Studies on growth rates of snakes have long been investigated (Barnard et al. 1979; Carpenter 1952; Ford 1974; Kauffeld 1943) and are still ongoing (Boback 2003; Hill and Beaupre 2008; Madsen and Shine 2001). There are two growth measurements that are generally recorded when measuring snakes: length and mass (Charland and Gregory 1989; Franz 1977; Kauffeld 1943; Myer and Kowell 1973). A third and easily acquired measurement is girth at mid-body but this is rarely reported. Straight-line length is occasionally used but the most commonly reported length measurement is snout-to-vent length (SVL; Seigel and Ford 1988). It is important to state which measurement technique is being used (Fowler and Salamao 1995).

In a study on Nerodia sipedon, Brown and Weatherhead (1999) reported two variables that are likely to affect snake growth rates: energy intake and climate. Laboratory investigations allow for control of both of these variables. Many studies hold temperature constant and investigate feeding regimes (Barnard et al. 1979; Dmi’el 1967; Ford and Seigel 1994). Myer and Kowell (1973) showed that frequency of feeding and food mass can affect growth in Thamnophis sirtalis. As a snake consumes more food its total body mass usually increases but this phenomenon may not accurately relate the size (mass) of a snake to its age because body mass can be impacted by multiple variables. Snake mass has been shown to fluctuate with feeding regimes (Myer and Kowell 1973) and varying reproductive efforts (Charland and Gregory 1989). Neonate Pantherophis guttatus have been shown to convert up to one-third of their food weight into added body mass (Love and Love 2005). However, age can be predicted based upon SVL if the sampling period of the growth model is large enough and the specimen collected is in close regional proximity to the growth model sample (Brown and Weatherhead 1999). Individual marine iguanas total length has been shown to shrink during times of low food availability (Wikelski and Thom 2000) but this growth reduction phenomenon has not been shown in snakes (Madsen and Shine 2001).

In an early field growth study, Kaufman and Gibbons (1975) evaluated the relationship of SVL and mass of thirteen species of snakes that were primarily road collected and reported a correlation coefficient between SVL and mass of ±0.82 with *P. guttatus* being 0.97. Barnard et al. (1979) investigated the growth rates of ten sibling *P. guttatus* for ca. 2 years in a laboratory setting. Snakes were fed weekly meals of mice and were measured (total length and mass) monthly. A correlation coefficient of 0.978 was reported between total length and mass. They found that growth is more dependent on food consumed rather than age, length is logarithmically related to body weight, and weight gain and length are related to the amount of food ingested.

Many investigators have evaluated snake growth at different feeding frequencies (Dmi’el 1967; Wharton 1966) but to our knowledge, none have evaluated snake growth when fed in a mass-ratio feeding category with a constant frequency. A mass-ratio (MR) feeding category is a mutually exclusive feeding category calculated as the percent of prey mass to snake mass (Mehta 2003). The objective of this study is to evaluate the growth (length, girth, mass, and shedding rates) of neonate *P. guttatus* when fed in mutually exclusive MR feeding categories. We collected data on the growth rates and shedding frequencies of captive *P. guttatus*.

**Materials and Methods.**—The 18 hatchling snakes used in this study came from the personal collection of David Penning. Parents of the offspring were originally obtained from Miles of Exotics in Kansas City, Missouri. All snakes shared the same father and came from one of two mothers. All hatchlings displayed phenotypically normal traits but carried various non-expressed alleles that their mothers displayed but they did not. The first clutch of snakes began hatching on 8 June 2010 and all snakes hatched by 15 June 2010. All snake eggs were incubated in the same type of incubator (Little Giant® Still Air Incubator) with the same average temperature (28°C) and humidity (≤80%).

Each neonate was held individually in a cage internally measuring 27.9 × 27.9 × 15.2 cm. A sliding, clear piece of glass was used for the lid. Multiple 5-mm holes were drilled into the backs and fronts of the cages for proper air exchange. This allowed proper ventilation without exposing each snakes to the visual cues of the other snakes. Ambient room temperature averaged 27.9°C. Each cage was spot cleaned daily and bedding was changed *pro re nata*. No mites or parasites of any kind were observed during the experiment. Water was available at all times.

Hatchlings were then checked once per week for their first shed. The feeding trials began the following scheduled feeding day upon the discovery of each snake's first shed. The order in which the snakes were placed into each category was determined by a random number generator. House Mice (*Mus musculus*) were the only food given to snakes in the experiment. Each snake was put into a feeding schedule of one meal per week. The two feeding categories were labeled as small and large. The small feeding category had a prey mass-ratio of 20–40% of the snake's mass while the large category had a ratio of 41–60% of the snake's mass. The original categories followed the format of Mehta (2003) but hatchlings were born at a small size (mean = 4.4 ± 0.68 g) that prohibited the narrower ranges. Snakes were weighed using an AWS high capacity precision pocket scale (0.1 g) the day prior to each feeding trial and prey mass range was calculated for them. A prey item within the snake's range was chosen ca. one hour before trials began. Mice were transported to the university in containers in which all individuals of similar mass were grouped together. Mice were then chosen at random and weighed to match the appropriate snake. Snakes that failed to eat were removed from the experiment.

**Acknowledgments.**—The author wishes to thank the Missouri Department of Conservation and the Missouri Bat Rookery for assistance. The author also thanks Dr. David Penning for providing the hatchlings for this experiment.

