A bottom-up mammoth population model predicts moderate densities and high vulnerability to hunting

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Abstract

During the last glacial, large grazers inhabited Eurasia's mammoth steppe. This cold steppe was productive enough to sustain a diverse assemblage of large mammals, but it remains controversial which population densities it could support. In sufficient densities, large herbivores can act as ecosystem engineers: creating and maintaining grassland habitat by means of disturbance and accelerated nutrient cycling. Estimating carrying capacity (i.e., long-term mean megafauna densities) of the Pleistocene mammoth steppe is therefore crucial for understanding this paleoecosystem. In this study, we developed a process-based grazer model, dynamically coupled with a dynamic global vegetation model, in order to simulate a range of plausible glacial grazer densities. In order to capture parameter uncertainty we defined prior probability/mass distributions from literature for all grazer parameters. We parameterized and simulated the woolly mammoth (*Mammuthus primigenius*) because it is the largest and metabolically most efficient megafaunal species; therefore its per-area mass densities mark an upper bound for whole-guild carrying capacity. We sampled the parameter space with Monte-Carlo Markov Chains to derive parameter sensitivity and a posterior probability distribution of megafauna densities. In absence of mammoth densities for model fitting we chose a likelihood function that maximizes mammoth survival over its climatic niche. This approach let densities emerge bottom up from the mechanistic model. Our results identify 4% annual mortality of adults as an upper limit to survival of mammoth populations, which corroborates their high vulnerability to human hunting. The resulting posterior densities for mammoth steppe carrying capacity range from 13 to 85 kg/ha (95% quantile), which lies in between lower and higher estimates from other publications. We discuss reasons why our results should be interpreted as an upper limit to mammoth steppe carrying capacity. Even though our approach could only capture part of the predictive uncertainty, our results prompt caution to extrapolate very high potential megafauna densities to global scale as a natural baseline.

Keywords:
megafauna, DGVM, Pleistocene, mammoth steppe, grazer

Introduction

During the last glacial period, the periglacial landscapes of Eurasia were dominated by steppe-like vegetation (Guthrie 1990; Zazula et al. 2006; Willerslev et al. 2014; Wang et al. 2021). Evidenced by numerous fossil records, this biome was productive enough to sustain a diverse assembly of large mammalian herbivores (Guthrie 1968; Kahlke 2014). The most prominent and ubiquitous megafauna species, the woolly mammoth (*Mammuthus primigenius*), inspired the name "mammoth steppe" for this biome (Guthrie 1982). Along with the warming climate towards the Pleistocene–Holocene boundary (~11.7 thousand years), most of the glacial steppe gave way to tundra, bogs, and boreal forest (Binney et al. 2017). Concomitant with this vegetation change, steppe-adapted megafauna populations declined and, in many cases, went extinct (Stuart 2015).

For understanding the mammoth steppe ecosystem and its vanishing, densities of large herbivores are pivotal. The Keystone Herbivore Hypothesis postulates that large herbivores were numerous enough to shape their habitat on biome scale (Owen-Smith 1987; Zimov et al. 1995): through feeding, trampling, accelerating nutrient cycling, and so on. The argument goes that large herbivores were themselves agents in maintaining the mammoth steppe as a productive habitat by suppressing mosses, lichens, and woody vegetation in favor of herbs and graminoids. Accordingly, the mammoth steppe vanished *after* the (human-inflicted) demise of keystone herbivore species, which gave way to tundra and forest at the end of the glacial. In contrast, the Climate Hypothesis sees climate change as the driver for the vanishing of the mammoth steppe and its megafauna (Guthrie 1990; Mann et al. 2015; Monteath et al. 2021). The Climate Hypothesis sees the cause of megafauna extinctions in habitat loss as trees, bogs, dwarf shrubs, and bryophytes increasingly competed with herbaceous steppe under the warmer and wetter climate of the deglaciation. This hypothesis does not require high megafauna densities. In fact, Guthrie (1990) has decisively argued for very low densities. Certainly it needs more than one catch-all hypothesis to accommodate this taxonomic, temporal, and spatial complexity of late-Quaternary extinctions (Lorenzen et al. 2011), but any more nuanced view on specific regions, times, and species will likewise rest upon an understanding of general megafauna carrying capacity.

Beyond the Quaternary sciences, estimates of "natural" densities of large terrestrial herbivores are of interest as a "natural baseline" for restoring modern-day ecosystems (Kemp et al. 2023) and understanding mankind's global impact on larger time scales. In search of such a baseline, different studies have extrapolated estimates of long-term megafauna carrying capacity to global scale (Barnosky 2008; Zimov and Zimov 2014; Smith et al. 2016; Zhu et al. 2018; Manzano et al. 2023) — arriving at quite different conclusions depending on their assumptions.

There are surprisingly few original studies quantifying possible megafauna densities in the mammoth steppe. Taphonomic studies used long-term bone accumulation rates in permafrost to estimate long-term animal densities (Zimov et al. 2012; Mann et al. 2013), but it is difficult to assess their error range. To our knowledge, these are the only density estimates based directly on fossil evidence. Some model-based estimates relied on comparatively simple calculations (Redmann 1982; Bliss and Richards 1982), neglecting important processes such as seasonal population bottlenecks (Matthewson and Weisberg 2009). Zhu et al. (2018) coupled a physiological grazer model with the dynamic vegetation model ORCHIDEE to simulate patterns of late-Pleistocene grazer populations. For the present study we developed a dynamic mechanistic grazer model, coupled with the dynamic vegetation model LPJ-GUESS (Smith et al. 2014). While Zhu et al. focused on spatio-temporal patterns we focus on analyzing the simulated processes and local-scale population dynamics with a particular emphasis on the uncertainty range of simulated megafauna densities.

A Bayesian approach lends itself to exploring the range of plausible megafauna densities because it quantifies error propagation and prediction uncertainty (Simmonds et al. 2024). Bayesian updating operates on the full range of plausible model parameter values (prior probabilities), then confronts the model with observations ("data") in order to derive posterior probability distributions of parameters and model output variables. Prior and data together constrain posterior parameter probabilities and model predictions. In our case, prior knowledge is given by the parameter ranges of the grazer model (Appendix C). Bayesian model fitting also needs observations. However, fitting our model to above-mentioned Pleistocene megafauna density estimates would result in circular reasoning. Instead, we aimed for independent, model-emergent densities.

Instead of fitting our model to megafauna densities, we defined a likelihood term that opti-

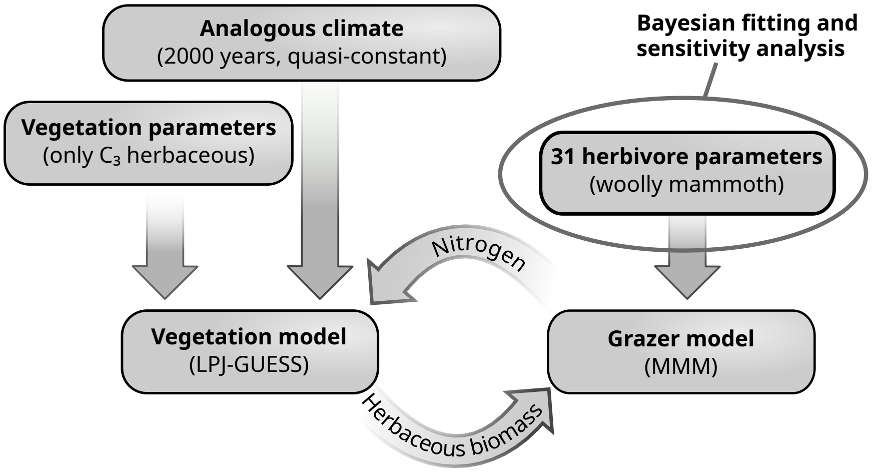

Figure 1. Schematic overview of the simulation components.

mized for population survival under environmental conditions similar to the Pleistocene mammoth steppe. Fortunately, decades of studies reconstructing paleoenvironments have given us considerable insight into the climate and environment of mammoth habitat (e.g., Hopkins et al. 1982; Axmanová et al. 2020; Wang et al. 2021; Huntley et al. 2023). This allowed us to choose environmental conditions analogous to the Pleistocene in order to drive our analysis. Our model fitting constrained posterior parameter values and population numbers to what is compatible with the mammoth's presumed fundamental climatic niche.

In addition to Bayesian simulations of mammoth densities, we also performed a global parameter sensitivity analysis, which aims to identify the most influential parameters. These parameters and the processes they control can in turn become the focus for future model development in order to iteratively reduce posterior uncertainties.

Our aim in this study is to quantify the range of plausible megafauna carrying capacity under conditions analogous to the Eurasian mammoth steppe of the Pleistocene. Here, plausible means compatible with physiological and demographic processes constraining population densities. The predictions of our bottom-up model are open-ended, independent from previous estimates, and quantify large parts of uncertainty. These properties allow them to provide one strand of evidence in the debate around Pleistocene megafauna densities (Traylor 2024). As the Keystone Herbivore Hypothesis postulates biome-scale ecosystem engineering by large herbivores in high densities, our results also inform the plausibility of this extinction pathway.

Methods

Basic Model Concepts

The goal of simulating extinct species in a non-analog paleobiome warrants a quite general model (Appendix B.1.1). While such generality naturally sacrifices realism in any particular application of the model (Levins 1966), it also allows for general conclusions: in this case about large herbivore population dynamics. The model is not tailored to any one particular megafauna species. Herbivores are represented by a set of parameters that characterize not so much species-specific attributes but rather by their ecological function (e.g., body size, digestion efficiency, and reproductive potential). Therefore we speak of herbivore functional types (HFTs; Pachzelt et al. 2013; Hempson et al. 2015). The megafauna model only becomes spatially and temporally explicit through LPJ-GUESS, which is driven by weather data on a grid cell basis. This makes the model applicable to different species, times, locations, and spatial scales.

Cohorts (annual age classes) are the basic herbivore entity. A cohort is defined by the state variables such as density (individuals per area), age, and amount of fat reserves (Appendix B.1.2). These represent an "average" individual in the respective age class. As opposed to an individual-based model, cohorts need fewer computational resources. All calculations are *per area*, which makes the model independent of grid cell size. Each cohort consumes herbaceous biomass (taken from the vegetation model) on a daily basis, according to its energetic needs and to fill up its body fat reserves. Ingested nitrogen is immediately returned to the plant-available soil pool (Appendix B.3.4). Energy expenditure is independent of the environment: basal metabolic rate scales allometrically with body mass and is multiplied with a constant coefficient to derive field metabolic rate (Appendix B.3.3). A cohort's density shrinks due to background mortality, old age, and — in case of very low body fat — starvation (Appendix B.3.3). Each year, a new cohort is created whose density is derived from the reproductive success of adult cohorts (Appendix B.3.3). The more body fat an adult cohort has, the more offspring it contributes.

The modeling goal is to estimate carrying capacity of large herbivores in the Pleistocene mammoth steppe. Following Dhondt (1988), we use the term carrying capacity as the animal density that can be sustained for a long period of time by primary production. On the timescale of centuries to millennia and a spatial scale of biomes, it appears reasonable to assume a long-term dynamic equilibrium between environment and herbivores. Under the premise that simulated herbivores are resource-controlled, net primary production (NPP) is obviously a key determinant of carrying capacity. Our simulations showed that not only multi-year average NPP is important, but also its seasonal availability. This is because mortality increases in winter, creating a bottleneck.

This way, population density emerges per grid cell from the intake–expenditure balance on the cohort level and the reproduction–mortality balance on the population level. Herbivores are completely bottom-up controlled by the availability of herbaceous forage. Herbaceous productivity of LPJ-GUESS in turn is controlled by soil properties and climate dynamics. The feedback from herbivores to vegetation is limited to biomass removal and a potentially accelerated nitrogen cycling. In short, the key mechanisms lie in climate-controlled grass productivity, digestive efficiency, fasting endurance, reproduction rate, and background mortality. We used MMM 1.1.5 (Traylor 2021) with a fork of LPJ-GUESS 4.1 with daily grass growth by Boke-Olén et al. (2018).

Among the large mammals of the glacial cold steppe in Eurasia, the woolly mammoth (*Mammuthus primigenius*) is generally considered the most influential ecosystem engineer (Zimov et al. 2012). Due to its size the mammoth has a lower metabolic rate per mass and can thus attain higher mass densities (Damuth 1981). Being so large, mammoths (at least as adults) evaded probably most non-human predation (Owen-Smith 1988), which gives reason to believe that their populations were resource-limited. Mammoths obviously shared resources (forage, space, water, etc.) with other large herbivore species. While there are attempts at reconstructing relative proportions of herbivore species of total mass density based on fossil abundances (Guthrie 1968; Mann et al. 2013), their generalizability is uncertain. Simulating coexistence and density proportions mechanistically is challenging. For these reasons, we focused on only the woolly mammoth whose population density (in mass per area) can be interpreted as an upper limit for the guild of large herbivores (Redmann 1982).

Bayesian Fitting

Bayesian inference allows us to use prior knowledge $\mathrm{Pr}(\theta)$ and observational data d to estimate unknown parameters θ in a given model M (Sivia and Skilling 2006). According to Bayes' rule (Bayes and Price 1763), this posterior parameter probability $\mathrm{Pr}(\theta|d, M)$ is proportional to the product of the prior probability and the probability (= likelihood) $\mathrm{Pr}(d|\theta, M)$ of reproducing the observations d with the model:

$$\mathrm{Pr}(\theta|d, M) \propto \mathrm{Pr}(\theta) \times \mathrm{Pr}(d|\theta, M) \tag{1}$$

In our case, prior knowledge, $\mathrm{Pr}(\theta)$, comprises conceivable parameter ranges for the woolly mammoth in MMM and some megafauna-related parameters in LPJ-GUESS. θ is then a vector of parameter values. Appendix C accounts in detail how we chose minimum and maximum values ($\theta_{i,min}$, $\theta_{i,max}$) for each parameter θ_i (Tables S14 and S15). In order to reflect our assumption that extreme values near $\theta_{i,min}$ and $\theta_{i,max}$ are less likely, we describe prior probabilities with a dome-shaped β distribution (dashed lines in Fig. 4):

$$\theta_i \sim \theta_{i,min} + \beta(2,2) \times \left(\theta_{i,max} - \theta_{i,min}\right) \tag{2}$$

Defining the likelihood is more difficult as there are no observational data on mammoth densities. That makes it impossible to fit the model's response variable to data, as is typically done in statistical modeling. However, we have some knowledge about the environmental conditions under which mammoths were able to survive. In other words, we do not know how many mammoths there were, but we know *that* they were there. If we imagine environmental variables, for instance annual precipitation and summer temperature, spanning a hyperdimensional space, the hypervolume enclosing conditions suitable for mammoth populations to thrive can be called their fundamental niche (Hutchinson 1957). In this sense, we take the fundamental niche reconstructed for mammoths as "observational" data d. Now we can say that the likelihood Pr$(d|\theta, M)$ should be higher the better the model (given parameters θ) reproduces viable mammoth populations within this environmental envelope. This approach makes no assumptions about population densities but only about their presence.

In practical terms, we simulated mammoths in a set of sample locations that fall within the mammoth's climate niche (Fig. 2*B*). We selected the locations manually to broadly represent regions that are considered partially analogous to Pleistocene steppe, excluding grid cells where LPJ-GUESS simulated no primary production at all. In the Arctic, partial analogs can be found where local-scale topography (slopes, bluffs, pingos) creates conditions for extrazonal steppe vegetation to persist (Yurtsev 1982; Lloyd et al. 1994; Marilyn D. Walker and Short 1991; Berman et al. 2011; Zimov et al. 2012; Reinecke et al. 2017). In mountainous regions of lower latitudes, high-elevation climate can provide region-scale conditions (low temperature, low precipitation) for grasslands and grazers (Guthrie 1982; Pavelková Řičánková et al. 2014; Pavelková Řičánková et al. 2015; Chytrý et al. 2019). We defined the likelihood as the proportion of locations where the model predicts viable populations ("viable" is defined below).

In order to obtain the posterior probability Pr$(\theta|d, M)$ we need to derive a normalizing constant for the right side of Equation 1. In fact, we are interested not only in the posterior probability for one value of the parameter vector θ but the whole posterior *distribution* $p(d, M)$ over the support of θ. In any but the simplest cases, this requires a numerical approach such as Monte Carlo Markov Chains (MCMC) (Hooten and Hefley 2021). In principle, this method repeatedly samples randomly (hence Monte Carlo) from the parameter space. By using its previous sample as a starting point to find the next one this procedure yields a Markov Chain. The chain will move to (i.e., accept) a new random proposal θ^* if the posterior probability Pr$(\theta^*|d, M)$ at that point is higher than at the current position θ. This principle ensures that, with increasing chain length, the density of accepted samples in parameter space converges to the posterior probability distribution $p(d, M)$.

