Assimilation efficiency and gut passage time in an African elapid snake, Hemachatus haemachatus

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Assimilation efficiency and gut passage time in an African elapid snake, *Hemachatus haemachatus*

**Graham J. Alexander**1*, Shirley A. Hanrahan1 & Duncan Mitchell2

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Abstract.—We measured apparent assimilation efficiency (AAE) and gut passage time in the African elapid snake *Hemachatus haemachatus* under laboratory conditions. AAE was dependent on food type, being 89.8% when snakes were fed frogs and 82.8% when fed mice. Differences in AAE for different meal types could be ascribed to the indigestible hair in mouse meals because differences were lost once this component of the mouse meals was removed from the calculation. AAE did not depend on snake body mass and there was no significant difference between AAE measures made at 20°C and 27°C for mouse meals. Gut passage time was 25% faster at 27°C than at 20°C, but was not affected by food type or snake body mass. Larger meals took longer to digest. Thus, *H. haemachatus* appears to offset reduced digestive performance at lower temperatures by retaining food in the gut for longer when at lower body temperatures (Tbs). These results fit an emerging pattern in snakes whereby digestive efficiency is generally high and insensitive to Tb over the selected thermal range, but may become dependent at lower Tbs when digestion is eventually arrested. The rate of digestion is highly temperature-sensitive and is fastest in the selected Tb range. Diet appears to affect digestive efficiency owing, mainly, to the presence of indigestible components such as hair. Using a comparative framework, venom does not appear to improve digestion for this species, at least over the temperature range tested, relative to other snake species in the literature.

Key words.—Digestive efficiency, net assimilation efficiency, rate of digestion, metabolisable energy coefficient, calorimetry

**INTRODUCTION**

Total food energy gain sets the upper limit to energy expenditure and so constrains many aspects of a species’ biology (Nagy 1983). Rates of energy acquisition may also constrain the set of life histories that are possible and affect time and energy allocations (Angilletta 2001) – factors that are critical to the fitness of organisms as they govern reproductive success. Since the gut does not absorb all of the food ingested by an animal, measures of the efficiency of absorption are necessary to estimate energy gains from measures of ingested food. This efficiency is usually expressed as a percentage of the total energy ingested, and is calculated using measures of energy ingestion (total energy of ingested food) and energy lost through defaecation (total energy of faeces derived from that food). Digestive efficiency (DE)
is sometimes also termed the apparent digestive efficiency (ADE) to take into account the fact that faeces include materials such as sloughed gut cells, secretions and associated gut bacteria, in addition to the undigested food (Mitchell 1964). It is not practical to separate these materials from the faecal waste and their inclusion results in a slight underestimation of the real digestive efficiency (McKinon & Alexander 1999). However, Greenwald and Kanter (1979) maintain that, in spite of this problem, ADE is a physiologically meaningful value as energy losses other than those due to non-absorption contribute to the energy debt.

Another commonly used measure of energy acquisition is apparent assimilation efficiency (AAE). This measure differs from ADE in that excreted nitrogenous waste is included in the measure of energy loss (McConnachie & Alexander 2004) and AAE is thus a measure of physiological fuel value to the organism (Greenwald & Kanter 1979). It is sometimes also referred to as the metabolisable energy (ME) and may be expressed as the metabolisable energy coefficient (MEC) (Beaupre et al. 1993). Reptiles and birds typically excrete nitrogenous waste in the form of urates, which may be voided as a discrete mass or mixed with the faecal matter, depending on the species and diet. When urates are not easily separated from faeces, it is more practical to measure AAE, which in snakes, is typically between 5 and 8% lower than ADE (Bedford & Christian 2000) depending on body temperature (Tb), species and diet. Beaupre et al. (1993) also argue that AAE is a more ecologically relevant measure than ADE in autecological studies because it is a better measure of catabolisable energy.

