PATTERNS OF GUT PASSAGE TIME AND THE CHRONIC RETENTION OF FECAL MASS IN VIPERID SNAKES

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Abstract: Passage of digesta (PT, ingestion to defecation) through the vertebrate gut exhibits considerable interspecific variation that appears to be greatest among snakes. We measured extraordinarily long PTs in stout and heavy, terrestrial species of snakes, which accumulate feces (5–20% of the body mass in *Bitis gabonica*) for periods of months sometimes exceeding a full year (maxima = 116 to 420 days in various vipers and pythons). In contrast, relatively short PTs characterize gracile arboreal species, which have low body mass and sometimes defecate within 24–48 h of ingesting a meal. Thus, storage of fecal mass in the snakes we examined complements a species' structural body mass. Available data indicate there is a positive correlation between PT and the relative body mass of snake species, which, in turn, generally reflects habitat and foraging mode. Extremely prolonged retention of feces, while pathological in humans, appears to be adaptive among ophidian taxa, possibly functioning as metabolically inert ballast in the heavier species while enhancing the uptake of water and nutrients. The "adaptive ballast" hypothesis seems especially appropriate to the biology of viperid snakes.

Introduction

Snakes exhibit complex specializations related to broad diversification of behavioral niches while retaining an elongate morphology without limbs (Greene, 1997). While many aspects of their biology have been the subject of scientific interest, trophic specializations are especially meaningful because they potentially integrate structure and function in numerous important contexts, including ecology, behavior, energetics, and life history. Many snake species, especially vipers that utilize ambush ("sit-and-wait") strategies, consume large meals at irregular and sometimes long intervals (Shine, 1991; Greene, 1992; Martin, 1992; Secor and Nagy, 1994). Although a fair amount is known concerning the mechanisms of prey capture and gastrointestinal digestion, there is relatively little information regarding the temporal and spatial regulation of storage function in the hindgut of snakes. In this paper we use the term "hindgut" synonymously with the large intestine, as is the usual usage for mammals (Stevens and Hume, 1995), and we include the cloaca as its terminus because of our emphasis on storage. This usage is in contrast to that of some authors who focus on morphology (e.g., Luppa, 1977). The terminology, however, reflects embryonic origins and functional divisions of the digestive tract (e.g., Kardong, 1995).

Following feeding, Sidewinder rattlesnakes (*Crotalus cerastes*) and Burmese Pythons (*Python molurus bivitattus*) exhibit increases of intestinal mass, upregulated transport capacity for uptake of nutrients, and dramatic increases in metabolic rate (Secor et al., 1994; Secor and Diamond, 1995). Thus, gut function in snakes can vary dramatically in relation to periodic ingestion of relatively large meals. This mode of feeding also influences behavioral activities of snakes in varied and complex ways.

Little is known quantitatively about the formation, storage, and evacuation of feces, and there are obvious and intriguing differences in these processes among species. In principle, the retention time for feces is a function of the gut volume and digestive flow rate (Penry and Jumars, 1987), and therefore retention time varies in relation to gut morphology and the plasticity of feeding. One possible consequence of variable fecal retention is its potential influence on digestive efficiency and the realized nutritional value of ingested prey items. Digestive efficiency also depends on many other factors, including temperature, enzymatic activities, and absorption rates for nutrients.

The duration of fecal retention is a key feature of digestive processing. Considering the relatively large size of meals that are ingested by snakes, the variable storage time of feces has important implications for adding a passive component to the magnitude of total body mass. Gut passage time, PT (defined as the time elapsed from ingestion to defecation), typically varies from hours or a few days in birds and mammals, to several weeks or longer in other vertebrates (Skoczylas, 1978; Guard, 1980; Parmenter, 1981; Warner, 1981; Bjorndal 1987, 1989). Numerous factors potentially influence the PT, including the texture and quality of food, meal size, feeding frequency, temperature, activity, gut morphology, and nutritional and physiological status of the animal.

Here we report the occurrence of unusually large PT values in ground-dwelling viperid and boid snakes that sometimes retain and accumulate fecal material for periods of months while on a regular feeding schedule. On the other hand, much shorter passage times appear characteristic of arboreal snake species

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Table 1. Measurements of gut passage times (PT, mean ± SE) in selected taxa of snakes. S = data based on single (but sometimes multiple) feedings.

