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Factorial scope of ingestion and the potential functional response of puff adders (*Bitis arietans*) to high prey abundance

Graham J. Alexander

Historically, snakes have been considered to have a weak functional response to changing prey abundance due to their ectothermic physiology and slow digestion. I measured aspects of food consumption in a captive colony of puff adders (*Bitis arietans*) to evaluate their functional response. I introduce a new metric for this evaluation, the 'factorial scope of ingestion', defined as the maximum food intake divided by maintenance consumption. Rates of weight loss during fasting were also quantified to assess the potential for puff adders to persist through periods of low prey abundance. To maintain a constant body mass, puff adders must consume 63% of their body mass in rodents annually. However, when provided with unlimited food, they increased their food intake by an average factor of 12 times above maintenance levels for extended periods, which resulted in dramatic increases in body mass. Regression analysis between annualized food intake and changes in body mass, and direct measures of weight loss, independently estimated an annualized weight loss of ~ 23% body mass for fasting puff adders while metabolising fat. This suggests that a puff adder with a high initial body condition index could fast for more than 2 years. The extreme flexibility of puff adder feeding biology suggests that this species has a significant functional response to high prey abundance, and this response is likely to be much more profound than the functional response of mammalian predators. These findings highlight the importance of snakes as potential ecosystem stabilizers and for the control of agricultural rodent pests.

Keywords Factorial scope of ingestion, Predator–prey interactions, Maximum food consumption, Weight loss, Fasting duration

The size of animal populations can be regulated through restriction of their food supply or predation[1], often being referred to as bottom-up or top-down regulation[2]. In times of plentiful food supply, highly fecund species with rapid growth rates and fast maturation can explosively increase population size. For example, many species of rodents are renowned for rapid increases in abundance to plague proportions[3] during years of higher rainfall[4], which can destabilize ecosystems and result in significant economic losses in agriculture[5,6]. Many species of snakes are considered specialist rodent predators[5], but Nowak et al.[7] have argued that due to their ectothermic physiology, snakes are only able to impact rodent populations when rodent abundance is low. However, Nowak et al.[7] conclusion does not correspond with the observed impacts of several invasive snake populations which have decimated prey populations[6,8]. The most notable examples are the establishment of Burmese pythons (*Python bivittatus*) in Florida[9], and brown tree snakes (*Boiga irregularis*) in Guam[10]. In these examples and others, predation by snakes has caused the local or total extinction of some prey species, suggesting that in at least some cases, snake species can have significant impacts on the abundance of their prey.

Predators can respond to changing prey abundance in two fundamentally different ways[11]. A functional response results in predators consuming more prey because more prey is available[12]. Alternately, predators can respond numerically, where increasing prey abundance leads to a concomitant increase in predator abundance because increased food consumption results in better breeding success of the predator[13]. Since it takes time for increased food resources to translate into increased predator numbers, numerical responses typically have a lag period (usually years) and this may lead to oscillations or instability in the relative numbers of prey and predators, depending upon the duration of the lag[12,13] and the reproductive biology of the prey[14]. In contrast,

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functional responses are more immediate since they depend primarily upon how many individuals of the predator species are in the system when prey numbers explode, and how the predators respond to changes in prey abundance[15,16]. Because functional responses are immediate, they can potentially have stabilizing effects on prey numbers since the more abundant the prey becomes, the greater the offtake by the predators[17]. Thus, predators that have an impactful functional response could be seen as system stabilizers if consumption rates are closely linked to prey abundance[18].

Holling[15] described three different functional response relationships between predators and their prey. Type 1 occurs when the number of prey consumed by predators is directly proportional to prey abundance. It is argued that this relationship occurs in cases where searching by the predator is random and remains constant with changing prey abundance until an upper threshold is reached due to satiation. This positive linear relationship may hold for filter feeders or prey-specialist ambush foragers where the number of prey passing ambush sites is directly proportional to prey abundance[19]. A Type 2 response differs from the first in that predation at high prey densities asymptotes rather than being limited by a hard threshold, possibly due to constraints caused by escalating prey handling time or digestive constraints. A Type 3 response is sigmoidal, with offtake rates at low prey abundance increasing exponentially due to increased searching[15] or prey switching by predators[20]. Although there are many other possible functional relationships[16,21], it is generally accepted that in most circumstances a functional response results in a positive relationship between prey abundance and offtake which should lead to a functional modulation of prey numbers by predators.

Although the functional response of predators to changing prey abundance has been widely debated, there are few direct empirical measures of the response[18]. More importantly, an aspect of the functional response of predators that has received almost no attention is the relative scope of the response of different predators to changing prey abundance. In all three of Holling's[15] proposed functional relationships, the upper limit of prey consumption is ultimately set by the predator's satiation, digestive system performance, prey handling time[22] or foraging time. The scope in the rate of consumption of prey between the minimum energy requirements and the maximum set by physiological, behavioural or ecological limits defines the relative magnitude of the possible functional response of predators (here termed the 'factorial scope of ingestion'; Fig. 1), but there have been no previously published measures of this scope. The period over which such a measure is made is also important and should be biologically relevant. For example, measures of factorial scope of ingestion made to assess the impact of the functional response of a predator to a rodent bloom should be measured over a period similar to the duration of a typical rodent bloom (~3 months)[4].

Snakes are ectothermic, gape-limited predators[23]. In a theoretical review on the importance of vipers as predators in the regulation of the prey populations, Nowak et al.[7] argue that ectotherm predator energetics are fundamentally different to those of endotherms[24] and concluded that vipers are likely to have only a small functional response to changing prey abundance. The reasoning given for the weak functional response is that the slow digestive rates in snakes limits how much food snakes can process in a given period. Snakes typically have very low minimum energy requirements in comparison to mammals but can consume meals that may exceed their own body mass[23]. However, Nielsen et al.[22] found that some species of snakes regain their appetite within 24 h of feeding. Studies have also shown that a high proportion of snake stomachs are empty at any given time[25] meaning that satiation or full digestive tracts may not always prevent increased consumption in snakes, so snakes could potentially increase consumption if prey becomes more abundant. In some ecosystems, the abundance of snakes may be much higher than the abundance of mammalian predators[26], more than compensating for lower individual consumption rates.