Snakes have become ‘model’ organisms in ecological studies (Shine & Bonnet 2000) and they possess several features that make them suitable for studies in energetics (Secor & Diamond 1998). For example, in snakes, measurement of AAE is easily achieved as meals invariably consist of completely intact prey (snakes cannot masticate food), making for easy and accurate quantification of food intake. Also, because many species of snakes naturally feed at infrequent intervals (Secor & Diamond 2000), meals can be spaced far-enough apart to allow collected faeces to be ascribed confidently to a particular meal. It is, therefore, surprising that relatively few studies have investigated digestive physiology of snakes. Most studies of ADE and AAE in snakes have focused on species in the Pythonidae (Vinegar et al. 1970; Bedford & Christian 2000; Toledo et al. 2003; Cox & Secor 2007), Colubridae (Gehrmann 1971; Smith 1976; Greenwald & Kanter 1979; Hailey & Davies 1987; Sievert et al. 2005; Britt et al. 2006) and Viperidae (McCue 2007; Tsai et al. 2008). Even within this limited taxonomic coverage, it is evident that the eight species of pythonids investigated appear to have DEs which are high in comparison with species in the Colubridae and Viperidae. However, with so few species investigated, it is not yet clear whether this finding is related more directly to ecological correlates or to phylogenetic patterning.

Several authors have proposed physiological and environmental attributes that could affect the performance of digestion in snakes. These include Tb, sex, meal size, body size, season (Bedford & Christian 2000), thermoregulatory opportunities, the effects of venom (Greenwald & Kanter 1979; McCue 2007; Chu et al. 2009), clutch effects (Cox & Secor 2007), life history (Tsai et al. 2008) and diet (Britt et al. 2006). Generally, DE appears to be relatively insensitive to Tb (Greenwald & Kanter 1979; Bedford & Christian 2000) over the ‘normal thermal range’ but Greenwald and Kanter (1979) and Tsai et al. (2008) do report decreased DE at low temperatures in
Pantherophis guttatus guttatus (as Elaphe guttata guttata; 20°C) and Viridovipera stejnegeri (as Trimeresurus stejnegeri stejnegeri; 15°C), respectively. Hailey and Davies (1987) also found a slight temperature effect on DE in Natrix maura. Most workers have found that the amount of food consumed, body size, season, and sex have little effect on DE. Only one previous study has compared the relative digestibility of two food types in a single species of snake: Britt et al. (2006) studied AAE in two populations of Thamnophis elegans, one of which specialised in feeding on slugs. They found that specialists were able to digest slugs more efficiently than were generalists, but were not compromised in their ability to digest fish. These differences indicate that dietary specialists are able to fine-tune their digestive systems so as to extract a greater proportion of the energy from their meals (and at reduced energy expenditure [Britt et al. 2006]). These findings warn against over-generalisation; snake digestive physiology may be more complex than the few published measures imply.

Unlike digestive efficiency, the rate of digestion appears to be highly temperature-dependent in snakes, with higher rates occurring at higher temperatures (Skoczylas 1970; Smith 1976; Greenwald & Kanter 1979; Naulleau 1983; Stevenson et al. 1985; Hailey & Davies 1987; Bedford & Christian 2000; Toledo et al. 2003; Sievert et al. 2005; Tsai et al. 2008). It is thus possible that in cases where measures of DEs are insensitive to Tb, temperature sensitivity of DE is offset by the meal spending longer periods in the gut. Rates of digestion also may set the upper limit to food consumption under some circumstances.

We measured AAE for two food types (mouse and frog) in the Rinkhals, Hemachatus haemachatus (Elapidae). For frog meals, urates were mixed with faeces, making separation of these two components, and thus measurement of ADE, problematic. To make measures comparable, we thus limited our assessment to measures of AAE for both food types. We also investigated the effect of Tb (at 20°C and 27°C) on AAE and on digestive rate, measured as gut passage time. Our study represents the first published measures of AAE in an elapid and thus serves to increase the taxonomic coverage of this measure in snakes.

**MATERIALS AND METHODS**

**Study Animal**

Hemachatus haemachatus (Rinkhals) is a diurnal (Alexander & Marshall 1998), cobra-like elapid restricted to the southern and eastern parts of southern Africa. In the wild, H. haemachatus is a generalist predator, feeding on a wide range of prey, including amphibians, rodents, lizards and other snakes (Broadley 1983). In parts of its range, H. haemachatus occurs at high altitudes (Branch 1998), up to 2500 m in South Africa (Bourquin 2004), where it is frequently exposed to sub-zero temperatures during winter. Alexander and Brooks (1999) found that H. haemachatus has reduced appetite during winter, even when kept at constant temperatures year-round. We have reported previously that H. haemachatus has a wide thermal tolerance in comparison to other snakes (Alexander et al. 1999). We thus expected H. haemachatus to exhibit digestive adaptations to low Tbs.