Species (N)	Gut passage time (days)	Defecation interval (max) (days)	Feeding interval (days)	Food/day (g)	Source
Boidae					
Arboreal					
Corallus caninus (8)	25.4 ± 4.1	18.3 ± 2.5 (45.1 ± 5.4)	11.3 ± 2.0	1.7 ± 0.3	This study
Morelia viridis (2)	6.5 ± 0.5		S	S	R. Mehta, unpublished
Terrestrial					
Morelia amesthistina (2)	20.5 ± 0.5		S	S	R. Mehta, unpublished
M. variegata (3)	16.0 ± 2.0		S	S	R. Mehta, unpublished
Python curtus (8)		74.9 ± 8.6 (196.6 ± 26.8)	16.1 ± 10.6	10.8 ± 1.8	This study
P. molurus (7)	35.4 ± 7.5	34.0 ± 4.2 (110.0 ± 14.7)	20.0 ± 7.0	90.6 ± 50.8	This study
P. regius (2)	16.5 ± 1.5		S	S	R. Mehta, unpublished
Colubridae					
Arboreal-Scansorial					
Elaphe obsoleta (9)	2.6 ± 0.2		S	S	This study
Uromacer oxyrhynchus (2)	1.8 ± 0.2		S	S	This study
Terrestrial					
Five species	3.5 to 7.0				Skoczylas, 1978
Leioheterodon geayi (7)	11.6 ± 0.5		S	S	R. Mehta, unpublished
Malpolon sp. (1)	5.3		S	S	This study
Viperidae					
Arboreal					
Atheris nitschei (3)	7.2 ± 0.2		S	S	This study
Trimeresurus stejnegeri (21)	3.5 ± 0.4				M. Tu, unpublished
Tropidolaemus wagleri (2)		(> 60)			R. Bartlett, unpublished
Terrestrial					
Bitis arietans (5)		29.5 ± 4.8 (74.2 ± 10.0)	23.9 ± 2.2	4.5 ± 0.4	This study
B. gabonica (8)	53 to 183	77.0 ± 12.4 (253.9 ± 22.1)	20.3 ± 1.4	5.4 ± 0.3	This study
B. nasicornis (7)		64.8 ± 8.8 (207.3 ± 21.7)	15.5 ± 1.8	6.4 ± 0.7	This study
Crotalus cerastes (35)	11 to 24				Secor and Diamond, 1995
C. horridus (27)	12.8 ± 1.1				F. Zaidan and S. Beaupre, unpublished
C. ruber (1)		(> 365)			G. Marsh, unpublished

which, in contrast with more massive terrestrial forms, have evolved comparatively gracile body shape and low relative mass. Our evaluation of available data suggests that the fecal mass retained by a snake can be a significant and possibly adaptive component of the total body mass, as the rates of passage (excretion or retention) of species complement their structural body mass. Comparatively large PT values of snakes in comparison with other vertebrates have been recognized (Skoczylas, 1978), but extremely long periods of fecal retention, measured in months, are known only as anecdotes. Therefore, we investigated fecal retention in captive snakes in order to provide comparative data on patterns of PT. A pronounced disparity of PT between snakes of small and large relative mass, respectively, appears to be generally characteristic in the three families of snakes we examined (Table 1).

METHODS

Passage Times

We obtained data for PTs from several sources (Table 1). Absolute PTs were measured as the time elapsed between feeding (with the gut empty) and the first appearance of feces during repeated feeding trials in the laboratory. These times corresponded to the time elapsed between feeding and the first appearance of plastic markers in *Elaphe obsoleta* or fluorescent dye in *Crotalus horridus*. In the case of select individuals of *E. obsoleta* and *Bitis gabonica*, we varied the rate of food presentation during separate feeding trials and recorded the mass of ingested food, snake mass, and both wet and dry mass of feces.

