Body size comparisons between wild and captive puff adders *Bitis arietans*

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Captivity can provide a resource-rich environment for snakes which may lead to over-conditioning of individuals. We compared captive and wild populations of *Bitis arietans* to see if a difference in scaled mass index (SMI) existed between the samples. Male *B. arietans* had significantly higher SMI in captivity than in the wild; there was no difference between wild and captive females. A sex-related difference in SMI between wild male and female *B. arietans*, evident in the wild, was not found in captivity. These results suggest that the captive management of *B.arietans* may require review to prevent over-conditioning of male snakes, and that this may be informed by further comparative research on wild and captive populations of this species.

Keywords: Body condition, captivity, scaled mass index, Viperinae

INTRODUCTION

Captivity can provide a resource-rich environment. However, it is often combined with behavioural restrictions, generally in the form of a reduction or inability to perform such energetically costly behaviours such as intense physical activity or reproduction (Estevez & Christman, 2006). Therefore, an excess of adipose tissue is a common problem associated with captivity across many vertebrate taxa (Frye, 1984; Wadsworth et al., 1984; Bradley & Wright, 2000; Goodchild & Schwitzer, 2008; Vester et al., 2008; Rawski & Józefiak, 2014; Stoskopf, 2017). This condition is associated with negative pathological conditions (Salas & Manteca, 2016; Caravaggi et al., 2018), a reduced life expectancy (Clubb et al., 2008) and may reduce welfare in animals throughout their lives (D'Eath et al., 2009). Clearly this is a state which is best avoided. A commonly used method of assessing whether an animal is at an ideal body condition is through quantitative assessment and comparison with wild conspecifics, and a better understanding of body condition in captive animals may guide the way for improvements in welfare.

Body condition in snakes has been investigated, however published data seem only available for studies under natural conditions as opposed to in a captive environment (Naulleau & Bonnet, 1996; Madsen & Shine, 2000; Aubret et al., 2002; Waye & Mason, 2008). The most appropriate way of calculating body condition is by using a scaled mass index (SMI) which takes into account the allometric nature of morphological features of an animal - in other words, there is not a simple linear relationship between the increase of length and the increase in mass (Falk et al., 2017). Typically, there is a sigmoid (cubic) relationship between linear measurement and mass in animals; that is, larger animals are proportionately heavier per unit of length than are smaller individuals. Therefore, larger individuals show a corresponding greater increase in mass for a given increase in length. The methodology of Peig & Green (2009) is deemed a suitable method for this reason. The same process of calculating body condition has been applied to introduced *Boiga irregularis* on the island of Guam (Waye & Mason, 2008) and *Acrochordus arafurae* in Australia (Madsen & Shine, 2000) to assess temporal variation of body condition.

Venomous reptiles are frequently kept in zoological and private collections all over the world and large, heavy-bodied vipers are among the more commonly exhibited venomous snakes. Multiple factors, including their generally manageable size as well as the intricate body patterns and attractive colours of many species influence these animals' popularity. Species360, an organisation providing members with data collection and management software known as the Zoological Information Management System (ZIMS), lists 4676 individual snakes in the family Viperidae currently held in zoos and aquariums around the world (accessed 7/1/22), with 1288 individuals contained in the subfamily Viperinae and 336 in the genus *Bitis*. Puff adders, *Bitis arietans*, comprise 96 of those individuals, making this one of the most abundant species of viper among Species360 members. In addition to this, an unknown number of these snakes are also maintained in non-registered zoological institutions and private collections around the world.

Published literature suggest that in a typical captive setting some reptiles have the potential to grow to body

conditions not often reached under wild circumstances (Beck, 2005; Mader, 2006). To further compound this, without recognised assessments for body condition in different reptilian taxa, there is often no clear-cut way to categorise physical states such as emaciation or obesity. Body condition scoring represents a standardised way for individuals using visual assessment to determine the body fat reserves of an animal (Vieira et al., 2015). To date only a small number of validated body condition scoring systems for reptiles exist (Deming et al., 2008; Thomson et al., 2009; Lamberski, 2013; Rawski & Józefiak, 2014; Falk et al., 2017). The many recognised diseases related to excess adipose tissue are likely to affect reptiles in the same way as demonstrated in other animals (German, 2006). Therefore, for individuals working directly with reptiles in ex-situ populations, having such information readily available is key to being able to provide the best welfare.