The colony of snakes that we used in our study consisted of 28 individuals (15 males, 13 females) that were collected from the wild in the vicinity of Johannesburg,
South Africa (26°S, 28°E, altitude >1600 m). Mean (± SD) body mass was 394±288 g, while mean (± SD) snout–vent length (SVL) was 794±212 mm. Snakes were housed individually in wooden cages and acclimatised to a constant ambient temperature (25°C) and lighting regime (12h:12h light:dark cycle; local dawn at 06:00) for a minimum of three months prior to experimentation. Snakes were maintained on a diet of mice or frogs, depending on individual preferences of the snakes, offered once per month (10–20% body mass per feed). We maintained snakes on a monthly feeding cycle since previous experience had shown us that more frequent feeding caused individuals of this species rapidly to become much heavier than wild specimens (Alexander 1996).

**Apparent Assimilation Efficiency**

Snakes were fed dead mice at two ambient temperatures, 20°C and 27°C, to test for the effect of temperature on the AAE. These temperatures represent the low and high extremes of the selected thermal range for *H. haemachatus* (for snakes given a wide thermal choice under laboratory conditions [Alexander 1996]). To test for the effects of food type on AAE, snakes were also fed frogs at 20°C. We chose to test for effects of food-type on AAE at 20°C because differences are likely to be more evident at low temperatures (Tsai et al. 2008). The temperature of the room housing the snake colony was set to the experimental temperature the day before feeding. In isothermal environments, the body temperature of *H. haemachatus* always was close to ambient temperature (Alexander 1996). Since snakes were not force-fed, the number of snakes that ingested food in each feeding trial depended on the individual snake’s food type preferences (*n* = 22 for both mouse-meal trials; *n* = 7 for snakes for frog meals).

We anchored plastic sheeting to the floor of the snake cages during feeding trials to facilitate the removal of excreta. Snakes were fed freshly killed mice (*Mus musculus* 8-week-old, strain MF1 males; average [± SD] mass 26.7±2.2 g) or frogs (*Xenopus laevis*; average [± SD] mass 51.0±15.4 g). For each feeding, meals weighed between 10 and 15% of the snake’s body mass for mouse meals and between 20 and 25% for frog meals (meal sizes were selected to standardise energy intake for the two meal types). We made up the required meal mass by feeding larger snakes more, rather than larger, food items. We offered food in the late afternoon, removing uneaten food the following morning. We collected excreta daily, when present, and dried it to constant mass at 50°C. Snakes were fed mice with dark fur on the feeds before and after the feeds for AAE measures, so that the undigested dark hair in the faeces could serve as a colour marker to confirm that we had collected all the excreta from the AAE trials.

The energy and water content of the food was measured in a representative sample of 10 mice and 10 frogs, which were killed, weighed and dried to constant mass at 50°C. Individual dried carcasses were then ground to a fine consistency by milling at 20000 revolutions per minute, for a minimum of 30 seconds (IKA Type A10 Mill), and four samples (between 0.5 and 0.7 g) were taken from each. Their energy content, and that of four samples of the excreta from each snake, was measured by bomb calorimetry (Digital Data Systems CP500 Calorimetry System, Johannesburg, South Africa). The heat of combustion of calorific-grade benzoic acid was used as a standard (26.4 kJ·g⁻¹) and the contribution of the fuse wire was taken into account.
We used analyses of variance (ANOVAs) to test for differences in energy contents among samples of each food type and among samples of excreta (energy content of food and excreta were normally distributed; Lilliefors test for normality; NS). We used two-tailed two-sample \( t \)-tests to test for significant differences among energy content of different food types, excreta derived from different food types and the excreta produced at different temperatures. Sequential Bonferroni adjustments for multiple paired comparisons (Rice 1989) were applied where appropriate (here and in the other statistical procedures of our study), in order to control for Type-I errors.

