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FUNCTIONAL MORPHOLOGY, STABLE ISOTOPES, AND HUMAN EVOLUTION: A MODEL OF CONSILIENCE

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Foraging is constrained by the energy within resources and the mechanics of acquisition and assimilation. Thick molar enamel, a character trait differentiating hominins from African apes, is predicted to mitigate the mechanical costs of chewing obdurate foods. The classic expression of hyperthick enamel together with relatively massive molars, termed megadontia, is most evident in *Paranthropus*, a lineage of hominins that lived about 2.7–1.2 million years ago. Among contemporary primates, thicker molar enamel corresponds with the consumption of stiffer, deformation-resistant foods, possibly because thicker enamel can better resist cracking under high compressive loads. Accordingly, plant underground storage organs (USOs) are thought to be a central food resource for hominins such as *Paranthropus* due to their abundance, isotopic composition, and mechanical properties. Here, we present a process-based model to investigate foraging constraints as a function of energetic demands and enamel wear among human ancestors. Our framework allows us to determine the fitness benefits of megadontia, and to explore under what conditions stiff foods such as USOs are predicted to be chosen as fallback, rather than preferred, resources. Our model predictions bring consilience to the noted disparity between functional interpretations of megadontia and microwear evidence, particularly with respect to *Paranthropus boisei*.

KEY WORDS: **Enamel thickness, fallback foods, foraging models, hominin evolution, *Paranthropus*, underground storage organs.**

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All animals must acquire and deliver food to their digestive systems. The mechanics of this process can result in the gradual wear, or senescence, of anatomical structures such as claws, beaks, and teeth. Such wear is detrimental to the foraging efficiency and reproductive success of a wide range of animals (Swennen et al. 1983; Raupp 1985; Juanes 1992; Juanes and Smith 1995; King et al. 2005; Roitberg et al. 2005). For mammals, the oral processing, or chewing, of food is a necessary wear-inducing behavior (Stirling 1969; McArthur and Sanson 1988; Skogland 1988; Perez-Barberia and Gordon 1998), and natural selection is predicted to favor dental attributes that prolong chewing efficiency. Accordingly, considerable attention has been focused on the microstructure, morphology, and functional ecology of mammalian molars, particularly the enamel.

Enamel is a hard, mineralized tissue covering the elastic and vascularized dentin, and rooted by cementum to the jaws of most mammals (Lucas 2004). Oral comminution of food before digestion is, today, a uniquely mammalian behavior (Lucas 2004), although gizzards and pharyngeal teeth serve this function in birds and some teleosts, respectively, and some ornithischian dinosaurs did comminute food orally (Weishampel et al. 2004). Some mammals have ever-growing teeth, but primates replace their molar teeth only once, after which they face an adult life of wear and occasional catastrophic damage (Constantino et al. 2010). Thus, adult primates must find a balance between the opposing advantages of enamel preservation and the consumption of foods with different propensities for enamel wear. In this vein, the identification of contemporary form–function relationships between tooth enamel and diet have been instructive for inferring foraging behavior in the fossil record, and dental enamel has long informed debate in the discipline of paleoanthropology (Ungar and Sponheimer 2011).

For example, among living mammals, relatively thick molar enamel is widely associated with the consumption of stiff, deformation-resistant (hard) foods, and it follows that hominins such as the genus *Paranthropus*, which possessed large "megadont" molars with hyperthick enamel (McHenry 1988), also consumed such foods (Kay 1981; 1985; Wood and Constantino 2007; Lucas et al. 2008a; b; Vogel et al. 2008; McGraw and Daegling 2012; McGraw et al. 2012; Wood and Schroer 2012; Constantino 2013). However, the identity of these stiff food objects has long-puzzled researchers and fueled hypotheses on the cost of dietary specialization (Balter et al. 2012). More recently, isotopic data from a range of hominin taxa, including *Paranthropus*, have revealed a heavy dependence on C_4-photosynthetic plants (which have tissues enriched in ^{13}C and include tropical grasses and sedges) or possibly animals that consumed these plants (Sponheimer and Lee-Thorp 1999; Ungar and Sponheimer 2011). Depending on the tissue, C_4 plants can be highly resistant to fracture or deformation, with mechanical attributes that are expected to induce wear or chip the enamel of molar teeth. Indeed, the molars of *Paranthropus boisei* are often heavily worn and deeply chipped (Constantino et al. 2010); and yet, paradoxically, the occlusal surfaces of nine well-preserved molars evince a microwear fabric that indicates a diet of soft, pliable foods (Ungar et al. 2008; 2010; 2012). These discrepant lines of evidence—indicating a diet of C_4 foods that are simultaneously hard and soft—have been challenging to reconcile, and it is sometimes referred to as the "C_4 conundrum."

For *Paranthropus*, the consumption of ^{13}C-enriched tissues might have included graminivorous insects and/or the leaves, seeds, and underground storage organs (USOs) of grasses and sedges (Sponheimer and Lee-Thorp 2003; Sponheimer et al. 2005; Yeakel et al. 2007; Cerling et al. 2011; Lee-Thorp 2011). Recently, the USOs—bulbs, corms, and rhizomes—of grasses and sedges have attracted special attention (Dominy 2012; Lee-Thorp et al. 2012) because they are widespread in many savanna habitats and a central food resource for some populations of baboons and humans (Post 1982; Barton et al. 1993; Youngblood 2004; Alberts et al. 2005). Corms in particular are stiff and deformation-resistant (Dominy et al. 2008) and a significant cause of tooth wear among savanna baboons (Galbany et al. 2011). However, the mechanical and nutritional properties of these potential foods, as well as the anatomical constraints of hominin dentition, are seldom factored into interpretations of hominin foraging behavior, and the diet of *Paranthropus* remains obscured by disquieting discrepancies (Grine et al. 2012). Here we attempt to bring consilience to these discrepancies by using a modeling framework.

The physiological and behavioral processes that yield inconsistent interpretations of diet can be explored with foraging models that depend on the anatomical and energetic states of potential foragers. Here we present a stochastic dynamic programming (SDP) model (Mangel and Clark 1988; Mangel and Ludwig 1992; Houston and McNamara 1999; Clark and Mangel 2000) to quantify the optimal foraging decisions for organisms that must balance energetic gain with enamel wear, while accounting for the stochastic effects of a variable environment. We base our model on measurements for anthropoid primates and focus specifically on decisions affecting hominins in savanna-woodland environments. We determine decision matrices in which specific food resources are chosen to maximize an animal's fitness conditional on two internal states: its energetic reserves and molar enamel volume.

This model-based approach is well suited to test a variety of important questions about the effects of dental enamel on foraging, and we focus on three potentially informative lines of inquiry. First, and most essential, how does the quantity of enamel influence the foraging strategies of savanna-woodland anthropoid primates, and how does megadont dentition alter these strategies? Second, to what degree do these foraging decisions depend on resource quality and quantity, where the quality and quantity of particular food items can vary depending on the environmental conditions? Third, can extradentary mechanical advantages, such as peeling, pounding, or cooking alter the influence of dental enamel, and to what extent do these alterations provide fitness benefits? Finally, we relate our model predictions to paleontological evidence of hominin diets, and conclude by showing that the model framework presented here can be used to both predict and inform paleodietary data.