PTs for other species, unless from literature, were calculated from data recorded in 1–3 year-long segments from daily records of captive snakes (maintained by E. Bessette, Ophiological Services, Archer, Florida). Absolute PTs were calculated for animals with records since birth as the time elapsed between the first feeding and first defecation. Similarly, for female pythons (*Morelia*, *Python*) laying eggs, absolute PTs were calculated as the time elapsed between the first feeding and first defecation following oviposition and egg incubation. Female pythons normally do not eat during the 4–5 months required for development and incubation of the eggs. For all other records that reflected uninterrupted feeding schedules, we calculated a "mean defecation interval" based on time elapsed between successive defecations. In these calculations, defecations less than three days apart were considered related to the same meal, with timing of defecation taken as the midpoint. When data were available, we also noted the timing and mass of feedings, and we calculated from this information the rate of food ingestion and mean feeding intervals expressed in days. Subjects were kept in individual cages, while ambient temperatures ranged from 26 to 32ºC and varied similarly for all animals.

Hindgut Volumes

In order to quantify the volumetric capacity of the hindgut in vipers that store feces and compare these with an arboreal species of snake characterized by much shorter PTs, we examined fresh tissues from snakes that were available to us for this purpose. Frozen cadavers of snakes were procured from our laboratory and from several other sources. We had access to only three *Bitis arietans,* so we made additional measurements from six *Crotalus adamanteus.* We based this decision on the impression that general hindgut structure was similar in these two species. We did not have access to sufficient arboreal vipers to enable comparisons within a single family, so we compared the viperid data with that from nine *E. obsoleta*, a highly scansorial, semi-arboreal colubrid.

For each subject we measured mass, snout-vent length (SVL), total length (TL), and body volume by water displacement. To measure the position and internal volume of the gut segments in situ, a ventrolateral longitudinal incision was made from the cardiothoracic region to the pyloric region of the stomach to expose the visceral organs. The incision proceeded posteriorly as gut segments were identified, and the position within the body cavity was measured. The incision was stopped anterior to the beginning of the large intestine in order for the integument to remain intact at that region during the volume measurements. Next, an incision was made in the posterior small intestine, and tygon tubing was inserted. Using this tube, the large intestine and cloaca were flushed with 0.9% saline solution to evacuate all feces that were present. On occasion, an incision in the cloacal region to ligate the ovarian ducts was required, such that infused saline did not escape from the gut. Once the hindgut was evacuated of all feces, saline and air, the tube was advanced to the beginning of the large intestine and securely fastened to ensure that no solution could leak. The cloacal opening was restricted and 0.9% saline was carefully injected into the empty hindgut with a syringe. The hindgut was distended in this manner to the extent where the volume expansion of the gut appeared to be restricted by the stretching skin of the animal. In this condition, the dorsal scales were separated, but the skin was not maximally strained. The volume of solution that so distended both the large intestine and cloaca was noted. The gut was then evacuated, and the longitudinal incision was continued posteriorad to identify and measure the position of the hindgut segments.

For statistical analysis, the measurements based on hindgut volumes were pooled for *B. arietans* and *C. adamanteus* and compared to the results from *E. obsoleta*. Differences between the two groups were ascertained using a Mann-Whitney U test, with alpha set at 0.05.

RESULTS

Gut Passage Times and Their Variability

Data from captive snakes were combined with measurements of our own and from the literature, and are summarized in Table 1. In general, arboreal species exhibit considerably shorter passage times than do terrestrial species, and this pattern appears to hold for the three families of snakes we examined. Colubrids, however, generally have shorter PTs than either of the other two families. Considering all data represented by mean values in Table 1, ANOVA and Fisher's post hoc tests (StatView 5.0) indicate differences between arboreal and terrestrial species that