**Author Information.**

DAVID A. PENNING
e-mail: Davidapenning@gmail.com

STEFAN CAIRNS
e-mail: cairns@ucmo.edu

University of Central Missouri, Department of Biology and Earth Science,
WCM 306, Warrensburg, Missouri 64093, USA

© 2012 by Society for the Study of Amphibians and Reptiles
to eat for four weeks in a row were removed from the study. A failed feeding trial was considered a period of 40 minutes at any point of the feeding trial in which the snake did not engage the prey.

Although previous studies measured snake length using snout to vent length (Fowler and Salamao 1995), we used snout to tail length for two reasons: the measurement data attained from this study came from a larger project requiring minimal handling; and to compare our data to that of Barnard et al. (1979). Because of this, snakes were digitally and not manually measured. Snakes were placed on a piece of 0.5 cm graph paper and photographed directly overhead approximately 100 cm above the snake. Pictures were then entered into the SnakeMeasurer© program to get total length. This allowed for the snake to orient its body in a natural position without being manually manipulated. Snake length was recorded to the 0.1 cm. Girth (in cm) was measured using a flexible measuring tape and wrapped around the snake at midbody and measured to 0.1 cm. Shedding events were recorded pro re nata. All statistical analysis was conducted on Minitab 14.

Results.—Snake mass is significantly related to the amount of food consumed in the small and large MR feeding categories (P < 0.05, small r² = 0.974, large r² = 0.949) and expressed by the following simple linear regression models: Small snake mass = 3.85 + 0.419 (total food consumed), Large snake mass = 4.84 + 0.395 (total food consumed). The intercepts and slopes of the regression models are not significantly different (General Linear Model, P > 0.05).

Snake length is significantly related to the amount of food consumed in the small and large MR feeding categories (P < 0.05, small r² = 0.795, large r² = 0.810) and expressed by the following simple linear regression models: Small snake length = 33.3 + 0.263 (total food consumed), Large snake length = 32.7 + 0.244 (total food consumed). The intercepts and slopes of the regression models are not significantly different (General Linear Model, P > 0.05).

Snake girth is significantly related to the amount of food consumed in the small and large MR feeding categories (P < 0.05, small r² = 0.807, large r² = 0.839) and expressed by the following simple linear regression models: Small snake girth = 2.23 + 0.0180 (total food consumed), Large snake girth = 2.21 + 0.0183 (total food consumed). The intercepts and slopes of the regression models are not significantly different (General Linear Model, P > 0.05). Regression models can be seen in Fig. 1.

Correlations were run among all three growth forms. All correlations are significant at P < 0.05. Mass and girth Pearson correlation coefficients are 0.912 for the small MR category and 0.934 for the large MR category. Mass and length Pearson correlation coefficients are 0.881 for the small MR category and 0.889 for the large MR category. Girth and length Pearson correlation coefficients are 0.853 for the small MR category and 0.922 for the large MR category.

Snake shed cycles from this experiment are presented in the same format as that of Myer and Kowell (1973) in Fig. 2.

Discussion.—In both the small and large MR feeding categories, growth in mass, length, and girth was significantly related to total food consumed. There was no significant difference
between the regression slopes of the small and large MR feeding categories for all three growth forms. This statistically supports the concept that food ingested (regardless of how it is ingested) will result in similar growth. Snakes in the larger MR category attained a larger mass, girth, and length by the end of the feeding trials but the overall growth models were not significantly different. It took the snakes in the small MR category longer to attain similar size in all growth forms but arrived at similar sizes as the large MR category per total food consumed. Mass, length, and girth gained by the snakes in this study depended upon the total amount of prey ingested. This supports the idea that snake mass is not dependent upon age alone. These findings agree with Barnard et al. (1979) in that snake mass is not an accurate estimation of age. These findings also support Barnard et al. (1979) in that variation (in mass) among individuals increased as amount of food increased and is presented in a similar format in Fig. 3. Snake size (mass) should not be used as an estimator of age beyond reproductive status (which generally accompanies a minimum age bracket).

We report a similar correlation coefficient as Barnard et al. (1979) between snake length and body weight (mass) in P. guttatus. A longer study is needed to specifically examine the growth associations in mutually exclusive MR feeding categories as Barnard et al. (1979) was a much longer study than the 22-week length of this experiment. In both the small and large MR feeding categories the correlation coefficients were similar for mass and length, mass and girth, and length and girth. These correlation coefficients suggest that there is a close association between the two MR feeding categories growth forms. Length, girth, and mass all covary with one another in a similar manner. Cornsnakes had a variable % mass gain (current pre-feeding snake mass – previous pre-feeding snake mass) / (prey mass from previous week)*100 in body weight per feeding event. Love and Love (2005) stated that neonate P. guttatus can convert up to 33% of their food (prey) weight into body mass. Snakes in this study had a percent mass gain range of -15% to 93% mass gain per feeding event. The average percent gain for the small MR feeding category was 40 ± 19.3%. The average percent gain for the large MR feeding category was 45 ± 22.4%. The averages suggest that it is more advantageous to eat larger prey (if the goal is mass gained) but when accompanied by the standard deviations there is no discernible difference between the percent mass gains of the two MR feeding categories. This observation is a much more variable number than the percentage presented by Love and Love (2005). There may be varying metabolic factors impacting mass gain that were not addressed in this study. A mass gain ratio does not appear to be a reliable measure of energetic (body mass) gain.

Acknowledgments.—We thank the Department of Biology and Earth Science’s faculty, staff, and graduate students, more specifically S. Wilson, K. Dean, and J. Mittelhauser. We also thank A. Brass, M. Perkins, and A. Bossert for their guidance and editorial reviews. This research was conducted under IACUC protocol #10-3212.

Literature Cited