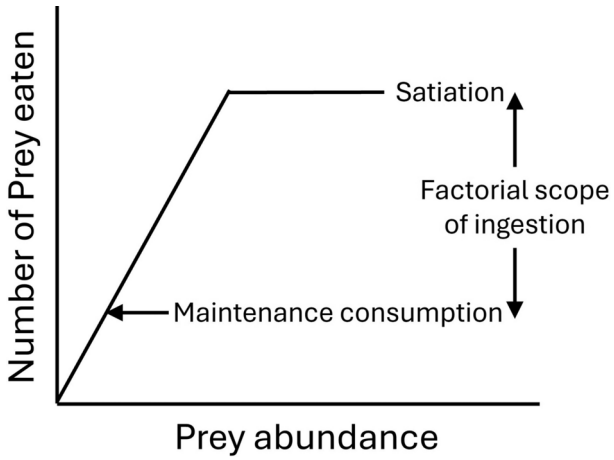

Fig. 1. The relationship between prey abundance and number of prey consumed in a Type 1 functional response (Holling[15]), showing the factorial scope of ingestion. Factorial scope of ingestion is calculated by dividing the maximum food intake (limited by satiation) by the maintenance food consumption (food intake for a constant body mass of the predator). The greater the factorial scope of ingestion, the greater the potential impact of the functional response of the predator on prey populations.

In this study I measured food consumption and changes in body mass of puff adders (*Bitis arietans*) in a captive colony using standardized feeding trials. Maintenance food requirements for constant body mass were estimated by measuring the relationship between food consumption and change in body mass over a range of moderate food intake. Maximum consumption was measured by feeding puff adders ad libitum over approximately 3-month trials. Factorial scope of ingestion was calculated and used to assess the potential functional response of puff adders to increased prey availability and to evaluate the potential the species has for top-down regulation of rodent populations during rodent blooms. I also drew on published measures of maintenance food requirements and maximum consumption rates of specialist mammalian predators to estimate and compare the factorial scope of ingestion for these species in comparison to puff adders. I used rates of weight loss during fasting as a means of broadly estimating possible duration of fasting in puff adders to evaluate how they may cope with times of low prey abundance. These findings, and comparisons to mammalian predators for which the appropriate measures were available, allowed for an evaluation of the importance of snakes as predators and ecosystem stabilizers.

Materials and methods

Study species

The puff adder (*Bitis arietans* Merrem, 1820) is the most widespread and abundant viper in Africa[27]. It occurs in a wide variety of habitats and is excluded only from true desert and forest[28]. Its geographic range includes most of sub-Saharan Africa and parts of the Arabian Peninsula[29]. It is an extreme ambush forager[30] and has all the morphological features typically associated with this foraging mode, such as a stout build, broad head, vertical pupils and is visually and chemically cryptic[31]. It spends extended periods in ambush for prey[30] and uses both caudal and lingual luring to attract prey[32]. It is a generalist feeder, preying on mammals, amphibians, birds and reptiles[25]. Adult snout-vent-length (SVL) is usually less than 1 m in southern African populations but may exceed 1.8 m in some populations in East Africa[27].

This study was conducted on a colony of 18 adult puff adders whose parents were from Dinokeng Game Reserve in Gauteng Province, South Africa (25° 38′ S; 28° 31′ E). All individuals were born in captivity and housed individually in cages (750 mm × 500 mm × 400 mm). Cages were lined with newspaper and drinking water, rocks and retreats were provided for each snake. The colony was housed in an isolated room in the Milner Park Animal Unit, University of the Witwatersrand, maintained at a temperature range of 27–30 °C (similar to selected temperatures of free ranging puff adders, unpublished data), photoperiod 12L:12D, and under positive air pressure with a filtered intake airflow. Snakes were fed only on rodents (rats and mice depending on availability) bred under controlled conditions (i.e., disease free) in the University of Witwatersrand Research Animal Facility, and the snake colony was thus considered to be parasite and disease free due to lifelong isolation, careful regulation and quality of food. Sex ratio of the puff adder colony was even, with male/female sibling pairs of known parentage (i.e. a female and male offspring from each of nine litters from different mothers were retained in captivity during data collection during another study[33]) and were of similar age (all born in January 2016). All individuals experienced the same environmental conditions and feeding regime during the first 4 years of growth into adulthood (sexually mature from 500 mm SVL[27]). Individuals reached adult body size and appeared to attain sexual maturity at the end of their third year. During this time, they were offered pre-killed mice making up approximately 10–15% body mass monthly.

Experimental design

Three different feeding trials designed to measure the relationship between food consumption and body mass in puff adders were conducted over a 4-year period (2019–2022). Trials included the measurement of change in body mass in relation to a range of moderate food consumption to elucidate the food consumption for the maintenance of constant body mass and to extrapolate rates of weight loss during fasting (Trial 1), maximum voluntary food intake (Trial 2) to calculate factorial scope of ingestion, and rates of weight loss during fasting (Trial 3) to estimate fasting duration. In all trials, each snake was used to provide a single measure for each metric to avoid pseudo-replication. Detailed information on the design of each of the trials is provided below:

Trial 1 (The effects of moderate food intake on body mass): Puff adders were offered food monthly (10–15% body mass at each feed). All food items (pre-killed mice or rats) were weighed to the nearest 0.1 g before being placed in the cages of individual puff adders. Consumption of food was checked and recorded 24 h after being place in cages. The effects of ecdysis on body mass change was controlled for by aligning the start and end of the feeding trial for each puff adder with its shedding cycle (i.e., since puff adders shed very infrequently, Trial 1 started immediately after a shedding event and ran to the next shedding event for each snake). Since puff adders also tend to defecate when they shed[31], this protocol also reduced error in measures of body mass due to the retention of faeces in the intestine[34]. Individuals were weighed and measured (SVL and tail length using ImageJ analysis of photographs) immediately after each shedding event.

