

Cooking and grinding reduces the cost of meat digestion

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Abstract

The cooking of food is hypothesized to have played a major role in human evolution partly by providing an increase in net energy gain. For meat, cooking compromises the structural integrity of the tissue by gelatinizing the collagen. Hence, cooked meat should take less effort to digest compared to raw meat. Likewise, less energy would be expended digesting ground meat compared to intact meat. We tested these hypotheses by assessing how the cooking and/or grinding of meat influences the energy expended on its digestion, absorption, and assimilation (i.e., specific dynamic action, SDA) using the Burmese python, *Python molurus*. Pythons were fed one of four experimental diets each weighing 25% of the snake's body mass: intact raw beef, intact cooked beef, ground raw beef, and ground cooked beef. We measured oxygen consumption rates of snakes prior to and up to 14 days following feeding and calculated SDA from the extra oxygen consumed above standard metabolic rate. Postprandial peak in oxygen consumption, the scope of peak rates, and SDA varied significantly among meal treatments. Pythons digesting raw or intact meals exhibited significantly larger postprandial metabolic responses than snakes digesting the cooked ground meals. We found cooking to decrease SDA by 12.7%, grinding to decrease SDA by 12.4%, and the combination of the two (cooking and grinding) to have an additive effect, decreasing SDA by 23.4%. These results support the hypothesis that the consumption of cooked meat provides an energetic benefit over the consumption of raw meat.

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1. Introduction

Food scientists typically advance three main reasons for why meat is cooked; improved palatability, preservation, and protection from pathogens and parasites (Charley, 1982; Lawrie, 1991; Barham, 2000; Warriss, 2000). By contrast, the consequences of cooking for net energy availability have conventionally been regarded as neutral or negative due to energy loss from drippings or the chemical degradation of amino acids (Borenstein and Lachance, 1988). However, anthropologists have recently proposed that there is an energetic benefit of cooking food and that the advent of cooking has had diverse effects on human evolution (Wrangham and Conklin-Brittain, 2003). Suspected outcomes of the increase in energy efficiency from consuming cooked food

include a reduction in gut size and an increase in daily energy expenditure. In support of the energetic significance of cooking, individuals that consume only raw food tend to be thin with little stored energy, with such women possessing impaired reproductive function (Koebnick et al., 1999). Also, there is ample information showing that cooking increases the digestibility of starch and the glycemic index of starchy foods (Olkku and Rha, 1978; Collings et al., 1981; Snow and O'Dea, 1981; Tester and Sommerville, 2000; Langkilde et al., 2002). Unfortunately, little empirical evidence exists that demonstrates the energetic benefits of cooking, especially the cooking of meat (Wrangham, 2006).

High temperature has two major effects on the physical properties of meat (Bouton and Harris, 1972; Purslow, 2005; Tornberg, 2005). At around 40 °C, muscle fiber proteins start to denature, leading to the contraction, drying and toughening of the meat. Between 50 and 60 °C, collagen denatures, causing gelatinization and solubilization of the connective tissues sheaths surrounding the muscle fibers. As cooking proceeds the meat becomes increasingly more tender and hence can be more easily

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chewed (Lucas, 2004). Meat quality and cooking method both determine the extent that heating impacts the shear values of the meat and the perception of its tenderness (Harris and Shorthose, 1988; Combes et al., 2003; Ruiz de Huidobro et al., 2005).

Conceivably, the denaturing of proteins and gelatinization of collagen from cooking should facilitate the digestive actions of gastric acids and proteolytic enzymes (Davies et al., 1987). Hence, cooking should decrease the cost and time of gastric and intestinal performance, thereby increasing net energy gain. Similarly, the grinding of meat, akin to chewing, should also decrease cost and increase gain. We tested the hypotheses that cooking and grinding reduce the cost of meat digestion using the Burmese python (*Python molurus*) as our experimental model (Secor and Diamond, 1998). Burmese pythons are strict carnivores and are able to ingest large intact meals that can exceed 50% of their body mass (Secor and Diamond, 1997). After feeding, pythons experience a large metabolic response [the specific dynamic action (SDA) of the meal], that is equivalent to 28–37% of the ingested meal's energy (Secor and Diamond, 1997). It is also known for the Burmese python that reducing the structural integrity of their meal lowers SDA (Secor, 2003). In this study we assessed the individual and combined effects of the cooking and grinding of meat on python SDA.