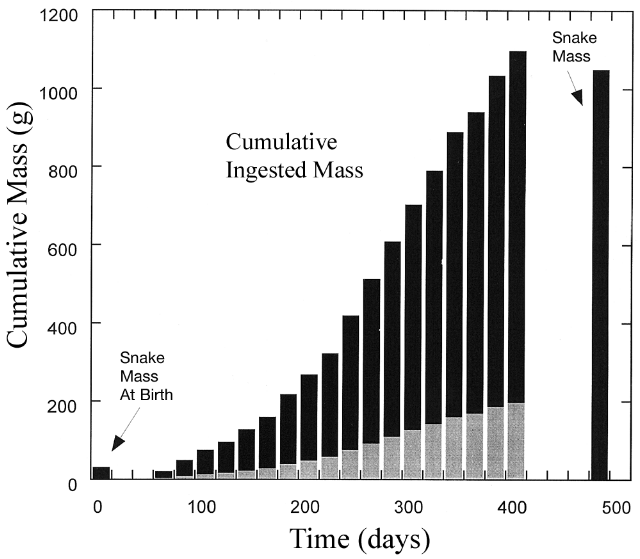

Fig. 1. Cumulative mass ingested by a single Gaboon Viper (*Bitis gabonica*) on a regular feeding schedule. Bars depict the cumulative mass of mice ingested during a 354-day period when feces accumulated between successive defecations on days 51 and 405. The lower gray areas of these bars indicate the proportion of ingested mass estimated to be stored as feces, based on calculations described in the text. Bars at the extreme left and right ends of the graph depict the snake's body mass that was measured at birth and at day 480, respectively. Using the latter measurement, the cumulative fecal mass that was stored during the 354 days was estimated to be 16% of the snake's structural body mass.

approach statistical significance ($P = 0.0618$), and there is no significant interaction with taxonomic category. Neither the feeding interval ($r = 0.065$, $P = 0.9098$) nor the rate of ingestion ($r = -0.238$, $P = 0.6737$) influenced defecation intervals based on uninterrupted feeding records.

It is instructive to consider the maximum defecation intervals that were observed. Maximum defecation intervals in terrestrial pythonids were 174 days in *P. molurus* and 386 days in *P. curtus*, whereas that of the arboreal boid *Corallus caninus* and pythonid *Morelia viridis* were 76 and 7 days, respectively. Similarly, maxima for defecation intervals among the terrestrial viperids *B. arietans, B. nasicornis*, and *B. gabonica* were 116, 286 and 420 days, respectively. In contrast, maximum retention of feces by the arboreal vipers *Atheris nitschei* and *Trimeresurus stejnegeri* were less than 10 days. The more gracile arboreal colubrids exhibited the shortest PTs, with minimum of 23 h in *Uromacer oxyrhynchus.*

The very long PTs are impressive because snakes were fed at rather regular intervals during the periods we examined (Table 1; Fig. 1). We quantified the

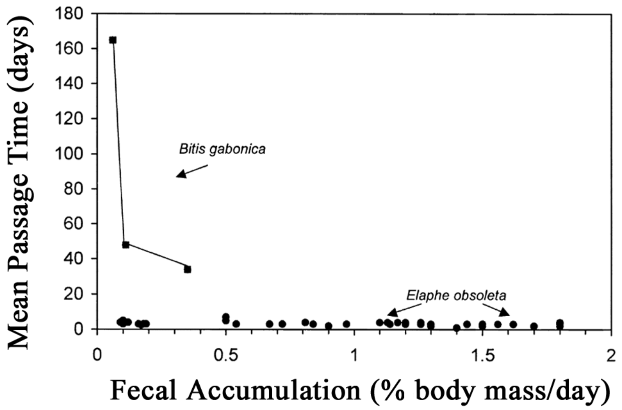

Fig. 2. Relationship between passage time and rate of ingestion expressed as fecal accumulation in percent body mass per day. In *Elaphe obsoleta*, which always defecates following a meal, the meal size was varied in 47 separate feeding trials involving ten different snakes. Note that passage time is independent of the fecal accumulation. In contrast, passage times vary inversely with feeding rate or fecal accumulation in a single *Bitis gabonica* fed on three different schedules.

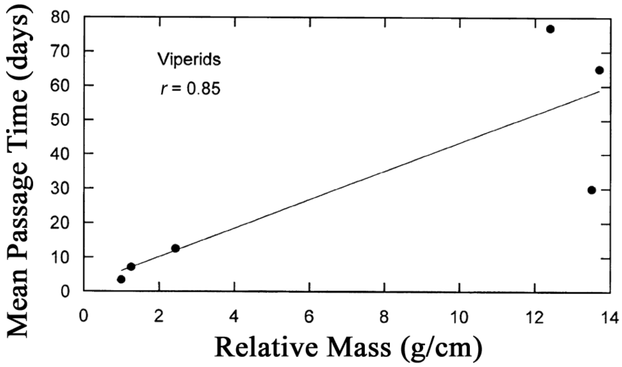

Fig. 3. Relationship between mean passage time (or period of feces accumulation) and the relative body mass (body mass/total body length) of viperid species for which data are available. The fitted line is based on simple regression.