Models and Analysis

Models based on stochastic dynamic programming are recognized as one of the best ways of predicting the evolutionary endpoints for natural selection. In this section, we outline the structure of the SDP model from which we determine fitness-maximizing foraging behaviors of hominin species. First, we define energetic state and enamel volume as the state variables of the model, and describe the processes that govern how these state variables change over time. We also introduce three factors that influence an organism's state: (1) the probability of finding different amounts of food (including not finding it); (2) the probability of losing a given amount of enamel as a function of chewing different foods; and (3) the quality of the environment at a given time. Second, we introduce the fitness function, which depends upon the state of the organism and time. Starting at a fixed final time, we show one can iterate the fitness function backwards in time, thus determining both fitness at earlier times and foraging decisions (the decision matrix) as a function of state. As the current time moves further and further from the final time, the decision matrix becomes independent of time (stationary), only depending upon physiological state. Third, we combine the stationary decision matrices with a Monte Carlo simulation going forward in time (forward-iteration) to examine the consequences of different foraging behaviors as a function of an organism's anatomical attributes and/or its ability to externally modify its food.

STATE DYNAMICS

We model the foraging decisions of an organism as a function of two principle state variables: (1) its net energy reserves at time t, $X(t) = x$; and (2) its enamel volume at time t, $V(t) = v$, where time is measured in days. We model a single unit of energy as 10 MJ, equivalent to 2388 kcal and roughly equal to the energy in 1 kg of animal tissue (Wolfram Research 2012). Accordingly, the maximum potential energy reserves for an organism, $x_{\max}$, is its body size, such that $x_{\max} = 70$ for a 70 kg organism. A unit of molar enamel volume v corresponds to 100 mm^3. Specific properties of molar anatomy correlate with body size (Shellis et al. 1998), and we use these relationships to approximate maximal (i.e., unworn) molar enamel volume, $v_{\max}$ as a function of $x_{\max}$, for both non-megadonts and megadonts (see Appendix S1 and Fig. S1). Both the potential energy gained from food and its impact on an organism's enamel change as a function of food mechanical properties. We consider an approximating measurement for the mechanical properties of food taking into account both the elasticity (Young's modulus, E_i, [MPa]) and the fracture toughness (R_i, [Jm^{-2}]) of food i, which approximates "hardness," measured as $\sqrt{E_i R_i}$ (Lucas et al. 2008b). We let η_i denote the digestibility of food i ranging between $\eta_i = 0$ (indigestible) and $\eta_i = 1$ (completely digestible; sensu Lucas et al. 2000). We assume that an individual dies when its energy reserves fall below $x_{\text{crit}} = (3/4)x_{\max}$ or its enamel volume falls below v_{crit} (see Appendix S1).

We let γ_i (in units of x) denote an organism's energetic gains for food type i (Table 1). Because larger animals gain relatively more calories per foraging bout, energetic gain is calculated as $\gamma_i = (\text{energydensity}/2388) \times (x_{\max}/10)$, where the constant (1/2388) normalizes the energy density of foods to units of x, and the modifier $(x_{\max}/10)$ ensures that gain scales weakly with body size. We assume that foraging behavior is governed primarily by caloric, or energetic, limitations (Rothman et al. 2011), and model the daily cost of foraging for food type i, c_i (in units of x), as a function of an organism's body size, and the aggregation of food on the landscape. We modified the estimates of daily energetic expenditure (kcal/day) by Leonard and Robertson (1997) to model daily energetic cost, such that $c_i = C_1 \times \text{RMR} \times (1/\xi_i)/2388$, and resting metabolic rate $(\text{RMR}) = 69.1x_{\max}^{0.761}$, where C_1 is the activity constant ($C_1 = 3.80$ for moderate activity), the constant (1/2388) operates as before, and ξ_i is the mean encounter rate for food i, such that $(1/\xi_i)$ is proportional to foraging time. Foods that are encountered more frequently (high ξ_i) thus have lower per encounter foraging costs. We assessed a costlier version of the model, where $c_i = (C_1 \times \text{RMR} \times (1/\xi_i) + C_2 \times \text{RMR})/2388$, where $C_2 = 1.2$, accounting for additional daily costs independent of food choice Leonard and Robertson (1997).

We identify four general food groups: (1) a nutritious, mechanically pliable, patchily distributed food (e.g., fruit); (2) a non-nutritious, mechanically hard, widely distributed food (e.g., leaves from C$_4$-photosynthetic grasses); (3) a nutritious, mechanically hard, widely distributed food (e.g., USOs); and (4) a highly nutritious, potentially hard, patchily distributed food (e.g., arthropods or more generally small quantities of animal tissue). We set the food energy density to be 717, 150, 785, and 1518 kcal/kg for fruit, grass leaves, USOs, and arthropods/animal tissue, respectively (Wolfram Research 2012). The mechanical properties of the food groups are measured by toughness [Jm^{-2}]: $R = (561, 330, 265, 1345)$, and Young's modulus [MPa]; these are $E = (1, 10, 5, 200)$ for fruits, grass leaves, USOs, and arthropods with fracture-resistant exoskeletons, respectively (Lucas 2004; Williams et al. 2005; Dominy et al. 2008; Yamashita et al. 2009). We used a conservatively low value for the fracture toughness of grass leaves in our model (330 Jm^{-2}; Lucas 2004). Although the fracture toughness of East African grasses is typically > 1000 Jm^{-2} (N.J. Dominy, unpubl. data), we assume that a grazing primate with bunodont molars would selectively consume tender grass leaves.

Many primates are known to modify the mechanical properties of foods before they are consumed (Altmann 2009). We consider four extradentary processing capabilities: (1) none, where the mechanical properties are as described; (2) peeling, pounding, or cooking USOs ($R_{\text{USO}} = 138$ and $E_{\text{USO}} = 5$; Dominy

Table 1. **Parameters and variables in the dynamic state variable model. Parenthetical values (except for ρ) are with respect to the foods: (fruit, grass leaves, USOs, arthropods). Values for *E* and *R* are those when no mechanical advantage is included. See methods for relevant references. Auto. = Autocorrelated.**

Parameter	Interpretation	Units	Value(s): Rich quality	Poor quality
$X(t) = x$	Energy reserves at time t	10 [MJ]	State variable	
$V(t) = v$	Enamel volume at time t	100 [mm^3]	State variable	
$K = k$	Number of food items found	Count	Stochastic variable	
$\Omega = \omega$	Basal enamel wear	[mm]	Stochastic variable	
γ	Energetic gain	10 [MJ]	(1.5, 0.3, 1.6, 3.2)	(1.4, 0.3, 1.4, 2.9)
c	Energetic cost (minimal)	10 [MJ]	(0.7, 0.5, 0.7, 2.2)	(1.1, 0.5, 0.7, 2.2)
	Energetic cost (maximal)	10 [MJ]	(1.4, 1.2, 1.4, 2.8)	(1.8, 1.2, 1.4, 2.8)
ξ	Mean encounter rate	time^{-1}	(3, 4, 3, 1)	(2, 4, 3, 1)
ν	Dispersion	NA	(3, 5, 3, 2)	(2, 4, 3, 1)
η	Digestibility	NA	(0.9, 0.7, 0.8, 0.9)	Same
A	Molar surface area	[mm^2]	$\sum_{m=1}^{3} \pi L_m^2$	Same
b	Slope of enamel wear	[mm/k]	0.0425	Same
E	Young's modulus	[MPa]	(1, 10, 5, 200)	Same
R	Fracture toughness	[Jm^{-2}]	(565, 330, 265, 1345)	Same
$\bar{\omega}$	Expected basal enamel wear	μm	0.24	Same
σ	Basal enamel wear SD	μm	1.6	Same
d	Prob. of death at time t	NA	e^{-10}	Same
$Q(t)$	Habitat quality at time t	binary	r	p
$\boldsymbol{\rho}$	Quality transition probability matrix: $(\rho_{rr}, \rho_{rp}; \rho_{pr}, \rho_{pp})$		Wet (0.8, 0.2; 0.2, 0.8) Dry (0.2, 0.8; 0.8, 0.2) Auto. (0.8, 0.2; 0.8, 0.2)	
Φ	Terminal fitness function ($t = T$)			
F	Fitness function ($t < T$)			
$D^*(x, v)$	Stationary decision matrix			
$\hat{F}$	Expected future fitness			

et al. 2008); (3) peeling arthropod exoskeletons ($R_{\text{arthropod}} = 306$ and $E_{\text{arthropod}} = 0.22$; alternatively, this mechanical advantage can account for swallowing arthropods with minimal chewing); and (4) a combination of mechanically altering both USOs and arthropods.