Herein, *B. arietans* are examined to explore the difference in SMI between wild and captive specimens. We view the most informative method of estimating the optimal body mass in relation to body length of captive *B. arietans* to be using data from wild populations of these animals, where a large enough dataset can be used to generate an 'ideal' value. This supposed ideal wild-population SMI can then be compared to ex-situ populations of *B. arietans*, with the null hypothesis that snakes in captivity will not differ in SMI from wild snakes. If this null hypothesis is rejected, and captive animals have a higher SMI, by lowering the SMI of the ex-situ population, welfare of these individuals may be increased. It is hoped that methods herein will allow an assessment of ideal SMI for this species to be quantified which may lead to a better understanding of fitness of the captive population as measured against the wild population.

METHODS

Total length and mass measurements of *Bitis arietans* were collected from published literature (Pitman, 1938; Rosi, 1988; Bonnet et al., 2001), institutional and personal correspondence (Liverpool School of Tropical Medicine [LTSM]; Ganger, E) field observations (Glaudas, X), and ZIMS (accessed 31/12/21). Wild snake length was typically measured directly while the snake was anesthetised (necessary for a separate telemetry study, for which ethical approval was granted), whereas in captivity snake length was calculated by photographing each snake next to a scale and digitally measuring total length via imageJ (Schindelin et al., 2012). A mean average of three lengths per captive snake was used to increase accuracy and precision (Fig. 1). Captive snakes were weighed using a digital balance (Adam Equipment CPWplus 15; Hendi 580233) and wild snakes with a portable electronic balance accurate to ± 1 g. All mass/length combinations were collected from individual snakes within one month of one another and without a feeding or defecation event in between to ensure that they were relevant to one another. Almost all

Figure 1. *Bitis arietans* from - **A)** Nigeria, **B)** Kenya, **C)** Tanzania and **D)** eSwatini. Each snake was photographed at the Liverpool School of Tropical Medicine by Edouard Crittenden. Black line illustrates measurements taken via ImageJ.

measurements were taken simultaneously. Data for other *Bitis* spp. were unavailable in appropriate numbers for analysis. Snakes were allocated as male or female, captive or wild. Data from snakes of unknown sex were excluded. Snakes less than 540 mm in total length were regarded as juveniles and data from these animals were also excluded. This measure was achieved using the smallest size recorded for a male snake showing courtship or reproductive behaviour (Glaudas et al., 2020b), minus 10 % range buffer to account for potential variance.

Scaled Mass Indices (SMIs; M_i) were calculated according to the methodology of Peig & Green (2009), using the formula:

$$\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

where M_i and L_i are the body mass and the linear body measurement of individual i respectively; b_{SMA} is the scaling exponent estimated by the standardised major axis regression (SMA) of M on L; L_0 is an arbitrary value of L (in this case the arithmetic mean of the study population); and $\hat{M}_i$ is the predicted body mass for individual i when the linear body measurement is standardised to L_0. We calculated bSMA using the method of dividing the slope from the standard ordinary least squares regression of M on L (bOLS) by the Pearson's correlation coefficient *r*.

We used Shapiro-Wilk tests to check data for normality and found that this assumption was not met; non-parametric analyses were therefore used. Data were log-transformed to ensure homoskedastcity, confirmed via Bartlett's test. Data were analysed using RStudio (Version 1.4.1717) with an alpha of 0.05. We

used the stats package (R Core Team, 2021) to perform Kruskall Wallis tests to investigate the effects of snake sex, source (wild or captive) and the interaction between these factors on SMI, and to use Mann-Whitney U tests to perform post-hoc comparisons, with Bonferroni corrections (adjusted alpha = 0.0083).

RESULTS

Masses and lengths of 84 wild (n male = 41, n female = 43) *Bitis arietans*, from Gauteng Province, South Africa, and 23 captive (n male = 17, n female = 12) *B. arietans*, from seven captive collections in Europe and the USA, were used for analysis (S1). Captive *B. arietans* with bloodlines originating from six countries were identified, and all but one individual were in captivity >12 months, with one female in captivity for nine months (S1). Data in the 'captive female' sample was comprised of 67 % snakes (n = 8) which did not reproduce in the same year in which weight was measured, 25 % (n = 3) snakes measured immediately prior to mixing male and female for breeding, following which each female produced a litter, and 8 % (n = 1) post-partum snakes. There was no information on reproductive status of wild snakes.

