

Growth rates of juvenile *Boa constrictor* under two feeding regimes

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Many husbandry routines in zoo herpetology are based on tradition, authoritarianism, anecdote, or speculation. However, relatively few empirical studies underlie many very common practices. We compared growth rates among littermates of *Boa constrictor* raised under two feeding regimes that were identical in terms of the mass of food ingested, but differed in weekly versus bi-weekly schedules. The growth rate of the group fed weekly was greater than the rate for the biweekly group. Snakes fed 10% of their body mass on a weekly regimen grew to a larger size, and at a faster rate, than did snakes fed 20% of their body mass on a biweekly regimen.

KEYWORDS

boidae, diet, evidence-based husbandry, snake

1 | INTRODUCTION

Growth rates in captive snakes have been a focus of study for many years, however, most published reports focus on colubrid snakes (e.g., Penning & Cairns, 2012; Scudder-Davis & Burghardt, 1996) or viperids (Taylor & Denardo, 2005), with relatively few reports on boids (but see Soares, Barbosa, Rodrigues, & Borges-Nojosa, 2015). Additionally, as with many aspects of herpetological husbandry in zoos, feeding regimes for collections generally are managed with more regard to tradition—the “folklore husbandry” posited by Arbuckle (2013)—than to empirical data. Generally, most snakes in captivity fall into the category of being fed weekly, especially younger snakes that may be physiologically inclined to allocate energy toward growth rather than toward fat reserves. Weekly feeding regimes also commonly are recommended in popular herpetocultural literature (e.g., de Vosjoli, 2004; Fogel, 1997) and followed by many herpetoculturists, sometimes with the goal of getting animals to reproductive size as quickly as possible. Likewise, efforts to maximize reproductive output with extra food provisioning are commonly referred to, even though such practices may be quite harmful to the snake (Fogel, 1997; Walsh, 1994). Nonetheless, it is our estimation that older or adult animals generally are fed less often than juveniles in captive collections, again typically based on tradition. In many cases, however, obesity is common in adult captive snakes (Huff, 1980) indicating that feeding regimes based on anything other than natural history data may be ill-advised. For some species, there are field

data on annual energy budgets with regards to diet, growth, and reproduction (e.g., Baron, Le Galliard, Ferrière, & Tully, 2013) which reveal subtle differences with regards to breeding year versus non-breeding years in females, for example. Other studies have found complex relationships in feeding frequency between sex and overall body size (Shine, Harlow, & Keogh, 1998).

Despite these available data, feeding regimes for even large adult snakes in captivity seem rarely to be based on natural history and more on convenience or institutional tradition (i.e., “We’ve always fed them this way.”). There are very few published data demonstrating the effects of differing feeding regimes on the actual growth rates of snakes. However, de Vosjoli (2004) pointed out, anecdotally, that snakes fed less frequently may show overall improved body condition, higher activity levels, but with reduced reproductive problems. Long-term field studies, such as Bronikowski and Arnold (1999), are few and indicate that the relationships between feeding schedules, growth, reproduction, and adult survivorship are complex and sometimes non-intuitive. As such, an optimal feeding regimen in one instance is unlikely to be transferrable to another.

In zoos and conservation breeding programs, where funds and resources often are limited, a more efficient means of rearing snakes may prove beneficial. Additionally, growing younger snakes in a more efficient and timely manner may be necessary to boost breeding populations that have shown poor recruitment, or to quickly grow young animals to larger sizes for reintroduction purposes (e.g., head-starting

programs). Alternatively, there may be any number of reasons for which an institution is uninterested in maximizing growth or reproductive output (e.g., spatial constraints), or specifically is disinclined to do so (e.g., space or health concerns). Here, we present an experimental study comparing growth rates of juvenile snakes between two feeding regimens.

Using a full-sibling litter of neonate *B. constrictor*, we measured growth rates between two treatment groups that were fed the same amount of total food, but per a weekly versus bi-weekly (i.e., every other week) schedule. The popularity of *B. constrictor* as pets has encouraged the publication of many popular articles and husbandry manuals (e.g., de Vosjoli, Klingenberg, & Ronne, 2004; Fogel, 1997; Russo, 2007). An example of a recommended feeding schedule from Fogel (1997) is once a week for juveniles and every 7–14 days for adult *B. constrictor*. Fogel (1997) further explicitly advised against over-feeding as a means of increasing or expediting reproductive output, citing concerns about animal health. A study similar to ours was reported by Soares et al. (2015) and revealed some noteworthy differences from ours; this will serve a basis for discussion. Finally, a controlled study on this topic is not possible in wild snakes, so we present our results toward the general body of knowledge of snake growth and physiology as well as a potential resource for managers of captive colonies.