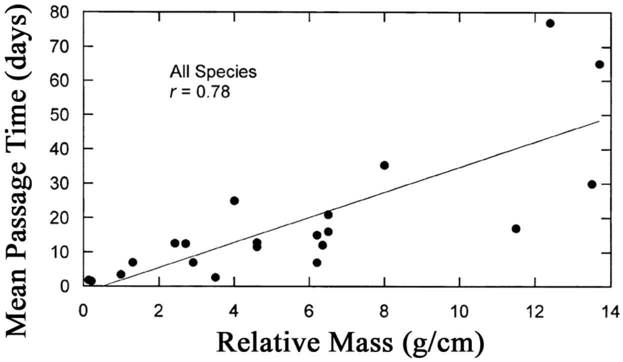

Fig. 4. Relationship between mean passage time (or period of feces accumulation) and the relative body mass (body mass/total body length) of all snake species for which data are available. The fitted line is based on simple regression.

Table 2. Data (mean ± SE) from 12 feeding trials in eight Gaboon Vipers (*Bitis gabonica*). * = cumulative fecal mass was estimated from the conversion (egesta/ingesta = 0.159 ± 0.047 SD) determined from four quantitative feeding trials. Ingestion data are courtesy of E. Bessette.

Snake Mass (kg)	Gut passage time (days)	Ingesta (g total mice)	Egesta (g feces*)	Egesta (% body mass)
1.172 ± 0.261	115 ± 22	581.3 ± 122.0	91.7 ± 19.2	9.2 ± 1.1

Table 3. Mean (± SE) morphometric measurements of snakes. The viperid category contains pooled data for *Crotalus adamanteus* and *Bitis arietans*. * = significant differences ($P < 0.05$) from Mann-Whitney U tests.

Measurements	*Elaphe obsoleta* (N = 9)	Viperids (N = 9)
Mass (g)	500.0 ± 29.60	945.4 ± 179.27*
SVL (cm)	111.8 ± 2.9	103.9 ± 6.37
Volume (ml)	485.9 ± 30	1013.9 ± 184.6*
Hindgut (HG = large intestine + cloaca)		
HG length (cm)	30.7 ± 2.42	18.4 ± 1.8*
HG length/SVL	0.26 ± 0.02	0.20 ± 0.02
(HG + small intestine)/SVL	0.45 ± 0.03	0.32 ± 0.02*
HG volume (ml)	41.8 ± 3.8	109.2 ± 20.3*
HG volume/HG length	1.39 ± 0.10	6.5 ± 1.67*
HG volume/SVL	0.38 ± 0.04	1.00 ± 0.16*
HG volume/body volume	0.09 ± 0.01	0.12 ± 0.02

storage of fecal mass for eight *B. gabonica*, which exhibited the longest PTs of all the species investigated. Using a food-to-feces wet mass conversion factor based on four quantitative feeding trials, we estimated the cumulative mass of feces over periods ranging from 36 to 291 days. These ranged from 5 to 20% of body mass ($\bar{x}$ = 9% body mass; see Table 2).

The cumulative mass of food ingested by a newborn *B. gabonica* during 354 days is shown in relation to the accumulated fecal mass in Figure 1. This figure illustrates the pattern of regular food intake during the year-long period between successive defecations. The total accumulation of feces during this time was estimated (by calculation as above) to be 16% of the structural body mass.

As the PT might be expected to vary with the periodicity of feeding, or rate of food ingestion, we tested this in *E. obsoleta,* a colubrid that defecates frequently, and in *B. gabonica*, a viperid that defecates infrequently. Whereas *E. obsoleta* always defecated following a meal, irrespective of the ingested volume, the *B. gabonica* we tested accumulated feces to volumes representing 5–12% of the body mass, irrespective of the feeding rate. Thus, our data demonstrate that PT was independent of the meal size in *E. obsoleta*, whereas in *B. gabonica* the PT varied with the rate of food ingestion (Fig. 2).

Although our data set is limited, we found there is a positive correlation between PT (hence retention of fecal mass) and the relative mass of snakes for which the requisite data are available (viperids, $r = 0.85$, $P = 0.0115$, Fig. 3; all species, $r = 0.78$, $P < 0.0001$, Fig. 4). Clearly, the greatest disparity in levels of stored fecal mass is seen between gracile, arboreal species and heavy-bodied, comparatively sedentary, ground-dwelling, ambush (“sit-and-wait”) predatory species.