AAE was calculated using Equation 1:

\[
\text{AAE} = \frac{\text{energy content of food}}{\text{energy content of faeces + urates}} \times 100 \quad (1)
\]

We used a \( t \)-test to test for differences in AAEs between the two temperatures and the two diets, and regression analyses to test for effect of snake body mass and relative meal size (meal mass/body mass) on AAE. We also computed net assimilation efficiency (NAE) for snakes that were fed mice at 20°C and used a \( t \)-test to establish if this differed from the AAE of snakes fed frogs at the same temperature. Measures of NAE were based on Greenwald and Kanter’s (1979) reported values for proportion of total energy made up by hair in mice (hair comprises 4.6% of the total energy in a 27.6 g mouse; the mice used in our study averaged a similar mass, 26.7 g).

**Rate of Digestion**

We assessed rate of digestion by measuring gut passage time. We recorded the number of days taken from feeding to first defaecation during the AAE feeding trials, as described by Greenwald and Kanter (1979). Differences in passage time between temperature regimes, and between diets, were assessed using \( t \)-tests. We used regression analyses to test if passage time was dependent upon relative meal size (meal mass/body mass). The residuals resulting from these relationships were regressed against body mass to test if passage time was affected by body mass.

**RESULTS**

ANOVAs revealed no significant variation in the energy content between the 10 mice \((F_{(9,40)} = 0.605; \text{NS})\), or between the 10 frogs \((F_{(9,40)} = 2.1; \text{NS})\). Also, we detected no significant differences in the energy content between excreta samples collected from snakes that consumed mice \((F_{(21,72)} = 1.6; \text{NS})\) or between samples collected from snakes that consumed frogs \((F_{(6,28)} = 0.4; \text{NS})\). Therefore, we pooled values and used average energy values for mice, frogs, and the excreta produced from each food type in our calculation of AAE (Table 1). Energy content of mice (kJ g\(^{-1}\) wet mass) was more than double that of frogs \((t = 23.1; P < 0.001)\). This difference was not entirely due to differences in water content, as the energy content per g dry mass also was significantly higher for mice \((t = 12.1; P < 0.001)\). The energy content of the excreta derived from mouse meals also was nearly double that derived from frog meals \((t = 13.3; P < 0.001)\). However, we found no significant differences in the energy content of excreta produced by snakes fed mice at 20°C and 27°C \((t = 0.05; \text{NS})\).
Apparent assimilation efficiencies for snakes fed mice were not significantly different at the two test temperatures \( t/C30.01; \text{NS} \), but were significantly lower at 20\( ^\circ \)C for snakes fed mice in comparison to those fed frogs \( t/C30.2.33; P/C30.028 \). These differences, however, were not significant once mouse meal AAE was converted to NAE \( t/C30.0.71; \text{NS} \), indicating that differences in AAEs in snakes fed mice and frogs was largely the result of the indigestible hair in mice. Regression analyses did not detect a significant relationship between AAE and relative meal size or between AAE and snake body mass.

On average, the first evidence of defaecation for snakes housed at 20\( ^\circ \)C and 27\( ^\circ \)C occurred at 5.2\( \pm \)1.6 and 3.9\( \pm \)1.0 days post-feeding, respectively. These intervals differ significantly \( t/C30.2.98; P/C30.006 \). Gut passage time did not differ between the mouse and frog meals \( t/C30.1.4; \text{NS} \) at 20\( ^\circ \)C. Regression analysis revealed a significant positive linear relationship between the number of days to first defaecation and relative meal size (Fig. 1). Although this relationship is significant, it explains only a third of the variation in gut passage time. Residuals from this relationship were not significantly related to body mass.

**DISCUSSION**

We found differences in assimilation efficiency with meal type (at 20\( ^\circ \)C only), but not temperature, in *H. haemachatus*. Also, snake body size and meal size appeared to have little effect on assimilation efficiency. Differences in AAE measures for the two meal types appeared to be largely the result of the indigestible hair in mouse meals. Unlike the AAE, the rate of digestion appeared to be highly temperature-dependent, as passage time was reduced by 25\% with a 7\( ^\circ \)C reduction in temperature. We also found that digestion of larger meals was slower, and this effect could not have been a simple surface area-to-mass effect, as larger meals consisted of more, rather than larger, food items.