Median SMI was 597.4 g, 799.9 g, 784.5 g and 890.1 g for wild male, wild female, captive male and captive female snakes, respectively. There was a significant effect of source (captive or wild) (X^2_1 = 8.25, p = 0.004; captive higher than wild) and sex (X^2_1 = 23.06, p < 0.0001; females higher than males) of animals, and the interaction between the two variables (X^2_1 = 35.05, p < 0.0001) on SMI. Post hoc comparisons (Table 1) showed that SMI of wild and captive females, and of captive males, did not differ significantly, but all three were significantly higher than wild males (Fig. 2).

DISCUSSION

The results of this research show evidence for higher SMI in captive male *Bitis arietans* than in wild conspecifics. By using the SMI developed by Peig & Green (2009) we accounted for both the allometric relationship between mass and length data (Falk et al., 2017) and also for differences in size distributions between populations, by relating all data to the arbitrary length value T_0. The SMI has also been validated against some snakes (Peig & Green, 2009) and found to outperform other mass indices in terms of correlation to tissue composition. In *B. arietans*, the effects of source and sex on SMI were due to the interaction between variables; wild male snakes were less well conditioned than wild females and both sexes in captivity. The SMI of these three groups did not differ from one another.

In the field, *Bitis* ssp. growth and body condition has been demonstrated to be linked to food availability. Growth rates differ between populations of *B. caudalis* from arid and intermediate habitat zones, with snakes from areas with greater food abundance growing more quickly and appearing 'less thin' (Shine et al., 1998). Furthermore, supplementary feeding of wild *B. arietans*

Table 1. P values derived from pairwise post hoc comparisons between scaled mass indices of wild and captive male and female *Bitis arietans*. An adjusted alpha of 0.0083 was used. Bold cells indicate a significant p value.

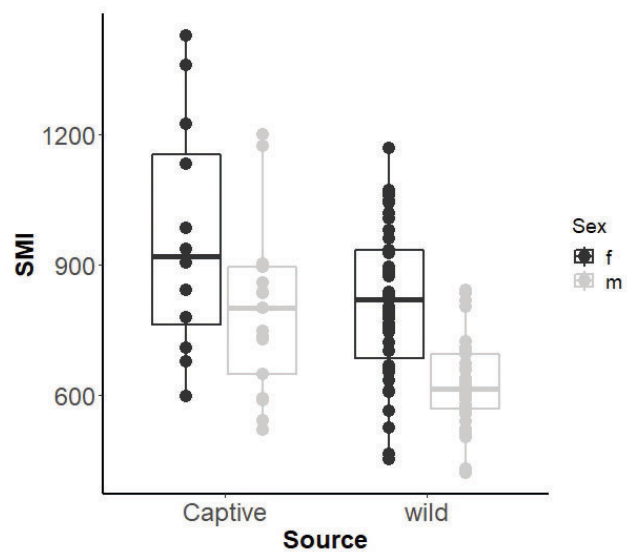|	Wild/ male	Wild/ female	Captive/ male	Captive/ female
Wild/male	x	x	x	x
Wild/female	**< 0.001**	x	x	x
Captive/male	**< 0.001**	0.9124	x	x
Captive/female	**< 0.001**	0.84148	0.77182	x

Figure 2. Median scaled mass index of 113 sampled *Bitis arietans* by source (captive or wild) and sex. Raw data are displayed for ease of interpretation; log-transformed data were analysed.

in South Africa showed changes in movement patterns when compared to control snakes, however home range remained similar (Glaudas & Alexander, 2017). Food intake was shown to directly affect allometric factors including growth rate, proportionate fang length and head width in captive juvenile *B. gabonica* (Bonnet et al., 2001). Data were not available for these features in our data set so they could not be compared. Food intake manipulation studies have revealed that growth rates can be substantially higher than those found under non-manipulated circumstances (Grubant et al., 1972), suggesting that growth in reptiles may be food-limited under certain natural conditions. Indeed, seasonal differences in food availability have been correlated with body condition of wild snakes (Madsen & Shine, 2000). This information should help inform husbandry aims and bring SMI of captive male *B. arietans* more in line with that of wild males.