Morphometrics and Storage Capacity of the Hindgut

The gut measurements are summarized in Table 3. Digestive tracts of all snakes were tubular and elongated. The esophagus was relatively thin and joined the stomach near the pericardial region. The stomach was thicker-walled and extended posteriorly, expanding in diameter until it narrowed and terminated at a junction between the pancreas, gall bladder and small intestine. A pyloric valve was identified at the posterior terminus of the stomach. The small intestine was convoluted and morphologically distinct from the stomach and large intestine. In arboreal *Elaphe,* feces were found in an elongated large intestine and cloaca, which showed comparatively little gross differentiation. In the viperid species, the cloaca was relatively short and morphologically distinct from the intestine, and as in *Elaphe*, stored feces were found in both regions. The large intestine was thin-walled and straight with no convolutions. Occasionally, a sphincter was identified between the large and small intestine in *B. arietans* and in *C. adamanteus.*

Measurements of body size revealed that, on average, viperids had twice the mass and volume as *E. obsoleta*, relative to generally similar SVL. The length of the hindgut in *E. obsoleta* was about 1.7 times longer than that in viperids and occupied a greater percentage of the body length. Additionally, the total intestinal length (hindgut plus small intestine) incorporated 45% of SVL in *E. obsoleta*, while only 32% of SVL in the viperids. However, volumetric measurements of the hindgut indicate that viperids have more than twice the absolute volume capacity than does *E. obsoleta.* Hindgut volumes expressed relative to SVL and hindgut length also were significantly greater in the viperids. Relative to the total body volume, however, hindgut volumes were similar among the species.

DISCUSSION

Variation of PT among Vertebrates

Gut PTs in vertebrates vary considerably within species and among different taxa of vertebrates. Coefficients of variation can be as high as 45% in humans, 21% in wild animals and 12% in farm animals (Warner, 1981). Shorter PTs are characteristic of very small birds and mammals, ranging from about 1 to 10 h (Warner, 1981). Among mammals, longer PTs are characteristic of arboreal folivores. Reptiles exhibit considerable variation in PT, and the total range of variation exceeds that of endothermic vertebrates. Relatively long PTs have been reported in tortoises, ranging up to 16 days (Bjorndal, 1987). Snakes, however, exhibit by far the greatest variation in PTs, as well as the longest PTs that have been measured in any vertebrate (Table 1).

Generally, high variation in PTs reflects a number of factors that can potentially affect gut function. For example, PT is influenced by properties of the digesta. Solutes usually have higher transit velocities through the gut than does particulate matter (Warner, 1981). The larger particles presumably are retained longer to increase the digestive efficiency. Increases in meal ration generally are followed by shorter retention times, presumably due to limited gut volume and decreased digestive efficiency (Warner, 1981). The nutritional value of ingested food also influences the PT, and meals having lower nutritional value or digestibility tend to be retained longer those having high nutritional value (Bjorndal, 1989; Wouter, 1992). Finally, the PT is often related directly to feeding frequency. Animals with short feeding intervals have relatively shorter PTs than do animals with considerably longer feeding intervals (Warner, 1981).

Attributes of the animal and its environment also can have considerable influence on gut function. The age of an animal can affect the PT. Although results vary among species, younger animals generally have shorter PTs than do adults. Pregnant and ovipositing females have shorter retention of feces, presumably caused by compression of the gut. Also, PTs can be shortened considerably by activity. High ambient temperatures are associated with longer PTs among endotherms, whereas in ectotherms higher temperatures elevate metabolic rates and thereby tend to shorten the PT (e.g., Wouter, 1992).

Variation of PT among Snakes

Factors influencing the variation of gut passage in snakes have not been well investigated. While some of the above-mentioned factors undoubtedly influence the PTs that have been reported for snakes, many can be eliminated as factors in the present investigation. Snakes that we tested for fecal retention were fed identical food (mice) while at similar body temperatures and at intervals appropriate for the metabolic requirements of species. Moreover, the extremes of variation reported exceed considerably any expected variation that might be attributable to properties of food and its ration characteristics. With respect to meal size and its periodicity, the arboreal species exhibit no variation of PT with rate of food ingestion attributable to differences in meal size, and the PT is the same for both small and very large meals (Fig. 2; H. Lillywhite, unpublished data for other species). On the other hand, data for *B. gabonica* suggest these snakes accumulate feces to what appears a maximum, or near maximum, of storage capacity, irrespective of the feeding rate. Thus, the PT can be shortened from nearly a year to about 1.5 months with increased rate of feeding. In consideration of these data, it is important to note that the feeding rate does not provide the total explanation for PT variation among species when heavy-bodied viperids are compared to gracile, arboreal species. The latter defecate soon after every meal, whereas even at the higher feeding rates terrestrial vipers retain feces until the accumulation from multiple feedings exceed some storage threshold.