Trial 2 (Maximum voluntary food intake rate): Trials for maximum food intake were initiated on an individual basis immediately after shedding during spring and summer, in some instances, ending as late as the early part of autumn. Food offered to snakes was increased to a minimum of 25% of snake body mass per feed every seven to ten days. Maximum voluntary food intake trials were conducted for approximately 80 days for each individual but were sometimes cut short due to shedding event. The duration of this feeding trial was aligned with the approximate duration of natural rodent blooms[4]. As with Trial 1, food was weighed, and uneaten food was removed from cages 24 h after presentation. Individuals that consumed all food offered at a particular feed were offered slightly more food in the subsequent feed in an attempt to offer ad libitum and to ensure that consumption was as close to maximum voluntary intake as possible. However, on occasion, food was limited by availability (limits to production). As in Trial 1, all individuals were weighed and measured at the start and end of the trial.

Trial 3 (Rates of weight loss during periods of fasting): Following the ad libitum feeding regime in Trial 2, feeding was suspended for a period of 5 months (January–May, inclusive). During Trial 3 all individual snakes were weighed and measured every 30 days. The colony was checked daily and all incidences of defecation of faecal matter were recorded. In order to factor out the effect of defecation on weight loss measures, faeces were weighed, and the recorded mass subtracted from the starting body mass of the snake in the 30-day time bin.

Data processing and analysis

All statistical analyses were conducted in Statistica (Version 8.0; Stat Soft Inc) and Excel (Version 2410; Microsoft 365).

Maintenance food consumption rate: (the annual food consumption that results in a constant body mass) was estimated using a regression analysis approach. Measurements of food consumption and changes in puff adder body mass (measured between two shedding events) in Trial 1 were annualized, and both expressed as a percentage of puff adder body mass. Prior to analyses, data were checked for normality (Lilliefors test). Differences in sex were tested using an analysis of covariance (ANCOVA; independent variable—food intake; dependent variable—change in body mass; covariate—sex). Because there was no significant difference between sexes, measures were pooled and analysed using regression analysis (independent variable—food intake; dependent variable—change in body mass). The regression line intercept of the x-axis provided an estimate of annual maintenance food consumption rate for a constant body mass. The y-axis intercept provided an estimate of rates of body mass loss per year at zero food intake (extrapolation based on non-fasting snakes).

Factorial scope of ingestion: (the factorial increase in food consumption above maintenance food consumption over a ~ 3-month period) was estimated for each puff adder. This was calculated by annualizing the food intake for Trial 2 (Maximum voluntary food intake rate) and expressing it as a percentage of puff adder body mass. This measure was then divided by the maintenance food consumption rate (measured in Trial 1, and also expressed as a percentage of puff adder body mass). Prior to analyses, data were checked for normality (Lilliefors test) and a paired *t*-test was used to test for differences due to sex (data pairs = sibling pairs).

Estimation of endothermic predator factorial scope of ingestion: In order to compare the range of puff adder food consumption characteristics, I searched the literature for studies that provided estimates of maintenance food consumption and maximum food consumption in prey specialist (prey mainly on a single prey species) mammalian predators. These measures were then used to estimate the factorial scope of ingestion for endothermic predators for comparative purposes.

Estimation of possible fasting duration: Two independent measures of rates of weight loss per year for puff adders in the test colony were used to estimate possible duration of fasting. The first method used the y-intercept of the regression between food consumption and change in body mass (Trial 1 data) while the second used direct measures of weight loss in fasting puff adders on a month-by-month basis (Trial 3 data). In the latter method, two estimates were calculated, the first included monthly measures of puff adders that shed, and the second excluded monthly measures with shedding events. The estimated rate of weight loss was then integrated with measures of body mass of puff adders after completion of Trial 2 and placed in the context of body condition index (BCI) measures of free ranging puff adders recorded in a large telemetry study[35]. Using positive residuals for puff adders that had been offered food ad libitum (Trial 2), it was then estimated how long fasting puff adders would take to reduce body mass to equal the general body condition of free ranging puff adders.

Ethics statement

Gauteng Province Nature Conservation issued a permit for this research (CPF6 000219) and the Animal Research Ethics Committee of the University of the Witwatersrand approved the experimental protocol used in the study as detailed in the application (clearance certificate 2020/11/04B). All procedures in this study were performed in accordance with the relevant guidelines and national regulations, and met the ARRIVE guidelines.

Results

Maintenance food consumption rates

Average number of days for feeding trials was 260 ± 104 days (Table S1). Measures of food consumption did not differ significantly from normality (Lilliefors; $P > 0.20$ for each sex). ANCOVA revealed that the sex of individuals did not have an effect on the relationship between food intake and change in body mass ($F_{1,16} = 0.05$; $P = 0.82$). Regression analysis (Fig. 2) revealed that maintenance food consumption for puff adders consuming rodents was 63% of body mass (x-intercept) per annum.

Factorial scope of ingestion

On average, ad libitum feeding trails lasted 77 days (s.d. 16) and puff adders increased food consumption dramatically, eating up to 10 rodents in a single feeding session (maximum offered) and were willing to feed again a week later at the next feeding session. On average, body mass of puff adders increased by 53.3% (s.d. 31.4; range 7.3–108.3) and SVL increased by 2.97% (s.d. 0.86; range 1.60–4.55) during these trails (Table S2). Measures of factorial scope of ingestion did not differ significantly from normality (Lilliefors test; $P > 0.20$ for each sex). There was no significant difference due to the sex of the puff adders (paired *t*-test; $t_8 = 0.70$; $P = 0.50$). The average factorial scope of ingestion measured was 12.0 (s.d. 3.9; range 4.6–19.8). Thus, puff adders in this study, on average, increased their food consumption 12-fold above maintenance levels over the feeding trial when fed ad libitum (Table S3). The best feeders raised consumption nearly 20 times above maintenance levels, demonstrating that puff adders are capable of very significant factorial scopes of ingestion.