In captivity, food provision may have a similar effect. Nutritional analysis of wild *B. arietans* prey is unknown, as for most snake species, however Dierenfeld et al. (2015) present a detailed nutritional analysis of the diet of wild *Drymarchon couperi*. Although this genus is phylogenetically distant from *Bitis*, the type of prey item consumed is broadly similar, both feeding on small mammals, amphibians and to a lesser extent birds and reptiles (Dierenfeld et al., 2015; Glaudas et al., 2017). Individual prey items in the diet of wild *D. couperi* contain 2-17 % crude fat. Crude fat percentage of lab-raised rats and mice, which are the staple food of many captive snakes including *Bitis* spp., average 20–30% (Dierenfeld et al., 2002). To potentially increase the effect of an excessively calorific diet in relation to a species' behaviour, an ambush predator such as *B. arietans* (Al-Sadoon, 1991) may be expected to expend few calories to find prey. Captive diets for *B. arietans* are likely substantially higher in fat than wild diets. Glaudas & Alexander (2017) demonstrated that supplementary-fed wild *B. arietans* improved their body condition and decreased travel distance compared to control snakes, which may further intensify the increase in SMI for captive snakes fed a typical high-calorie diet of commercially raised mice and rats.

As well as higher fat content in captive diets, overall food quantity and feeding frequency may be higher. On average, *B. arietans* in South Africa feed once every 10 days through the active season. It is estimated that an adult male will feed on 12–15 occasions and consume 384–480 g, or 48–60 % of average body mass (Glaudas & Alexander, 2017). In captivity, adult *B. arietans* are often fed around once every two to three weeks (Rosi, 1988; pers. obs., D. Kane) which may resemble typical wild feed frequency. However, even being fed a modest sized commercially raised rodent of 80 g for nine months of the year (a typical 'active season' for a male *B. arietans*) would result in a food intake of 1440 g, or at least three times more than would be expected for a wild snake. This difference in prey mass intake can be explained by the fact that wild *B. arietans* will feed on relatively small prey, potentially of a size which may not be offered to captive snakes. Seasonality in feeding of wild *B. arietans* from more temperate latitudes is expected as this species is known to undergo bouts of torpor under unfavourable climatic conditions, and male snakes consume less food during the breeding season than at other times of year (Phelps, 2010). When viewed holistically, the factors outlined here lend support to the notion that the more food-rich the environment, the shorter distance a snake will move while foraging. The thermal environment, and likely also the space and complexity of the captive environment available to a typical squamate, dictates to a large extent the behaviour of the animal (Thomas et al., 2019). Therefore, when unnatural diet type is combined with artificially controlled environmental parameters the risk of serious obesity and other disease (Frye, 1984; Simpson, 2006) developing in captive snakes may be further increased. To counteract this effect in captivity it is recommended to provide food items most similar in size, frequency, and nutritional composition to those included in the diet of wild snakes.

The effect of increased dietary intake may be exacerbated by reduced opportunity to expend calories. A measure of space requirement can be inferred from daily movement patterns. Free-ranging, reproductively active, male *B. arietans* move 80 m day^{-1} during the breeding season, whereas non-breeding males and females generally move <10 m day^{-1} (Alexander & Maritz, 2015). Furthermore, the motivation, ability, or need, for a captive viper to exhibit movement patterns comparable to snakes in the wild may be reduced, again intensifying the effects of a diet excessively rich in calories.

Our findings point to a resource-rich environment in captivity generating male snakes with elevated body condition. Male snakes are likely less well conditioned than females in the wild due to seasonal resource expenditure in finding and courting females (Daltry et al., 1998; Glaudas & Alexander, 2017). Female snakes may also have an overall high threshold level of energy reserves to compensate for reproductive expense (Duvall et al., 1992). In captivity, however, this effect disappears such that sexes have similar body conditions. The trend for male *B. arietans* to have a higher SMI in captivity than in the wild is likely due to an increased intake of food in terms of quantity and calorific value, and less need to expend energy on active behaviours including foraging, mate-searching and other behaviours related to reproduction, when compared to wild males. This is a non-negligible difference, with captive male snakes having on average an SMI nearly 33 % larger than wild conspecifics.