The energetic and enamel state of an organism change over time, and these changes are due to both deterministic and stochastic processes. The energetic state of an organism depends primarily on the number of resources found and the amount of energy spent in a given foraging period. We let the random variable K represent the number of food items found in a single foraging period and that with probability $f_K(k)_i$ an individual finds k items of food type i. In Appendix S2, we derive the negative binomial model used for food encounters. We maintain this notation, upper case for random variables and lower case for specific values, for all stochastic variables. Because an organism's daily consumption is limited by gut volume, daily caloric gain is bounded by $x_s = (1/5) \times x_{\max}$ (proportional to average anthropoid % gut volume; Milton 1989). Thus, if k items of food type i are found in period t

$$X(t+1) = X(t) + \min(k\eta_i\gamma_i, x_s) - c_i. \quad (1)$$

Enamel volume decreases as an animal consumes resources. Although the underlying mechanisms of enamel loss are poorly understood (Lucas et al. 2008a), siliceous particulate matter is probably the most significant cause of abrasion (Lucas et al. 2012). We assume that hard foods (high $\sqrt{E_i R_i}$ values) promote increased use of the dentition (cf. Organ et al. 2011), and that such use induces wear regardless of the specific cause. We set enamel wear, $\Delta v(\Omega)$, to be a function of: (1) the mechanical properties of food i and (2) a stochastic decrease in enamel volume (determined by Ω). Because enamel is a nonrenewable resource, this wear cannot be undone. Teaford and Oyen (1989) showed that the consumption time for vervet monkeys (*Chlorocebus*) that ate a diet of raw Purina monkey chow was 8× greater than that for vervets fed on premashed monkey chow. With respect to enamel wear, this is equivalent to chewing 8× as much food. Teaford and Oyen also showed that the enamel thickness decreased by about 0.58 μmday^{-1} when vervets fed on the raw diet, versus ca. 0.24 μmday^{-1} when they fed on the pre-mashed diet. We assumed a linear relationship between the loss of enamel thickness (Teaford and Oyen 1989), and consumption time, or, alternatively, the amount of food consumed, k (with a slope $b = 0.0425$). The lower bound of this relationship ($\bar{\omega} = 0.24$ μm) represents the expected basal enamel wear that occurs irrespective of consumption, and we used it to parameterize the stochastic variable Ω. Accordingly, given that A is the molar enamel surface area and E_{MC} and R_{MC} are scaling constants denoting the average Young's modulus (50.44 MPa) and fracture toughness (1030.55 Jm^{-2}) of monkey chow, respectively (Williams et al. 2005), when k items of food type i are found in period t

$$V(t+1) = V(t) - \underbrace{\frac{A}{250}\left(\frac{bk\sqrt{E_i R_i}}{\sqrt{E_{MC} R_{MC}}} + \Omega\right)}_{\Delta v(\Omega)}. \tag{2}$$

The constant 1/250 scales tooth wear to ensure the organism attains its expected longevity (Lindstedt and Calder III 1981), and accounts for (1) overestimation of molar enamel area (our allometric estimation includes the lateral aspects of molar surfaces); and (2) the notion that wear is a complex action affecting a small fraction of the occlusal surface at a given time (Lucas 2004).

The basal loss of enamel thickness has an expected value $\mathrm{E}(\Omega) = \bar{\omega} = 0.24$ μm. As such, chewing and the daily wear unassociated with chewing have variable effects on enamel wear (Lucas 2004). Specifically, enamel wear is typically small, but occasionally large, and is realized when the organism chips or looses a tooth or part of a tooth (cf. Boccara 2004). To capture this property, we model the probability that Ω falls within the small interval ω and ω + dω, $f_\Omega(\omega)$, by a lognormal distribution, where $\mathrm{E}(\Omega) = \bar{\omega}$ and $\mathrm{Var}(\Omega) = \sigma^2$ (see Table 1).

Finally, we introduce changing habitat quality as a stochastic environmental variable that affects both the nutritional gains and foraging costs of foods at a given time. Habitat quality can be rich ($Q(t) = \mathrm{r}$) or poor ($Q(t) = \mathrm{p}$) at time t, and changes through time according to a transition probability matrix $\boldsymbol{\rho} = (\rho_{\mathrm{rr}}, \rho_{\mathrm{rp}}; \rho_{\mathrm{pr}}, \rho_{\mathrm{pp}})$, where—for example—$\rho_{\mathrm{rp}}$ is the probability of transitioning from a rich quality habitat at time t to a poor quality habitat at time $t+1$. Changes in habitat quality alter energetic gain, the mean encounter rate, and the dispersion of different foods. We set energetic gain to decrease by 10% in poor quality habitats relative to rich-quality habitats. Moreover, the mean encounter rate (ξ_i) as well as the dispersion of food (ν_i) are modified by $Q(t)$, such that food resources are more easily found (higher ξ_i) and are less patchily distributed (higher ν_i) in rich quality habitats (see Appendix S2 for a detailed derivation of dispersion and encounter rates of foods). USOs are stored underground and have evolved to retain high nutrient loads during periods of environmental stress (Copeland 2004). We incorporate this quality by holding the energetic gain, encounter rate, and dispersion of USOs constant, irrespective of habitat quality.

With this basic framework, we assess the influence of "wet," "dry," and "autocorrelated" environmental conditions on foraging decisions. Wet environments have high values of ρ_{rr}, ρ_{pr}, and low values of ρ_{rp}, ρ_{pp} (such that habitat quality is generally rich), whereas dry environments are the opposite. Autocorrelated environments are unlikely to change from their current state, and thus have high values of ρ_{rr}, ρ_{pp}, and low values of ρ_{rp}, ρ_{pr} (see Table 1). We recognize that natural systems are more idiosyncratic, however this simplification allows us to assess the effects of changing habitat quality over time with minimal added complexity.

MAXIMIZING FITNESS BY FOOD CHOICE

We consider a nonbreeding interval of length T during which only foraging decisions influence fitness. This interval will ultimately become sufficiently large so that we can use decisions that are independent of time (cf. Mangel and Clark 1988; Clark and Mangel 2000), and assume that at the end of this interval, the fitness of an individual with energy reserves x and enamel volume v is $\Phi(x, v)$. For numerical computations we use

$$\begin{aligned} \Phi(x, v) &= \frac{1}{2}\left(2 - \frac{x_{\mathrm{crit}}}{x} - \frac{v_{\mathrm{crit}}}{v}\right), \text{ where } \begin{cases} x > x_{\mathrm{crit}} \\ v > v_{\mathrm{crit}} \end{cases}, \\ \Phi(x, v) &= 0, \qquad\qquad \text{otherwise.} \end{aligned} \tag{3}$$

The maximum fitness at $t = T$ is realized by an organism with $X(T) = x_{\max}$ and $V(T) = v_{\max}$, and the rate of fitness decline increases as x and v approach x_{crit} and v_{crit}. We explored alternatives such as $\Phi(x, v) = (1 - x_{\mathrm{crit}} x^{-1})(1 - v_{\mathrm{crit}} v^{-1})$ and they had little effect on the qualitative predictions. We scaled the terminal fitness function to be 1, so it is easiest to consider it as survival after T for an individual whose end state is $X(T) = x$, $V(T) = v$.

