 2022). Similar to anecdotes

TABLE 2.—Summary statistics for multiple regression models that used SVL and BCI as predictors of organ dry mass in starved Western Rattlesnakes (*C. oreganus*).

Organ	n	R^2	F statistic$_{(df)}$	P value	Explanatory variable	β	P value
Heart	37	0.377	$11.91_{(2,34)}$	0.0001	BCI	0.357	0.0007
					SVL	0.004	0.0004
Liver	20	0.884	$73.22_{(2,17)}$	<0.0001	BCI	3.499	<0.0001
					SVL	0.033	<0.0001
Kidneys	20	0.692	$22.29_{(2,17)}$	<0.0001	BCI	3.626	<0.0001
					SVL	0.026	0.0006

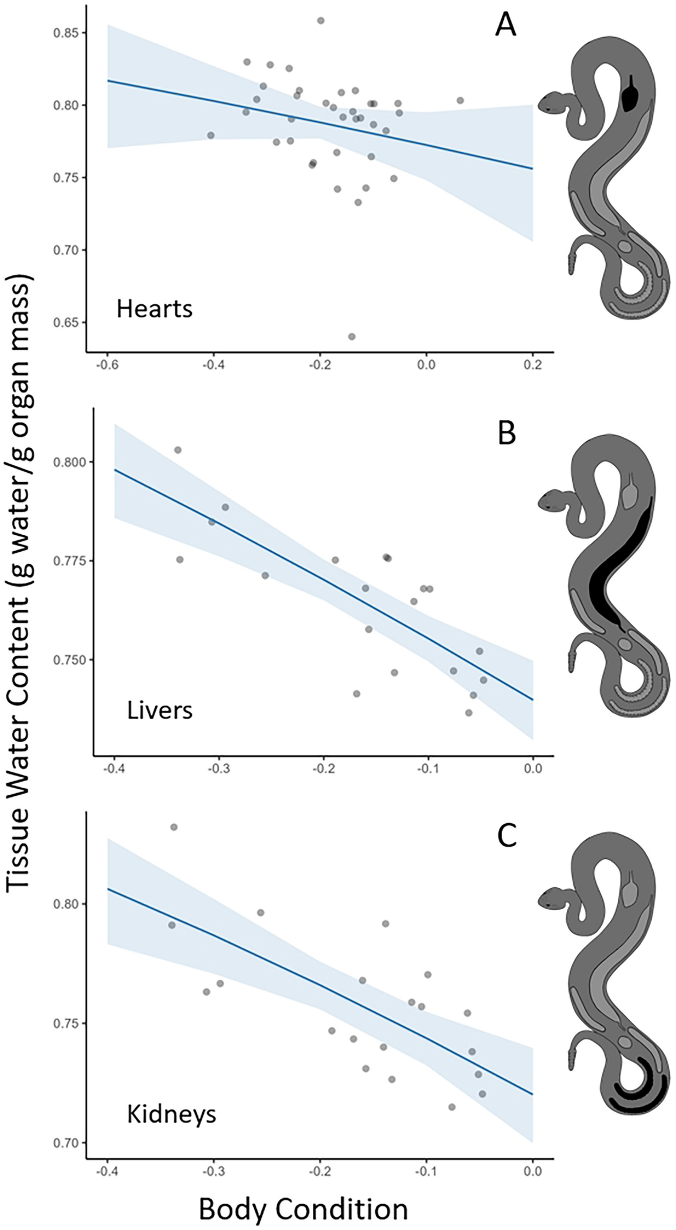

FIG. 6.—Beta regression scatter plots showing body condition plotted against tissue water content (grams of water/grams of total mass) of visceral organs of rattlesnakes starved to varying degrees. There was no relationship between body condition and tissue water content for hearts (A), but there were negative relationships for livers (B) and kidneys (C). The lower the body condition (indicating a more severely starved snake), the higher the tissue water content of the organs. The shaded regions are 95% confidence intervals based on standard error of the mean.