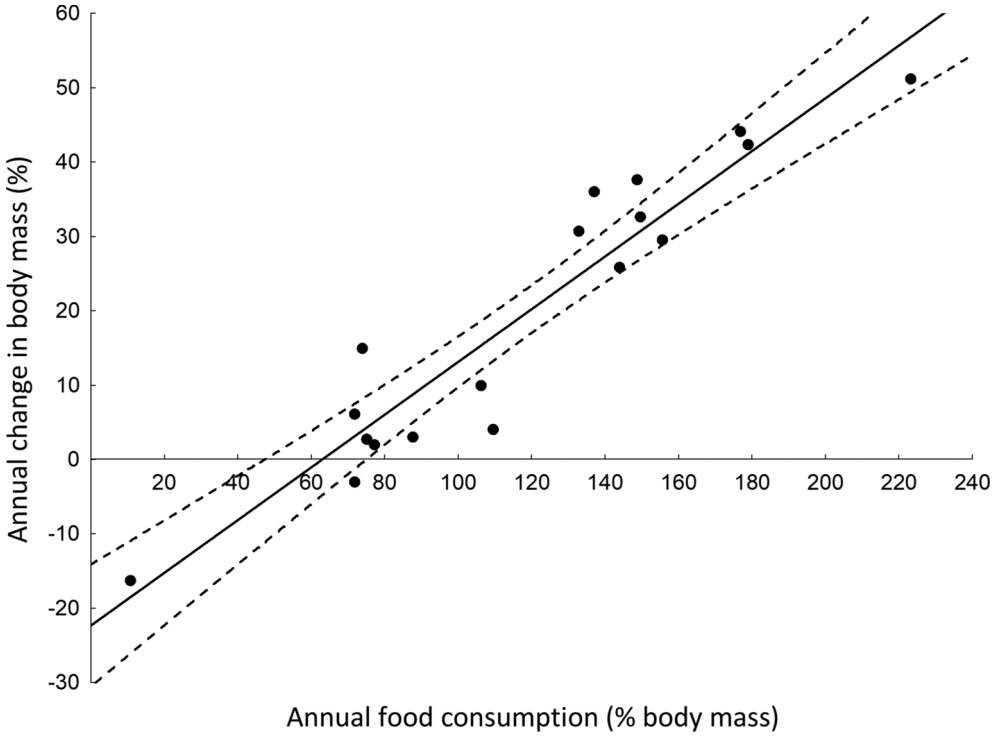

Fig. 2. The relationship between annualized food consumption (rodents), and annualized change in percentage of body mass in puff adders. The x-intercept (63%) is the maintenance food consumption rate, while the y-intercept (-22.3%) is an estimate of weight loss over a year in a fasting puff adder. $y = 0.35x - 22.3$; $F_{1,17} = 138.3$; $N = 18$; $R^2 = 0.90$; $P < 0.001$. Dashed lines define the 95% confidence intervals.

Estimation of endothermic predator factorial scope of ingestion

Few published studies provided the necessary information (maintenance food consumption and maximum voluntary consumption) to estimate factorial scope of ingestion in endothermic predators. However, Sundell et al.[36] provide estimates of maintenance food consumption of one vole (*Microtus* spp.) per day for the least weasel (*Mustela nivalis nivalis*). In an experimental setup with high vole abundance (100 per 0.5 ha), least weasel kill rate peaked at 11 voles over three days. If this measure is taken as the maximum rates of predation, least weasel factorial scope of ingestion would be approximately 3.5 over three days. O'Donoghue et al.[17] provides estimates of lynx (*Lynx canadensis*) maintenance consumption of 0.4 to 0.5 snowshoe hares (*Lepus americanus*) per day and reports a maximum kill rate of 1.2 hares per day during times of high hare abundance. This equates to a factorial scope of ingestion of approximately 3.

Estimation of possible fasting duration

Using extrapolation of the regression analysis between food consumption and change in body mass (Fig. 2), weight loss was estimated to be 22.3% body mass loss per year (95% confidence range 12–30%) excluding the impact of shedding (trials were run between shedding events). Using direct monthly measures of weight loss, annualized rate of weight loss was estimated to be 28.8% without the exclusion of shedding events. However, when measures of weight loss excluded months of measurement when individuals shed, direct measure of rate of weight loss was estimated to be 23.9% per annum. Thus, both estimates using direct measures of weight loss (including and excluding the effects of shedding) fall within the 95% confidence range of the estimate using regression analysis. The relationship between SVL and body mass in free ranging puff adders was $y = 0.00000244x^{2.95}$ ($N = 75$; $R^2 = 0.90$). Based on this relationship, at the end of the ad libitum feeding trials, puff adders were on average 38.8% (s.d. 23.5; range 5.1–92.2%) heavier than average free ranging puff adders of the same SVL (Fig. 3). This suggests that the puff adders which greatly increased BCIs through increased food consumption during a rodent bloom could potentially fast for approximately 2 years before body mass is reduced to average or slightly below average BCI of free ranging puff adders.

Monthly weight loss of shedding snakes was 6.22% body mass ($N = 8$ snake months), while monthly weight loss for individuals that did not shed was 1.99% ($N = 75$ snake months; Fig. 4). These rates were significantly different (Two sample *t*-test; $t = 5.61$; $P < 0.001$). This suggests that shedding results in an increase of weight loss of approximately 4.2% body mass. On average there were 243 days between shedding events, ranging from 35 days between sheds to 742 days ($N = 85$ shedding events).

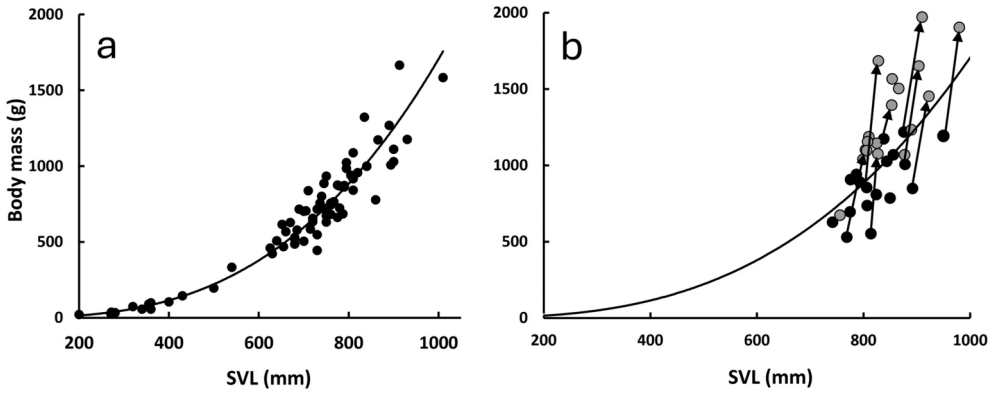

Fig. 3. The relationship between length (SVL) and body mass in puff adders. 'a' shows the relationship between SVL and body mass in free ranging puff adders (*Bitis arietans*); $y = 0.00000244^{*}x^{2.95}$; $N = 75$; $R^2 = 0.90$; $P < 0.001$. Increased positive residuals due to ad libitum feeding (Trial 2) are represented in 'b'. Arrows provide examples of mass increase in individual puff adders from initial body mass (black markers) to body mass at the termination of the ad libitum feeding trial (grey markers) superimposed over the regression line from 'a'. Arrows lean to the right due to growth of SVL (2.97%, s.d. 0.86) during trials.