2 | MATERIALS AND METHODS

Three species are now recognized in the genus *Boa* (Card et al., 2016), with *B. constrictor* occurring in South America, *B. imperator* along the Atlantic Coast of Mexico and Nuclear Central America into South America, and *B. sigma* along Mexico's Pacific Coast. Many subspecies originally referred to the taxon *B. constrictor* have been described (Uetz, Freed, Hošek, 2017), however, their taxonomic validity is highly questionable. This species also is popular in commercial trade and has many informal names associated with various patterns of coloration produced through selective breeding or based on general localities of founder breeding stock. The exact locality of the breeding pair that produced the snakes used in this study is unknown as they were confiscated as juveniles by the United States Fish and Wildlife Service at Atlanta's Hartsfield–Jackson International Airport. There is indirect evidence that they likely originated from Peru. The dam, sire, and offspring all correspond closely in coloration to snakes generally referred to as Red-tailed boas deriving from the Upper Amazon Basin. Hence, we refer the snakes in this study to *B. constrictor* with no subspecific notation. *Boa constrictor* was amenable to our study as it is commonly kept in all sectors of the captive animal field, produce relatively large litters of young, and they generally accept frozen/thawed rodent prey readily through all life stages.

Twenty neonate *B. constrictor* (11 male, 9 female) from a litter born on September 2, 2014 were placed into individual sliding-rack system enclosures (Vision Products® V-70 11 level rack), with each enclosure measuring 86.4 × 44.5 × 13.5 cm. Each enclosure was identical, with newspaper substrate, a round glass water bowl (80 × 40 mm), and a

plastic shelter (42 × 30 × 10 cm; TROFAST; IKEA brand) lined with slightly dampened newspaper to provide a humid retreat with access holes on top which were enlarged as necessary to accommodate the growing snakes. Enclosures were cleaned as needed. Flexible heat cable was installed underneath the back half of each enclosure to provide a thermal gradient. A rheostat (Zilla® Temperature Controller) was used to control temperatures and set to keep the warm end of each enclosure ~29–32°C. As it was possible that the uppermost enclosures could experience slightly higher ambient temperatures, we rotated all enclosures top-to-bottom weekly to allow individuals to experience all possible thermogradients equivalently throughout the study. We placed two data loggers (Lascar Electronics, Inc. model EL-USB-2) in each of two enclosures from January 2, 2015 through the remainder of the study, with one placed on the warm end of the enclosure and the other on the cooler end away from the heat source. Hourly temperature data were then compared to determine if the cooler ends and warmer ends of the two exemplar enclosures were similar as they rotated vertical positions over the course of the study.

We chose to use a full-sibling litter specifically to reduce the effects of genetic variance among the study subjects (Alford & Harris, 1988). *Boa* spp. are wide-ranging species that show considerable population-level variation in adult size (Boback, 2006; Card et al., 2016). Variation in adult size across populations of snakes has a clear genetic component, and quite likely so do parameters of growth (Avery, 1994). Our design used full siblings to ensure that all individuals were equivalently genetically related. An alternative design, using individuals from different sets of parents would necessarily be confounded by the fact that individual subjects would be differentially related to one another with respect to the unknowable tokogeny of individuals of a wide-ranging species. Our study was not designed to characterize growth in *B. constrictor* in general, but rather to control for genetic relatedness across subjects so as to better understand the influence of feeding frequency on individual snakes.

Two groups of 10 snakes each were randomly assigned to each of two feeding regimens immediately after birth; sex ratios of each group were as close to equal as was possible with the sample group (Group 1 = 5.5, Group 2 = 6.4). All snakes were fed mice and/or rats. Our study was designed based strictly on food-item mass, we did not distinguish between species of rodent. Individuals in Group 1 were fed a prey mass equal to 10% of their own body mass weekly. Individuals in Group 2 were fed a prey mass equal to 20% of their own body mass biweekly (every other week). The mass of the prey items offered was regulated by augmenting a single rodent with anatomical pieces culled from other rodents and inserted into the coelom until the total mass of the rodent-plus-pieces was at the desired level, or with parts removed to reduce mass to desired level (e.g., removing parts of the tail). In no case were multiple prey items offered. The mass of each snake was recorded on the day of birth and then afterwards at 2-week intervals immediately prior to feeding. The study proceeded for thirteen months (September 2, 2014–October 2, 2015). We measured mass biweekly, rather than weekly, to reduce the likelihood that snakes may have an accumulated fecal bolus that would artifactually contribute to their total body mass. *Boa constrictor* defecates relatively infrequently (RLH,

pers. obs.) and the feces passed may be of considerable mass (e.g., the “adaptive ballast” concept articulated by Lillywhite, de Delva, & Noonan, 2002). Accurate measurements of length from snakes are essentially impossible to achieve for a variety of reasons (Astley, Astley, Brothers, & Mendelson III, 2017). The digital methods proposed by Astley et al. (2017) require the snake be in a flat position relative to the substrate during photography, and we found this to be unworkable as the snakes in our study typically adopted defensive postures (i.e., head raised and oriented nearly vertically) in the presence of a researcher. We chose not to use a press-box method to restrain such easily agitated snakes. Thus, we excluded length as a measured variable in this study.