Among available MCMC approaches, Metropolis–Hastings updating (Metropolis et al. 1953) is simple and widely applicable (Hooten and Hefley 2021). Here, the chain starts at an initial parameter vector θ^0, which we manually defined as a set of parameter values that worked to yield viable mammoth populations (Tab. S14). Starting at $k = 1$, a proposal θ^* for next chain position θ^k is drawn from a proposal function, which we defined as Gaussian: $\theta^* \sim N(\theta^{k-1}, 0.05)$ (second argument is standard deviation, manually tuned for effective sampling). Note that each dimension of the parameter space is normalized to the interval $[0, 1]$ corresponding to $[\theta_{min}, \theta_{max}]$. Then the Metropolis–Hastings ratio is calculated as

$$mh = \frac{\text{Pr}(\theta^*) \times \text{Pr}(d|\theta^*, M)}{\text{Pr}(\theta^{k-1}) \times \text{Pr}(d|\theta^{k-1}, M)}. \tag{3}$$

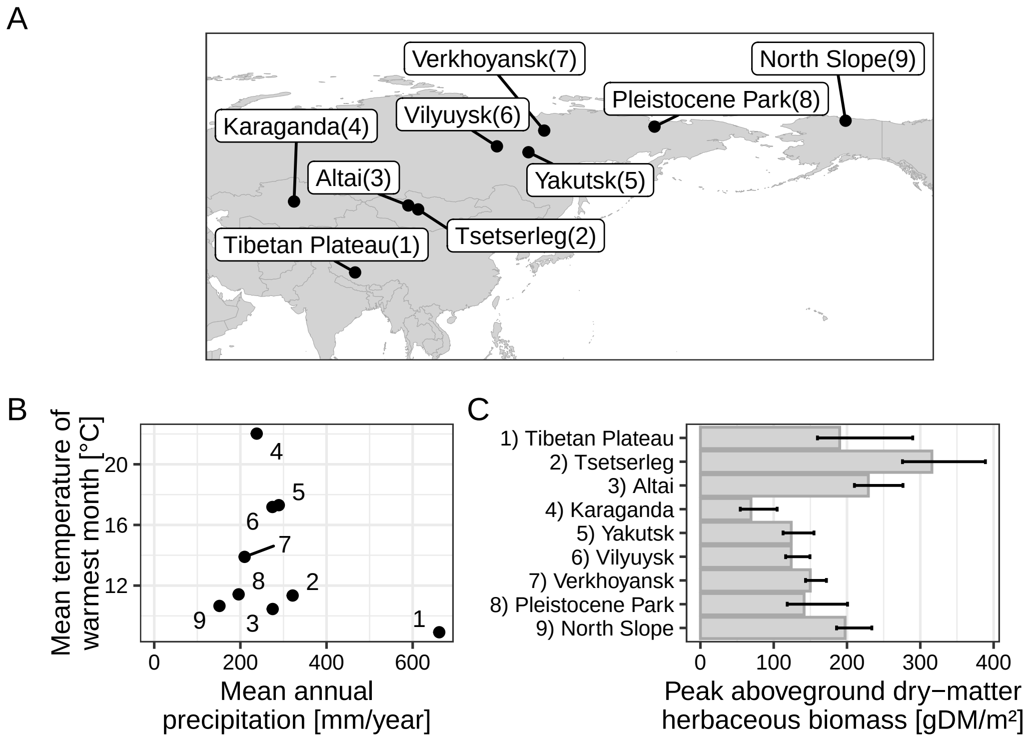

Figure 2. Locations for mammoth density simulations. *A,* Map of manually selected grid cells used for fitting (names only serve as memory aid). *B,* Mean climate of grid cells used to drive simulations (CRU-NCEP 1960–1990). *C,* Mean simulated peak aboveground dry-matter (DM) biomass without herbivory. Bars show 95% quantiles.

The proposal is accepted (i.e., $\theta^k := \theta^*$) with a probability of min$(mh, 1)$; otherwise the previous value is retained (i.e., $\theta^k := \theta^{k-1}$) for the next iteration. This means that a better proposal (i.e., higher posterior probability) always gets accepted, and a worse proposal may or may not, depending on the ratio mh. Then k is incremented and the above steps repeated until the chain has reached a desired length (in our case 2500). To ensure a thorough exploration of the whole parameter space we ran 27 chains in parallel. Using trace plots (sampled values over iterations by chain for each parameter, not shown) we determined that chains were well mixed after 250 iterations, which we defined as burn-in period and discarded from the posterior distribution. We implemented the Bayesian sampling in in R 4.3.1(R Core Team 2023).

By sampling the full prior parameter space, Bayesian simulations naturally propagate all input uncertainty to the output. However, predictive uncertainty related to model parameters has actually three different components (Dietze 2017). Parameter *uncertainty* itself is the variance of the parameter values in general. It is reflected in the width of the (marginal) posterior distribution resulting from MCMC sampling. Parameter *variability* refers to parameters changing through time and space or between taxonomic units, populations, or individuals. We neglect parameter variability because its role is probably small in comparison with other sources of uncertainty, and evolutionary adaptations or variability within populations are very difficult to quantify sufficiently. Finally, parameter *sensitivity* describes how strongly the model output is affected by changes in parameter values. This is not directly evident from the Bayesian fitting but should be evaluated in a sensitivity analysis.

Sensitivity Analysis

For studying the behavior of a complex model a new layer of abstraction is helpful: a metamodel describing the relationships between varying parameters (predictor variables) and the simulated output (response variable). Such a metamodel should learn from given data with few prior assumptions and be able to handle interactions between predictors and non-linear responses. Machine learning fulfills these requirements, in particular boosted regression trees (Elith et al. 2008), which compare well to other metamodel methods in sensitivity analysis (Prowse et al. 2016). Regression tree approaches repeatedly create splits at those values of predictor variables that are most decisive for the outcome. Many such splits form a decision tree whose leaves represent values on the outcome scale. Boosting iteratively aggregates such trees to create a more robust average. We tuned hyperparameters (interaction depth, number of trees, and learning rate) manually, minimizing root mean squared error (RMSE) with 25 bootstrapping iterations.

Boosted regression trees provide valuable diagnostic output: importance ranking and partial dependence plots. Importance ranking relies on the effect of splits: The more often a predictor variable was selected for new splits in the decision trees and the larger the resulting predictive improvement, the higher is this predictor's importance rank (Friedman 2001). Partial dependence plots visualize how the response variable behaves to changes of *one* predictor variable, with all other predictors held constant (Friedman 2001). They capture the nature of the dependence but may give an incomplete picture in case of higher-level interactions (Elith et al. 2008). All predictors were automatically z-scored (centered at zero and divided by the standard deviation). For calculations, we used the packages `caret` 6.0-93 (Kuhn 2022), `gbm` 2.1.8 (Greenwell et al. 2020), and `pdp` 0.8.1 (Greenwell 2017) in R 4.3.1(R Core Team 2023).

We were interested how sensitive mean herbivore density is towards the choice of parameter values. In order to maximize the number of simulations to train the metamodel, we included output of all simulations from the Bayesian MCMC — both the accepted and rejected parameter samples. Since the Bayesian fitting already includes the likelihood (i.e., confronts the model with data), the resulting parameter sensitivity should only be interpreted in context of this particular application. Even a global sensitivity analysis over all prior probabilities would only give results that are still contingent on priors, vegetation model, and climate drivers. Therefore this is not a sensitivity analysis of MMM in general.

For simplicity's sake we only defined *marginal* prior probability distributions: one range per parameter. This generates many non-viable combinations: e.g., very low intake with very high expenditure. As a result, the volume of viable combinations in parameter space is much smaller than the prior probability volume. Therefore we removed all simulations on grid cells that didn't yield a "viable" population and used only the mean herbivore mass density ($^{kg}/_{ha}$) after the initial rise as response variable (see definitions below). This approach will give the model's parameter sensitivity *given* that the parameter combinations are sensible. In total, this left 26,562 samples to train the metamodel.

Simulation Setup

Environmental changes through time are of little concern in this study, as it aims at long-term carrying capacity. Therefore we chose to drive simulations with climate data that lacks any dynamics above decadal scale. This approach leads mammoth populations into a long-term equilibrium with a quasi-constant environment. Even though Pleistocene Eurasia presented anything but a constant environment (Wolff et al. 2010) and mammoths experienced repeated range shifts (Markova et al. 2013), each equilibrium simulation can estimate potential carrying capacity for one point in climate space. With changing climate, animals likely moved to more suitable regions in order to remain within their fundamental niche in climate space (Lorenzen et al. 2011). Accordingly, our approach — despite using real-world locations — is geographically inexplicit and operates in climate space.

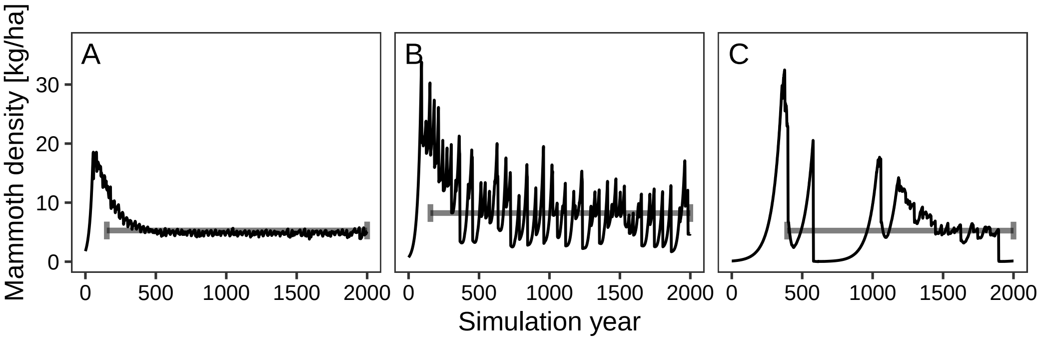

Figure 3. Example time series of simulated mammoth populations. Horizontal gray lines indicate the calculated mean density after the end of the first rise. Depending on the parameter combination, populations can be quite stable (*A*), fluctuating (*B*), or prone to crashes (*C*).

LPJ-GUESS and the climate driving it provide a quasi-constant environment for the mammoth populations (Fig. 1). LPJ-GUESS was set up to simulate 3000 years of spin-up data (cf. Appendix B.3.1), in which it repeats a detrended monthly climate time series of 1960–1990 from the CRU-NCEP dataset (Wei et al. 2014), which includes atmospheric CO_2 concentrations. Each location is a cell from the 0.5°×0.5° CRU-NCEP grid. Mammoths are established after 1000 years of vegetation spin-up, which is the time when the grass biomass reaches equilibrium. In the following 2000 years, a mammoth population can reach its dynamic equilibrium; the "historical" period after the spin-up period is of no interest in this study. Stochastic disturbance and fire are disabled in LPJ-GUESS. In all locations, the model simulates only grassland, without competition. This makes "C_3 grass" the only plant functional type representing all herbaceous vegetation. We used daily allocation (Boke-Olén et al. 2018) and the adjustments discussed in Appendix B.3.4. Nitrogen limitation was enabled and nitrogen deposition set to the default pre-industrial value of 2 kg N/ha/year. Soil codes are taken from Sitch et al. (2003). Figure 2*C* shows the resulting aboveground net primary production simulated by LPJ-GUESS.

The locations chosen for simulation approximate the breadth of a hypothesized fundamental niche of the woolly mammoth (and the mammoth steppe in general). Aridity, cold winters, and short vegetation periods generally characterized the mammoth steppe climate (Guthrie 1984). With increasing precipitation and temperature, forest, tundra, or wet- and peatlands may take over (Binney et al. 2017). For approximately covering the niche of woolly mammoth we hand-selected grid cells from around the Northern Hemisphere (Fig. 2*A*) that are either in steppe regions today considered modern mammoth steppe analogs or relics (Walker et al. 2001; Pavelková Řičánková et al. 2014; Reinecke et al. 2021); or thought to be climatically suitable if tundra were to give way to grassland (Zimov et al. 2012). Plotted as summer temperature over annual precipitation (Fig. 2*B*), climate space covered by the selected grid cells broadly corresponds to the L-shaped climatic envelope that Zimov et al. (2012, Fig. 2) suggest for the mammoth steppe. Using paleoclimate simulation output instead of modern-day climate would be desirable, but uncertainties of currently available data products (Liu et al. 2009; Armstrong et al. 2019) can lead to unrealistic net primary production and thus distort inference (cf. Zhu et al. 2018). Note that the climate envelope along annual precipitation and summer temperature does not make an assumption to what extent large herbivores "engineered" their habitat. The model assumes steppe vegetation, but without representing the mechanism for maintaining it: be it ecosystem engineering by megafauna or environmental factors.

Defining Viable Populations

A simulated mammoth population in a grid cell is defined as viable if it has reached a (dynamic) equilibrium well above establishment density. All populations start with an exponential growth until they reach a first peak, after which they oscillate with varying amplitude (Fig. 3). The initial

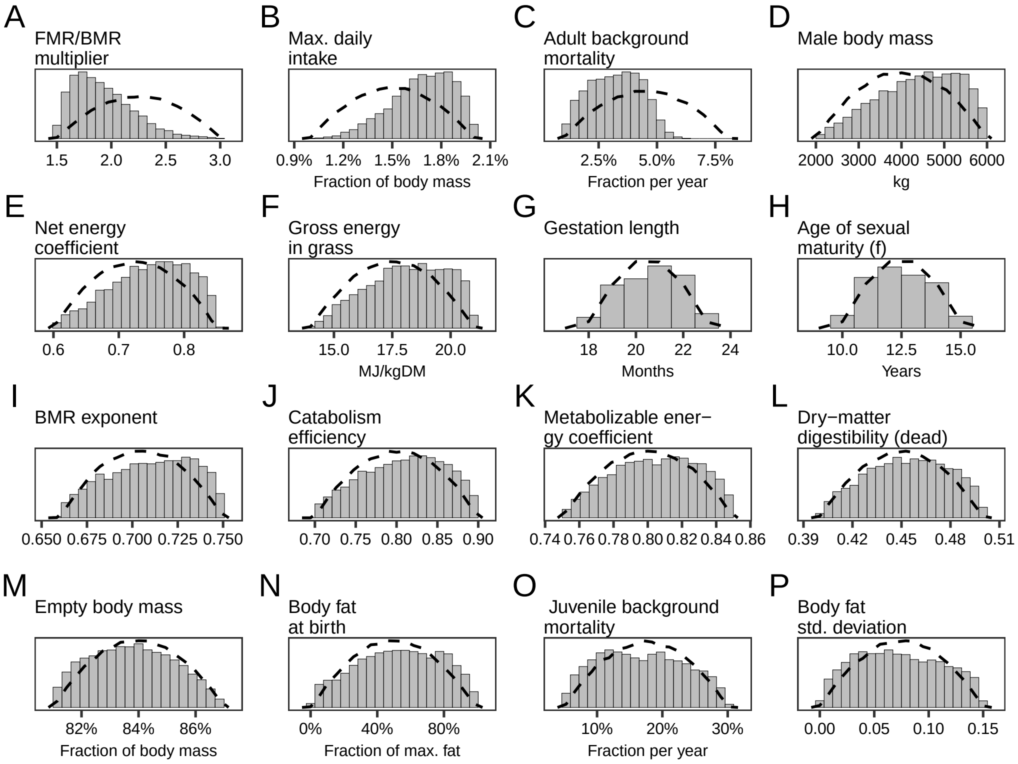

Figure 4. Marginal prior (dashed lines) and posterior (histogram columns) probability/mass distributions of woolly mammoth parameters, ordered by prior–posterior shift. The posteriors of the remaining 15 parameters match the priors and are not shown. Note that female body mass is derived from male body mass by a factor (not shown); hence *D* is to be interpreted for both sexes.

rise is not representative of the long-term equilibrium. In a moving window the mean herbivore mass density of each year is compared with 50 years prior. The first peak is reached when this difference first drops below 5% of the overall mean density. The first 100 years of the time series are ignored because an initial drop after establishment can give a false signal. The time until the first peak varies substantially. Therefore only the time between the first peak and the end of the simulation period is used to calculate the arithmetic mean density used for further analysis. A mean of less than twice the establishment density (0.01 ind/km²; Appendix C.2) indicates that the population kept crashing immediately after being (re-)established. Such simulations with non-viable populations are discarded. This leaves mean herbivore densities that approximate a hypothetical carrying capacity for the given climate.

Preregistration and Data Availability

In order to avoid potential biases, modelers should be wary of altering their simulation setup after seeing their model results (Traylor 2024). Still, modeling remains an iterative process. We left parameter ranges and megafauna model unchanged after the first simulation on selected locations[1]. Afterwards we introduced Bayesian fitting and adjusted the simulation locations and postprocessing to make inference more meaningful. Software and data to reproduce the analysis are available under 10.5281/zenodo.4972504.