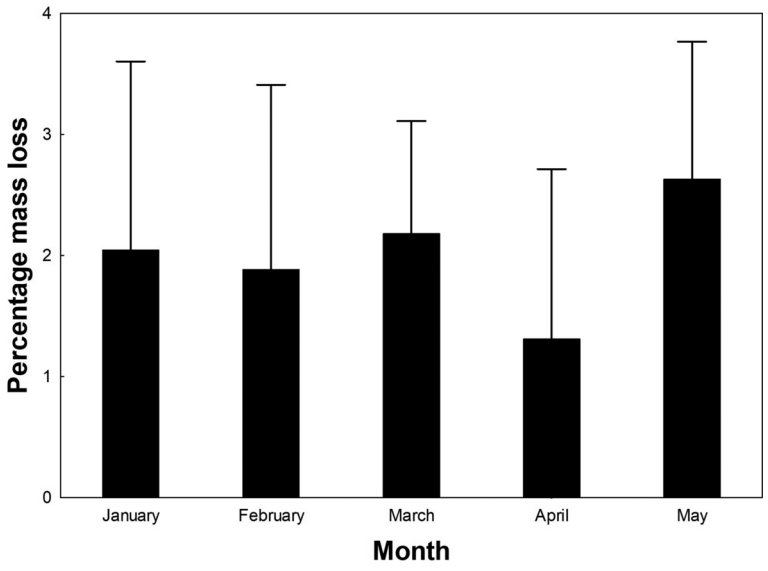

Fig. 4. Monthly percentage mass loss of fasting puff adders (*Bitis arietans*) excluding the effect of shedding by removing measures of snakes that shed in any given month. Average monthly weight loss was 1.99% (s.d. 2.4). No trend over the five months is evident and there is no significant difference between months ($F_{72,4} = 0.65$; $P = 0.60$).

Discussion

Annualized maintenance food consumption rates for constant body mass in puff adders was shown to be low and to be less than two thirds (63%) of body mass when feeding on rodents. Feeding trials also revealed that puff adders were able to dramatically increase food consumption for months at a time and consume many prey items in a feeding session. The most willing feeder in the trials increased intake almost 20 times maintenance rates. This resulted in rapid increases in body mass which provides puff adders with sufficient fat reserves to sustain fasting for extended periods, likely approximately 2 years in duration in some cases. These findings demonstrate that puff adder ingestion and digestion traits are extremely flexible, allowing them to survive through times of food limitations and to respond functionally to increases in food availability. Additionally, the low metabolic expenditure of ectotherms results in fasting puff adders losing less than a quarter of their body mass per year when the effect of shedding is removed. In addition to being capable of enduring periods of low food availability, puff adder's average factorial scope of ingestion was more than 12 times maintenance levels. This appears to be far higher than the factorial increases in food consumption of mammalian predators. Factorial scope of ingestion represents a novel metric that provides information on the magnitude of the functional response that a predator may have on a prey population. In general, these findings suggest that puff adders potentially have a

large functional response to prey abundance and are likely to be ecosystem stabilizers in reducing the impact of rodent blooms. If other species of snakes have similar flexibility in feeding abilities, it suggests that conservation of snake assemblages is important both for ecosystem stability and financial savings in agriculture[6] and should be promoted.

The puff adder is a dietary generalist[25] and it is therefore most likely that the species would have a Type 3 functional response (sigmoidal) that includes the effects of prey switching[36]. For example, the two most important taxa in puff adder diet are rodents and frogs[25] and it is possible that foraging puff adders would select different ambush sites depending on the relative abundance of different prey types. At times of low rodent abundance, it is likely that puff adders would select ambushing sites in areas where frogs are abundant but switch to ambushing next to rodent runs based on the chemical signature when rodents are abundant[37]. Such prey switching would result in an exponential increase in predation on rodents when rodent abundance is low but rising, leading to the sigmoidal relationship in a Type 3 functional response curve. Thus, for example, puff adders in an area where rodent numbers are low would be able to survive for extended periods of low rodent abundance not only through their ability to fast for extended periods but also by switching to amphibians as a primary food source. Prey switching to rodent prey during rodent blooms effectively increases the potential for puff adders to regulate rodent populations.

The measure of food consumption for maintenance of constant body mass in puff adders in this study was lower than most estimates of food consumption in other species of snakes. For example, Beaupre[38] estimates consumption of between 113–193% body mass for western diamondback rattlesnakes (*Crotalus atrox*), tiger rattlesnakes (*Crotalus tigris*) and black-tailed rattlesnakes (*Crotalus molossus*), while Clark[39] estimates 100% body mass for timber rattlesnakes (*Crotalus horridus*). Beck[40] estimates consumption for maintenance ranging between 91 and 98% body mass for western diamondback rattlesnakes, black-tailed rattlesnakes and tiger rattlesnakes. However, it should be noted that these estimates are not for maintaining a constant body mass, but rather for 'maintenance, growth and reproduction' and were calculated indirectly using measures of energy expenditure on free ranging snakes integrated with lab measures of metabolic expenditure. Other studies have reported maintenance consumption measures that are more in line with measures for puff adders. For example, Zaidan and Beaupre[41] estimate a maintenance consumption for constant body mass of only 56.3% in timber rattlesnakes and highlight several issues with metabolic measures that could impact these estimates. Although few other studies have measured maintenance consumption rates directly with a protocol similar to the current study, Alexander[42] found that the actively foraging rinkhals (*Hemachatus haemachatus*) had a maintenance consumption of 71.1% when consuming rodents, and Barends[43] reports a consumption of 62.3% of body mass for rhombic egg-eater (*Dasypeltis scabra*) feeding on bird eggs. Thus, rates measured for puff adders are consistent with measures for some other species, especially where measures were made directly with a protocol similar to that used in this study.