We assume that natural selection has acted on behavioral decisions concerning diet (food choice) conditioned on energetic state, enamel volume, and the probability of transitioning from rich or poor habitat quality. We define fitness functions

$$\begin{aligned} F_{\mathrm{r}}(x, v, t) = \max_i \mathrm{E}\{&\Phi(X(T), V(T)) | X(t) = x, \\ &V(t) = v, Q(t) = \mathrm{r}\}, \end{aligned} \tag{4a}$$

$$\begin{aligned} F_{\mathrm{p}}(x, v, t) = \max_i \mathrm{E}\{&\Phi(X(T), V(T)) | X(t) = x, \\ &V(t) = v, Q(t) = \mathrm{p}\}, \end{aligned} \tag{4b}$$

where the maximization over i chooses the food that maximizes fitness given energy reserves, enamel volume, and habitat quality. By definition, at time T

$$F_{\mathrm{r}}(x, v, T) = F_{\mathrm{p}}(x, v, T) = \Phi(x, v).$$

For time periods before the terminal time $t = T$, an organism must survive mortality independent of starvation or enamel loss and choose the fitness maximizing food, given the stochasticity in food encounter. If the probability of death in a single period is set to ($m \approx \mathrm{e}^{-10}$ or 4.5×10^{-5}, estimated for a subadult male chimpanzee; cf. Bronikowski et al. 2011), then $F_{\mathrm{r}}(x, v, T)$ and $F_{\mathrm{p}}(x, v, T)$ satisfy the equations of SDP, such that

$$F_{\mathrm{r}}(x, v, t) = \max_i (1 - m) \left(\sum_{k=0}^{k_{\max}} f(k_{\mathrm{r}})_i (\rho_{\mathrm{rr}} \mathrm{E}_\Omega \{ F_{\mathrm{r}}(x_{\mathrm{r}} + \min(k\eta_i \gamma_i, x_s)_{\mathrm{r}} - (c_i)_{\mathrm{r}}, v - \Delta v(\Omega), t + 1)\} \right.$$
$$\left. + \rho_{\mathrm{rp}} \mathrm{E}_\Omega \{ F_{\mathrm{p}}(x_{\mathrm{r}} + \min(k\eta_i \gamma_i, x_s)_{\mathrm{r}} - (c_i)_{\mathrm{r}}, v - \Delta v(\Omega), t + 1)\}) \right), \tag{5a}$$

$$F_{\mathrm{p}}(x, v, t) = \max_i (1 - m) \left(\sum_{k=0}^{k_{\max}} f(k_{\mathrm{p}})_i (\rho_{\mathrm{pr}} \mathrm{E}_\Omega \{ F_{\mathrm{r}}(x_{\mathrm{p}} + \min(k\eta_i \gamma_i, x_s)_{\mathrm{p}} - (c_i)_{\mathrm{p}}, v - \Delta v(\Omega), t + 1)\} \right.$$
$$\left. + \rho_{\mathrm{pp}} \mathrm{E}_\Omega \{ F_{\mathrm{p}}(x_{\mathrm{p}} + \min(k\eta_i \gamma_i, x_s)_{\mathrm{p}} - (c_i)_{\mathrm{p}}, v - \Delta v(\Omega), t + 1)\}) \right), \tag{5b}$$

where the expectation E_Ω is taken with respect to the random variable Ω (eq. 2). These equations identify the food i that maximizes fitness for given energetic reserves $X(t) = x$, enamel volume $V(t) = v$, and habitat quality $Q(t)$ at time t. As equations (5a,5b) are solved backward in time, in addition to obtaining the values of fitness, we create decision matrices $D_{\mathrm{r}}(x, v, t)$ and $D_{\mathrm{p}}(x, v, t)$, characterizing the optimal choice of food in a rich or poor environment given that $X(t) = x$ and $V(t) = v$. Thus, the two decision matrices (for rich and poor quality) depend upon the habitat quality transition matrix $\boldsymbol{\rho}$, but we suppress that notation for ease of reading.

As t moves backward further and further away from T, the fitness maximizing decisions become independent of time and depend only upon state, which accords with the intuition that far from the time at which fitness is assessed, the behavior of an organism is predicted to depend on its state and on the environment, but not on the current time. Decisions that maximize fitness at $t \ll T$ are thus stationary with respect to time. We used these stationary decisions, which we denote by $D_{\mathrm{r}}^*(x, v)$ and $D_{\mathrm{p}}^*(x, v)$ for further analysis. We confirmed stationarity by calculating the summed square differences between decision matrix solutions from $t + 1$ to t, such that $\Delta D(t) = \sum_{v,x} (D(x, v, t + 1) - D(x, v, t))^2$, for $t = T - 1$ to $t \ll T$ and we assumed stationary decisions had been reached when $\Delta D(t) \to 0$ for $t \ll T$ (e.g., see Fig. S2).

FORWARD ITERATION

We used a Monte Carlo simulation moving forward in time (forward iteration algorithm; Mangel and Clark 1988; Clark and Mangel 2000) to assess the impact that fitness maximizing foraging decisions (given by $D_{\mathrm{r}}^*(x, v)$ and $D_{\mathrm{p}}^*(x, v)$) have on the expected future fitness of individuals by iteratively solving for the state dynamics of simulated foragers over time, given the state dynamics in equations (1) and (2). We let τ denote forward-iterated time units experienced by simulated individuals making foraging decisions in accordance to the stationary decision matrices, as opposed to the time units t used to calculate stationary decision matrices. At each time τ, the nth simulated individual with states $X_n(\tau)$ and $V_n(\tau)$ forages for the food i determined by the decision matrices $D^*(X_n(\tau), V_n(\tau) | Q(\tau))$.

To test whether and to what extent mechanical advantages conveyed fitness benefits to hominin primates, we quantified expected future fitness, $\hat{F}(\tau | D^*, Q(\tau))$, for $n = 1, 2, \ldots, N = 100$, 50 kg individuals, with maximal foraging costs for days $\tau = 1$ to $\tau_{\max} = 10950$ (expected life span of 30 years) given both the stationary decision solutions and habitat quality. As energy reserves and/or enamel volume decrease over the lifetime of an individual, $\hat{F}$ is expected to decrease similarly. We quantified the expected future fitness at time τ of a population,

$$\hat{F}(\tau | D^*, Q(\tau)) = \frac{1}{N} \sum_{n=1}^{N} F^*\big(X_n(\tau), V_n(\tau) | D^*, Q(\tau)\big), \tag{6}$$

where $F^*(X_n(\tau), V_n(\tau) | D^*, Q(\tau))$ is the optimal fitness for individual n at time τ given its physiological states and the environment.

We explored the potential adaptive benefits of megadontia and extradentary mechanical advantages using two approaches. First, we compared the proportions of foods identified to maximize fitness in accordance to the stationary decisions $D_{\mathrm{r}}^*(x, v)$ and $D_{\mathrm{p}}^*(x, v)$. Organisms that are predicted to use a particular resource across a greater proportion of states (x, v) may have fitness benefits in environments where those resources are plentiful. However, although the percentage of foraging choices in decision matrices is an efficient summary of potential dietary behavior, it should not be viewed as the proportional contribution of food to an individual's diet over time, which is calculated with the forward iteration algorithm. To determine whether megadontia provided fitness benefits over the lifetime of an individual organism, we compared expected future fitness, $\hat{F}$, for populations of individuals with and without megadont dental anatomy (incorporated into the model by altering $v_{\max}$; see Appendix S1), mechanical advantages, and during both wet environments (where rich quality habitats are more likely) and dry environments (where poor quality habitats are more likely).