Results

The Bayesian fitting yielded a joint posterior probability/mass distribution for 31 model parameters (Fig. 4). Most of these correspond to their prior distribution, which indicates that the data did

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[1] Archived on Open Science Framework: https://osf.io/tmyf7

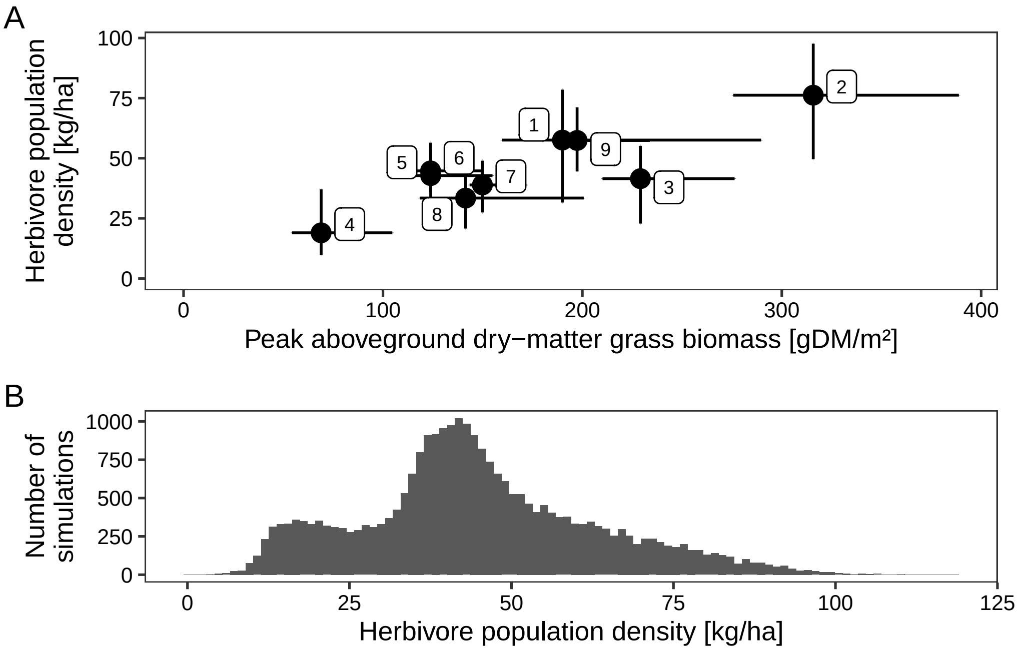

Figure 5. Mean mammoth density of simulations accepted in the Monte-Carlo Markov Chains. *A,* Simulated mammoth mass density means over peak aboveground dry-matter (DM) grass biomass (net primary production, from vegetation-only simulations) of the respective location (cf. Fig. 2); bars indicate 95% intervals and dots medians. *B,* Histogram of mammoth densities from all simulations, which can be interpreted in Bayesian terms as a posterior probability distribution. Note that the bimodal shape is an artifact from the small number of locations.

not substantially constrain these parameters. (Note however that the marginal distributions don't show the covariance structure of the joint posterior, which reflects parameter "trade-offs" not included in the prior: e.g., between maximum intake and gross grass energy content.) For some parameters, the posterior is shifted from the prior: maximum daily intake, adult background mortality, field metabolic rate, net energy coefficient, and body mass. In particular, the posterior distributions suggest that (1) a field metabolic rate exceeding twice the basal metabolic rate is unlikely (Fig. 4*A*); that (2) energy intake requires some optimization towards high caloric density in forage (Fig. 4*F, L*), high daily intake (*B*), and high forage utilization efficiency (*E, J, K*); that (3) lower fractional intake rates (Fig. 4*B*) can only be sustained by larger-bodied animals (*D*); and that (4) annual mortality rates of adults above 4% are implausible (Fig. 4*C*), which has implications for extinction pathways discussed below. In short, physiological and demographic traits need to be optimized for populations to survive the full spectrum of abiotic conditions.

Simulated mean mammoth densities strongly depend on primary production (Fig. 5*A*), which reflects that the modeled herbivore populations are strongly bottom-up controlled. Within each location, the distribution of mass density means takes the shape of a log-normal distribution, just as real-world population densities (Limpert et al. 2001). This is remarkable because it shows that there is not only an upper limit given by primary production but also a lower limit given by model mechanics and priors: If a parameter combination yields "viable" populations (as defined above), these also attain substantial densities. From a Bayesian point of view there is no difference between MMM's parameters and its output (mass density), as all of them are unknown estimands, whose posterior probabilities are proportional to the product of prior and likelihood. That we let mass density emerge from the model without further constraints is equivalent to assigning a uniform prior. Accordingly, the histogram in Figure 5*B* displays the posterior probability distribution of mammoth density in the sampled climatic niche of the mammoth steppe — given all model as-

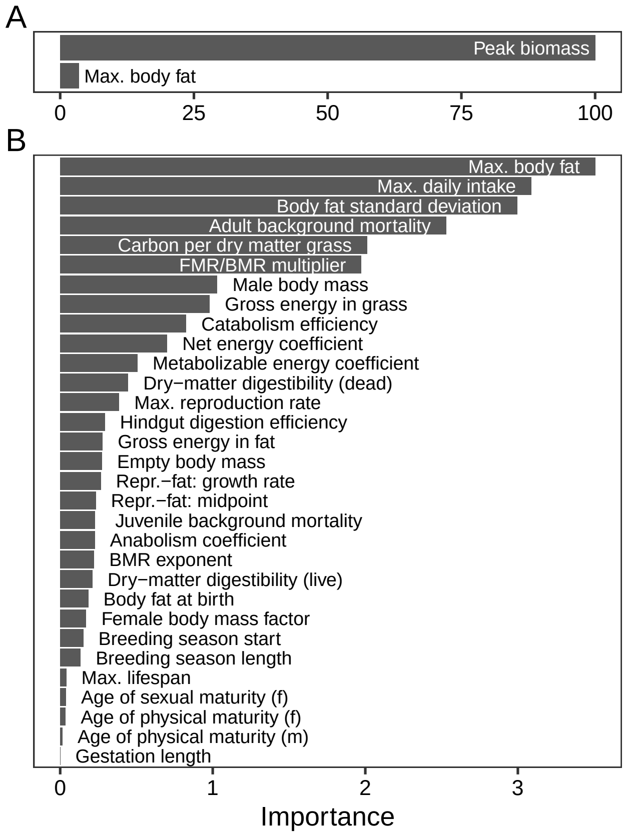

Figure 6. Relative influences of, *A,* annual peak aboveground herbaceous biomass (as a measure of net primary production) and, *B,* model parameters on simulated mean mammoth densities, based on a boosted regression trees metamodel and scaled to 100 for highest importance. The diagram is split to make the scale legible.

sumptions. Based on annual aboveground dry-matter forage production of ca. 70–315 $^{g}/_{m^2}$, 95% of the simulated mammoth densities fall into a range of 13–85 $^{kg}/_{ha}$.

Boosted regression trees show which parameters the model is most sensitive to. Hyperparameter tuning achieved RMSE = 4.52 (z-scored) and $R^2 = 0.95$ with interaction depth = 4, learning rate = 0.05, and tree count = 6000. Figure 6 shows the relative importance of predictor variables in the metamodel. Available forage (peak biomass) is by far the most important predictor for mean herbivore density (cf. Fig. 5*A*). Of MMM's parameters, a group of parameters related to energy budget dominates the outcome. Among them, only body fat standard deviation (Appendix C.2.9) is a tuning parameter without physiological basis. The partial dependence plots (Fig. 7) help visualize the kind of influence a single predictor has on the output (positive/negative, linear/saturating, etc.). Note that partial dependence curves become unreliable where there are no or few simulations, such as where adult background mortality exceeds 4%. The most important parameters all show linear relationships on their respective value range, except for body fat standard deviation, whose influence saturates towards higher values.

Discussion

We used a dynamic grazer–vegetation model to derive potential mammoth densities from physiological and population-theoretical principles, considering megafauna parameter uncertainty. The resulting 95% compatibility interval of 13–85 $^{kg}/_{ha}$ lies in the same magnitude as extant densities of wild large herbivores (Tab. 1). This is insofar remarkable as it suggests that our knowledge of metabolic and reproductive parameters for an extinct species and a few theoretical assumptions are

Table 1. Published large herbivore densities for Pleistocene mammoth steppe (*upper part*) and extant ecosystems (*lower part*)

Domain	Density (kg/ha)*	Reference
Mammoth in climate envelope (model)	13–85†	This study
Herbivore guild in grassland (model)	83–120	Redmann (1982)
Circumpolar Arctic in LGM (model)	0–40	Zhu et al. (2018, Fig. 3c)
Pleistocene NE Siberia (bone count)	105	Zimov et al. (2012)
Late-glacial Alaska (bone count)	88	Mann et al. (2013)
Herbivore guild in steppe-tundra (model)	8–15	Bliss and Richards (1982)
Arctic and alpine tundra	0.3–4.3	Redmann (1982)
Temperate grasslands and forests	9–36	Redmann (1982)
Pleistocene Park (2014)	10–30	Reinecke et al. (2021)
Various African game parks	4–190	Pachzelt et al. (2013)

* Density ranges represent lowest and highest reported values.

† 95% quantile of posterior density distribution.

enough to model plausible population densities as an emergent property. The bottom-up, highly mechanistic model works well without being tuned to specific population densities. Despite the high number of parameters, the model is well constrained by prior knowledge about the physiologically plausible parameter ranges. Requiring the presumed mammoth steppe climatic envelope to produce viable populations did little to narrow posterior parameter distributions: most posteriors resemble priors. Still, the Bayesian model fitting demonstrates that mammoths required an optimal intake–expenditure balance, benefited from larger body size, and were particularly sensitive to adult mortality above 4% annually (Fig. 4). The high importance of maximum body fat (Fig. 6*B*) indicates that starvation capacity is critical for surviving the winter.

Net primary production (NPP) has a much higher influence on population density than all herbivore-related parameters (Fig. 6*A*). Higher NPP means more fresh forage in the growing season and more standing dead grass in winter, which allows more animals to survive until spring. This important role of resource limitation underscores the need for a sophisticated dynamic vegetation model, such as LPJ-GUESS. Moreover, it demonstrates how the priors on herbivore parameters sufficiently constrain predictions by the grazer model.

The Bayesian approach has the benefit of transparently propagating errors from a-priori uncertainty to a-posteriori credibility. The challenge lies in including all sources of a-priori uncertainty (Simmonds et al. 2024). The present analysis only considers prior probability distributions of MMM's parameters. Not included are uncertainties stemming from environmental drivers, the grass production model of LPJ-GUESS, and model structure. Any model is a simplification and might neglect processes that are actually important. Before putting the results into context of other attempts to reconstruct glacial megafauna densities, we will discuss limitations of the three model components climate, vegetation, and herbivores along two dimensions: prediction uncertainty and bias towards over- or underestimation (Tab. 2).

Model Limitations

Climate Drivers

The coupled herbivore–vegetation model is built on the concept that environmental conditions define primary production, which in turn defines mammoth densities. Therefore the impact of uncertainties in climate increases by propagation through multiple model layers. We used a spatiotemporally inexplicit climate envelope to cover a conceivable range of environmental conditions. This circumvents the uncertainty inherent in gridded paleoclimate reconstructions (e.g., Liu et al. 2009; Armstrong et al. 2019). On the other hand, the samples (locations) in climate space do not represent relative prevalence of the respective climatic conditions of a particular region or time. In the mammoth steppe, some conditions occurred more often than others, but this is challenging

Table 2. Possible reasons why the predicted mammoth densities could be over- or underestimating megafauna carrying capacity in the glacial mammoth steppe

Overestimation	Underestimation
Modern CO_2	No migration
No smaller megafauna species	No functional diversity
No snow covering forage	No demographic compensation by other megafauna
No climate variability	
High-productivity sites in our sample	
LPJ-GUESS overestimates NPP (Fig. S8)	
No predation	
Carbon as the only limiting resource	

to reconstruct quantitatively and therefore not reflected in our choice of location samples. This means that the posterior density distribution (Fig. 4) gives a *range* of plausible mammoth densities but does not allow inference about relative prevalence: i.e., how common higher densities were compared to lower ones. Inference about *total* global wild herbivore biomass (Barnosky 2008; Zimov and Zimov 2014) would require projecting climate space to geographic range in the glacial: a challenging step because of high uncertainty in paleoclimate projections.

Spanning environmental space with only annual precipitation and summer temperature is actually rather simplistic and may not do justice to the distinct characteristics of a glacial cold steppe. Annual precipitation sum can be a poor surrogate for moisture availability during the growing season (Swemmer et al. 2007). While summer air temperature certainly is a proximal driver for primary production, it does not necessarily capture variation in length of growing season, which is critically determined by snow melt and soil thaw. A logical next step would be to simulate megafauna densities in a large number of random locations, evenly sampled from modern analog regions.

Disentangling potential environmental drivers determining steppe vegetation and its productivity was not the aim of this study. We tried to avoid presuming either the Climate Hypothesis (e.g., Guthrie 2001) or the Keystone Herbivore Hypothesis (e.g., Zimov et al. 1995). By choosing the large climatic envelope suggested by Zimov et al. (2012), we aimed to encompass a wide range of conceivable environments. It would be worthwhile to refine this approach by simulating megafauna densities under conditions that correspond in detail more closely to what different hypotheses postulate.

Driving simulations with virtually no interannual variability generates a rather artificial long-term carrying capacity as it avoids the question of climatic perturbations. However, these fluctuations may have determined the very character of glacial steppes (Lister and Sher 1995; Mann et al. 2019). If the glacial mammoth steppe was indeed characterized and maintained by constant climatic fluctuations and plant communities in disequilibrium, the effects are probably less relevant for the scope of this study: The vegetation model neglects both competition and dispersal but simply prescribes herbaceous plants, and the megafauna model neglects mobility and spatial heterogeneity. This way, the model setup circumvents the question how climate fluctuations have influenced vegetation composition.

This leaves us with climate perturbations possibly diminishing megafauna populations repeatedly, which would keep them below potential carrying capacity (e.g., Aanes et al. 2000; Solberg et al. 2001; Kaczensky et al. 2011). This is not represented by the model either. With its slow reproduction rate, the woolly mammoth would have recovered slowly from such events. On the other hand, there is good reason to surmise that total biomass of the large grazer community as a whole may have remained rather stable (Prins and Douglas-Hamilton 1990). Faster reproducing grazers could temporarily "fill the gap" left by slowly reproducing ones. Nonetheless, carrying capacity simulated in artificially stable climate should be interpreted as an upper limit of plausible ranges (Tab. 2).

Vegetation Model

The parameter sensitivity analysis identified annual aboveground net primary production as by far the most important determinant of carrying capacity in the model (Fig. 6*A*). Variance in primary production is composed of natural heterogeneity as well as uncertainty of the vegetation model, which is in turn comprised of driver, parameter, and conceptual uncertainty (Dietze 2017). At this point, we cannot disentangle these components. It would require a global parameter uncertainty analysis of the LPJ-GUESS with daily grass growth as well as scrutinizing how well the model represents processes critical for glacial steppe productivity: e.g., drainage, snow melt, soil temperature, nutrient cycling, in particular herbivore-accelerated nitrogen turnover. Unfortunately, this is beyond the scope of this study because LPJ-GUESS is a very complex model not designed to be routinely subjected to uncertainty/sensitivity analyses (but see Pappas et al. 2013; Bagnara et al. 2019).

Critical parameters for daily grass growth have been calibrated with Australian sites (Boke-Olén et al. 2018). Still, the grass model does reproduce the magnitude of grassland production measured in temperate, alpine, and arctic sites (Fig. S8), and the annual aboveground dry-matter NPP in the arcto-alpine sites of this study (Fig. 2c) falls into the range of measured Arctic tundra and grassland productivity (Bliss 2000, p. 25; Tieszen 1972, Tab. 3; Chapin III et al. 2011, p. 151; Gough and Hobbie 2003, Fig. 1a; Velichko and Zelikson 2005; Reinecke et al. 2021). In addition to primary production, decay rates of standing grass in winter is critical — as winter survival turns out to limit population size in the model. For more solid inference about potential megafauna densities, the sources of uncertainty in LPJ-GUESS need to be quantified in the same detail as we have done for MMM.

We have neglected the fact that atmospheric CO_2 concentrations were much lower during the glacial, which can drastically reduce primary production (Gerhart and Ward 2010; Poorter et al. 2022). LPJ-GUESS does include a mechanism to reduce primary production under lower CO_2, but accuracy and uncertainty of this mechanism remain to be evaluated (cf. Kastner et al. 2022). In any case, grass productivity simulated with modern CO_2 is certainly an overestimation of glacial conditions (Tab. 2).

Megafauna Model

In its current form the model rests on two balances: energy intake–expenditure and reproduction–mortality balance, both mediated by fat storage, with winter survival as bottleneck. In this simplicity, the model necessarily neglects other potential population-limiting resources: e.g., sodium availability (Davydov et al. 2020), protein intake (Matheus 2003), and freshwater access (Velichko and Zelikson 2005; Wang et al. 2018). In addition, snow can substantially reduce available winter forage (Schwartz and Thompson 1985; Rutley and Hudson 2001). That all these factors could further reduce carrying capacity estimates confirms that our results should be interpreted as upper limits (Tab. 2). On the other hand, an important shortcoming of the model is the lack of spatial heterogeneity and movement. These factors could actually increase density estimates.

In real-world herbivore systems, intake patterns are always shaped by spatial heterogeneity of resources (Owen-Smith 2004). In contemporary migratory systems, large herbivores attain higher densities thanks to movement by avoiding predators and exploiting different patches at peak resource availability (Sinclair 2003). Mammoths may not have been limited by predation but they may have conceivably migrated long distances (Wooller et al. 2021; Kowalik et al. 2023) — although not necessarily seasonally (Widga et al. 2021). In a dynamic model, local population crashes can be buffered or avoided by movement (Stratmann et al. 2023). On a regional scale, seasonal migrations in north–south trajectory could effectively distribute grazing pressure during summer to northerly areas. At the end of summer, this would leave more forage in southern patches, where animals would aggregate again during winter. How much this hypothetical mechanism could increase winter survival and overall population density would have to be tested in simulations.

Modeling only one megafauna species may either over- or underestimate carrying capacity (as biomass per area) (Tab. 2). Due to the allometric scaling of metabolic rate, large species require less forage per kilogram body mass than smaller ones (Peters 1983). Therefore a community composed of large-bodied animals will attain higher densities of biomass per area (Redmann 1982; Zhu et al. 2018). In this way, modeling only mammoths will overestimate megafauna densities. On the other hand, a functionally diverse community may utilize resources more completely, with different species specializing on different forage types (Pansu et al. 2022). Modeling this mechanism would not only require multiple herbivore species and plant types but also increased net primary production resulting from plant functional diversity. Since the plant functional type "grass" already represents all herbaceous vegetation, trees and shrubs — providing forage for browsers — could potentially increase whole-ecosystem net primary production. However, because browse is less nutritional we conjecture the effect to be small at best.