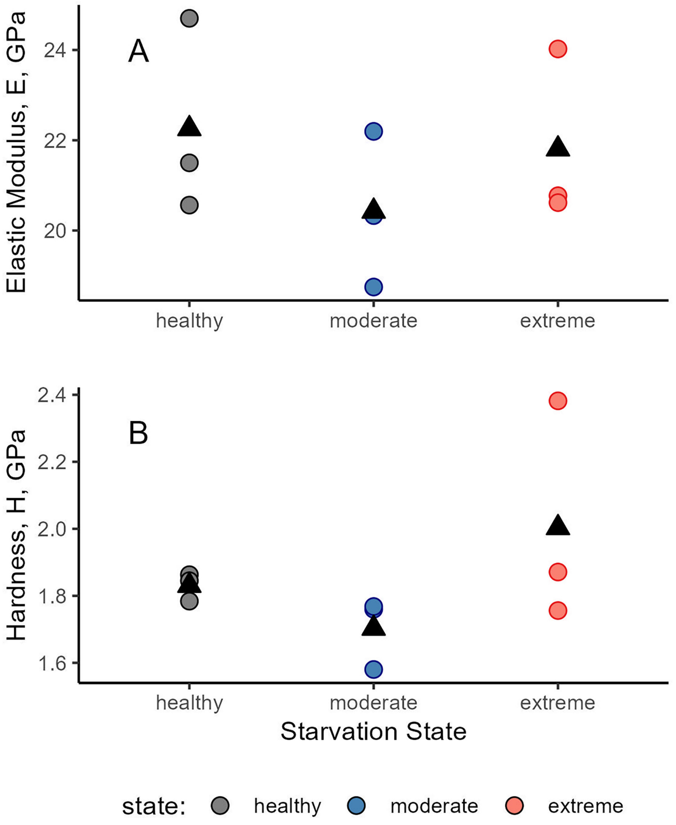

FIG. 7.—Starvation is not related to material properties of cortical bone in Western Rattlesnakes (*C. oreganus*). We used nanoindentation on rib cross sections of snakes binned into three starvation states (n = 3 per state) to determine effects on elastic modulus (A) and hardness (B). Colored dots represent the average value for an individual snake, and black triangles represent the group mean.

of emaciated captive snakes dying shortly after consuming a meal, it is likely that the snakes completely lacking fat bodies in our study were starved to an extent where recovery via natural feeding was impossible.

Our nanoindentation tests found no significant differences in elastic modulus or hardness in the bones of healthy, moderately starved, and extremely starved Western Rattlesnakes. These results do not support our hypothesis that bones of starved rattlesnakes would be more prone to damage through elastic or permanent deformation as a result of the snakes assimilating resources like minerals from them. We also found no evidence that the degree of starvation affects the amount of cortical bone in rattlesnake ribs, offering no support of our hypothesis that layers of bone may be degraded sequentially as snakes starve. However, we cannot be certain whether these results are a product of our limited sample sizes or if there is truly no effect of starvation on bone integrity. Bone mineralization can be a highly extended process in long-lived species, occurring over the course of an animal's life (Bala et al. 2010). In light of this consideration, it may be the case that resource assimilation from bones is excessively slow, and even the timescale of extreme starvation is too short to substantially influence their composition. Instead, the individual history of each animal preceding starvation may be more influential on the properties of their bones. Despite our expectation that extreme starvation would impact bone integrity, perhaps resilience to bone degradation should be expected in ambush hunters like rattlesnakes. While many cases of degradation in bone quality have been linked to disuse atrophy, the lives of rattlesnakes are characterized by extended bouts of inactivity, and they may have evolved to be resistant to the deterioration of their bones as a result of this activity pattern (Brent et al. 2021).

We selected nanoindentation to assess the properties of snake bones because it can be used to test the material properties of samples, irrespective of physical size. The technique has only been used to explore reptile biology relatively recently, and most of the studies concerning reptiles have focused on skin and osteoderms with the aim of developing novel materials via biomimicry (Sun and Chen 2013; Iacoviello et al. 2020). We believe there is also great potential in using this methodology to bolster a new dimension in reptile osteology, as introducing more quantitative approaches into this historically descriptive subdiscipline could greatly diversify the types of hypotheses we may be able to test (e.g., differences in material properties between species, sexes, age classes, ecological specializations, etc.). Future work should use the techniques described here on a larger scale that can provide greater statistical power.

Conclusions

We found that most organs of Western Rattlesnakes were extraordinarily responsive to starvation. Almost all types of organs measured showed dramatic shrinkage commensurate with the extent of starvation experienced, showing an impressive capacity to tolerate protein breakdown in order to sustain survival. Although rattlesnakes break down their body's proteins to a high degree, the tissue water content of vital organs is either maintained or increased with the level of starvation, suggesting adaptations allowing the snakes to concentrate their body fluids where they are most needed. We measured the material properties of bones for the first time in any snake species. These data suggest that the skeletal system of *C. oreganus* is not compromised as the animals experience starvation, but more extensive testing is needed.

Ethical guidelines should, and will, continue to constrain experiments on extreme starvation. However, we have demonstrated that research groups can work opportunistically to produce novel insights into starvation in the aftermath of inhumane treatment of animals. Should the opportunity arise, future work should attempt to investigate extreme starvation at different levels of biological organization. Namely, molecular processes occurring at extreme stages of starvation remain poorly studied. Hopefully, this study and related research will prove informative to fields such as wildlife rehabilitation and management, veterinary sciences, animal husbandry, and many others.

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SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpeto-logica-D-25-00018.S1; https://doi.org/10.1655/Herpetologica-D-25-00018.S2; https://doi.org/10.1655/Herpetologica-D-25-00018.S3; https://doi.org/10.1655/Herpetologica-D-25-00018.S4; https://doi.org/10.1655/Herpetologica-D-25-00018.S5; https://doi.org/10.1655/Herpetologica-D-25-00018.S6; https://doi.org/10.1655/Herpetologica-D-25-00018.S7; https://doi.org/10.1655/Herpetologica-D-25-00018.S8.

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