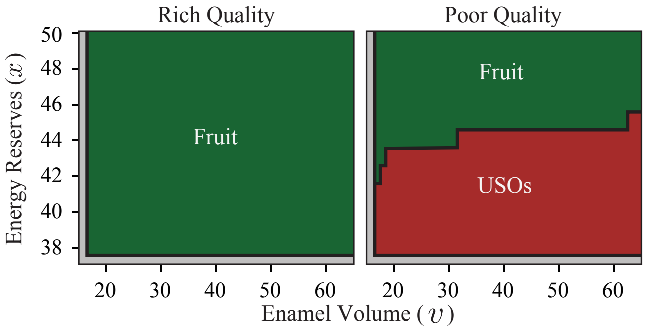

Figure 1. Stationary solutions to the fitness-maximizing equations $F_r(x, v)$ (rich-quality habitat) and $F_p(x, v)$ (poor-quality habitat) for a 50-kg anthropoid primate with no mechanical advantages. There are no qualitative differences between wet, dry, or autocorrelated conditions. Gray elements to the left and bottom of the plots denote values of (x, v) resulting in mortality.

Results

Based on the stationary solutions, we predict that energy reserves and enamel volume have large consequences for diet choice. In rich-quality habitats, foods with the energetic and mechanical properties of fruit maximize the fitness of animals without an extradentary mechanical advantage across all potential states (x, v) (Fig. 1). In poor-quality habitats, such food maximizes fitness only if energy reserves are high; as reserves decline, the optimal resource shifts from fruit to plant USOs. Plant USOs confer similar energetic gain as fruit, however we hold the mean encounter rate and dispersion of USOs constant in both rich- and poor-quality habitats, whereas fruits are patchier in poor habitats (Table 1). As enamel volume declines with age, the mechanical hardness of USOs, which produce greater enamel wear, is predicted to promote an increased reliance on riskier but mechanically pliable foods such as fruit.

Stationary decision matrices reveal that hominins with megadontia can maximize fitness by incorporating a relatively greater proportion of obdurate foods in poor-quality habitats. With no mechanical advantage, megadont decision matrices show a reduction in the percentage of fruit, and an increase in USOs relative to non-megadonts (Fig. 2). As mechanical advantages are introduced, megadont decision matrices show similar percentages of each food item as those of non-megadonts with one important difference: regardless of the mechanical advantage, megadont decision matrices include a greater percentage of USOs.

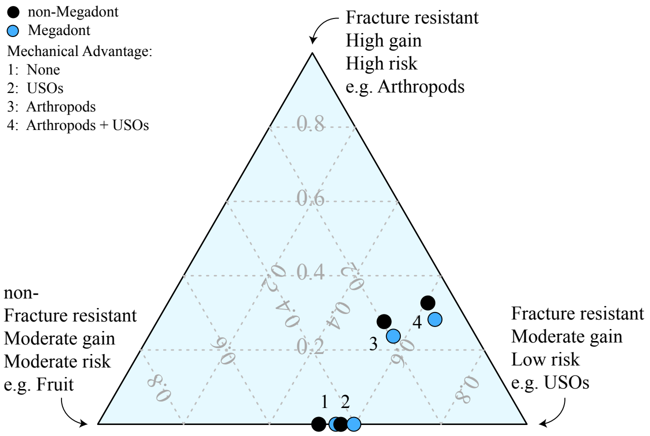

Figure 2. Ternary diagram showing the proportional contribution of fruit, USOs, and arthropods to the decision matrices of both 50-kg non-megadont and megadont primates under each mechanical advantage scenario. Results are shown for autocorrelated environmental conditions; results for wet and dry conditions were qualitatively similar.

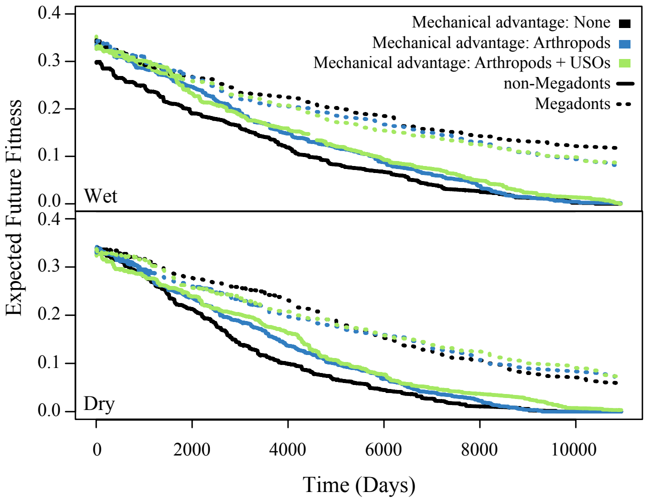

Figure 3. Expected future fitness trajectories for $N = 100$, 50-kg non-megadont (solid) and megadont (stippled) hominins over an estimated life span with varying mechanical advantages (none, arthropods, arthropods + USOs), during both wet and dry environmental conditions.

For all simulated populations, forward iterations reveal that expected future fitness decreases sharply early in life, but saturates as the population reaches its expected life span of 30 years (10,950 days; Fig. 3). This is due to wear on enamel and potential decline in energy reserves going forward in time, resulting in lower future fitness. Because the decision matrices for the USO mechanical advantage are nearly identical to the no mechanical advantage scenario, we show only forward iteration results for the latter. Our results point to an important difference between the three mechanical advantage scenarios that are considered (none, arthropods, arthropods + USOs; Fig. 3; solid lines). Both arthropod and arthropod + USO mechanical advantages appear to have large impacts on expected fitness. For both wet and dry environmental conditions, having either mechanical advantage provides large fitness benefits, but the difference in fitness *between* mechanical advantages is small, particularly when habitat quality is generally rich (wet conditions).

The fitness advantages of megadontia are more obvious. Populations with this character trait have greater expected future fitness than those without megadontia—irrespective of mechanical advantage—and these differences are more exaggerated later in life (Fig. 3; stippled lines). Moreover, the predicted fitness benefits generated by a mechanical advantage are generally less for populations with megadontia.

Because foraging costs scale nonlinearly with body size, optimal foraging decisions vary accordingly. For larger animals and for each environmental scenario in our model (wet, dry, and autocorrelated), a poor habitat quality is strongly associated with the consumption of riskier foods with higher energetic yields such as fruit, whereas more ubiquitous foods such as USOs are an important supplement (Fig. 4 A). Animals with smaller body sizes tend to rely on USOs exclusively. When habitat quality is rich, both smaller- and larger-bodied animals switch to a diet of energy dense foods (fruit). In the absence of an extradentary mechanical advantage, extremely energy dense, but relatively rare foods such as arthropods are avoided by animals of any size, regardless of habitat quality. As body size increases, the role of plant USOs remains constant, however arthropods (highest nutritional gain and lowest probability of encounter) become favored over fruit (Fig. 4). Thus, in both rich- and poor-quality habitats, large-bodied animals increase the percentage of risky foods if their mechanical properties can be altered to preserve enamel (Fig. S3). Smaller-bodied animals lack the energetic reserves required to forage on rare, but energy dense foods such as arthropods, regardless of their mechanical advantages.