An asset of the model is that vegetation and herbivores interact dynamically. Inherently, grazing, nutrient distribution, and disturbance are spatially heterogeneous (Hobbs 2006). Large herbivores tend to forage in the most nutritious or snow-free patches; by excreting urine and feces they redistribute nutrients in the landscape; as herds they trample some areas more intensively than others, etc. But is this heterogeneity on a local scale relevant on a regional scale (Hobbs 2003; Holyoak and Wetzel 2020)? Must these mechanisms be considered in order to understand large-scale carrying capacity? Proponents of the Keystone Herbivore Hypothesis might argue for it (Owen-Smith 1987; Zimov et al. 1995; Zimov et al. 2012). However, to our knowledge, no published study has tried to quantify the large-scale effect of these mechanisms on carrying capacity. At each step in "zooming out" from local, to landscape, to regional scale it is paramount to understand which sources of uncertainty (*sensu* Dietze 2017) dominate and to decide at which point inference or prediction become impossible. Such an analysis could identify critical mechanisms currently missing in MMM.

Population Densities in Context

Given the above considerations, the simulated mammoth densities could be interpreted as either over- or underestimating mammoth steppe carrying capacity (Tab. 2). In our assessment, arguments for them being overestimations weigh stronger: High CO_2 overestimates glacial NPP; constraining mechanisms such as snow foraging and interannual variability are missing; and the large herbivore guild is only represented by its metabolically most efficient member. Metabolic efficiency allows high animal mass densities (Redmann 1982; Zhu et al. 2018). In this light, it stands out that high densities (ca. >80 kg/ha) are already rare (Fig. 5*B*) and only achieved in the most productive site (site 2 in Fig. 2 and 5*A*). This contrasts with higher carrying capacity of the mammoth steppe estimated by some authors (Tab. 1).

Redmann (1982) formulated a simple model of production and diversity in large-herbivore communities. He assumed an annual aboveground net primary production of 150 g/m^2, which would be all consumed by a guild of grazers. Forage requirements scale with body mass and an allometric exponent of ¾. Keeping whole-guild forage intake constant, total grazer density varies with body sizes. Depending on the body size composition of the grazer guild, this model predicts megafauna densities of 83–120 kg/ha. While the principle assumptions of Redmann's bottom-up approach resemble ours, it overlooks seasonality and winter bottlenecks, which our study identified as particularly important. Also Matheus (2003) has criticized Redmann's densities as much too high. He pointed out that Redmann's model would predict bison densities in pre-European Great Plains of 25 ind/km^2, which are twice as high as even optimistic pre-European bison density estimates (Epp and Dyck 2002). In contrast to Redmann's assumption of high primary production, Bliss and Richards (1982) calculate with a less productive ecosystem of sedges, shrubs, mosses, and lichens, consequently arriving at a very low estimate of 8–15 kg/ha (which is still much higher than today). However, more recent evidence for herb- and graminoid-rich vegetation during the glacial (e.g., Zazula et al. 2003; Zazula et al. 2007; Wang et al. 2021) points to higher primary production. Zhu et al. (2018) used a mechanistic grazer model, which shares many concepts with this study and was likewise coupled with a dynamic vegetation model. They arrived at densities of 0–40 kg/ha for mammoth steppe areas in the late-Pleistocene, which might be so low because of bias in the paleoclimate driving data.

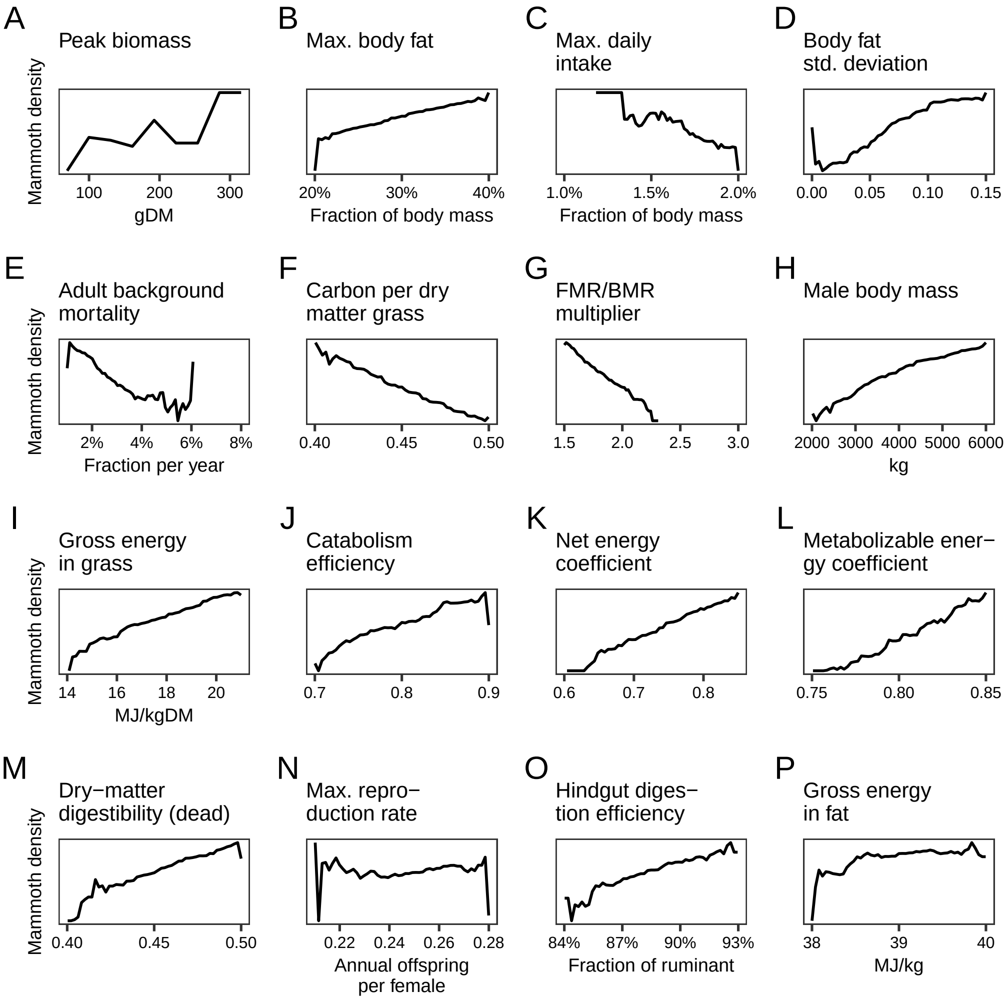

Figure 7. Partial dependence plots from boosted regression trees. Only the 16 most influential parameters are shown, ordered by descending influence. Plots show general trends of how each parameter influences simulated mean mammoth densities over its value range (x axis). Trajectories should be interpreted qualitatively (increase, decrease, thresholds), which is why the y axis scale is not shown. Irregularities near the edges are artifacts.

More proximal inference about glacial megafauna densities comes from long-term bone accumulation rates in permafrost. To our knowledge, only two studies have applied this approach: In northeastern Siberia, Zimov et al. (2012) calculate 105 kg/ha total herbivore biomass; and in Alaska, Mann et al. (2015) calculate 88 kg/ha total grazer biomass. Unfortunately, both studies do not quantify uncertainties in their calculations, which makes their results difficult to compare. Other proxies for megafauna abundance are not mature yet. Attempts at using ancient DNA to infer effective population sizes per region suffer from very wide credibility intervals (Debruyne et al. 2008), and there are no quantitative models (yet) to relate dung fungal spores (Gill et al. 2013) to population size. Recreating ecosystems resembling the mammoth steppe, as intended by the Pleistocene Park in northeast Siberia (Zimov 2005), might reveal upper limits of carrying capacity in high latitudes, but that still needs time and is inhibited by the lack of very large ecosystem engineers (Reinecke et al. 2021). In light of the evident uncertainties in estimates of Pleistocene megafauna densities, large-scale extrapolations of these numbers for defining a baseline of potential global herbivore biomass (e.g., Barnosky 2008; Zimov and Zimov 2014; Smith et al. 2016; Manzano et al. 2023) should be interpreted with caution.

Implications for Late-Quaternary Extinctions

Why over a third of Eurasia's large-bodied (>45 kg) mammals went extinct during the Late Quaternary remains debated (Stuart 2015; Mann et al. 2019; Fordham et al. 2022; Svenning et al. 2024). In addition to climate-induced habitat changes, hunting pressure by *Homo sapiens* is a likely extinction cause (Barnosky et al. 2004). Our simulation results mark a continuous annual mortality rate of 4% for adult woolly mammoths as a maximum below which the population won't survive (Fig. 4*C*). In the model, this threshold emerges from the maximum reproduction rate and the number of fertile life years in females. The dynamic model confirms Bliss and Richards (1982) who calculated a maximum of 4% of harvestable biomass from a mammoth population. Congruent with observations in extant large herbivores (Garrott et al. 2003) both survival and density of our simulated mammoth populations are largely unaffected by juvenile mortality. Therefore, hunting dynamics on adult animals are key for understanding the extinction patterns of woolly mammoths.

Pleistocene carnivores might have been able to prey on adult mammoths in larger groups (Van Valkenburgh et al. 2016), but human hunters were probably a bigger threat (Owen-Smith 1987; Chatters et al. 2024). It is well documented that slowly reproducing animals were particularly at risk of extinction (Johnson 2002), but a human preference for large-bodied prey is not necessary to explain this extinction bias (Zuo et al. 2013). On the contrary, ethnographic records from pre-firearms societies suggest that hunting proboscideans, especially adults, was too dangerous for regular meat procurement and done only on rare occasions for prestige (Lupo and Schmitt 2023). On the other hand, humans desired meat probably less than fat, which is much more abundant in adult animals than juveniles (Ben-Dor and Barkai 2024).

Predator–prey dynamics are highly dynamic, and a long-term average mortality rate is of limited value to reconstruct potential extinction pathways. As with other animal species, population densities of prehistoric humans must have fluctuated and, at times, overshot their long-term carrying capacity (Alroy 2001). Whatever the baseline preference of human hunters was, overpopulation must have pushed towards exploiting all potential resources. This kind of hunting pressure lasted shorter but was more intense than the long-term average. Future dynamic modeling studies should explore what role such shorter-term mortality events could have played in the extinction of Pleistocene megafauna.

The Keystone Herbivore Hypothesis suggests that population reduction from human hunting also cascaded into a collapse of the steppe ecosystem itself (Owen-Smith 1987; Zimov et al. 1995). The hypothesis hinges on megafauna occurring in densities high enough to act as biome-scale ecosystem engineers (Tab. 1; Zimov et al. 2012). The low mammoth densities of our study do not point in that direction. Therefore, our results are more compatible with other extinction pathways such as the Climate Hypothesis (Guthrie 1990).

Conclusions

Our mechanistic, bottom-up simulations of woolly mammoth densities add to existing attempts at reconstructing carrying capacity for large herbivores in the Pleistocene mammoth steppe. Our results for carrying capacity fall somewhere in the middle of the range of previous estimates but should be interpreted as lending more support to lower herbivore densities. Lower herbivore densities are less compatible with biome-scale ecosystem engineering as postulated by the Keystone Herbivore Hypothesis. Our results also have implications for defining a pre-Anthropocene baseline of potential wild herbivore biomass. Our credibility interval captures uncertainties stemming from the megafauna population model so that future studies should focus on analyzing and improving the vegetation model and climatic drivers. Our simulations also demonstrated a maximum mortality tolerance in adult mammoths, which highlights their vulnerability to human predation. The mechanistically detailed, bottom–up approach of modeling vegetation and large herbivores dynamically coupled has proven valuable in reconstructing a no-analog paleoecosystem.

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Author Contributions (CRediT)

- **W.T.** — Conceptualization, methodology, software, formal analysis, investigation, writing (original draft), visualization
- **M.F.** — Conceptualization, methodology, writing (review and editing), supervision
- **T.H.** — Conceptualization, methodology, writing (review and editing), supervision, funding acquisition

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Appendices

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A NPP Evaluation

In order to verify that the daily grass growth scheme yields realistic NPP for high-latitude grasslands, we collected published aboveground NPP measurements from alpine and arctic grasslands (Tab. S3 on page 31). For each measurement location, we let LPJ-GUESS simulate C3 grass on the corresponding grid cell with CRU-NCEP climate (Wei et al. 2014). Most of the studies we included used peak standing dry biomass as a surrogate for annual aboveground NPP. Therefore, we compared them with the maximum of daily aboveground leaf biomass values from LPJ-GUESS. For simplicity, we converted carbon mass from LPJ-GUESS to dry matter with a factor of 2 (but compare variable `c_in_dm_forage` in Sec. B.3.3 and Tab. S15). Figure S8*A* shows simulated over measured aboveground NPP in grasslands. Generally, LPJ-GUESS is in the right magnitude, but appears to overestimate grass productivity. However, this pattern is dominated by a cluster of "typical steppe" plots in north-east China. Overall, we consider the evaluation result acceptable for our purposes, but it remains desirable to calibrate the grass model to arcto-alpine grasslands

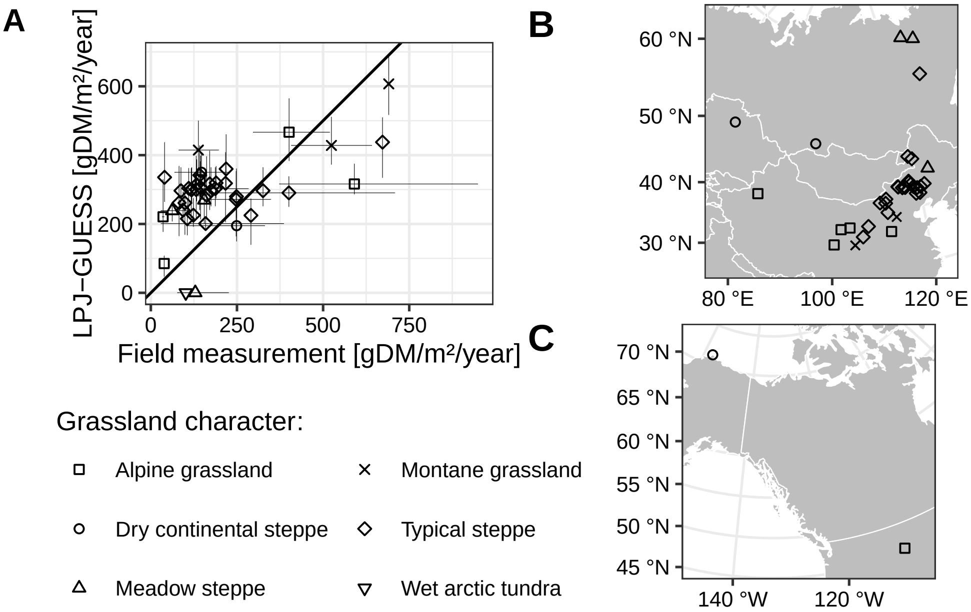

Figure S8. Evaluation of daily grass model. *A,* Correlation of simulated peak aboveground leaf biomass in dry matter (DM) over published measurements (Tab. S3). LPJ-GUESS was run with daily grass allocation and driven by monthly CRU-NCEP climate in the respective grid cell (0.5°×0.5°) of the measurement site. Whiskers show minima and maxima: measured range along x axis, where available, and simulated range over years where measurements were taken along y axis. *B, C*, Maps of Asia and North America with measurement sites.

Table S3. Measurements of aboveground net primary production in northern-hemisphere grasslands used for evaluating the daily grass growth model in LPJ-GUESS

Country	Location	Character	Longitude	Latitude	Peak Biomass*	Years	Method†	Reference
Kazakhstan	Shortandy	dry continental steppe	71.00	51.67	103–330	1975–1979	NPP	Gilmanov et al. (1997)
China	Aohan	typical steppe	119.87	42.28	217	1984–1989	PLAB	Ni (2004)
China	Baimu	alpine grassland	112.32	36.50	143	1987–1989	PLAB	Ni (2004)
NA	Bairin Youqi	typical steppe	118.65	43.53	117	1983–1992	PLAB	Ni (2004)
NA	Bairin Zuoqi	typical steppe	118.15	44.05	218	1983–1989	PLAB	Ni (2004)
China	Bayan Tal 1	typical steppe	120.30	43.28	99	1983–1984	PLAB	Ni (2004)
China	Bayan Tal 2	typical steppe	118.65	43.53	110	1983–1988	PLAB	Ni (2004)
China	Bayan Xil	typical steppe	116.63	43.72	97–283	1979–1986	PLAB	Ni (2004)
China	Bultai Sum	typical steppe	111.85	42.22	132	1984	PLAB	Ni (2004)
China	Darhan	typical steppe	110.42	41.68	94	1983–1987	PLAB	Ni (2004)
China	Da Yultuz	alpine grassland	82.37	41.53	39	1985–1987	PLAB	Ni (2004)
China	Eco-station	typical steppe	116.63	43.72	326	1979–1982	PLAB	Ni (2004)
China	Gaxun Ula	typical steppe	116.58	43.78	175	1980	PLAB	Ni (2004)
China	Gongnai Sum	typical steppe	116.67	43.67	87	1980	PLAB	Ni (2004)
China	Guyuan	typical steppe	106.28	36.00	672	1986	PLAB	Ni (2004)
China	Haibei	alpine grassland	101.63	37.37	297–518	1980–1989	PLAB	Ni (2004)
China	Haijinshan	typical steppe	118.97	42.28	144	1984–1986	PLAB	Ni (2004)
China	Haniwula	typical steppe	114.97	44.03	123	1981–1984	PLAB	Ni (2004)
China	Hulun Buir 4	typical steppe	119.67	48.22	171	1982–1992	PLAB	Ni (2004)
China	Inner Mongolia 1	typical steppe	118.75	48.77	162	1981–1992	PLAB	Ni (2004)
China	Inner Mongolia 2	typical steppe	117.73	44.40	142	1983–1992	PLAB	Ni (2004)
China	Inner Mongolia 3	typical steppe	115.05	43.95	106	1983–1991	PLAB	Ni (2004)
China	Inner Mongolia 4	typical steppe	111.95	39.87	40	1987–1992	PLAB	Ni (2004)
China	Jinqiang River	alpine grassland	103.53	37.66	373–948	1980–1981	PLAB	Ni (2004)
China	Kailu	typical steppe	121.30	43.60	291	1991–1993	PLAB	Ni (2004)

continued

Table S3. (continued)