2. Materials and methods

2.1. Study animals and their maintenance

Hatchling Burmese pythons (*P. molurus*) (~120 g) were purchased commercially (Bob Clark Captive Bred Reptiles, Oklahoma City, OK, USA; Strictly Reptiles Inc., Hollywood, FL, USA) and maintained individually in 20-L plastic cages within customized racks (Animal Plastics, Johnston, IA, USA). Embedded in the rear of each rack is a heat conductive cable that maintains a rear to front gradient of 30–26 °C within each cage. Pythons were kept under a 14 h:10 h light:dark cycle, fed pre-killed laboratory rodents every two weeks, and provided with water ad libitum. Prior to the start of metabolic experiments, we

withheld food from pythons for a minimum of 30 days to ensure that they were postabsorptive (Secor and Diamond, 1995).

2.2. Metabolic response to meal treatments

For each metabolic trial, pythons (mean body mass \pm 1 SE = 569 \pm 19 g, $N=16$) were fed either an adult rat or one of four experimental beef meals; intact raw beef, intact cooked beef, ground raw beef, and ground cooked beef. Lean beef (eye of the round, less than ~5% fat) was purchased fresh for each trial from a local meat supplier (South's Finest Meats, Tuscaloosa, AL, USA) and cut to weigh 25% of the snake's body mass. For ground treatments, meat was ground using a manual meat grinder (Universal, L.F. & C. New Britain, CT, USA). For cooked treatments, intact or ground raw meat was placed in a covered dish and microwaved (Sharp R-409EW, Mahwah, NJ, USA) to an internal temperature of 80 °C. Any water lost from the meat during cooking was collected from the cooking dish and added to the meal when fed to the pythons such that there was no loss of meal mass due to cooking. All snakes were carefully force fed meals either directly through their mouths (intact meals) or through a feeding tube (ground meals) (Fig. 1). We also fed eight pythons each a single adult rat equaling 25 \pm 1% of their body mass to compare the metabolic responses of rat-fed pythons with those of snakes fed the beef meals.

We measured rates of oxygen consumption ($\dot{V}O_2$) of pythons using closed-system respirometry (Vleck, 1987; Secor and Diamond, 1997). Fasted pythons were placed into individual respirometry chambers (9-L plastic containers fitted with inflow and outflow stopcocks) and maintained within a temperature-controlled environmental chamber at 30 °C. For each sampling period, a 50-ml gas sample was drawn from each chamber, the chambers were sealed, and a second gas sample was drawn 1–2 h later. Gas samples were injected into an O_2 analyzer (S-3A/II, AEI Technologies, Naperville, IL, USA) after passing through a column of water absorbent (Drierite) and CO_2 absorbent (Ascarite). We calculated $\dot{V}O_2$ (ml h^{-1}) after correcting for standard pressure and temperature as described by Vleck (1987). We measured $\dot{V}O_2$ of fasted pythons at 12-h intervals for 4 days