In *H. haemachatus* that ate mice, AAE was the same at ambient temperatures of 20\( ^\circ \)C and 27\( ^\circ \)C, which implies that, within this range, the ability of this species to extract energy from its food does not depend on body temperature, even though gut passage time does. This result is in broad agreement with those of Greenwald and Kanter (1979), Bedford and Christian (2000), and Tsai *et al.* (2008), who reported

<table>
<thead>
<tr>
<th>Measures</th>
<th>Mouse meals</th>
<th>Frog meals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Energy content of food (dry; kJ g(^{-1}))</td>
<td>26.6( \pm )1.1</td>
<td>18.0( \pm )2.0</td>
</tr>
<tr>
<td>Dry mass/wet mass of food (%)</td>
<td>32.1( \pm )2.1</td>
<td>22.3( \pm )1.1</td>
</tr>
<tr>
<td>Energy content of food (wet; kJ g(^{-1}))</td>
<td>8.5( \pm )2.3</td>
<td>4.0( \pm )0.2</td>
</tr>
<tr>
<td>Energy content of dry excreta (kJ g(^{-1}))</td>
<td>15.3( \pm )2.4</td>
<td>8.3( \pm )0.3</td>
</tr>
<tr>
<td>AAE (%) at 20( ^\circ )C</td>
<td>82.9( \pm )3.9 (n = 22)</td>
<td>89.8( \pm )3.9 (n = 7)</td>
</tr>
<tr>
<td>AAE (%) at 27( ^\circ )C</td>
<td>82.8( \pm )3.7 (n = 22)</td>
<td></td>
</tr>
<tr>
<td>NAE (%) at 20( ^\circ )C</td>
<td>87.0( \pm )3.9 (n = 22)</td>
<td></td>
</tr>
</tbody>
</table>

Note: Values are mean\( \pm \)SD.
temperature-independence of digestion and assimilation at temperatures above 20°C for other species of snakes. However, in studies where lower temperatures were tested (Greenwald & Kanter 1979; Hailey & Davies 1987; Tsai et al. 2008), efficiency appeared to become temperature dependent. Relatively few studies have included measures at low temperatures because snakes are disinclined to feed at these temperatures and the incidence of regurgitation increases dramatically below 15°C (Hailey & Davies 1987; Tsai et al. 2008).

We found that food type had a significant effect on AAE in H. haemachatus. Digestive efficiency of snakes fed mice (82.8%) was significantly lower than for those fed frogs (89.8%), but the indigestibility of mouse hair was probably largely responsible for the differences in AAEs; faeces passed by snakes eating mice contained undigested hair and had a significantly higher energy content than faeces passed by snakes eating frogs. Differences in AAE were lost once hair indigestibility was factored out of the measure. Britt et al. (2006) found similar differences in AAE for Thamnophis elegans eating slugs and fish but, in their case, differences could not be ascribed wholly to indigestible components. Thus, meal type appears to be an important determinant of AAE in snakes.

Our measure of AAE for H. haemachatus eating mice (82.8%) was lower than those for various species of pythonids eating rodents (Table 2; average 88%) but is slightly higher than measures for vipers (81%). The only comparative measure for a colubrid is 88% for P. guttatus (Smith 1976). AAE for frog meals has been recorded previously only by Smith (1976), who measured an AAE of only 84% for Heterodon platyrhinos feeding on toads (Anaxyrus terrestris as Bufo terrestris). This AAE is lower than the 89.8% measured for frog meals in the present study, but the comparison should be assessed with caution as the food species are different. The low numbers of species for which measures of AAE exist make it impossible to ascertain if these differences are a result of phylogeny or are set by ecological and life history characteristics. Such uncertainties will be resolved only when measures are collected for more species.

Figure 1. Regression showing the relationship between the number of days to first defaecation and relative meal size (meal size divided by body mass).
Notes: Linear regression equation: \(y = a + bx\); \(a = 1.23\); \(b = 12.17\); \(R^2 = 0.34\); \(n = 22\); \(P = 0.005\).
Table 2. Summary information on the digestion and assimilation characteristics of snakes.