Country	Location	Character	Longitude	Latitude	Peak Biomass*	Years	Method†	Reference
China	Maqen	alpine grassland	100.23	34.65	33–38	1991	PLAB	Ni (2004)
China	Ongniud Qi	typical steppe	119.45	43.22	148–348	1983–1992	PLAB	Ni (2004)
China	Sidunzi	typical steppe	107.50	37.80	94–708	1988	PLAB	Ni (2004)
China	Siziwang Qi	typical steppe	111.68	41.52	82	1982–1991	PLAB	Ni (2004)
China	Taihang	montane grassland	113.77	38.90	408–641	1988–1989	PLAB	Ni (2004)
China	Xi Ujimqin Qi 4	typical steppe	117.72	44.62	190	1984–1986	PLAB	Ni (2004)
China	Xilin Gol	typical steppe	116.63	43.72	133	1985–1988	PLAB	Ni (2004)
China	Xilin River 2	typical steppe	116.63	43.72	119	1982	PLAB	Ni (2004)
China	Zhang County	montane grassland	104.58	34.57	691	1985	PLAB	Ni (2004)
Russia	Kolyma	meadow steppe	129.00	68.60	77–225	2015	NPP	Reinecke et al. (2021)
Russia	Lena	typical steppe	130.00	61.60	29–385	2015	NPP	Reinecke et al. (2021)
Russia	Yana	meadow steppe	134.00	67.60	29–114	2014	NPP	Reinecke et al. (2021)
Russia	Tuva	dry continental steppe	94.42	51.83	69–224	1979–1985	NPP	Scurlock et al. (2002)
USA	Bridger	montane grassland	-109.22	45.78	81–196	1970–1971	NPP	Scurlock et al. (2002)
China	Tumugi	meadow steppe	123.00	46.00	155	1981–1990	PLAB	Scurlock et al. (2002)
China	Xilingol	typical steppe	116.00	43.71	249	1980–1989	PLAB	Scurlock et al. (2002)
USA	Barrow	wet arctic tundra	-156.79	71.29	102	1972	PLAB	Tieszen (1972)

[*] in g leaf dry matter per m² and year

[†] PLAB = peak leaf aboveground biomass, NPP = aboveground net primary production

B ODD Model Description

This model description follows the ODD (Overview–Design–Details) standard by Grimm et al. (2020). The focus lies on the Modular Megafauna Model (MMM) (Traylor 2021), which can be coupled with different grass models. As its name suggests, MMM is composed of modules, which can be enabled and disabled in various combinations. Here, we describe only the model setup and its parameters that produced the simulation results of this study.

MMM integrates with the dynamic vegetation model LPJ-GUESS 4.0 (Smith et al. 2014), including the daily grass growth scheme introduced by Boke-Olén et al. (2018). A full ODD description of LPJ-GUESS would be beyond the scope of this study. Therefore, we refer to Smith et al. (2014) and Boke-Olén et al. (2018) for published model descriptions and only focus on the coupling with MMM (Sec. B.3.4).

Besides LPJ-GUESS our model development also relied on another, very simple, grass model in some simulations to illustrate model behavior under "controlled" conditions — i.e., without input data influencing the outcome. We describe this "demo simulator" briefly in Section B.3.5, but refer to LPJ-GUESS in the remaining description. During model development we also parameterized steppe bison (*Bison priscus*) and horse (*Equus ferus*), which therefore appear in model description and parameterization.

B.1 Overview

B.1.1 Purpose and Patterns

The purpose of the model is to quantitatively estimate regional- to continental-scale population densities of megafaunal grazers in the Pleistocene paleobiome of the mammoth steppe. The special focus is on the "three big grazers," which are prominent in the fossil record of Beringia and Northern Eurasia (Guthrie 1968): woolly mammoth (*Mammuthus primigenius*), steppe bison (*Bison priscus*), and horse (*Equus ferus*). Specifically, the model's objective is to give answers to the following questions:

- What large herbivore densities could primary production potentially sustain?
- What are the key mechanisms or parameters in herbivore physiology and in grass–grazer interaction that influence herbivore populations?

The fact that the mammoth steppe ecosystem lacks direct modern analogs (Guthrie 1990) and that most large herbivore species are extinct (Stuart 2015) necessitates a strict mechanistic, bottom-up modeling approach. This means that grazer densities (the outcome variable) must emerge from lower-level mechanisms and that parameter values must come from physiological analogs. The model assumes that climate (i.e., temperature, precipitation, and solar radiation) drives grass growth, which in turn determines grazer density.

The model should reproduce the following patterns:

- Herbivore body condition (i.e., stored fat) fluctuates seasonally, bottoming in late winter to early spring (Arnold 2020) — the time of increased starvation mortality (Reimers 1983).
- Herbivore populations fluctuate between years because of density dependence mediated through grass forage as the limiting resource.
- Differences in climate through space and time result in differences in herbivore populations.

B.1.2 Entities, State Variables, and Scales

The following entities are included in LPJ-GUESS coupled with MMM: grid cells, patches, herbivore cohorts, grass cover.

Vegetation and herbivores are simulated in square **grid cells,** which are all independent of each other. Grid cells are spatially explicit in two dimensions, identified by **longitude** and **latitude.** Time is represented in discrete **daily time steps.** Climate input (Sec. B.3.2) defines the resolution and extent of the simulated grid as well as the simulated time frame. Soil input defines a set of soil properties for each grid cell. Unless stated otherwise, all simulations were run with one patch per grid cell.

Each grid cell contains a fixed number of **patches** (LPJ-GUESS parameter `npatch`), each containing vegetation and herbivores. Patches are independent of each other and have different histories of disturbance and succession, but they share the same climate and soil in a grid cell. Patches serve as replicate samples, whose output is aggregated to provide mean values for the grid cell.

The vegetation consists of only one **C_3 grass** entity (in LPJ-GUESS called "individual") per patch. This "grass" represents all graminoid and herbaceous ground vegetation. It is parameterized with **plant functional type (PFT)** parameters. Please see Smith et al. (2001) and Smith et al. (2014) for a description of the state variables in LPJ-GUESS. Boke-Olén et al. (2018) provide the state variables for the daily carbon allocation in grasses, based on Johnson and Thornley (1983).

Herbivores are simulated as **cohorts** of **herbivore functional types (HFTs).** Each cohort represents individuals that were born in one particular simulation year. In each patch there may be at most *one* cohort for each year, HFT, and **sex** (male/female). The **age** of a cohort is given in days. An amount of **body fat** [$^{kg}/_{ind}$] represents an average value of energy stored in each individual of the cohort. Each cohort is associated with one patch as its habitat and remains there stationary. In analogy to PFT, an HFT is a set of constant parameters that characterize a species, which may in turn be interpreted as representing an entire herbivore guild. In this study, the HFTs are woolly mammoth, horse, and steppe bison.

B.1.3 Process Overview and Scheduling

Grid cells are simulated independently of each other, possibly in parallel. The model updates entities within each grid cell *daily* in this order:

1. Prepare climate for this day (Sec. B.3.2).
2. Vegetation (LPJ-GUESS):
    1. Update daily climate drivers.
    2. Calculate day length, insolation, and potential evapotranspiration.
    3. Loop through all patches:
        1. Update daily soil drivers including soil temperature.
        2. Update leaf phenology.
        3. Interception: Calculate loss of water and energy through evaporation of rain or snow intercepted by the canopy.
        4. Derive and re-distribute rain-melt.
        5. Simulate photosynthesis, respiration, and evapotranspiration.
        6. Simulate soil water dynamics.
        7. Allocate sequestered carbon to grass biomass.
        8. Simulate soil organic matter and litter dynamics.
        9. On last day of the year: Simulate establishment, mortality, and fire disturbance.
3. Herbivores: Loop through all patches:
    1. Establish or re-establish herbivores (Sec. B.3.1).
    2. Loop through herbivore cohorts in this patch (asynchronous updating):
        1. Increment age.
        2. Catabolize fat (Sec. B.3.3).
        3. Calculate this day's energy expenditure (Sec. B.3.3).
        4. Calculate this day's offspring (Sec. B.3.3).
        5. Reduce cohort density by applying mortality (Sec. B.3.3–B.3.3).
    3. Feed herbivores.
        1. Calculate demands: expenditure plus potential fat anabolism (Sec. B.3.3, B.3.3).

        2. Distribute available forage (Sec. B.3.3).
        3. Anabolize fat if possible (Sec. B.3.3).
    4. Remove consumed forage carbon from the patch (synchronous updating; Sec. B.3.4).
    5. Remove dead cohorts (Sec. B.3.3–B.3.3).
    6. Create newborn cohorts or increment existing ones by today's offspring (Sec. B.3.3).
    7. Aggregate output data by grid cell and HFT (Sec. B.2.8).

Technical notes:

- Each day, herbivore simulations start only after vegetation simulations are finished. The reason for this is purely technical: because the Modular Megafauna Model (MMM) manages its own entities independently of LPJ-GUESS.
- It is irrelevant for the model mechanics in which order entities (patches or cohorts) are looped over; the software implementation can define that freely.
- Herbivore entities perform asynchronous updates because they are implemented strictly object-oriented. Only removing *all* consumed forage carbon in the patch is done synchronously in order to reduce calculation steps.

B.2 Design Concepts

The following design concepts are not applicable: Learning, Prediction, Collectives.

B.2.1 Basic Principles

On the herbivore side, the critical process is the balance of energy intake and expenditure. The energy intake model is based on a long tradition of, chiefly agricultural, research (Ferrell and Oltjen 2008): The combustible (gross) energy of ingested forage matter gets converted to "net energy," which can be used by the animal to balance energy expenditure and build up (anabolize) fat reserves. The scaling of simulated energy expenditure is based on metabolic theory of ecology (Brown et al. 2004). Fat reserves can be burned (catabolized) to meet energy needs in times of scarcity, which makes them the key limiting factor for winter survival (Millar and Hickling 1990; Trondrud et al. 2021) and reproductive success (Wade and Schneider 1992).

B.2.2 Emergence

The bottom-up approach of this model consists of scaling up from rather well-known and parameterizable physiological processes to unknown densities of herbivores in an ecosystem that no longer exists. Therefore grass growth and sward density, herbivore density dependence, and carrying capacity emerge from simulations.

B.2.3 Adaptation

Herbivores don't act in if–then–else decisions, but two critical behaviors are adapted to internal state and external circumstances: How much to eat and how much to reproduce. Herbivores "seek" to ingest as much forage as possible, but are constrained by available forage, gut capacity, and a maximum of possible body fat. In terms of reproduction, female herbivores "seek" to maximize the number of offspring, but are constrained by their body condition (fat reserves) at the time of mating. Since grass is the single limiting resource and herbivores neither move nor directly compete with each other (i.e., no interference competition), herbivores have no further options to adapt to changing environment.

B.2.4 Objectives

The proximate goal of herbivores is to maximize energy intake and storage, which ultimately serves to maximize lifetime reproductive success.

B.2.5 Sensing

Herbivores don't sense anything other than forage quality and quantity in their patch. In particular, other herbivores and other patches don't influence them.

B.2.6 Interaction

Herbivores reduce the amount of grass in their patch through feeding. They don't compete directly for grass because, if grass is scarce, the available forage is distributed in a fair manner among herbivore cohorts, proportional to their demands.

Since there is only *one* grass individual, there is no interaction within the vegetation.

B.2.7 Stochasticity

In the herbivore model, there is no stochasticity. In LPJ-GUESS, stochastic disturbance and fire are disabled.

B.2.8 Observation

At the end of each simulation day, MMM queries state variables from model entities and aggregates them first by patch (and HFT, if applicable), then by grid cell. Here, aggregating means calculating (weighted) arithmetic means. For daily output, the mean for each output variable is printed immediately to the respective output file.

In the case of annual output, the mean, m, for each output variable (per grid cell) from the current day, $t+1$, gets merged into the existing mean, M_t, which already aggregates t days. The new aggregate mean, M_{t+1}, is then

$$M_{t+1} = \frac{t M_t + m}{t+1}. \tag{4}$$

On Julian day 365 (disregarding potential leap years), M_t is printed to file, and t is set to 0.

Some output variables directly correspond to state variables (Sec. B.1.2), others are derived:

- Output of herbivore **individual density** [ind/km^2] is the arithmetic mean of the corresponding state variable across all cohorts of one HFT in a grid cell.
- To calculate **mass density** [kg/km^2] of an HFT in a patch, each cohort's individual density is multiplied with its body mass [kg/ind] (see Sec. B.3.3 for how body mass is calculated). For output, these values are then averaged per HFT and grid cell.
- Proportional **body fat** [kg/kg] is the state variable fat mass [kg/ind] divided by body mass [kg/ind]. In contrast to herbivore density, body fat refers to individuals, not patches or grid cells. Therefore, averaging cohorts for one HFT in a patch weights body fat with the cohort's individual density. (Aggregation across patches in a grid cell and over time (for annual output) does not weight body fat by individual density.)
- **Grass forage** available to herbivores [kg DM/km^2] comes from the vegetation model (Sec. B.3.4). Since it is already per patch, it only gets aggregated across patches and over time (if output is annual).
- **Digestibility** [fractional] refers to available grass forage and not the patch. Therefore, if there is no grass forage at all, digestibility is not available (compare for example Fig. S15*B left*). Otherwise, digestibility gets aggregated like grass forage.

B.3 Details

B.3.1 Initialization

- Soil codes
- Establishment and re-establishment of herbivores
    - Initial values of state variables
    - Age range and density at establishment
- Spin-up time: 100 years without nitrogen plus 1000 years without herbivores plus 1900 years with herbivores

Table S4. LPJ-GUESS parameters defining simulation spin-up

Identifier	Unit	Description
`nyear_spinup`	years	Total spin-up time with constant climate
`freenyears`	years	Spin-up time without nitrogen limitation
`free_megafauna_years`	years	Spin-up time without herbivores

Table S5. Parameters pertaining to herbivore establishment

Identifier	Unit	Explanation
`hft.establishment.age_range`	years	Youngest and oldest age of cohorts to create at establishment.
`hft.establishment.density`	$^{ind}/_{km^2}$	Total population density for establishment in one patch.
`simulation.establishment_interval`	days	Days between checking if re-establishment is necessary.

Spin-up

The simulation begins with a user-defined **spin-up time** with stable climate before the **historic climate** of the input data set sets in (cf. Sec. B.3.2). Usually, the simulated ecosystem is supposed to "spin up" to an equilibrium state, from which it can react to changes in subsequent historic climate. However, we don't intend to study ecosystems in recent times, but rather use the spin-up phase to study how simulated herbivore populations develop and behave under a stable climate that exhibits some supposed characteristics of continental climate in the Pleistocene. The historic period is therefore less relevant.

To generate a spin-up climatology, LPJ-GUESS takes the first 30 years of monthly values from the historic period. For each climate variable (i.e., precipitation, solar radiation, air temperature, and rainy days), it then removes any interannual linear trend in the 30-years data. Consequently, the annual means of the resulting detrended climatology show no increase or decrease in linear regression anymore. This detrended 30-years climate then drives the whole spin-up period by repeating itself.

The parameters in Table S4 define the lengths of three different phases in spin-up:

1. Spin-up without herbivores and without nitrogen limitation: for building up a nitrogen pool.
2. Spin-up with nitrogen limitation, and still without herbivores: for establishing equilibrium in a nitrogen-limited vegetation.
3. Spin-up with herbivores: for establishing equilibrium between primary producers and consumers.

Herbivore Establishment

Herbivores of one HFT are created in a patch on the first day after the herbivore-free spinup time is over (*cf.* Sec. B.3.1). For each year in a specified age range (`hft.establishment_age_range`), one female and one male cohort are created. Each new cohort has the same density [$^{ind}/_{km^2}$] so that the sum of all new cohorts matches the value given in parameter `hft.establishment_density`. Newly established cohorts start with maximum fat reserves (cf. Sec. B.3.3) so that they have a chance of survival even if created in winter.

B.3.2 Input Data

The simulations in this study use climate data in 0.5° × 0.5° spatial resolution over the historic period of 1901–2015 CE from the CRU-NCEP data set (Wei et al. 2014). But note that this study only uses spin-up data as described there. Climatic variables are monthly means of temperature at sea level [Kelvin], precipitation [$^{mm}/_{day}$], downwelling short-wave radiation [$^{W}/_{m^2}$], and rainy days per

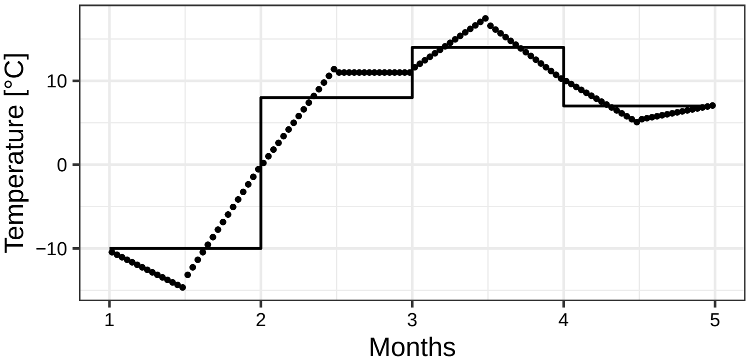

Figure S9. Example of how LPJ-GUESS interpolates monthly means (*solid line*) to quasi-daily values (*dots*). Strong temperature shifts — typical in arctic climate — can result in daily values far above or below the monthly mean.

month [month^{-1}]. Figure S9 illustrates how LPJ-GUESS converts monthly to the quasi-daily values for simulation: It linearly interpolates from the middle of one month to the next, while preserving the mean of the month. The linear interpolation yields daily values that are higher and lower than the monthly mean — something to be aware of when interpreting sudden seasonal changes.