Snakes allocate a significant proportion of stored reserves to meet metabolic costs associated with reproduction (Santos & Llorente, 2004). It is likely that any single breeding event may lower the female body condition below a reproductive threshold, with a corresponding decrease in SMI. Female *B. arietans* from wild and captive populations do not differ significantly in median SMI (799.9 g vs. 890.1 g). Wild female *B. arietans* are thought to reproduce infrequently on account of their large litter sizes and females are not equally fecund due to differing body conditions (Maritz & Alexander, 2013; Glaudas et al., 2020a). Our captive sample contains female snakes in a range of reproductive statuses, whereas the reproductive state of wild females is not known. Our sample size increases the validity of our results by reducing the likelihood of small sample size intensifying natural skew of snakes being allocated to either 'reproductive' or 'non-reproductive' body conditions and thus influencing results. Compared to male *B. arietans*, female *B. arietans* are relatively sedentary in the wild (Alexander & Maritz, 2015) so there may be less of an energy expenditure difference between wild and captive females compared to between wild and captive males. This may account for the difference in SMI between these four populations. It is unclear why wild and captive females do not significantly differ in SMI; the very high p value from the post-hoc comparisons suggests that the lack of difference is unlikely to be an

artefact of sample size. It is possible that differences in behaviour (seasonally or otherwise) allow them to secure more prey items in the field, or create a smaller difference in energy expenditure between field and captive conditions. A factor we could not control for with our sample size was the origin of the snakes. Data from all wild snakes were from Gauteng province, South Africa, while none of the captive snakes were known to originate from this country. The possibility exists that cryptic lineages are hidden within '*B. arietans*' (Barlow et al., 2013) and future work may recognise multiple species. While wild and captive snakes originating from a broader geographic range would have provided the opportunity to test for locality or institution-specific differences in SMI, this was outside the scope of this work.

It is important to acknowledge limitations to BCIs based on morphometrics. However, as the differences in SMI between wild and captive populations of male *B. arietans* were significant, this is likely to have a real impact on the fitness of the captive population. Numerous pathologies associated with excess adipose tissue are reported from various taxa (Clubb et al., 2008; D'Eath et al., 2009; Salas & Manteca, 2016; Caravaggi et al., 2018). Clearly, unnatural levels of adipose tissue, likely linked to a high SMI, is a condition to be avoided should captive snake welfare be maximised. Snakes may be difficult to assess for body condition, however several studies have shown temporal variation in BCI (Madsen & Shine, 2000; Waye & Mason, 2008) albeit purely in wild populations. The reproductive state of snakes in this study was not considered as this information was not available for the majority of specimens; it is likely that female snakes in particular may show an elevated SMI prior to and during a reproductive season whereas male SMI decreases from the beginning to the end of the breeding season (Glaudas et al., 2020a). This highlights the need for long term data collection on body condition, preferably over several active seasons, from which reliable results can be inferred (as in Madsen & Shine, 2000). In the present work, we suggest that proportions of captive animals in different reproductive states in our data set do not differ significantly from those expected in a natural population; while this does not allow us to quantify the effects of reproductive state, it allows us to discount them in our comparisons.

Therefore, we suggest that a validated scoring system for body condition of *B. arietans*, based on visual appearance in conjunction with SMI calculations, may better account for the differing structural composition of an animal (Santos & Llorente, 2004; Jayson et al., 2018) and might be useful in informing the captive management of this species. Data on health impacts of high SMI in *B. arietans* are not available, therefore we suggest that future research should focus on health issues linked to body condition in this and other snake species.

In conclusion, the data presented in this study suggest that, on average, wild male *B. arietans* have a significantly lower SMI than do their captive counterparts whereas female snakes show no difference. Taking the median SMI of wild male snakes as ideal for this sex, captive male snakes appear to be over-conditioned. Applying the same comparison to female snakes suggests the body conditions of the two populations are the same. Given the negative pathologies associated with excess adipose tissue, linked to calorific imbalance and a higher SMI, the SMI of wild snakes is a condition which should be aimed for in a typical captive environment. The natural ambush-foraging behaviour of these snakes, and ability to ingest large meals, may predispose male snakes to maintaining an unnaturally high SMI, more so than other species with a higher metabolic rate (Al-Sadoon, 1991; Secor & Diamond, 1998). However, more detailed analysis is outside the scope of this work. The importance and benefits of maintaining captive vipers at an ideal wildtype SMI is, however, clear to be understood.

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