An interesting finding is the positive correlation between PT (hence retention of fecal mass) and the relative mass of snakes (Figs. 3–4). Clearly, the greatest disparity in levels of stored fecal mass is seen between gracile, arboreal species and ground-dwelling, heavy-bodied, comparatively sedentary, ambush (sit-and-wait) predatory species. In the latter category, the presumably adaptive "extremes" of stout body form and high relative mass have evolved among the boids and viperids. Considering the present data for vipers, the PTs of arboreal species are much shorter than are those for strictly ground-dwelling species. Whereas the arboreal species have more streamlined body shapes, the ground-dwelling species in our comparison are very stocky in body shape. In general, the latter species may be relatively less mobile and more dependent on ambush foraging tactics (e.g., Greene and Santana, 1983; Greene, 1992). A more inclusive multivariate analysis of the various factors potentially affecting PT is not yet feasible because of limited, taxonomically uneven, and in many cases inadequate availability of the appropriate measurements.

There is a trend among snakes as well as other vertebrates for more active species to have shorter PTs than do sedentary species (Skoczylas, 1978; Guard, 1980; Parmenter, 1981; Warner, 1981). Therefore, one might assume that activity levels and foraging behavior might influence PT and the retention of feces. More active and mobile species will benefit, by means of economical and effective locomotion, from lighter mass associated with frequent defecation. While the trend in all snake taxa we examined was for arboreal species to have shorter PTs than their ground-dwelling relatives, especially among viperids, it is interesting to note the arboreal viper *Tropidolaemus wagleri* tends to be relatively sedentary in captivity and may retain feces for periods exceeding two months (R. Bartlett, unpublished). Thus, PT of the *T. wagleri* appears at least 8-fold longer than that of the more active arboreal viper *Atheris nitschei* (Table 1). Similarly, differences in PT exhibited by *C. caninus* and *M. viridis* might reflect evolution of behavioral differences not yet appreciated or understood from behavioral or ecological research. Although some arboreal species of snakes might be sedentary to varying degrees (e.g., Henderson, 1982), field studies suggest arboreal snakes generally forage actively or move frequently between foraging sites (Henderson et al., 1981; Plummer, 1981; Chandler and Tolson, 1990; Rodda, 1992; Henderson, 1993; Tu et al., 2000). More detailed field observations are required on movements of arboreal snakes before defecation patterns can be adequately evaluated in relation to the activity patterns of species. However, factors such as camouflage and support by unstable substrata of branches might also be important in relation to selection for low body mass and therefore frequent defecation.

The consideration of activity raises the question as to what extent the longer PTs we observed are artifacts of captivity. While this is an important question, all of the data being considered are from captive animals, so the factor of captivity alone does not explain what appear to be characteristic interspecific differences in the tendency to retain or evacuate feces. Further, in preliminary trials we "exercised" one individual of *B. gabonica* by causing it to crawl upon the laboratory floor periodically during a trial of feedings (while feces were accumulating), and the activity did not induce "premature" (early) defecation uncharacteristic of the individual's defecation pattern. We also noted that neither skin shedding nor drinking induced early defecation in this particular snake. Nonetheless, in light of the general question, it would be of much interest to investigate defecation patterns of snakes during normal cycles of activity in the field.

Gut Storage and Anatomy

The large intestine of vertebrates generally appears specialized for the purpose of reabsorbing water and electrolytes, while forming and storing fecal material. In terrestrial squamates the large intestine and cloaca also store urates. Anti-peristaltic movements mix urates with the feces, and a sphincter prevents backflow into the small intestine (Stevens and Hume, 1995). Our inspection of the gut in the colubrid *E. obsoleta*, and viperids *B. arietans* and *C. adamanteus* confirm that fecal materials are stored in both the posterior large intestine and cloaca, which are thin-walled and considerably wider in diameter than is the small intestine. In *E. obsoleta*, the fecal material is relatively loose and mixes with urates, whereas in the viperids (and some boids) fecal matter usually appears more compacted and separated from the urate mass. In our captive specimens of *B. gabonica*, the urates may also be very compacted and can be voided independently of feces during a long period of fecal accumulation (H. Lillywhite, unpublished).