<table>
<thead>
<tr>
<th>Species</th>
<th>ADE (%)</th>
<th>AAE (%)</th>
<th>T_b (°C)</th>
<th>Meal type</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pythonidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Antaresia childreni</em></td>
<td>89-97</td>
<td>78-92</td>
<td>24-33</td>
<td>Rats &amp; mice</td>
<td>Bedford &amp; Christian</td>
</tr>
<tr>
<td><em>Antaresia stimsoni</em></td>
<td>95-97</td>
<td>87-94</td>
<td>24-33</td>
<td>Rats &amp; mice</td>
<td>Bedford &amp; Christian</td>
</tr>
<tr>
<td><em>Aspidites melanocephalus</em></td>
<td>89-96</td>
<td>78-88</td>
<td>24-33</td>
<td>Rats &amp; mice</td>
<td>Bedford &amp; Christian</td>
</tr>
<tr>
<td><em>Liaxis fuscus</em></td>
<td>95-98</td>
<td>91-93</td>
<td>24-33</td>
<td>Rats &amp; mice</td>
<td>Bedford &amp; Christian</td>
</tr>
<tr>
<td><em>Liaxis olivaceus</em></td>
<td>94-97</td>
<td>84-92</td>
<td>24-33</td>
<td>Rats &amp; mice</td>
<td>Bedford &amp; Christian</td>
</tr>
<tr>
<td><em>Morelia spilota variegata</em></td>
<td>96-97</td>
<td>90-92</td>
<td>24-33</td>
<td>Rats &amp; mice</td>
<td>Bedford &amp; Christian</td>
</tr>
<tr>
<td><em>Morelia spilota spilota</em></td>
<td>95-97</td>
<td>88-92</td>
<td>24-33</td>
<td>Rats &amp; mice</td>
<td>Bedford &amp; Christian</td>
</tr>
<tr>
<td><em>Python bivittatus</em></td>
<td>91</td>
<td>84</td>
<td>28</td>
<td>Mice</td>
<td>Cox &amp; Secor (2007)</td>
</tr>
<tr>
<td><em>Python curtus</em></td>
<td>93-98</td>
<td></td>
<td></td>
<td>Rats &amp; mice</td>
<td>Vinegar <em>et al.</em> (1970)</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>95</td>
<td>88</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Colubridae</strong></td>
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</tr>
<tr>
<td><em>Heterodon platyrhinos</em></td>
<td></td>
<td>83</td>
<td>25</td>
<td>Toads</td>
<td>Smith (1976)</td>
</tr>
<tr>
<td><em>Natrix erythrogaster</em></td>
<td>80</td>
<td></td>
<td></td>
<td>Thermoreg.</td>
<td>Gehrmann (1971)</td>
</tr>
<tr>
<td><em>Natrix maura</em></td>
<td>85-95</td>
<td></td>
<td></td>
<td>Minnows</td>
<td>Hailey &amp; Davies (1987)</td>
</tr>
<tr>
<td><em>Pantherophis guttatus</em></td>
<td>85-89</td>
<td></td>
<td>20-31</td>
<td>Mice</td>
<td>Greenwald &amp; Kanter</td>
</tr>
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<td><em>Pantherophis guttatus</em></td>
<td>87-95</td>
<td></td>
<td>23</td>
<td>Neonatal mice</td>
<td>Sievert <em>et al.</em> (2005)</td>
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<tr>
<td><em>Pantherophis guttatus</em></td>
<td>88</td>
<td>25</td>
<td></td>
<td>Mice</td>
<td>Smith (1976)</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>87</td>
<td>82</td>
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<td></td>
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<tr>
<td><strong>Elapidae</strong></td>
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<tr>
<td><em>Hemachatus haemachatus</em></td>
<td>83-90</td>
<td></td>
<td>20-27</td>
<td>Mice &amp; frogs</td>
<td>Present study</td>
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<td><strong>Viperidae</strong></td>
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<td><em>Viridovipera stejnegeri</em></td>
<td>70-88</td>
<td></td>
<td>15-35</td>
<td>Mice</td>
<td>Tsai <em>et al.</em> (2008)</td>
</tr>
<tr>
<td><em>Viridovipera stejnegeri</em></td>
<td>73-93</td>
<td>69-87</td>
<td>14-24</td>
<td>Mice</td>
<td>Chu <em>et al.</em> (2009)</td>
</tr>
<tr>
<td><em>Viridovipera gracilis</em></td>
<td>83-96</td>
<td>79-90</td>
<td>14-24</td>
<td>Mice</td>
<td>Chu <em>et al.</em> (2009)</td>
</tr>
<tr>
<td><em>Crotalus atrox</em></td>
<td>79-80</td>
<td></td>
<td>27-30</td>
<td>Mice</td>
<td>McCue (2007)</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>86</td>
<td>81</td>
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Notes: ADE, apparent digestive efficiency; AAE, apparent assimilation efficiency; T_b, body temperature (or range) at which experiments were conducted.
At ambient temperatures within its thermal range, *H. haemachatus* had passage times that were strongly dependent on temperature. The seemingly modest increase in ambient temperature from 20 to 27°C caused gut passage time to decrease by 25%, or by more than a day. This result agrees with the trend recorded by other studies (Skoczylas 1970; Smith 1976; Greenwald & Kanter 1979; Naulleau 1983; Stevenson et al. 1985; Hailey & Davies 1987; Bedford & Christian 2000; Toledo et al. 2003; Sievert et al. 2005; Tsai et al. 2008). Gut passage time was, however, independent of food type, in spite of the differences in AAE, and the energy content of the food and excreta. Within the range of masses of the snakes we observed, gut passage time also was independent of body mass. We did find a weak, but significant, relationship between the number of days to first defaecation and relative meal size. An increase in passage time with an increase in relative meal size implies that small prey items, relative to snake size, would be digested more rapidly than larger prey items. Naulleau (1983) reported such a trend in *Vipera aspis* and argued that it was the result of the relatively greater surface area available for digestion in small prey items. In our study, however, the size of the food item offered to snakes was not dependent on snake size. Larger snakes were fed more mice rather than larger mice and we found no relationship between snake mass and passage time. An alternative explanation for slower passage times for relatively larger meals is that these larger meals take longer to digest because digestive enzymes are diluted more by the larger meal.