Given that the food choices in our SDP model are associated with a distribution of δ^{13}C values, we can use a forward iteration framework to explore how the accumulated δ^{13}C values of individuals within a population change over time as a function of energetic reserves, enamel volume, and the prevailing environmental conditions (see Appendix S3, for details). Our results show that the δ^{13}C values of a simulated population of $N = 100$, 50 kg anthropoid foragers capable of mechanically altering both arthropods and USOs is influenced by both energetic reserves and enamel volume. In dry environments and where foraging costs are minimal, the mean δ^{13}C value of simulated foragers remains relatively high ($\delta^{13}C_{\mathrm{avg}} \approx -10.5‰$; Fig. 5 A), due to a greater reliance on USOs (Fig. S3). After day 3500, $\delta^{13}C_{\mathrm{avg}}$ declines to $-11.2‰$ as the proportional contribution of USOs decreases and that of fruits increases (Fig. 5 B). This highlights the increasing importance of foods that are less obdurate as enamel is worn—despite greater energetic costs—as well as the accompanying decrease in the mean δ^{13}C value of a consumer population over its life span.

If foraging costs are too great, low-risk, obdurate foods are preferred despite greater enamel wear, resulting in a higher $\delta^{13}C_{\mathrm{avg}} \approx -8.8‰$ (Fig. 5 C). In this case, our model predicts δ^{13}C values equivalent with those observed for *Australopithecus africanus* and *Paranthropus robustus* (Ungar and Sponheimer 2011). In costlier environments (where energetic cost includes both foraging costs as well as daily costs independent of food choice), USOs tend to maximize fitness until late in life (Fig. 5 D), when the cost of reduced enamel volume supersedes the risks of foraging on pliable but rare foods.

Under the conditions imposed by our model, C_4 grass leaves cannot maximize fitness. However, we can explore under what conditions grass leaves do maximize fitness by altering model properties. We find that grass leaves become represented in the decision matrices of hominins both with and without megadontia if the abundance of grass is exaggerated (such that the encounter rate of grass leaves is increased from 4 to 5; Fig. 6 A,B). Still, the consumption of grass leaves is shown to be a fallback behavior *in extremis*, selected only when enamel volume is high and energy reserves are extremely low. Moreover, megadontia leads to a relatively greater percentage of states where grass leaves maximize fitness (Fig. 6 B), and this is in accordance with the elevated δ^{13}C values observed for species in the genus *Paranthropus*.

Discussion

Models have been used to explore the foraging behaviors of humans (Belovsky 1988), nonhuman primates (Boyer et al. 2006; Sayers et al. 2010), and their mutual interactions (Levi et al. 2011), but few have been applied to extinct primates (Dunbar 1993; Janssen et al. 2007; Griffith and Long 2010), and none have accounted for nonrenewable resources such as dental enamel. This omission is surprising given the functional and adaptive significance prescribed to molar enamel thickness. In this vein, an SDP model is attractive because it demands the explicit expression of processes that determine fitness, as well as sources of external and internal stochasticity (Mangel and Clark 1988; Clark and Mangel 2000). We have developed an SDP model that assesses directly the role of enamel volume on food selection and fitness while quantifying the extent to which anatomical and behavioral attributes can alter foraging behaviors.

THICK ENAMEL CONFERS A FITNESS ADVANTAGE

The relatively massive molar teeth of *Paranthropus* are invested with hyperthick enamel (Shellis et al. 1998; Lucas et al. 2008a). This combination of traits, or megadontia, is coupled with robust jaws and large chewing muscles, which together enable an immense bite force (Demes and Creel 1988; Constantino et al. 2010). Functional interpretations of these traits have long stressed the consumption of hard or obdurate foods (Kay 1981; Osborne 1981; Macho 1999), although a recent trend has emphasized tough

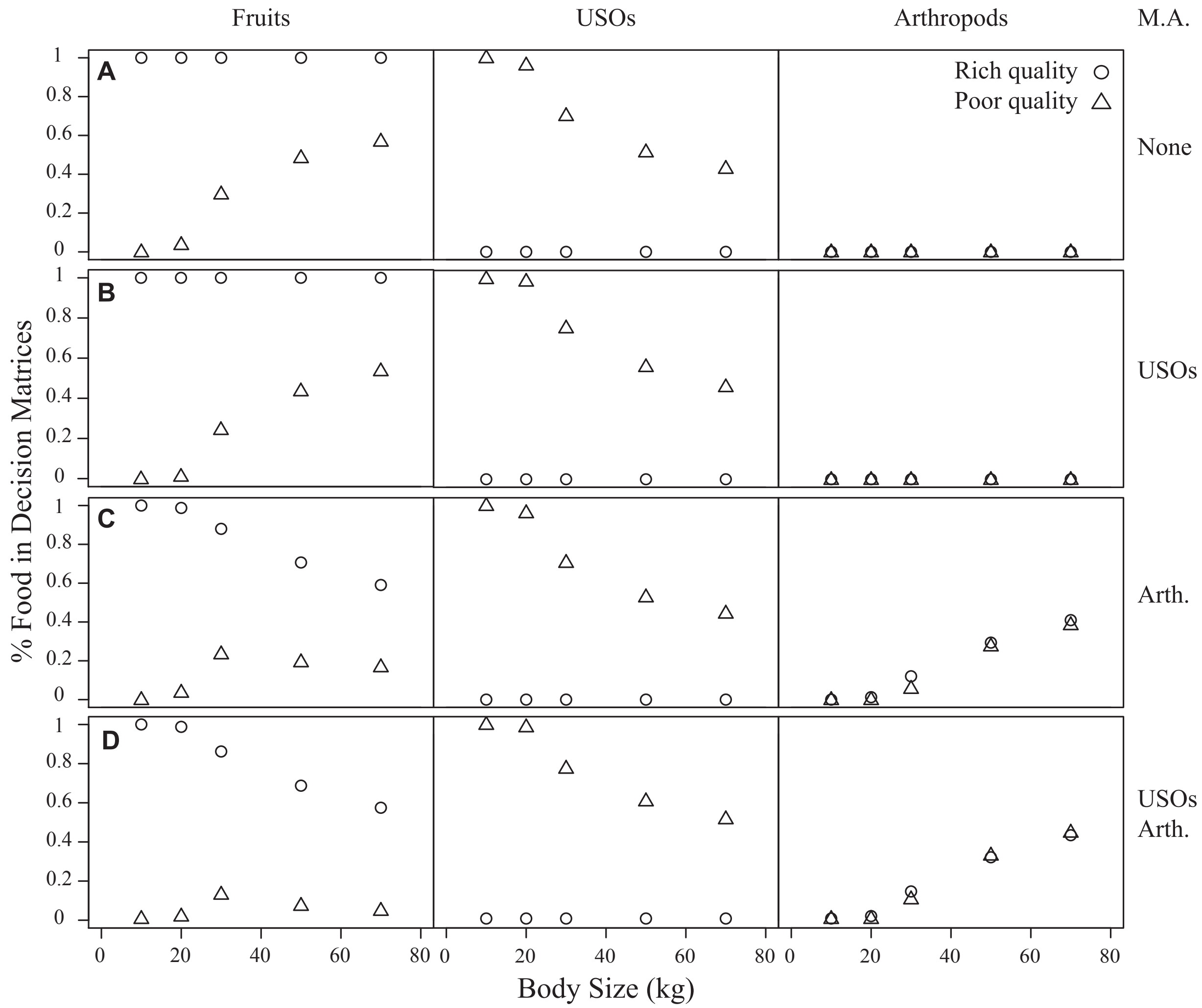

Figure 4. The proportional contribution of foods to the decision matrices of anthropoid primates with body sizes ranging from 10 to 70 kg. Contributions of foods for the no mechanical advantage scenario (A), the USO advantage scenario (B), the arthropod advantage scenario (C), and the arthropod + USO advantage scenario (D). Grass leaves are not found to be optimal foraging solutions in any decision matrix. Results are shown for autocorrelated environmental conditions; results for wet and dry conditions were qualitatively similar.