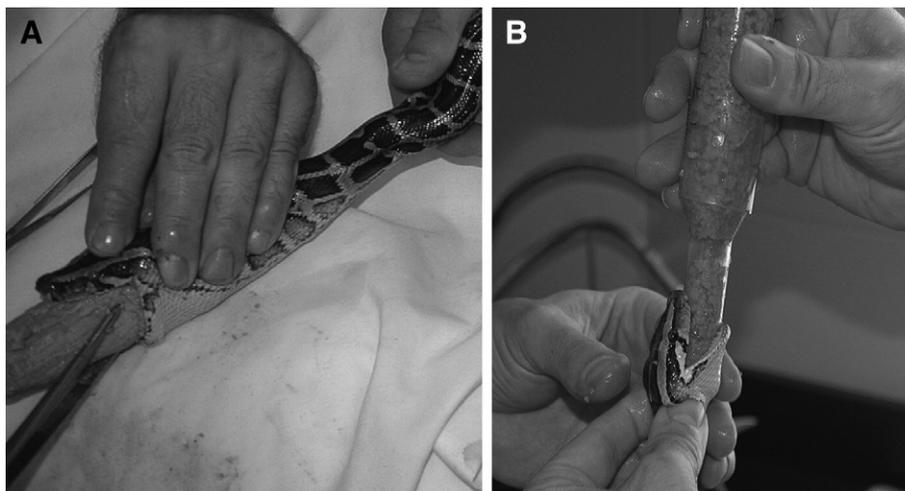


Fig. 1. Force-feeding pythons intact cooked (A) and ground cooked meat (B).

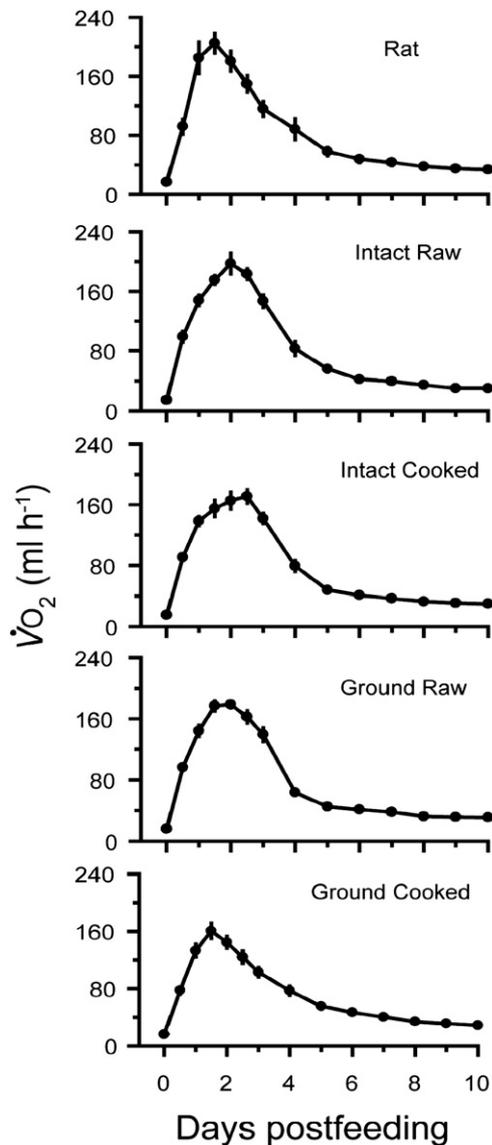


Fig. 2. Mean oxygen consumption ($\dot{V}O_2 \pm 1$ SE) of Burmese pythons (*Python molurus*) prior to day 0 and up to 10 days after consuming meal treatments equaling 25% of snake body mass ($N=8$ for each meal treatment). Cooked treatments (intact and ground) were obtained by microwaving lean (<5% fat) raw meat to an internal temperature of 80 °C. See Materials and methods for details.

and assigned the lowest measure $\dot{V}O_2$ of each individual as its standard metabolic rate (SMR). The morning following SMR measurements, snakes were removed from their respirometry chambers, fed their prepared meals, and returned to their chambers for subsequent metabolic measurements. We measured $\dot{V}O_2$ of fed snakes at 12-h intervals for 3 days and thereafter at 24-h intervals for 11 more days.

2.3. Quantifying the cost of digestion

We examined the postfeeding metabolic response to digestion, absorption, and assimilation of each meal treatment by measuring the following variables: 1) SMR, the minimum $\dot{V}O_2$ measured in the 4 days prior to feeding; 2) peak $\dot{V}O_2$, the highest $\dot{V}O_2$ measured

during digestion; 3) the factorial scope of peak $\dot{V}O_2$, peak $\dot{V}O_2$ divided by SMR; 4) duration, the number of days that postfeeding $\dot{V}O_2$ was significantly greater than SMR; 5) SDA, the summed total energy expended above SMR during the postfeeding period of significantly elevated $\dot{V}O_2$; and 6) SDA coefficient, SDA quantified as a percentage of ingested energy. We quantified SDA from the amount of extra O_2 consumed above SMR during the duration of significantly elevated $\dot{V}O_2$ and converted this value to kilojoules assuming 19.8 J expended per ml O_2 consumed (Geesaman and Nagy, 1988).