We used the time to first defaecation as a measure of gut passage time, which we assumed to be an index of digestion rate. Peterson et al. (1993) argue that time to first defaecation may not be a good measure of digestion rate in snakes, because snakes can hold faeces in their large intestine for a considerable time. This may be valid especially for heavy bodied, ambush-foraging species (Lillywhite et al. 2002), as defaecating while in ambush might reveal the presence of the snake to prey and predators, and stocky builds allow for the retention of faecal matter. However, *H. haemachatus* is an active forager with a relatively slim build. Greenwald and Kanter (1979) contend that, since some species of snakes produce several defaecations per feed, intestinal volume does not permit storage of all the faeces from a meal and faeces formed early must be voided to accommodate succeeding deposits. Even if this is not the case, we contend that time to first defaecation is at least a relative measure of passage time since inconsistencies in measures owing to faecal retention were likely to have affected gut passage time in a similar way at both our trial temperatures.

It has long been supposed that the venoms in some snakes, especially those that are predominantly proteolytic in action, enhance the digestion of prey. Thus, venomous snakes might be expected to have higher DEs, or faster digestion. Thomas and Pough (1979) showed that mice envenomated with *Crotalus atrox* venom were digested faster by several species of non-venomous snakes than were non-envenomated mice, especially at low temperatures. However, McCue (2007) found no venom effects on DE or speed of digestion in *C. atrox* itself, while Chu et al. (2009) have shown that venom has no beneficial impact on DE for *Viridovipera gracilis* and *V. stejnegeri*, even at low temperatures. Our relatively low measures of AAE for *H. haemachatus* support this conclusion, and the emergent trend, so far, is for venomous snakes to have lower efficiencies than do non-venomous ones. These findings challenge the long-standing paradigm that snake venom facilitates digestion (Chu et al. 2009).
We studied snakes in the laboratory, at constant and controlled temperatures, and presented them with adequate, high-quality food. This approach allowed us to dissect out physiological attributes of digestion in the snakes, and it provided some of the information necessary to analyse the contribution of food energy gain to the energetics of the species, adding to the understanding of digestion efficiencies and rates for snakes in general. Our approach eliminated the effects of thermoregulatory behaviour, food availability and prey capture. We can conclude, for example, that the higher energy content of mice more than compensates for *H. haemachatus*’ lower AAE for this food type. The average energy content of the *M. musculus* was more than twice that of *X. laevis* per gram of fresh mass. *Hemachatus haemachatus* eating frogs would have to eat approximately twice as much *X. laevis* by mass to gain the equivalent energy, even after adjustments have been made for the different AAEs. Much of the discrepancy is the result of the water content of frogs greatly exceeding that of mice. This comparison does not include considerations of differences that snakes may experience in the costs of prey capture, which may still make frogs the preferred diet of *H. haemachatus* in their natural habitat.

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