Our statistical approach first used Shapiro–Wilks tests for normality to confirm appropriateness of parametric methods. We then used Levene's test to compare variances between the treatment groups, and a two-tailed *t*-test to compare mean masses of snakes in each group at the start and end of the study. Growth rates were compared following methods of Olsson and Shine (2002), computing the regression coefficient for the growth rate of each group and compared using one-way ANOVA, again with Levene's test to assure equality of variances. Because our sample size is relatively small, we also performed a nonparametric Kruskal–Wallis rank sum test, in order to evaluate the robustness of our data with regards to analytical technique. To test for equivalence of temperatures among enclosures, we used a Granger test (Diks & Panchenko, 2006; Granger, 1969). This test typically is used to evaluate causality, but it also can be used to compare any two datasets to determine how predictive they are of one another and is suitable for comparing autocorrelated, time-series data. In other words, if our temperature profiles through the study were similar, then data from one datalogger will be able to predict the data from the other logger. To determine whether the snakes experienced broadly different temperature regimes, we used the Granger test on the stationary-transformed daily temperature data to ensure agreement between the readings from each enclosure (defined at $p < 0.05$). All analyses were conducted using R-software (R Core Team, 2013).

3 | RESULTS

Comparison of the temperature loggers placed at the warmer and cooler sides of the enclosures indicated that the snakes experienced similar thermal regimes during our study (Granger test, warmer sides: $F = 3.89$, $df = 270, 271$, $p = 0.049$; cooler sides: $F = 6.18$, $df = 270, 271$, $p = 0.013$). Tests of normality confirmed appropriateness of parametric methods (all $W > 0.94106$, p -value > 0.2511).

Reductions in body mass were only recorded after birth and prior to the first feeding, with the single exception of snake 14 M on August 21, 2015. Otherwise, mass increased at every measurement throughout the experiment. Nearly all individuals fed consistently throughout the study, with the exceptions of snakes 1 M, 10 M, and 20 F refusing their first offered food item and snakes 21 and 15 M refusing their 2nd and 49th offerings, respectively.

The variances of the two groups were not different at birth ($F = 1.158$, $df = 1, 18$, $p = 0.269$), nor were the means of the masses

(Table 1; $t = 1.4000$, $df = 18$, $p = 0.1785$). At the end of the study, variances of the two groups ($F = 0.7001$, $df = 1, 18$, $p = 0.4137$), and mean masses of the two groups were different at the end of the study, with the 10% weekly group having a greater mean mass than did the 20% biweekly group (Table 1; $t = 8.060$, $df = 18$, $p < 0.001$). The total relative growth of individuals in each group ranged from 1,233 to 1,426% (median = 1,307%) in the 10% feeding group, and was less in the 20% feeding group, with a range of 995–1233% (median = 1,036%). The variances of growth rate between the two groups were not different ($F = 0.318$, $df = 1, 19$, $p = 0.5769$). The growth rate of the 10% weekly group was greater than was the rate for the 20% biweekly group (Figure 1; $F = 73.031$, $df = 1, 18$, $p < 0.001$). Analysis of the same data, using the non-parametric Kruskal–Wallis rank sum test also indicated greater growth rate for the 10% weekly group (Growth ~ group, Kruskal–Wallis $\chi^2 = 14.286$, $df = 1$, p -value = 0.0001571). In summary, the snakes fed 10% of their body mass on a weekly regimen grew to a larger size, and at a faster rate, than did snakes fed 20% of their body mass on a biweekly regimen, even though total mass of prey ingested over the term of the experiment was equivalent.