LPJ-GUESS receives atmospheric CO_2 concentrations as annual global means. For the historic period (1901–2015 CE), we used the CO_2 time series from the global carbon project (Le Quéré et al. 2018). Soil codes, which define various soil texture properties per grid cell, are the same as in Sitch et al. (2003). Nitrogen deposition is constant at the default pre-industrial value of 2 kg N per hectare and year.

B.3.3 Grazer Submodel (MMM)

A note on units:

Most herbivore submodels calculate *per individual* (e.g., intake as $\mathrm{kg\,DM/ind}$) To derive the *per-area* values of herbivore cohorts, the model framework multiplies the *per-individual* values with the cohort density [$\mathrm{ind/km^2}$].

Re-Establishment

Counting from the first day after herbivore-free spinup (Sec. B.3.1), every n days a check for re-establishment is performed: If all cohorts of one HFT in a patch are dead, the HFT is re-established in the same way as in the initial establishment (Sec. B.3.1). The number of days, n, is given by the parameter `simulation.establishment_interval` (Tab. S5).

Daily Forage Intake

There is no distinction between young and adult cohorts in terms of feeding. Also newborn cohorts feed on grass, and lactation is not represented in the model.

How much forage an herbivore ingests each day is defined by the lowest value of any of these intake constraints:

- Available forage in the habitat (Sec. B.3.3).
- Digestive limit (Sec. B.3.3).
- Demand — i.e., energy required to balance energy expenditure (Sec. B.3.3) plus energy that can be used to anabolize fat (Sec. B.3.3).

In reality, other factors can constrain forage intake as well, namely searching for and handling food items (Spalinger and Hobbs 1992; Farnsworth and Illius 1996; Hobbs 2003). Dispersal of forage patches (i.e., low encounter rate) may limit intake on the scale of hours or a few days at most, which herbivores can usually compensate by increasing daily foraging time or feeding speed (Romney and Gill 2000; Thompson and Barboza 2013). Short-term searching and handling constraints

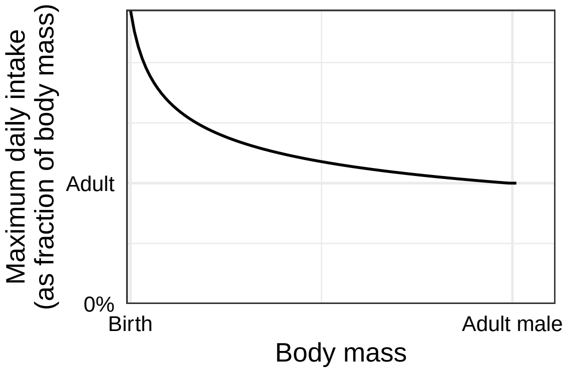

Figure S10. Allometric scaling of digestion-limited intake per body mass. In this example plot, the exponent for basal metabolic rate is 0.75 ("3/4 power law"), which is matched by the *relative* intake scaling with an exponent of −0.25.

are the mechanisms behind the Type II functional response (Holling 1959) frequently observed in large grazers (e.g., Fortin et al. 2002). However, on the seasonal scale, digestive capacity is more likely the limiting factor (Owen-Smith 2002). Consequently, a functional response — as used by Illius and O'Connor (2000) — can be appropriate for models on very short time scales, but has little effect on long-term population dynamics.

Digestive Limit

The parameter `hft.digestion.allometric.fraction_male_adult` [kg DM/(kg day)] defines the digestion-limited daily dry-matter intake as *fraction* of live body mass; the given value applies to the body mass of an adult male animal, BM_{ad}. It corresponds to ad-libitum intake in feeding experiments. From this value, the digestive limit for other body weights is derived with an allometric formula of the form $a = b \times BM^c$ (Fig. S10). It is important to scale the intake with body mass using the same allometric exponent as for energy expenditure (Sec. B.3.3) because otherwise young (small) cohorts are at a disadvantage because of their higher per-mass expenditure and might not be able to meet their intake needs at all. (This strict requirement is in part a model artifact because simulated young animals can't compensate for their higher per-mass expenditure by nursing or selecting high-quality forage.)

Consequently, the allometric exponent for digestion, `hft.digestion.allometric.exponent`, must correspond to the expenditure exponent `hft.expenditure.basal_rate.exponent`, x. The digestive limit is *relative* to body mass (kg DM/(kg day)) while expenditure is *absolute* (MJ/day). Therefore, relative digestive limit scales with BM^{x-1}. The constant coefficient b in the allometric formula $b \times BM^{x-1}$ is derived from the value defined in `.fraction_male_adult` so that the resulting formula for the *relative* digestive limit looks like this:

$$\text{digestive limit}_{[\text{kg DM/(kg day)}]}\left(BM_{[\text{kg}]}\right) = \left(\frac{\text{digestive limit of ♂ adult}_{[\text{kg DM/(kg day)}]}}{BM^{\text{x}-1}_{ad,\,[\text{kg}]}}\right) \times BM^{\text{x}-1}_{[\text{kg}]} \qquad (5)$$

Distribute Forage Among Herbivores

Every day, the model distributes available forage among herbivore cohorts according to demand. The **demand** [kg DM/km²] of a cohort is the grass dry matter it would ingest if grass were unlimited. It is the sum of forage mass needed for balancing energy expenditure (Sec. B.3.3) and anabolizing fat (Sec. B.3.3); it depends on the herbivore's digestive efficiency (Sec. B.3.3). Whether all cohorts can satisfy their demands depends on how much grass [kg DM/km²] is available in the patch (Sec. B.3.4). Grass can be abundant or scarce:

- **Abundance:** If the cumulative demand [kg DM/km²] of *all* herbivore cohorts in the patch is less

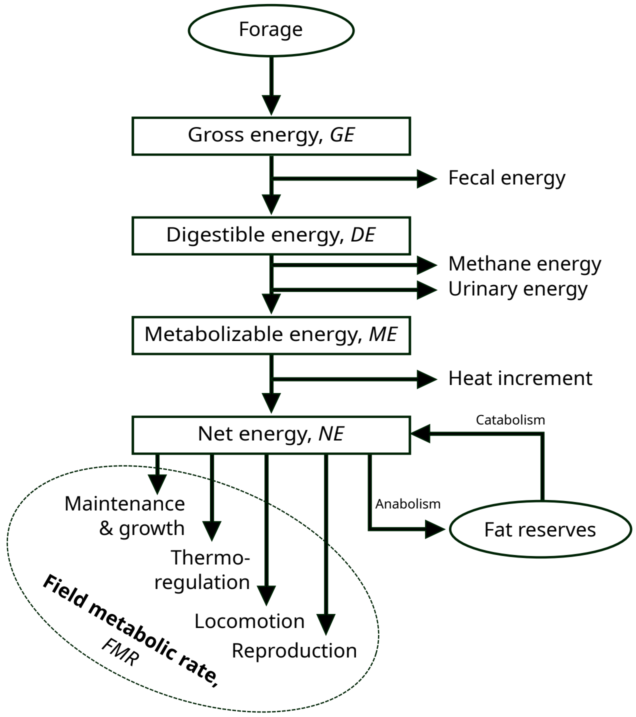

Figure S11. Schematic overview on how herbivores use forage energy.

than or equal to the available forage biomass, each herbivore cohort receives the amount it demands.

- **Scarcity:** If the cumulative demand is greater than the available forage biomass [kg DM/km²], each cohort receives a portion of the available forage in proportion to its demand:

$$\text{cohort's intake}_{[\text{kg DM/km}^2]} = \frac{\text{cohort's demand}_{[\text{kg DM/km}^2]}}{\sum \text{demands}_{[\text{kg DM/km}^2]}} \times \text{available forage}_{[\text{kg DM/km}^2]} \tag{6}$$

The model defines "demand" solely by what herbivores would potentially eat. It does not take fat reserves (i.e., body condition) into account. A cohort at the edge of starvation may therefore have the same potential intake ("demand") as one that has almost full fat reserves — however, both will get the same amount of forage. In consequence, one cohort might starve to death while the other one is thriving. Through this **exploitative competition** (i.e., cohorts competing for the same finite resource) those herbivore populations will ultimately thrive that use their forage most efficiently for reproduction. Here it would be desirable to have mechanisms in place that facilitate coexistence.

Forage Energy Content

Herbivores "pay" for energy expenditure (Sec. B.3.3) and the building of fat reserves (Sec. B.3.3) with **net energy,** NE [MJ]. Forage dry matter contains a certain **gross energy,** GE [MJ/kg DM] (`forage.gross_energy.grass`), which is the energy per dry matter[2] released by combustion and typically measured in a bomb calorimeter. In the process of converting gross to net energy, losses occur at different stages (Fig. S11). These losses define overall digestive efficiency and are modeled as follows.

First, the energy *not* lost in feces is called **digestible energy,** DE [MJ/kg DM] and given by forage **digestibility** — the fraction of ingested dry matter the animal retains and does not excrete. While the model treats digestibility as a property inherent to the forage, herbivore species actually differ

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[2] All forage energy content variables are *per dry matter.*

Table S6. Parameters pertaining to herbivore digestion and forage energy content

Identifier	Unit	Explanation
`hft.digestion.k_fat`	MJ/MJ	Coefficient, k_f, for converting metabolizable energy to fat gross energy.
`hft.digestion.allometric.fraction_male_adult`	kg DM/(kg day)	Digestion-limited maximum daily dry-matter intake as fraction of live body mass.
`hft.digestion.allometric.exponent`	—	Allometric exponent for intraspecific scaling of digestive intake limit.
`forage.gross_energy.grass`	MJ/kg DM	Gross energy, GE, in grass forage per dry matter mass.
`hft.digestion.digestibility_multiplier`	—	Coefficient to adjust ruminant-specific digestibility to the efficiency of other digestion types.
`hft.digestion.me_coefficient`	MJ/MJ	Metabolizable energy coefficient, ME/DE, for converting digestible to metabolizable forage energy content.
`hft.digestion.k_maintenance`	MJ/MJ	Fraction, k_m, of metabolizable energy that is available as net energy.

in how much dry matter they retain during digestion (Clauss, Jürgen Streich, et al. 2007; McDonald et al. 2010, p. 250). Therefore, effective digestibility is modeled as a product of a digestibility value that applies to livestock ruminants and a modifying HFT-specific constant (`hft.digestion.digestibility_multiplier`):

$$\text{effective digestibility} = \text{digestibility}_{\text{ruminant}} \times \text{modifier} \tag{7}$$

Second, the digestible energy not lost in methane and urine is called **metabolizable energy,** ME [MJ/kg DM]. It is derived from the digestible energy, DE, by multiplication with the efficiency coefficient `hft.digestion.me_coefficient`, ME/DE.

Third, the fraction of metabolizable energy lost due to heat production is known as **heat increment.** The coefficient k_m (`hft.digestion.k_maintenance`) denotes the fraction of metabolizable energy that is retained and available as net energy.

In summary, net energy content, NE, is given as a fraction of gross energy, GE, based on a number of explicitly represented and measurable parameters (Tab. S6):

$$NE_{[\text{MJ/kg DM}]} = ME_{[\text{MJ/kg DM}]} \times k_m = GE_{[\text{MJ/kg DM}]} \times \text{eff. digestibility} \times \left(\frac{ME}{DE}\right) \times k_m \tag{8}$$

The partitioning of metabolizable energy has a long tradition in agricultural research. Ferrell and Oltjen (2008) give an historical overview. Birkett and Lange (2001) summarize its conceptual shortcomings and difficulties in practical methodology.

Fat Storage

If the net energy content (Sec. B.3.3) of the ingested forage mass exceeds the energy expenditure (Sec. B.3.3) within one day, the extra energy is converted into fat mass. The process of building up body fat is called fat anabolism.

Metabolizable energy, ME [MJ], from forage is converted to fat mass [kg] by the product of fat gross energy [MJ/kg] (`hft.body_fat.gross_energy`) and the net energy coefficient for fattening, k_f (`hft.digestion.k_fat`):

$$\text{anabolized fat}_{[\text{kg}]} = k_f \times \frac{ME_{[\text{MJ}]}}{\text{fat gross energy}_{[\text{MJ/kg}]}} \tag{9}$$

The maximum attainable body fat is defined by the parameter `hft.body_fat.maximum` [fraction].

Table S7. Parameters pertaining to herbivore fat reserves

Identifier	Unit	Explanation
`hft.body_fat.maximum`	kg/kg	Maximum body fat as fraction of total live weight.
`hft.body_fat.catabolism_efficiency`	—	Conversion coefficient to turn body fat gross energy into net energy.
`hft.body_fat.gross_energy`	MJ/kg	Combustible energy in live body fat mass.

Table S8. Parameters pertaining to daily energy expenditure of herbivores

Identifier	Unit	Explanation
`hft.expenditure.fmr_multiplier`	—	Constant factor to convert from basal metabolic rate (BMR) to field metabolic rate (FMR).
`hft.expenditure.basal_rate.mj_per_day_male_adult`	MJ/day	Basal metabolic rate (BMR) of an animal with the body mass of an adult male.
`hft.expenditure.basal_rate.exponent`	—	Allometric exponent for intraspecific scaling of basal metabolic rate.

In one day, an animal will not ingest more forage energy than it can burn and convert to fat.

Fat reserves are catabolized ("burned") to meet energy expenditure (Sec. B.3.3) if the net energy content (Sec. B.3.3) of the forage ingested that day is less than the energy expenditure. The fat mass [kg] that needs to be catabolized is determined with the parameters `hft.body_fat.catabolism_efficiency` [unitless] and `hft.body_fat.gross_energy` [MJ/kg] and the required *net* energy [MJ] (while not exceeding the current fat mass, of course):

$$\text{burned fat}_{[\text{kg}]} = \min\left(\frac{\text{required energy}_{[\text{MJ}]}}{\text{efficiency} \times \text{fat gross energy}_{[\text{MJ/kg}]}}, \text{current fat}_{[\text{kg}]}\right) \tag{10}$$

Energy Expenditure

Daily energy expenditure is modeled as a constant rate that is independent of the environment. This field metabolic rate, FMR [MJ/day], of an individual is difficult to measure and extrapolate across body sizes (Nagy 2005). Therefore, FMR is modeled as a multiple (`hft.expenditure.fmr_multiplier`) of the basal metabolic rate, BMR [MJ/day], which is easier to measure.

$$FMR_{[\text{MJ/day}]} = \text{multiplier} \times BMR_{[\text{MJ/day}]} \tag{11}$$

BMR is given as a parameter (`hft.expenditure.basal_rate.mj_per_day_male_adult`) for the body mass of an adult male, BM_{ad} [kg]. From this datum, the BMR for other body weights, BM [kg], is derived with an allometric formula of the form $a = b \times BM^c$. The exponent for this intraspecific scaling relationship is given by the parameter `hft.expenditure.basal_rate.exponent`, which corresponds to `hft.digestion.allometric.exponent` (cf. Sec. B.3.3). So the BMR for any body weight within one HFT is given by this formula:

$$BMR_{[\text{MJ/day}]}\left(BM_{[\text{kg}]}\right) = \left(\frac{BMR\left(BM_{ad,\,[\text{kg}]}\right)}{BM_{ad,\,[\text{kg}]}^{\text{exponent}}}\right) \times BM_{[\text{kg}]}^{\text{exponent}} \tag{12}$$

Body Composition and Growth

In the model, the live **body mass** (BM) of an herbivore is composed of two parts: **lean mass** and **body fat** (Fig. S12):

Table S9. Parameters pertaining to herbivore body composition and ontogenetic growth

Identifier	Unit	Explanation
`hft.body_mass.birth`	kg	Live body mass of a newborn herbivore, irrespective of sex.
`hft.body_fat.birth`	kg/kg	Body fat at birth as a fraction of total live body mass.
`hft.body_mass.female/.male`	kg	Live body mass of female and male herbivores at the age of physical maturity and with half of maximum fat reserves.
`hft.body_mass.empty`	kg/kg	Fraction of live body mass that is not ingesta, blood, hair, antlers/horns, etc.
`hft.life_history.physical_maturity_female/_male`	years	Age when adult body mass is reached.

$$BM_{\text{[kg]}} = \text{lean mass}_{\text{[kg]}} + \text{fat mass}_{\text{[kg]}} \tag{13}$$

Lean mass is the fat-free body and composed of the empty body mass and the structural mass. **Empty body mass** is the live body mass minus those parts that are typically removed before chemical analysis: ingesta, blood, antlers, etc. **Structural mass** (SM) is the fat-free tissue, muscle, bones, etc. Structural mass is lean mass minus the aforementioned removable parts, such as ingesta and blood. The **fat fraction** of the body is the total lipid content of the *empty* body mass. The body fat fraction is variably also called ether extract, free lipid content, or crude fat (Hyvönen 1996). The reason for modeling body composition this granular is that the literature usually reports body fat measurements as fraction of *empty* body mass while allometric relationships refer to *total* (live) body mass.