This study appears to be one of the first that has attempted to quantify maximum voluntary food consumption in snakes under ad libitum conditions. Although it has been acknowledged that under some circumstances snakes may be willing to consume meals in quick succession[22,44], snakes are generally considered to be greatly limited in their ability to consume multiple meals in a short period due to their slow ectothermic digestive physiology. It has been argued that this limitation is likely to reduce their functional response to changing prey abundance[7]. However, puff adders in this study consumed up to 10 rodents per feed and were willing to feed again a week later. In fact, it is possible that in some cases, the food offered was not truly ad libitum (puff adders often consumed everything offered in a feeding session) due to difficulty in producing enough food for each feed during Trial 2. Some individuals in the colony consumed more than 2 kg of rodents during the trial, and several individuals consumed more than twice their body mass in less than 3 months. These results suggest that ad libitum feeding trials in other species of snakes would be informative and would provide more information on the potential functional response of snakes in general.

Rough estimates of factorial scope of ingestion in mammal predators suggest that endothermic predators are far less flexible than puff adders with regard to rates of food ingestion. It is also likely that the estimates of factorial scope of ingestion of approximately 3 for the least weasel and lynx is an overestimate for these species. In the case of the least weasel, measures of maximum consumption were made over a period of only three days[36], whereas the average trial duration for puff adders in this study was 77 days. It is likely that least weasels would not be able to sustain the reported peak rates of consumption continuously for months due to satiation limiting consumption. In addition, Sundell et al.[36] and O'Donoghue et al.[17] report that there were surplus killings (prey killed that were not consumed) by least weasels and lynx at high prey abundance, and unlike snakes, mammalian predators do not always consume the entire prey item, especially when nearing satiation[17]. However, it should be noted that predators killing without consuming prey would still have an impact on prey numbers. A simple thought experiment also supports these findings: could you imagine more than trebling your normal food consumption for months? Humans can only manage this level of scope during single events such as their birthday dinner or Christmas lunch. Thus, it is plausible that puff adders have a much larger factorial scope of ingestion than is typical for an endothermic predator, and it is likely that this would apply to most other snake species, especially ambush forages with stocky bodies that can accommodate many prey items and store large fat reserves[7]. These findings go against the conventional view that snake digestive physiology is slow with low performance and suggests that snakes have the potential to have an impactful functional response.

Fasting puff adders were estimated to lose weight at an average rate of 22.3% and 23.9% (indirect and direct measures) body mass per year when factoring out weight loss due to shedding. Shedding events did have a significant impact on weight loss, increasing average total weight loss to 28.8% per annum, with single shedding events reducing body mass by approximately 4%. Although puff adders shed very infrequently, shedding events were impactful on weight loss and should be explicitly measured when measuring weight loss in snakes. Reported measures of weight loss in other species of snakes are generally higher than rates recorded in puff adders[45,46],

but these studies do not take shedding or the impact of defecation into account. It is also important to note that the two measures of weight loss in puff adders in this study were derived from two independent analyses, one extrapolating weight loss in feeding snakes on a moderate diet and the other directly measuring changes in body mass in fasting snakes. The estimates derived from these two independent trials differed by less than 2%, with the slightly higher estimate of weight loss recorded in fasting puff adders.

The similarity of estimates of weight loss using different protocols in puff adders suggest that it is unlikely that puff adders will respond to fasting with a depression of metabolic rate. However, this would need to be confirmed with direct measures of metabolic rates in fasting puff adders as it may be dependent on the duration of fasting. McCue[45] has reported depression of metabolic rate in fasting ball pythons (*Python regius*), western diamondback rattlesnakes and ratsnakes (*Pantherophis obsoletus*) but De Figueiredo et al.[46] did not find changes in metabolic rates in fasting boa constrictors (*Boa constrictor*). Leite et al.[47] also found no change in metabolic rate fasting South America rattlesnakes (*Crotalus durissus*) but noted that rates of weight loss were not constant over a year. The triphasic nature of weight loss appears to be dependent upon the preferential burning of carbohydrates, lipids and proteins[48]. Thus, rates of weight loss in puff adders could change with the duration of fasting, with increased rates of weight loss on the depletion of fat reserves.

This study was lab-based, and trials were run under standardized conditions. Performing such studies in a lab-setting results in both strengths and weaknesses on the research. Much of the empirical research on functional responses of predators to prey abundance has been aimed at measuring the number of prey items eaten by single predators housed in small cages. As pointed out by Abrams and Ginzburg[18], this precludes the possibility of detecting anything other than the effect of prey abundance on predator response. However, in this study, the primary aim was to evaluate the flexibility and physiological limits of prey ingestion and weight loss of puff adders so that the species potential for an impactful functional response could be evaluated. In addition to the lab setting allowing for the accurate quantification of ingested food, shedding, defecation and changes in body mass, it allowed for the standardization of puff adder age, sex ratio and ensured that the colony was disease and parasite free. In some studies of this nature, it could be argued that individuals housed in captivity are forced to be more sedentary than free ranging individuals[42]. However, this is not likely to be a major factor with puff adders since free ranging individuals have an average daily displacement of less than 10 m, usually move on fewer than five occasions per month[35] and may spend weeks in ambush at the same site[30]. Puff adders in the colony were also observed to be reactive to researcher presence, and it is thus possible that movement and metabolic expenditure of these captive puff adders was at least as high, if not higher, than free ranging puff adders.