4 | DISCUSSION

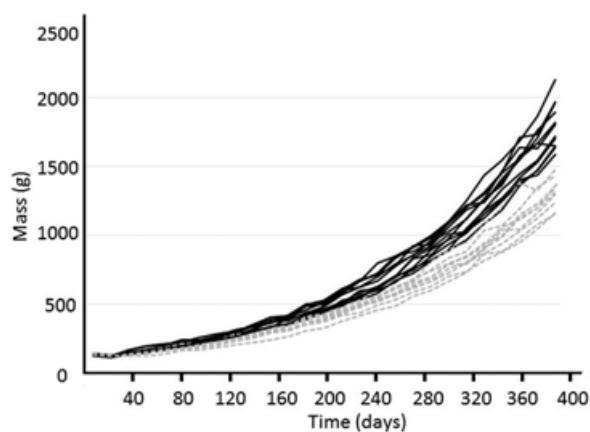
Our results indicate that feeding schedule has more influence on total growth of juvenile snakes than does total prey mass ingested over time. The reasons for this differential growth are unclear, but these general results echo the idiosyncratic results reported from the field in other snakes (e.g., Bronikowski & Arnold, 1999). Repeated experiments on other taxa will be necessary before any general conclusions can be drawn. In any case, we suggest that our results may reflect the cumulative energy spent on meal digestion and assimilation, termed the specific dynamic action (SDA; McCue, Guzman, & Passemont, 2015). In pythons, SDA can account for 20–30% of the energy ingested (Secor, 2009). Part of the costs of SDA stem from significant amounts of anatomical growth in the digestive tract and associated organs that are initiated after ingestion of a meal (Andrew et al., 2015; Secor & Diamond, 1998). In our case, even though the amount consumed over the course of the experiment was equivalent in both treatments, the snakes that were fed larger-sized meals (at 20% body mass bi-weekly) grew less than the snakes receiving the smaller, more frequent meals. In this sense, our results match perfectly the summary of Secor (2011) and the empirical data of Crocker-Buta and Secor (2014) who indicated that increased meal size increases the work of digestion and assimilation to increase the SDA.

While Soares et al. (2015) came to essentially the same conclusion as we did, their results were marked by some notable differences from our own. For example, Soares et al. (2015) reported numerous instances of decreases in mass in their biweekly 20% mass feeding group. We note that they recorded mass weekly in both of their treatment groups, whereas we recorded mass biweekly for both groups. Our design was intended to reduce likelihood of our data including the mass of any retained feces from previous feedings.

TABLE 1 Mean mass and standard deviation for each treatment of *Boa constrictor* in this study

Group	N	Mass		Overall growth
		Initial	Final	
10% weekly	10	135.0 ± 6.3	1818.2 ± 111.6	1683.2 ± 113.8
20% biweekly	10	138.2 ± 3.5	1425.2 ± 21.0	1287.0 ± 121.3

Although Soares et al. (2015) did not report timing of fecal passage in their snakes, according to our experience with juvenile *B. constrictor*, we suggest that this may have been a factor in their data. We note that, with only a single exception, we never found a decrease in the mass of our study animals once feeding trials had been initiated. We also highlight the remarkable differences in the initial and final sizes of the snakes used by Soares et al. (2015) compared to the snakes in our study. In our study, the final mass of every snake was $\geq 10X$ that of their initial mass. In Soares et al. (2015), despite starting with smaller snakes (<60 g compared to >120 g in this study), final mass of the snakes was only $\sim 4\text{--}5X$ that of the original mass. Although Soares et al. (2015) conducted a shorter study (10 months vs. 13 months), by the 10-month mark in our study all snakes were already approaching $\sim 10X$ their starting mass. *Boa constrictor* is well-known for very rapid growth capacity based on food intake under captive situations (Russo, 2007) and it is unclear why snakes from our study grew at a much higher rate than those described in Soares et al. (2015). We did not see a change in willingness to feed overall within our study group once snakes had begun feeding, with the lone exception of snakes 15 and 21 M (each refused a single meal throughout the study); we observed no instances of regurgitation. Soares et al. (2015) reported, especially at the 7-month mark, numerous food refusals and regurgitations. This seems highly unusual to us, given that the feeding regimens involved in both studies were not extreme with respect to traditional husbandry practices and the natural history of this species. We suggest that their snakes may have become influenced by some environmental or

**FIGURE 1** Comparison of growth rates between sibling *Boa constrictor* maintained on a weekly diet comprising 10% of their body mass (black lines, each representing one snake) versus a biweekly diet comprising 20% of their body mass (gray lines). The growth rate of the 10% weekly group was greater than was the rate for the 20% biweekly group ($F = 73.031$, $df = 18$, $p < 0.001$)

pathogenic factors during the course of their study, which could also explain the differences in the final relative sizes of the snakes in their work.

In summary, our data indicate that managers of captive colonies of snakes should pay attention to the energetics of digestion. Larger meals are more physiologically expensive to process so, as a general rule-of-thumb, moderated growth, and reduced risk of obesity may be achievable with fewer, but larger, meals. We emphasize, however, the results from one life-stage, sex, species, or even population may not be applicable to another group of animals.

5 | CONCLUSIONS

1. Weekly, or otherwise regular feeding of snakes is deeply entrenched in the traditions of herpetological husbandry.
2. We found that the feeding schedule of snakes has a greater influence on growth rate and mass than does the amount of food ingested.
3. These results have significant implications for avoidance of obesity in captive animals, head-start and release conservation programs, and also for budgetary resource allocations across captive snake collections.

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