Structural mass at birth (age $= 0$) is derived from live weight at birth, `hft.body_mass.birth` [kg] and proportional fat content, `hft.body_fat.birth`:

$$SM_{\text{birth, [kg]}} = BM_{\text{birth, [kg]}} \times \text{empty frac.} \times \left(1 - \text{fat frac.}_{\text{birth}}\right) \tag{14}$$

The fraction of the body that is "empty" (`hft.body_mass.empty`) and the maximum body fat fraction (`hft.body_fat.maximum`) apply to all ages. The body mass parameters for adults (BM_{ad}, `hft.body_mass.female` and `.male` [kg]) include *half* of the maximum attainable fat reserves (Fig. S12). From these parameters, the structural mass for an adult is derived:

$$SM_{\text{ad, [kg]}} = BM_{\text{ad, [kg]}} \times \text{empty frac.} \times \left(1 - \frac{\text{fat frac.}_{\text{ad}}}{2}\right) \tag{15}$$

Until physical maturity (`hft.life_history.physical_maturity_female` and `_male` [years]), the structural mass on each day is interpolated between the value at birth (age $= 0$) and at physical maturity (age $= maturity$). For simplicity's sake, this growth "curve" is actually a linear interpolation:

$$SM_{\text{[kg]}}(\text{age}) = SM_{\text{birth, [kg]}} + \frac{\text{age}_{\text{[days]}}}{\text{maturity}_{\text{[days]}}}\left(SM_{\text{ad, [kg]}} - SM_{\text{birth, [kg]}}\right) \tag{16}$$

In summary, lean mass is completely decoupled from the energy budget and grows with age until physical maturity is reached ("prescribed growth"). Absolute fat mass, on the other hand, grows only with a positive energy balance. Consequently, young animals can grow in total mass while their *relative* body fat decreases if their intake is not sufficient to increase absolute fat mass.

Reproduction

The number of newborn herbivores [ind/km²] is calculated for each cohort every day. Only female cohorts that have reached **sexual maturity** will produce offspring, and only within the **breeding**

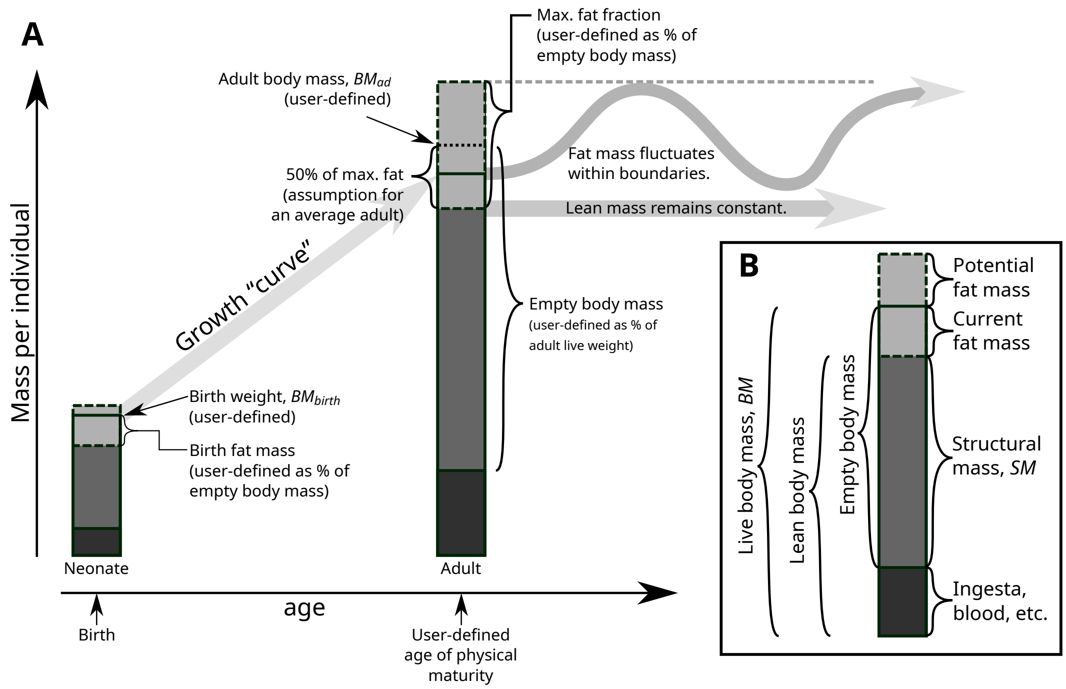

Figure S12. Body composition of an herbivore individual in the model. *A,* Ontological development. *B,* Overview on all body components.

season.

A female cohort has reached sexual maturity when its age in days divided by 365 is greater than or equal to the value in years in the parameter `hft.life_history.sexual_maturity`. The breeding season is defined by the two parameters `hft.breeding_season.start` [Julian day] and `hft.breeding_season.length` [days].

Every day within the breeding season, the number of births of a cohort is based on the **body condition at the day of conception.** The day of conception is given by counting back by the length of gestation. The length of gestation is given in months (`hft.reproduction.gestation_length`) and converted to days by multiplication with 30. Body condition is defined as the current fat mass divided by the *potential* maximum fat mass (see Sec. B.3.3).

The maximum number of offspring that one sexually mature female can produce *anually* is given by the parameter `hft.reproduction.annual_maximum`. This annual maximum is converted to a *daily* maximum by multiplying it with `hft.reproduction.breeding_season_length` divided by 365. The potential maximum daily reproduction within the breeding season is constant. The *total* number [$^{\text{ind}}/_{\text{km}^2}$] of maximum daily offspring for a cohort is simply calculated by multiplying the individual value [fraction] with the cohort density [$^{\text{ind}}/_{\text{km}^2}$].

The relationship between body condition at the time of conception and the daily offspring of a female cohort within the breeding season is modeled as a logistic function (Fig. S13):

$$\text{today's offspring}_{[\text{ind/km}^2]} = \frac{\text{maximum daily offspring}_{[\text{ind/km}^2]}}{1 + e^{-\text{growth rate} \times (\text{body condition} - \text{midpoint})}} \tag{17}$$

The midpoint and growth rate are given by the parameters `hft.reproduction.logistic.midpoint` and `hft.reproduction.logistic.growth_rate`.

The body mass of newborn herbivores is defined by the parameter `hft.body_mass.birth` [kg], and the fractional body fat is defined by the parameter `hft.body_fat.birth` [$^{\text{kg}}/_{\text{kg}}$] (see Sec. B.3.3).

Two **new cohorts** (females and males) for the newborn herbivores are created at the first day of the breeding season at which the number of total offspring of one HFT in the patch is a positive

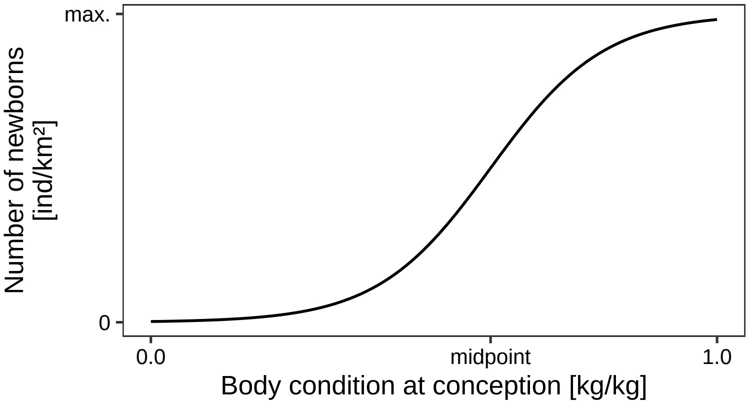

Figure S13. Logistic correlation between body condition (fat mass/max. fat mass) at the time of conception and number of births of a female cohort in a day within the breeding season.

Table S10. Parameters pertaining to herbivore reproduction

Identifier	Unit	Explanation
`hft.life_history.sexual_maturity`	years	Age of female sexual maturity in years.
`hft.breeding_season.start`	Julian day	First day of the season in which new herbivores are born.
`hft.breeding_season.length`	days	Length of the breeding season.
`hft.reproduction.gestation_length`	months	Time between conception and parturition.
`hft.reproduction.annual_maximum`	ind/year	Number of newborns a sexually mature female can produce per year if body fat is maximum at the time of conception.
`hft.reproduction.logistic.midpoint`	kg/kg	Body condition at the time of conception for which a female cohort reaches *half* of its potential maximum number of daily offspring in the breeding season.
`hft.reproduction.logistic.growth_rate`	—	Parameter defining the *slope* of the logistic relationship between body condition at the time of conception and reproduction rate.

number. These new cohorts are created with an age of 0 days. Subsequent offspring are *merged* to this existing "newborn cohort" by increasing its density [ind/km^2]. The age [days] of the existing cohort remains unchanged, but a new, mean body fat is calculated, weighted by the density [ind/km^2].

Background Mortality

The fraction by which to reduce an herbivore cohort is calculated each day as the sum of a constant background mortality and a dynamic starvation mortality.

Mortality patterns in wild herbivores suggest a partitioning into juvenile and adult mortality (Caughley 1976, p. 191). The parameter `hft.mortality.juvenile_rate` [fraction] defines a constant annual background mortality rate for herbivore cohorts in their first 365 days of life. The parameter `hft.mortality.adult_rate` [fraction] defines annual mortality for all older cohorts.

Since mortality is applied daily, the annual rate is converted to a daily rate:

$$\text{daily mortality}_{[\text{day}^{-1}]} = 1 - \left(1 - \text{annual mortality}_{[\text{year}^{-1}]}\right)^{1/365} \tag{18}$$

Applying this daily rate 365 times would have the same effect as applying the annual rate once.

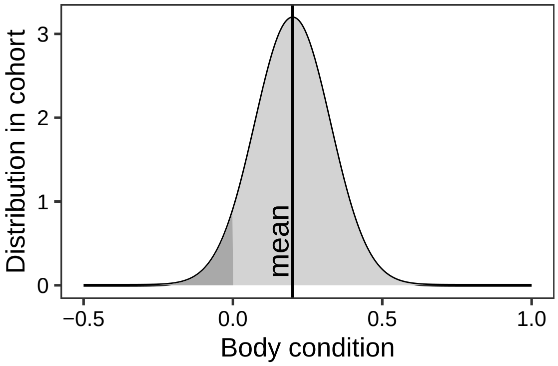

Figure S14. Normal distribution of body condition within an herbivore cohort. Body condition is current fat mass divided by maximum fat mass. The fraction with zero (or "less") body fat is considered dead due to starvation.

Starvation Mortality

The body fat [kg] state variable is considered a *mean* across individuals of one cohort. The **body condition** [kg/kg] is defined as the current fat mass divided by the potential maximum fat mass (cf. Sec. B.3.3). In order to define a fraction of individuals that dies each day, the distribution of body condition among individuals *within* a cohort is modeled as a **normal distribution** (Fig. S14) with the mean μ, following Illius and O'Connor (2000). The standard deviation, σ, is given by the parameter `hft.body_fat.deviation` [kg/kg]. The fraction with zero or negative body condition is removed from the cohort once every day. This **starved fraction** (dark area in Fig. S14) is given by the cumulative normal distribution function F at position $x = 0$:

$$\text{starved}_{\text{[frac.]}} = F(0; \mu, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^{0} \exp\left(-\frac{(t-\mu)^2}{2\sigma^2}\right) dt \tag{19}$$

Juveniles (<1 year of age) have no body fat variance because it would subject newborns immediately to starvation mortality if body fat at birth is not very high. This compensates for the lack of lactation in the model, which would protect lean juveniles from starvation.

By removing starved individuals, the fat mass per area [kg/km²] in the herbivore population should remain unchanged because, conceptually, only individuals with zero body fat die. Therefore, when reducing the density [ind/km²] of a cohort, the mean fat mass [kg/ind] of the surviving herbivores increases:

$$\text{new fat mass}_{\text{[kg/ind]}} = \frac{\text{total fat mass}_{\text{[kg/km²]}}}{\text{surviving density}_{\text{[ind/km²]}}} \tag{20}$$

$$= \frac{\text{density}_{\text{[ind/km²]}} \times \text{fat mass}_{\text{[kg/ind]}}}{\text{density}_{\text{[ind/km²]}} \times (1 - \text{starved}_{\text{[frac.]}})} \tag{21}$$

Whether the body fat value of the cohort is shifted in such a way can be controlled with the parameter `hft.mortality.shift_body_condition_for_starvation`.

Lifespan Mortality

The lifespan of an herbivore is limited by the parameter `hft.life_history.lifespan` [years]. When the age [days] of an herbivore cohort reaches 365 times `hft.life_history.lifespan`, it is removed.

B.3.4 Vegetation Submodel: LPJ-GUESS

We don't describe the vegetation model LPJ-GUESS in detail here. That would be beyond the scope of this study because LPJ-GUESS is very large and complex. The publications by Smith et al. (2001),

Table S11. Parameters pertaining to herbivore mortality

Identifier	Unit	Explanation
`hft.mortality.juvenile_rate`	year^{-1}	Annual background mortality for herbivore cohorts in their first year of life.
`hft.mortality.adult_rate`	year^{-1}	Annual background mortality for all herbivore cohorts of an age ≥ 365 days.
`hft.body_fat.deviation`	kg/kg	Standard deviation in body condition (current fat mass/max. fat mass) within one cohort.
`hft.life_history.lifespan`	years	Maximum age of an herbivore.
`hft.mortality.shift_body_condition_for_starvation`	boolean	Whether to "redistribute" the "negative" fat mass of the starved fraction in a cohort.

Table S12. LPJ-GUESS plant functional type (PFT) parameters for the integration with MMM

Identifier	Unit	Explanation
`digestibility`	frac.	Digestibility of live grass (growing and expanded leaves).
`digestibility_dead`	frac.	Digestibility of "dead" grass (senescing leaves).
`c_in_dm_forage`	$\mathrm{g\,C}/\mathrm{g\,DM}$	Fraction of carbon in forage dry matter.

Smith et al. (2014), and Boke-Olén et al. (2018) have described those pieces of LPJ-GUESS that are relevant for our simulations. If you want to request access to the LPJ-GUESS code base, please contact the maintainers: https://web.nateko.lu.se/lpj-guess/contact.html

Our "megafauna" fork of LPJ-GUESS 4.1 includes MMM in version 1.1.5 and the changes of the trunk version until Subversion revision 10716 and the daily grass growth scheme by Boke-Olén et al. (2018) from revision 9461 (branch `daily_grass`). We will describe the changes we made to integrate LPJ-GUESS with the Modular Megfauna Model.

Available Forage

The daily grass growth model (Johnson and Thornley 1983; Boke-Olén et al. 2018) has 4 **leaf compartments:** growing leaves, first and second fully expanded leaves, and senescing leaves. LPJ-GUESS represents each of them as carbon and nitrogen mass per area [$\mathrm{g\,C}/\mathrm{m}^2$]. Senescing leaves don't contribute to photosynthesis, which is why we consider them dead standing grass biomass. Carbon biomass translates to dry matter per area with the conversion coefficient `c_in_dm_forage` (Tab. S12). The sum of all aboveground grass dry-matter biomass is then available for herbivores to eat.

Consequently, grass appears as *one* amount of forage to herbivores, and they can't preferentially select between leaf compartments. This is for simplicity's sake in this early model development phase. Although field studies have well documented that large grazers feed preferentially on young leaves (Merkle et al. 2016) and modeling studies indicate that switching forage types can stabilize populations (Owen-Smith 2002), the mechanism would introduce too many variables to MMM at this stage. Therefore, each grass leaf compartment gets eaten and reduced in proportion to its carbon mass. All eaten carbon disappears into the atmosphere, and eaten nitrogen enters the soil pool (see Sec. B.3.4).

The 4 compartments represent a grass life cycle. Each day, a fraction of each grass compartment transforms to the following one (growing to expanded to senescing leaves, and, finally, to the litter pool). This **senescence factor** is a function of dynamic water and temperature stress, and the constant leaf longevity PFT parameter. In the original implementation, the senescence factor is the same for all leaf compartments; growing leaves turn into expanded leaves at the same rate as

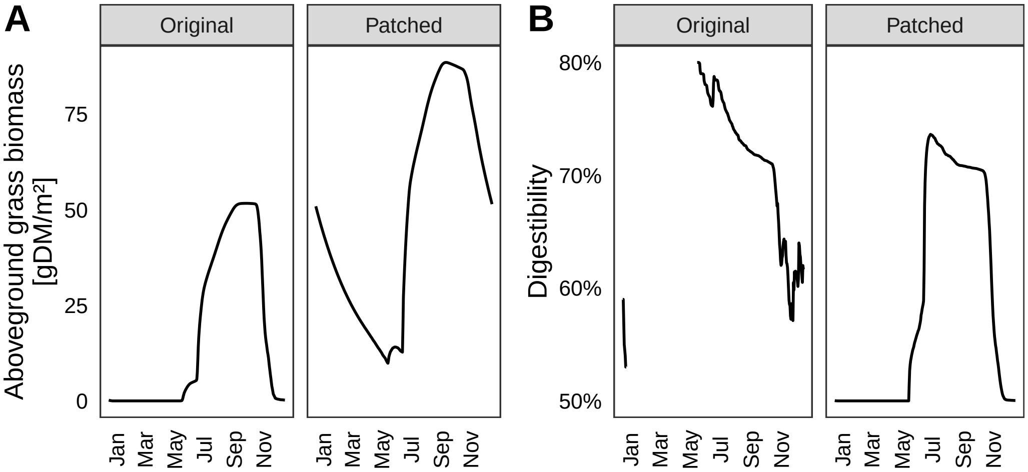

Figure S15. Difference in simulated grass forage between original LPJ-GUESS daily grass growth model and a patch where freezing suspends decay of senescing leaves. The patched version provides winter forage for herbivores. *A,* Aboveground dry-matter (DM) grass forage available to herbivores. *B,* Digestibility (i.e., forage quality), peaking in spring. Arbitrarily chosen arctic location: 156.75 °E, 62.25 °N. Driving data: monthly CRU-NCEP climate, 1900–2015.

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senescing leaves turn into litter.