2.4. Bomb calorimetry

We determined the energy content of each experimental meal by multiplying its wet mass by its mass-specific energy value (kJ g^{-1} wet mass) as determined by bomb calorimetry. For the rat meal, eight rats (132 ± 5 g, range 117–161 g) were weighed, dried at 60 °C, reweighed, ground into a fine powder using an electric grinder, and pressed into pellets. For each beef treatment, four 30–70 g samples of meat were taken from four different pieces of beef, and weighed, processed as above (intact raw, ground raw, intact cooked, and ground cooked), dried at 60 °C, reweighed, ground into a fine powder, and pressed into pellets. For each rat or meat sample, three pellets were ignited in a bomb calorimeter (1266, Parr Instruments Co., Moline, IL, USA) to determine energy content. Wet mass energy content was calculated as the product of dry mass energy equivalent as determined by bomb calorimetry, and the sample's percent dry mass. Rats had an energetic equivalent of $6.96 \pm 0.11 \text{ kJ g}^{-1}$ wet mass. We found no significant difference (P values > 0.28) in either the dry or wet mass energy content among the four beef treatments and therefore elected to use the wet mass energy value determined from the intact raw beef samples ($6.59 \pm 0.14 \text{ kJ g}^{-1}$ wet mass) to calculate meal energy for all beef treatments. Meal energy was therefore used to calculate the SDA coefficients for each metabolic trial.

2.5. Statistical analysis

For each meal treatment we used a repeated-measures analysis of variance (ANOVA) to test for an effect of time (days postfeeding) on $\dot{V}O_2$. Each ANOVA was followed by a post hoc pairwise mean comparison to determine when postfeeding $\dot{V}O_2$ was no longer significantly different from SMR. To examine the effects of meal treatment, we tested for differences in body mass, meal mass, and metabolic measures among the four beef meals using ANOVA for body mass and mass-specific metabolic measures, and ANCOVA (body mass as the covariate) for meal mass and whole-animal metabolic measures. When effects of meal treatment were significant, we used pairwise mean comparisons to identify those treatments that differed significantly from each other. For all statistical comparisons, we set $\alpha=0.05$ and report mean values as means ± 1 SE.

3. Results

The digestion of the intact beef meal generated nearly identical metabolic response to that stemming from the digestion

Table 1
Body mass, meal mass, standard metabolic rate (SMR) and five variables of the metabolic response to digestion for Burmese pythons (*Python molurus*) digesting rats and four beef meals

Variable	Rat	Intact raw beef	Intact cooked beef	Ground raw beef	Ground cooked beef	<i>F</i>	<i>P</i>
<i>N</i>	8	8	8	8	8	–	–
Body mass (g)	588±31	572±23	582±18	586±20	580±43	0.04	0.987
Meal mass (g)	147±8	143±6	146±5	147±5	145±11	1.12	0.359
SMR (ml h ⁻¹)	16.5±0.7	14.5±0.9	15.0±0.8	15.8±0.9	16.3±1.1	1.18	0.335
SMR (ml g ⁻¹ h ⁻¹)	0.028±0.001	0.025±0.001	0.026±0.001	0.027±0.001	0.028±0.001	1.41	0.259
Peak $\dot{V}O_2$ (ml h ⁻¹)	217±15	203±13 ^c	180±10 ^{a,b}	183±6 ^{b,c}	161±10 ^a	5.84	0.003
Peak $\dot{V}O_2$ (ml g ⁻¹ h ⁻¹)	0.379±0.035	0.354±0.013 ^b	0.309±0.015 ^a	0.316±0.012 ^a	0.280±0.009 ^a	6.02	0.003
Scope of peak $\dot{V}O_2$	13.2±0.7	14.0±0.3 ^c	12.1±0.5 ^b	11.9±0.7 ^b	10.0±0.4 ^a	10.4	0.0001
Duration (days)	8	8	7	7	7	–	–
SDA (kJ)	299±17	303±11 ^c	262±10 ^b	263±8 ^b	232±12 ^a	9.14	0.0002
SDA (kJ kg ⁻¹)	509±23	532±16 ^b	452±19 ^a	452±16 ^a	411±30 ^a	5.72	0.0035
SDA coefficient	29.0±1.33	32.3±1.0 ^b	27.4±1.2 ^a	27.4±1.0 ^a	24.9±1.8 ^a	5.72	0.0035