foods that require repetitive loading (grinding) of the jaws and teeth (Ungar and Sponheimer 2011), particularly with respect to *Paranthropus boisei* (Ungar et al. 2008; 2012). In either case, debate has focused on a diet of grass seeds (Jolly 1970) or plant USOs as the primary drivers of this robust morphology (Laden and Wrangham 2005; Sponheimer et al. 2005; Yeakel et al. 2007; Dominy et al. 2008). The results of our SDP model agree well with these hypotheses by showing that hyperthick molar enamel reduces the mechanical costs of chewing harder foods over a greater proportion of internal states (x, v) (Fig. 2). Megadontia, then, provides an adaptive advantage in poor-quality environments where hard foods such as grass seeds and USOs are relatively abundant.

Hominins were doubtless tool users, and the ability to alter the physical properties of wear-inducing foods is expected to both increase dietary breadth and decrease fitness costs. In support of this prediction, the inclusion of an extradentary mechanical advantage in our model increased the proportion of high-risk foods in the predicted decision matrices (Fig. 2). A USO mechanical advantage increased the proportion of USOs in the diet, albeit marginally, whereas the consumption of fruit declined. By comparison, the extradentary mechanical advantage associated with arthropods or both arthropods and USOs had a large effect on the decision matrices. Arthropods were fitness-maximizing foods for hominins both with and without megadontia because they decreased the risk of obtaining rare or patchily distributed foods, while reducing their reliance on fruit. Extradentary processing is therefore advantageous; however, it is telling that USOs always maximized fitness across a greater proportion of states for hominins with greater enamel volume.

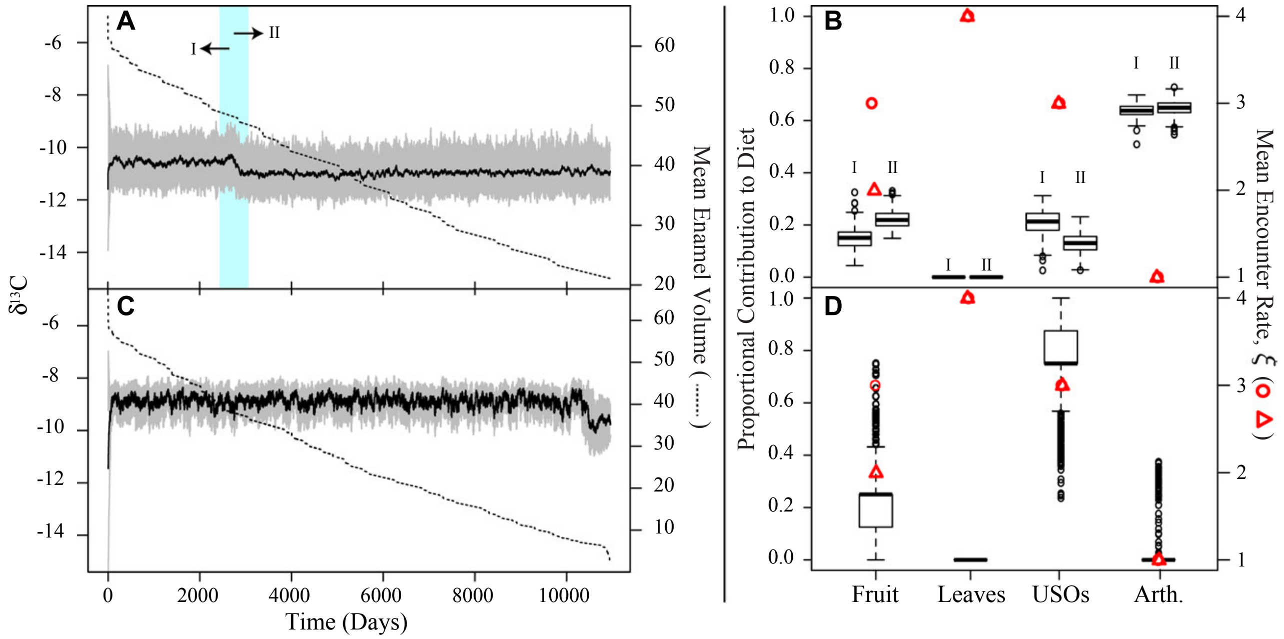

Figure 5. Forward simulation of the δ^{13}C values (black line denotes running mean; gray band denotes maximum and minimum values), mean enamel volume, and the proportional contribution of food-items to the diets of $N = 100$, 50-kg individuals foraging in a dry environment over an estimated life span. (A,B) When foraging costs are minimal, a dietary switch is observed to occur near day 3500, and labels I and II denote the pre- and post-diet switch. (C,D) The same simulation when foraging costs are elevated. In panels B and D, the red circles and triangles denote the mean encounter rate for each food in rich- and poor-quality habitats, respectively.

Importantly, the predicted fitness advantages of thick enamel are variable due to the different rates of enamel wear over a lifetime (Fig. 3). In this regard, our process-based model is relatively simplistic in that life-history stages are excluded; however, these simplifications enabled us to test and affirm three predictions regarding hominin foraging behavior: (1) behaviors that alter the mechanical properties of hard foods result in greater fitness; (2) these benefits are primarily realized in dry environments, where

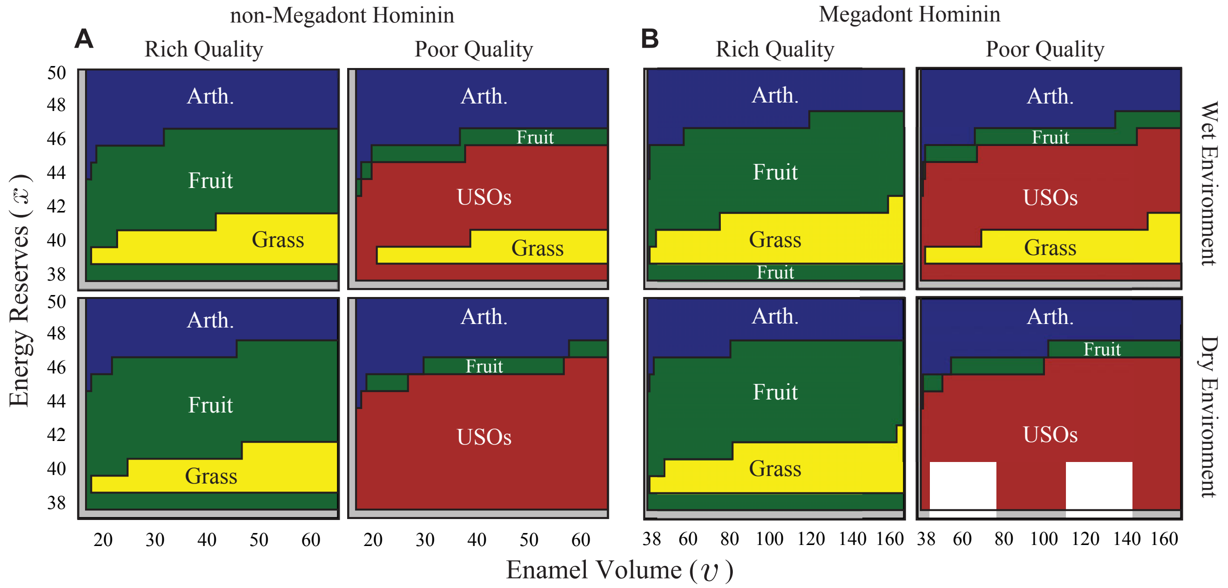

Figure 6. Stationary solutions for the fitness-maximizing equations, $F_r(x, \upsilon)$ and $F_p(x, \upsilon)$, as a function of energy reserves x and enamel volume υ for both non-megadont and megadont hominins when grass leaves are hyper-abundant and for the arthropod + USO mechanical advantage scenario. Gray elements to the left and bottom of the plots denote values of (x, υ) resulting in mortality.

habitat quality is more likely to be poor and hard foods are relatively more abundant; and, (3) because megadontia results in relatively slower rates of wear, it confers relatively higher fitness, and these benefits are primarily realized later in life.