Despite all puff adders in this study being from a single population, of similar age and raised under identical conditions, there were clear differences in the willingness of different individuals in the colony to feed, and in their responses to the presence of the researcher and handling. These consistent behavioural differences between individuals suggest that members of the colony have different personalities, an observation supported by Skinner et al.[49,50]. For example, one individual in the colony (67M) had been a fussy eater since birth, resulting in slower growth, lower body mass and body length in comparison to the other members of the colony. This individual experienced significant weight loss during Trial 1 and the lowest increase of body mass in Trial 2. Its body mass had a positive residual of only 5% on the BCI curve after the ad libitum feeding trial (Trial 2). It should be noted that the primary aim of the study was to assess the extent of the factorial scope of ingestion of puff adders, and 67M's, and some other members of the colony scores brought down the averages of the scope of ingestion. The most willing feeders in the colony should thus be used to define the possible performance limits of puff adder consumption physiology. Although the average scope of ingestion was ~ 12, the maximum measured factorial scope of ingestion recorded for 73M was 19.8 and should represent a measure of possible performance for puff adders. Viewed from this perspective, puff adders appear to easily outperform endothermic predators in factorial scope of ingestion and should be considered as potential top-down predators in the regulation of prey species.

Few previous studies have evaluated the impact of snakes as predators in predator prey relationships, and knowledge of the importance of snakes as ecosystem components is thus limited[26]. The most thorough and wide-ranging review on the topic is by Nowak et al.[7] who conclude that energy expenditure and feeding rates of vipers are very low in comparison to endothermic predators, resulting in vipers having a very low functional response and a slow numeric response. However, more recent studies have revealed cases where digestion in snakes can be rapid, voluntary consumption relatively high[51], and abundance of snakes in natural habitats can be very much higher than mammalian predators[26,52]. Thus, the lower energy consumption of snakes in comparison to mammalian predators can be compensated by their higher abundance. Wilson and Winne[26] highlight the fact that because snakes tend to be secretive and highly cryptic, with few robust measures of abundance, snakes are generally undervalued as predators. Given their high factorial scope of ingestion, their ability to consume multiple rodents when given the opportunity, the ability to persist through long periods of low food availability, and their abundance, puff adders likely provide important ecological services that have stabilizing effects on rodent blooms. This probably also applies to many other snake species. Given that snakes are generally not considered in conservation management plans and are not appropriately valued in agricultural systems[6], there is a need for more focused research on assessing aspects of predator prey relationships.

Data availability

Data are presented in the supplementary files. Correspondence and requests for materials should be addressed to G.A.