Our method of measuring gut volumes was developed as a practical means of quantifying the in situ volume capacity of the hindgut, as it relates normally to compliances of the gut wall, body wall and integument. Relative to both hindgut length and total body length, hindgut volumes of the viperids are several-fold larger than in *E. obsoleta,* and they occupy a more posterior position of the gut (Table 3). Thus, vipers compact a larger relative volume of fecal mass in more posterior positions relative to body length. When gut volumes are expressed relative to the total body volume of species, however, there is no significant difference between these taxa. Thus, increased fecal storage capacity evidently has evolved along with increased mass and body volume in the viperid snakes, while the location of storage has shifted posteriad. Of course, these measurements of storage maxima do not necessarily reflect functional volumes or their exact body position, which might vary through time and among individuals. We note, however, that volume maxima determined from the anatomical estimates correspond reasonably well with storage maxima (based on relative mass) actually measured in snakes (Table 2).

Fecal Mass and Body Mass

The rates of fecal passage complement the total body mass characteristic of species. Clearly, a large mass is disadvantageous for arboreal species that are often supported by comparatively weak and unstable substrata of branches. Generally, arboreal snakes are gracile and have low relative mass in comparison with terrestrial relatives (Lillywhite and Henderson, 1993). As such, arboreal species minimize excess mass by voiding feces quickly, thereby increasing mobility and decreasing energy expenditure required to counteract gravity. In contrast, many terrestrial species are larger and heavier than are their arboreal relatives. The contrast in extremes of morphology begs the question: Why are the “megasnakes” such as pythons and terrestrial vipers so massive? While there is no definitive answer to this question at present, a large mass confers mechanical advantages to the capture and handling of large and potentially dangerous prey (Pough and Groves, 1983; Slip and Shine, 1988; Shine, 1991; Greene, 1992).

Stored feces contribute a labile component to body mass that is free of metabolic maintenance cost and requires no energy expenditure so long as the animal is sedentary. For whatever reason arboreal snakes evolved small structural mass, the rapid voiding of feces helps keep the total body mass low. Contrariwise, for whatever reason(s) heavy-bodied, terrestrial ambush predators (“megasnakes”) have evolved large structural mass, the prolonged and cumulative retention of feces contributes inert ballast to their mass. Thus, natural selection for either small or large body mass might also act with respect to the defecation patterns associated with either respective context.

Recent analyses by Cundall (this volume) indicate that both viperids and boids not only possess a comparatively stout trunk, but also the mass is relatively more concentrated in the posterior trunk region compared with the anterior body behind the head. Retained fecal mass also has a posterior position. Therefore, these additive features might well serve to maximize the static friction force and inertia of the posterior body, thereby reducing the reaction distances moved by the posterior trunk while the anterior trunk is accelerated rapidly during predatory strikes. Similarly, a large posterior mass might assist to “anchor” a snake that might be holding onto a large prey item while on open ground, as during constriction in boids or following fang penetration in some viperids.

The prolonged residence time of fecal material in the gut also potentially increases the absorption of nutrients and water. However, maximal absorption efficiency is dependent on physiological transport and diffusion processes (and possibly gut transmural pressures) which theoretically might require days or perhaps weeks, but surely do not require multiple months, of time. Moreover, preliminary data indicate that changes in PT do not improve digestibility in Timber Rattlesnakes (*Crotalus horridus*; F. Zaidan and S. Beaupre, unpublished).

Further research is required to substantiate the “adaptive ballast” hypothesis and to elucidate the facultative mechanisms that might control extremely prolonged retention and storage of fecal material in the ophidian hindgut. There are records of extreme constipation lasting for months in humans, but this condition is clearly pathological (e.g., Hurst, 1921). Research toward understanding of adaptive constipation might possibly provide insights on the causes and cures of pathological constipation. Viperid snakes appear to be remarkably appropriate animals for such investigations. Moreover, research on mechanical and storage aspects of digestion might further our integrated understanding of viperid evolution.

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