In summary, our SDP model demonstrates that different foraging choices are predicted to maximize fitness among hominins with varying degrees of megadontia, and that these foraging strategies have different expected lifetime fitness values. In the following sections, we discuss how a forward iteration approach can be used to examine the isotopic differences observed among hominin species, and whether the mechanical and physiological constraints imposed by our model are predictive of the isotopic patterns observed in the fossil record.

COMPARING MODEL PREDICTIONS TO ISOTOPIC DATA

Results from simulations of the δ^{13}C values accumulated over a lifetime of a hominin population help to resolve occasional discrepancies between craniodental morphology (indicating hard foods) and molar microwear (indicating soft foods; Grine et al. 2012). Molar enamel is formed early in life (Lucas 2004) when food selection tends toward mechanically hard foods with high δ^{13}C values (Fig. 5A,B). As enamel is worn, softer, less abundant foods with lower δ^{13}C values are shown to maximize fitness. Because fossilized microwear is formed shortly before death (the "last supper effect"), our model results suggest that softer, more pliable foods will have a disproportionately large influence on the microwear of teeth, particularly for older individuals. Moreover, simulated foragers incorporated foods in proportions that are not predicted by their relative abundance on the landscape (Fig. 5 B,D), highlighting the importance of considering both mechanical and energetic constraints in addition to resource abundance.

FALLBACK FOODS ARE BODY SIZE DEPENDENT

Multiple lines of evidence suggest that plant USOs were important foods for early hominins. Plants with geophytic structures are both diverse and abundant in arid habitats (Pate and Dixon 1982; Vincent 1985; Procheş et al. 2006), and modern hunter-gatherers use these resources extensively, particularly in marginal environments (Campbell 1986; Marlowe 2003; Marlowe and Berbesque 2009). Associations between mole rats—known USO specialists—and hominins suggest that human ancestors lived in USO-abundant habitats (Laden and Wrangham 2005), and stable isotope analysis of both modern and fossil mole rats confirm that USO specialists have isotopic values similar to those of *A. africanus* and *P. robustus* (Yeakel et al. 2007). It is widely assumed that USOs served as fallback rather than preferred foods due to their lower nutritional content and relative availability (Schoeninger et al. 2001). The results of our model are in general agreement with this assumption, but show that the role of USOs as fallback foods varies—in part—as a function of an organism's energy reserves and enamel volume, as well as body size.

In general, the consumption of USOs is predicted if enamel volume is relatively high and energy reserves are relatively low (Fig. 1). However, our model also predicts a trade-off with respect to the role of USOs as fallback foods as body size is altered. Smaller-sized animals tend to use nutritious foods such as fruit in rich-quality habitats and less nutritious but more ubiquitous foods such as USOs in poor-quality habitats (Fig. 4A). Thus, as energetic reserves become more limiting, as they are for smaller organisms with relatively higher resting metabolic rates, fruit and USOs alternatively serve as preferred foods when habitat quality is rich and poor, respectively. By comparison, larger body size enables riskier foraging even when habitat quality is poor, and such risky foraging becomes commonplace if an organism can alter its food mechanically (Fig. 4B–D). For all scenarios, larger animals resort to USO consumption when energy reserves are low. Accordingly, USOs are relegated to a fallback status, and are consumed if the act of foraging for preferred foods incurs relatively greater fitness costs on the organism. Although consumption of USOs reduces the costs of foraging in poor-quality environments, our results also show that widespread but nutritionally poor and mechanically obdurate foods such as grass leaves are actively avoided, even when there are enamel and energetic reserves to spare.

GRASS LEAVES DO NOT MAXIMIZE FITNESS

Despite the ubiquity of C_4 grass leaves in hominin habitats, this potential food resource is an unlikely solution to the SDP, consistent with the aversion to C_4 plants that is evident among savanna-dwelling chimpanzees (Sponheimer et al. 2006), modern lemurs (Crowley and Samonds 2013), and some hominin species including *Ardipithecus ramidus* (White et al. 2009) and *Australopithecus sediba* (Henry et al. 2012). Because we used a conservatively low value for the fracture toughness of C_4 grass leaves (see Methods), the absence of this food from hominin decision matrices is a telling argument against the concept of a grazing hominin. The underlying reasons for this aversion are unknown, but C_4 grass leaves are often more fracture-resistant (Boutton et al. 1978) and less nutritious (Barbehenn et al. 2004) than C_3 leaves, possibly due to the presence of bundle sheath cells. These factors have been cited to explain the avoidance of C_4 plants by herbaceous insects in grassland communities (Caswell et al. 1973; Boutton et al. 1978; Pinder III and Kroh 1987).

Yet, megadont hominins such as *P. boisei* have δ^{13}C values $\approx 0‰$, which corresponds to a diet of 75–80% C_4 foods (Ungar and Sponheimer 2011). Such a heavy dependence on C_4 foods has led to speculation that *P. boisei* was potentially a grazing hominin (Lee-Thorp 2011; Rabenold and Pearson 2011). Our model results indicate that grass leaves do have the potential to maximize fitness in extreme circumstances, although the benefits of this food source decline quickly as enamel is worn. This suggests that C_4 grass leaves are unlikely to confer fitness advantages even for hominins with megadontia.

Conclusion

Foraging behaviors are a consequence of both the mechanical and energetic costs of food and the constraints imposed by an organism's dentition. Dental enamel thickness is a highly conserved trait among individuals within modern human populations (Lucas et al. 2008b), yet it varies considerably across hominin lineages in the fossil record. This variability is an evolutionary consequence of interactions between the dentition and food, and process-based models that integrate these ingredients can inform both the possible roles of certain foods as well as the potential fitness benefits of different dental morphologies or extradentary mechanical advantages. Along this line, a similar SDP approach could be used to investigate the roles of different types of USOs—foods that include corms, tubers, bulbs, and rhizomes. Because these plant parts are distributed differently across C_3 and C_4 plant species, the preference or avoidance of such potential foods—as a function of energetic and mechanical gains and costs—may help explain the surprisingly high $\delta^{13}C$ values of hominins such as *P. boisei*. Regardless, we believe that the integration of data obtained from the fossil record with mechanistic models that set physical constraints on potential behaviors will expand our understanding of these enigmatic organisms.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. A cross-section of a molar.

Figure S2. Summed square differences between decision matrices from $t+1$ to t for $t \ll T$ to $t = T - 1$, where $\Delta(t) = \sum_{v,x}(D(x,v,t+1) - D(x,v,t))^2$.

Figure S3. Stationary solutions for the fitness-maximizing equations $F_{\mathrm{r,p}}(x,v)$ as a function of energy reserves x and enamel volume v.