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References

1. Monadjem, A. & Unwin, M. *African Ark: Mammals, Landscape and the Ecology of a Continent* (Wits University Press, 2023).
2. Martínez-Abraín, A., Llaneza, L., Ballesteros, F. & Grandal-d'Anglade, A. Do apex predators need to regulate prey populations to be a right conservation target?. *Biol. Conserv.* **261**, 109281 (2021).
3. Makundi, R. H., Oguge, N. O. & Mwanjabe, P. S. *Rodent pest management in East Africa: An ecological approach*. in *Ecologically-Based Rodent Management* (eds G. Singleton, L. Hinds, H. Leirs and Z. Zhang) 460–476. (ACIAR Monograph **59**, Brown Prior Anderson, Melbourne 1999).
4. Leirs, H., Verhagen, R., Verheyen, W., Mwanjabe, P. & Mbise, T. Forecasting rodent outbreaks in Africa: An ecological basis for *Mastomys* control in Tanzania. *J. Appl. Ecol.* **33**, 937–943 (1996).
5. Krishnakumar, B. M., Guptha, B., Ramanujam, E. & Ganesh, S. R. Rodent Surveys reveal good insights into the snake fauna in an agro-pastoral ecosystem in southern India. *Biol. Stud.* **6**, 230–240 (2023).
6. Shine, R., Dunstan, N., Abraham, J. & Mirtschin, P. Why Australian farmers should not kill venomous snakes. *Anim. Conserv.* **27**, 415–425 (2023).
7. Nowak, E. M., Theimer, T. C. & Schuett, G. W. Functional and numerical responses of predators: Where do vipers fit in the traditional paradigms?. *Bio. Rev.* **83**, 601–620 (2008).
8. Alexander, G. J. & Wang, T. Snake foraging ecology and digestive physiology: Integrative biology and evolving paradigms. In *Snakes Morphology, Function, and Ecology* (ed. Penning, D.) 313–342 (Nova Science Publishers, 2023).
9. Dorcas, M. E. et al. Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *PNAS* **109**, 2418–2422 (2012).
10. Rodda, G. H. & Savidge, J. A. Biology and impacts of Pacific island invasive species. 2. *Boiga irregularis*, the brown tree snake (Reptilia: Colubridae) 1. *Pac. Sci.* **61**, 307–324 (2007).
11. Elton, C. *Voles, Mice and Lemmings: Problems in Population Dynamics* (Clarendon Press, 1942).
12. Solomon, M. E. The natural control of animal populations. *Anim. Ecol.* **18**, 1–35 (1949).
13. Brand, C. J., Keith, L. B. & Fischer, C. A. Lynx responses to changing snowshoe hare densities in central Alberta. *J. Wildl. Manage.* **40**, 416–428 (1976).
14. Korpimäki, E. & Norrdahl, K. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecol.* **72**, 814–826 (1991).
15. Holling, C. S. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol.* **91**, 293–320 (1959).
16. Taylor, R. J. Ambush predation as a destabilizing influence upon prey populations. *Am. Nat.* **118**, 102–109 (1981).
17. O'Donoghue, M. et al. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* **79**, 1193–1208 (1998).
18. Abrams, P. A. & Ginzburg, L. R. The nature of predation: Prey dependent, ratio dependent or neither?. *TREE* **15**, 337–341 (2000).
19. Formanowicz, D. R. Jr., Bobka, M. S. & Brodie, E. D. Jr. The effect of prey density on ambush-site changes in an extreme ambush-type predator. *Am. Midl. Nat.* **108**, 250–255 (1982).
20. Breisjøberget, J. I., Odden, M., Wegge, P., Zimmermann, B. & Andreassen, H. The alternative prey hypothesis revisited: Still valid for willow ptarmigan population dynamics. *PLoS ONE* **13**, e0197289 (2018).
21. Jeschke, J. M., Kopp, M. & Tollrian, R. Predator functional responses: Discriminating between handling and digesting prey. *Ecol. Monogr.* **72**, 95–112 (2002).
22. Nielsen, T. P., Jacobsen, M. W. & Wang, T. Satiety and eating patterns in two species of constricting snakes. *Physiol. Behav.* **102**, 110–114 (2011).
23. Greene, H. W. *Snakes: The Evolution of Mystery in Nature* (University of California Press, 1997).
24. Campbell, E. W. C. III., Adams, A. A. Y., Converse, S. J., Fritts, T. H. & Rodda, G. H. Do predators control prey species abundance? An experimental test with brown treesnakes on Guam. *Ecology* **93**, 1194–1203 (2012).
25. Glaudas, X., Kearney, T. C. & Alexander, G. J. Museum specimens bias measures of snake diet: A case study using an ambush-foraging snake, the puff adder (*Bitis arietans*). *Herpetologica* **73**, 121–128 (2017).
26. Willson, J. D. & Winne, C. T. Evaluating the functional importance of secretive species: A case study of aquatic snake predators in isolated wetlands. *J. Zool.* **298**, 266–273 (2016).
27. Phelps, T. *Old World Vipers: A Natural History of the Azemiopinae, and Viperinae* (Edition Chimaira, 2010).
28. Branch, W. R. *Field Guide to the Snakes and Other Reptiles of Southern Africa* (Struik Publishers, 1998).
29. Spawls, S. & Branch, W. R. *The Dangerous Snakes of Africa* (Bloomsbury Publishing, 2020).
30. Glaudas, X. & Alexander, G. J. Food supplementation affects the foraging ecology of a low-energy, ambush-foraging snake. *Behav. Ecol. Sociobiol.* **71**, 5 (2017).
31. Miller, A. K., Maritz, B., McKay, S., Glaudas, X. & Alexander, G. J. An ambusher's arsenal: Chemical crypsis in the puff adder (*Bitis arietans*). *Proc. R. Soc. B* **282**, 20152182 (2015).
32. Glaudas, X. & Alexander, G. J. A lure at both ends: Aggressive visual mimicry signals and prey-specific luring behavior in an ambush-foraging snake. *Behav. Ecol. Sociobiol.* **71**, 2 (2017).
33. Glaudas, X., Rice, S. E., Clark, R. W. & Alexander, G. J. The intensity of sexual selection, body size and reproductive success in a snake mating system with presumed male-male combat: Is bigger better?. *Oikos* **129**, 998–1011 (2020).
34. Lillywhite, H. B., de Delva, P. & Noonan, B. P. Patterns of gut passage time and the chronic retention of faecal mass in viperid snakes. In *Biology of the Vipers* (eds Schuett, G. W. et al.) 497–506 (Eagle Mountain Publishing, 2002).
35. Alexander, G. J. & Maritz, B. Sampling interval significantly impacts the estimation of movement parameters in African snakes. *J. Zool.* **297**, 309–318 (2015).
36. Sundell, J., Norrdahl, K., Korpimäki, E. & Hanski, I. Functional response of the least weasel, *Mustela nivalis nivalis*. *Oikos* **90**, 501–508 (2000).
37. Clark, R. W. Timber Rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *J. Chem. Ecol.* **30**, 607–617 (2004).
38. Beaupre, S. J. Field metabolic rate, water flux, and energy budgets of mottled rock rattlesnakes, *Crotalus lepidus*, from two populations. *Copeia* **1996**, 319–329 (1996).
39. Clark, R. W. Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. *Copeia* **2006**, 181–187 (2006).
40. Beck, D. D. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *J. Herpetol.* **29**, 211–223 (1995).
41. Zaidan, F. III. & Beaupre, S. J. Effects of body mass, meal size, fast length, and temperature on specific dynamic action in the timber rattlesnake (*Crotalus horridus*). *Physiol. Biochem. Zool.* **76**, 447–458 (2003).
42. Alexander, G. J. *Thermal Physiology of Hemachatus haemachatus and its Implications to Range Limitation*. *PhD thesis* (University of the Witwatersrand, Gauteng, South Africa, 1996).
43. Barends, J. M. *Autecology of the Rhombic Egg-eater*, *Dasypeltis scabra*. *PhD thesis* (University of the Western Cape, Western Cape, South Africa. 2022).
44. Clark, R. W. The hunting and feeding behavior of wild rattlesnakes. In *Rattlesnakes of Arizona* Vol. 2 (eds Schuett, G. W. et al.) 58–91 (ECO Wear and Publishing, 2016).
45. McCue, M. D. Snakes survive starvation by employing supply-and demand-side economic strategies. *Zool.* **110**, 318–327 (2007).
46. de Figueiredo, A. C., de Barros, F. C. & de Carvalho, J. E. Effects of prolonged fasting on postprandial metabolic rates of *Boa constrictor* Linnaeus, 1758 (Serpentes: Boidae). *Herpetol. Notes* **13**, 621–625 (2020).

47. Leite, C. A. C. et al. Loss of the ability to control right-to-left shunt does not influence the metabolic responses to temperature change in long-term fasting in the South American rattlesnake *Crotalus durissus*. *Physiol. Biochem. Zool.* **87**, 568–575 (2014).
48. Wang, T., Hung, C. C. Y. & Randall, D. J. The comparative physiology of food deprivation: From feast to famine. *Annu. Rev. Physiol.* **68**, 223–251 (2006).
49. Skinner, M., Brown, S., Kumpan, L. T. & Miller, N. Snake personality: Differential effects of development and social experience. *Behav. Ecol. Sociobiol.* **76**, 135 (2022).
50. Skinner, M., Kumpan, T. & Miller, N. Intense sociability in a "non-social" snake (*Python regius*). *Behav. Ecol. Sociobiol.* **78**, 113 (2024).
51. Jones, P. C., King, R. B., Stanford, K. M., Lawson, T. D. & Thomas, M. Frequent consumption and rapid digestion of prey by the Lake Erie watersnake with implications for an invasive prey species. *Copeia* **2009**, 437–445 (2009).
52. King, R. B., Stanford, K. M. & Jones, P. C. Sunning themselves in heaps, knots, and snarls: The extraordinary abundance and demography of island watersnakes. *Ecol. Evol.* **8**, 7500–7521 (2018).

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Author contributions
All aspects of the work were conducted by G.A.

Declarations

Competing interests
The authors declare no competing interests.

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