Values are presented as means±1 SE and *F* and *P* values result from either ANOVA or ANCOVA analysis of the four beef treatments. For variables with significant ANOVA or ANCOVA, different superscript letters denote significant ($P < 0.05$) differences between the means as determined by post hoc pairwise comparisons (see text for details).

of the more natural rat meal (Fig. 2). Both meals resulted in more than a 13-fold increase in $\dot{V}O_2$, an 8 day duration of elevated metabolism, and very similar SDA (Table 1). Given this match in the metabolic responses between the rat and intact raw beef meals, we focused our remaining comparisons on the four beef treatments.

Python body mass, meal mass, and SMR (mass-specific and whole animal) did not significantly differ among the four beef treatments (Table 1). For each treatment, $\dot{V}O_2$ of pythons had increased significantly (P values < 0.0002) within 12 h after feeding, peaked between 1.5–2.5 days postfeeding, and remained significantly elevated above SMR for a total of 7 or 8 days (Fig. 2). Both the postprandial peak in $\dot{V}O_2$ and the factorial scope of peak $\dot{V}O_2$ varied significantly (P values < 0.004) among treatments (Table 1). We found that meals of intact raw beef generated significantly (P values < 0.035) higher peaks in $\dot{V}O_2$ (203±13 ml h⁻¹) compared to both whole (180±10 ml h⁻¹) and ground (161±10 ml h⁻¹) cooked meals. In addition, ground raw meals expressed a significantly ($P = 0.042$) higher $\dot{V}O_2$ peak compared to ground cooked meals (Table 1). Correspondingly, the factorial scope of peak $\dot{V}O_2$ was significantly greater (P values < 0.013) for the intact raw meals (14.0±0.3) compared to the other three beef meals. When digesting the intact cooked

meals (12.1±0.5) or the ground raw meals (11.9±0.7), pythons possessed significantly (P values < 0.014) higher scopes compared to when digesting the ground cooked meals (10.0±0.4) (Table 1). For the intact raw meals, pythons maintained elevated rates of metabolism for 8 days, whereas for the other three meal treatments, metabolism was elevated for seven days (Table 1).

The total energy expended on digestion, absorption, and assimilation (SDA), quantified as kJ, kJ kg⁻¹, and as a percentage of meal energy, differed significantly (P values < 0.004) among meal treatments (Table 1). The consumption of the intact raw meals resulted in a significantly greater SDA (303±11 kJ) compared to that generated by the other three meals. Both the whole cooked (262±10 kJ) and ground raw (263±8 kJ) meals generated significantly greater SDA compared to the ground cooked meal (232±12 kJ). This pattern was repeated with the analysis of mass-specific SDA (kJ kg⁻¹; Table 1). When calculated as a percentage of meal energy, SDA was significantly ($P = 0.002$) higher for the intact raw meal (32.3±1.0%) compared to the ground cooked meal (24.9±1.8%; Table 1).

4. Discussion

We found using Burmese pythons that the cooking of meat significantly reduces the combined costs of its digestion and assimilation, the meal's SDA. When the intact or ground meat was microwaved, the SDA fell by an average of 12.7%. Likewise, the grinding of meat (raw or cooked) reduced SDA by an average of 12.4%. Together, cooking and grinding lowered SDA by 23.4% (Fig. 3). These results demonstrate that cooking and grinding separately, and in combination, decrease the amount of energy required to digest and assimilate a meal. The similarities in the decrease in SDA due to cooking and grinding and their additive effects suggest that the cooking of meat has as much impact on facilitating digestion as grinding or chewing.

Since snakes do not masticate their food, the stomach alone must break down each meal into a soup-like chyme suitable for passage into the small intestine (Secor, 2003). If the integrity of their intact meal is compromised by grinding then some of the mechanical and chemical digestion normally performed by the

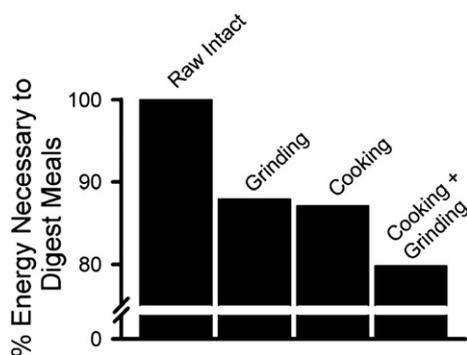


Fig. 3. The effect of grinding and cooking meat on the energy needed to digest, absorb, and assimilate meat meals in pythons. Bars are scaled as a percentage of intact raw meat.

stomach has already been accomplished, thus decreasing gastric effort. This was observed when pythons were fed homogenized rats and the resulting SDA was 75% of that generated by the digestion of intact rats (Secor, 2003). Likewise we found in this study that the grinding of meat significantly reduces SDA.

Compared to the raw meals, the cooked meals took less time (for intact meals) and energy (for intact and ground meals) to digest and assimilate. Cooking softens and solubilizes the collagen-rich connective tissues that surround the muscle fibers thereby increasing access of the tissue to gastric acids and proteolytic enzymes. Therefore like grinding, cooking reduces the structural integrity of the meat, thereby speeding up gastric digestion.

As implied, we suspect that the reduction in SDA for ground and cooked treatments is due to a decrease in the efforts of the stomach. For Burmese pythons digesting intact rodent meals, an estimated 55% of the SDA is attributed to gastric performance, i.e., production of HCl and gastric enzymes (Secor, 2003). Oxynticopeptic cells of the python's gastric mucosa actively pump H^+ into the gastric lumen, via the H^+/K^+ ATPase, which joins with released Cl^- to form HCl (Guyton and Hall, 2000). For the python, the high cost of gastric performance is incurred by the rapid and continuous production of HCl that results in gastric pH dropping from fasting levels (7.5) to postprandial levels of 1–2 within 24 h after feeding, levels which are maintained for approximately 6 more days of digestion (for meals equaling 25% of snake body mass; Secor, 2003). It is predicted that one molecule of ATP is used to pump one molecule of H^+ into the gastric lumen (Reenstra and Forte, 1981). The metabolic machinery for ATP production and the cellular site of oxygen consumption are mitochondria, which fill 40% of the pythons' oxynticopeptic cells (Secor, personal observation). Thus, any process that reduces the structural integrity of the meal, would decrease the amount of HCl and enzymes needed to prepare the meals for entry into the small intestine.

The findings of this study indicate that cooking, by disrupting muscle structure, decreases the cost of gastric digestion. An added benefit of the softening effects of cooking is that less time and effort is expended on chewing (Lucas, 2004). For rats, it has been shown that the softening of their food (by increasing air content) reduces SDA and increases energy gain (Oka et al., 2003). These combined benefits to oral and gastric digestion support the hypothesis that by cooking meat, humans experience an energy savings (Wrangham, 2006). The magnitude of such a savings has not yet been experimentally quantified. However for humans digesting a standard diet that includes cooked items, SDA is low (6–7% of ingested energy; Swindells, 1972; Ravussin et al., 1986; Maffei et al., 2001) compared to that of fishes (12–20%; Beamish, 1974; Fu et al., 2006), amphibians (13–35%; Secor and Boehm, 2006; Secor et al., 2007), reptiles (12–33%; Secor and Diamond, 2000; McCue, 2006), birds (11–13%; Bech and Præsteng, 2004; Green et al., 2006), and other mammals (13–16%; Gallivan and Ronald, 1981; Costa and Kooyman, 1984) digesting raw intact food items. This study serves to lay the groundwork for future investigations on the effects of cooking on SDA using more relevant mammal species and humans. Combined with models of human energy flux,

these studies will be instrumental in demonstrating the impact of cooking on human energetics and its role in the evolution of human life history.

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