The dynamic senescence factor increases with lower temperature (cold stress) and low soil moisture (drought stress). It makes sense for live leaves to die off (i.e., turn into senescing leaves) due to frost and drought damage, but dead standing grass (i.e., senescing leaves) decomposes (i.e., enters the litter pool) more *slowly* under dry and cold conditions. In arctic and temperate winter, snow cover or continuous freeze can preserve dead standing biomass for many months. In fact, it is considered important winter forage for large grazers, especially in the Pleistocene cold steppe (Guthrie 1990). If senescing leaves enter the litter pool at the rate of the dynamic senescence factor, they disappear immediately at the onset of arctic winter (Fig. S15*A*). This leaves no forage for herbivores at all, and they die in the long winter. In order to simulate available forage in winter, we simply disabled decay on days when air temperature is below freezing (Fig. S15*B*). This should be considered an ad-hoc solution. In order to apply the model to tropical grass–grazer systems, forage must remain available during the drought season, and the decay should be slowed down by desiccation.

Digestibility

Dry-matter digestibility is the indicator of forage quality — that is, energy content (cf. Sec. B.3.3). It is highest in young leaves, which are rich in nitrogen and low in hard-to-digest compounds like lignin. Over the course of the growing season, as graminoids and forbs age, digestibility increases because the plant matter contains more lignin for structural support. Therefore, tall grass is typically less digestible than short grass.

Pachzelt et al. (2013) have modeled digestibility as a simple function of grass density: the more grass, the lower its digestibility. However, this creates the artifact of herbivores "increasing" digestibility simply by removing forage. Since the new daily grass growth model of LPJ-GUESS explicitly represents four different growth stages (compartments), we can calculate digestibility in a more sophisticated way. Digestibility is highest in growing leaves (parameter `digestibility`; Tab. S12), lowest in senescing leaves (parameter `digestibility_dead`), and linearly interpolated for the two compartments of expanded leaves (Fig. S16). Total digestibility is the mean of the four compartments, weighted by their respective carbon mass per area. With this mechanistic formulation, digestibility peaks in spring, declines throughout the growing season, and stays at the minimum in

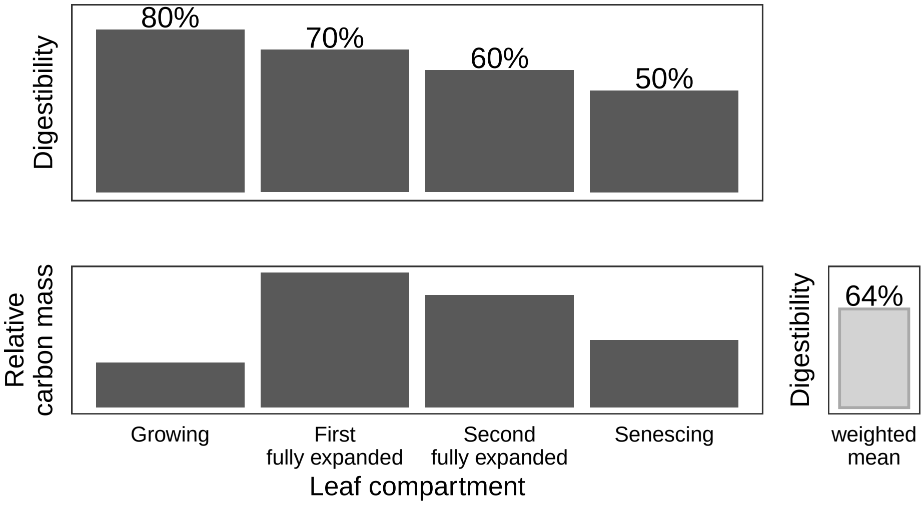

Figure S16. Example calculation of grass digestibility, using the leaf compartments of the LPJ-GUESS daily grass growth scheme to build a weighted average (*bottom right*).

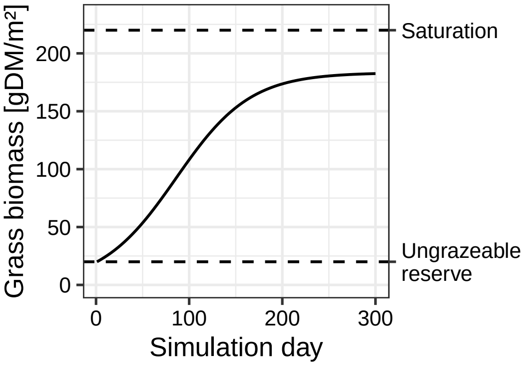

Figure S17. Aboveground grass dry-matter (DM) biomass as simulated by the demo simulator in the absence of herbivory and with constant parameters. Note that the growth rate decreases with increasing biomass (logistic growth), the decay rate is constant; that's why the effective saturation is lower than the user-specified parameter.

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winter, when only senescing leaves are available (Fig. S15*B*).

Nitrogen

Nitrogen consumed by herbivores enters the soil NH_4 pool directly and is thus available to plants. The fact that herbivores retain nitrogen in digestive tract and body tissue is neglected. (This assumption remains only valid in the absence of movement; otherwise redistribution of nitrogen in the landscape may play a significant role.) Decomposition time of excretions and carcasses as well as losses to the atmosphere are also neglected.

B.3.5 Vegetation Submodel: Demo Simulator

The demo simulator of the Modular Megafauna Model provides a very simple grass model with logistic growth (Fig. S17). It is similar to the grass model used by Owen-Smith (2002). Grass grows in daily time steps up to a saturation level. The daily increment is proportional to the standing grass and is a balance between growth rate and decay rate. An ungrazeable reserve (`grass.ungrazeable_reserve` [gDM/m²]), which cannot be consumed by herbivores, guarantees that grass can always regrow. The daily proportional net growth on day d is given by:

Table S13. Parameters for MMM's demo simulator with a simple logistic grass model

Identifier	Unit	Explanation
`general.years`	years	Number of simulation years.
`grass.daily_decay_rate`	day^{-1}	Proportional rate of senescence/ attrition.
`grass.daily_growth_rate`	day^{-1}	Proportional *maximum* growth rate.
`grass.digestibility`	fraction	Measure of forage quality.
`grass.initial_mass`	$\text{g DM}/\text{m}^2$	Grass dry matter at the beginning of the simulation.
`grass.saturation_mass`	$\text{g DM}/\text{m}^2$	Maximum standing grass mass; asymptote of logistic curve.
`grass.ungrazeable_reserve`	$\text{g DM}/\text{m}^2$	Grass biomass unavailable to herbivores; necessary for regrowth.

Note: Growth rate, decay rate, and digestibility can be specified per month.

$$\text{prop. increment}_{[\text{day}^{-1}]}(d) = \text{growth}_{[\text{day}^{-1}]} \times \left(1 - \frac{\text{standing grass}_{[\text{g/m}^2]}(d)}{\text{saturation}_{[\text{g/m}^2]} + \text{reserve}_{[\text{g/m}^2]}}\right) - \text{decay}_{[\text{day}^{-1}]} \quad (22)$$

The new standing grass biomass on the following day ($d + 1$) is then:

$$\text{standing grass}_{[\text{g/m}^2]}(d+1) = \text{standing grass}_{[\text{g/m}^2]}(d) \times \text{prop. increment}_{[\text{day}^{-1}]}(d) \quad (23)$$

If decay rate $= 0$, the grass will grow to an asymptote of `saturation_mass` plus `ungrazeable_reserve`. With decay enabled, that saturation level will effectively not be reached (Fig. S17).

C Parameterization

In choosing parameter ranges, we aired on the side of caution, rather choosing a wider than a narrower range. In our case, overestimating uncertainty is better than underestimating it.

Vegetation parameters are like for modern (high-latitude) grasslands, which assumes basic physiological conservatism. Herbivore parameters are more specific, the modeled species are extinct, and observational or experimental studies on modern Arctic large herbivores are rather rare. Therefore we followed this order of preference for basing herbivore parameters on:

1. Evidence from fossil record
2. Closest living relatives (e.g., Asian elephant for woolly mammoth, American bison for steppe bison)
3. Other wild large herbivores, preferably in the Arctic (e.g., reindeer)
4. Domesticated large herbivores (e.g., cows and horses)
5. General patterns in mammals (e.g., allometric scaling relationships)

Table S14. Parameter ranges defined for specific Pleistocene herbivore functional types (for literature references and discussion, see the associated text sections)

Identifier	Unit	Mammoth		Horse	Bison	Section
		Fixed	Range			
`body_mass.birth`	kg	100		36	25	C.2.10
`body_mass.female`	kg	2200	50–57% of ♂	300	550	C.2.10
`body_mass.male`	kg	4000	2000–6000	300	800	C.2.10
`digestion.allometric.fraction_male_adult`	kg DM/kg	2%	1–2%	4%	3.6%	C.2.19
`digestion.digestibility_multiplier`	fraction	0.9	0.84–0.93	0.9	—	C.2.14
`expenditure.basal_rate.mj_per_day_male_adult`	MJ/day	200	159–361	36	105	C.2.20
`life_history.lifespan`	years	70	60–80	20	22	C.2.17
`life_history.physical_maturity_female`	years	30	25–35	4	4	C.2.2
`life_history.physical_maturity_male`	years	40	35–45	4	6	C.2.2
`life_history.sexual_maturity`	years	12	10–15	3	3	C.2.3
`mortality_adult.adult_rate`	year^{-1}	1%	1–8%	10%	10%	C.2.5
`mortality_adult.juvenile_rate`	year^{-1}	5%	5–30%	30%	30%	C.2.5
`reproduction.annual_maximum`	year^{-1}	0.28	0.21–0.28	0.7	0.75	C.2.23
`reproduction.gestation_length`	months	20	18–23	11	9	C.2.16

C.1 Plant Parameters

C.1.1 Carbon Concentration in Dry Matter

- Chapin III et al. (2011, pp. 124–25):
  - "The carbon concentration of organic matter is also variable but averages about 45% of dry weight in herbaceous tissues and 50% in wood (Gower et al. 1999; Sterner and Elser 2002). … Because of the relative constancy of the carbon and energy contents of organic matter, carbon, energy, and biomass have been used interchangeably as currencies of the carbon and energy dynamics of ecosystems."
  - We could not find any number in Gower et al. (1999) about carbon content in dry matter. The reference might be a bit misplaced.
  - In the Google Books preview of Sterner (2002), we only found this on page 181:
    - "In most biological materials, carbon is 40–50% of dry weight (Chapter 2)."
    - In Chapter 2 we only found figures for specific chemical components of biomass (lipids, proteins, etc.).
- Pachzelt et al. (2013):
  - "Our model calculates the grass biomass (V_{total}) as the grass leaf carbon mass times two (as approximately half of the leaf dry biomass is carbon) …"
  - Unfortunately, a citation is missing here.

Conclusion: If dry herbaceous tissue is on average 45% carbon, then a conservative range might be 40 to 50%.

C.1.2 Forage Digestibility

- DMD = dry-matter digestibility
- Minson (1990): *Lolium perenne* has about 75% in fresh growth and 65% in hay. *Dactylis glomerata* has 70% in fresh growth and 62% in hay.
- Klein and Bay (1994): *Salix arctica* had in vitro dry matter digestibility of 37% to 60%. *Carex stans* ranged from 51% to 66%.
- Illius and O'Connor (2000): 40% digestibility for dead grass. 70% digestibility for live grass.
- Peltier et al. (2003): Hay DMD between 82 and 88%.
- Cornelissen et al. (2004, Fig. 1): In-vitro digestibility of subarctic graminoids and forbs range approximately from 40% to 80%.
- Pachzelt et al. (2013): 40% digestibility for dead grass. Flexible digestibility for live grass.

Conclusion: The digestibility of senescing leaves may range from 40 to 50% and freshly grown leaves from 70 to 80%. We have not investigated the effect of different measurements. If this parameter is highly effective, it will be worth to explore a mechanism for digestibility, e.g., to derive it from nitrogen content (in case LPJ-GUESS is sufficiently accurate there).

C.1.3 Forage Gross Energy

- Golley (1961): gross energy in various ecological materials
  - also cited by Robbins (1983, p. 10) and by Hobbs (1989)
  - We translate the coefficient of variation (CV) to a range of about 96% of the observations. The CV multiplied by the mean is the standard deviation (SD), and the mean ±SD makes our range.
  - 1 calorie is 4.184 joules
  - Table 1: Average energy values for parts of plants, based on determinations from 57 species: Leaves: 13.6 to 21.8 $^{MJ}/_{kg}$ (n=260)
  - Table 3: Average energy values of dominant vegetation in ecological communities.

Table S15. Parameter ranges defined for all Pleistocene herbivore functional types (for literature references and discussion, see the associated text sections)

Identifier	Unit	Fixed	Range	Section
`hft.body_fat.birth`	fraction	25%	0–max.	C.2.6
`hft.body_fat.catabolism_efficiency`	fraction	0.9	0.7–0.9	C.2.13
`hft.body_fat.deviation`	—	0.075	0–0.15	C.2.9
`hft.body_fat.gross_energy`	MJ/kg	39	38–40	C.2.7
`hft.body_fat.maximum`	fraction	30%	20–40%	C.2.8
`hft.body_mass.empty`	fraction	0.84	0.81–0.87	C.2.15
`hft.breeding_season.length`	days	15	1–30	C.2.12
`hft.breeding_season.start`	month	May	March–June	C.2.12
`hft.digestion.k_fat`	fraction	0.7	0.5–0.7	C.2.4
`hft.digestion.k_maintenance`	fraction	0.85	0.60–0.85	C.2.22
`hft.digestion.me_coefficient`	fraction	0.85	0.75–0.85	C.2.21
`hft.establishment.age_range.first`	years	1	—	C.2
`hft.establishment.age_range.last`	years	19	—	C.2
`hft.establisment.density`	ind/km^2	0.01	—	C.2
`hft.expenditure.basal_rate.exponent`	—	0.75	0.66–0.75	C.2.20
`hft.expenditure.fmr_multiplier`	—	1.5	1.5–3.0	C.2.20
`hft.mortality.minimum_density_threshold`	fraction	0.5	—	C.2
`hft.reproduction.logistic.growth_rate`	—	15	10–50	C.2.24
`hft.reproduction.logistic.midpoint`	fraction	0.3	0.2–0.7	C.2.24
`simulation.establishment_interval`	days	365	—	C.2
`simulation.gross_energy.grass`	MJ/kg DM	18	14–21	C.1.3
LPJ-GUESS: `c_in_dm_forage`	kg C/kg DM	50%	40–50%	C.1.1
LPJ-GUESS: `digestibility`	fraction	80%	70–80%	C.1.2
LPJ-GUESS: `digestibility_dead`	fraction	50%	40–50%	C.1.2

        - *Andropogon* field: 12.9 to 19.7 MJ/kg (n=143)
        - Herb old-field: 14.1 to 20.8 MJ/kg (n=35)
        - *Poa* old-field: 14.9 to 19.2 MJ/kg (n=115)

- Schwartz and Thompson (1985, p. 29): “Gross energy (or combustion energy) in plant samples is routinely about 18.8 kJ/g dry matter,[80, 81] but may be higher when plants contain high levels of fats or oils. However, variation in gross energy content is of little significance to the animal.”
    - Ref. 80: Garret \& Johnson (1983): Nutritional energetics of ruminants
    - Ref. 81: Milchunas et al. (1978): In vivo/in vitro relationship of Colorado mule deer forages. Colo. Div. Wildl. Spec. Rep.
- Givens et al. (1989):
    - “In the absence of energetic data, it has been common to calculate ME from DOMD content. MAFF et al. (1984) stated that for a wide range of feedstuffs ME may be calculated as 0.015 X DOMD. This is based on the assumption that the GE of digested OM is 19.0 MJ kg^{-1} together with a ME/DE ratio of 0.81.”
    - ME = Metabolizable Energy [MJ/kg]
    - DE = Digestible Energy [MJ/kg]
    - GE = Gross Energy [MJ/kg]
    - OM = Organic Matter [kg]
    - DOMD = Digestible Organic Matter Content [percent] = digestibility for dry matter forage
- McDonald et al. (2010): Table 11.1 on page 259 gives some gross energy values for different feeds. They range between 17.9 (mature grass hay) and 19.5 (dried, mature ryegrass).

Conclusion: The seasonal variation in Golley (1961) seems to us small. We will assume a constant value. The variation of gross energy in the wild as put together by Golley (1961) seems to be much higher than what is listed in the agricultural publications. But since we am dealing with wild herbivores, a range of 14 to 21 MJ/kg seems reasonable.

C.2 Herbivore Parameters

There are some parameters that have no ecological basis and are only needed for the simulation procedure. However, they can create artifacts in the output of the sensitivity analysis simulations. For example, the higher the establishment density, the higher the mean density — but without ecological significance. Therefore the following parameters are set to fixed values:

- `hft.establishment.age_range.first` and `hft.establishment.age_range.last`: For simplicity’s sake we want to keep them the same for all HFTs, which means that the upper age range is limited by the lowest lifespan. That makes a range of 1–19 years.
- `hft.establishment.density`: If spinup time is long enough, the populations can grow from any very low density. The establishment density must be low enough that it is not overstocking even very low-productive sites. Matheus (2003) estimates mammoth density at 0.079 ind/km^2. A value of 0.01 ind/km^2 should be low enough; it means that 1 animal has 100 km^2 to graze.
- `hft.mortality.minimum_density_threshold`: A value of 0.5 allows room for some population decline immediately after establishment without accidentally deleting a potentially viable population. Some loss is to be expected since we establish in winter, on January 1st.
- `simulation.establishment_interval`: By setting the establishment density to 365d̃ays, every year around January 1st, herbivores are re-established if they have died out.

C.2.1 Age of Menopause (Mammoth)

- Owen-Smith (1988, p. 145): “The proportion of African elephant females pregnant is highest (43%) in the age group 31–40 years. Fertility declines rapidly after 50 years of age.”
- Whyte et al. (1998): “Unlike humans, they remain fertile until into their late fifties.”
- Moss (2001): “In Amboseli, unlike Addo (e.g., Whitehouse \& Hall-Martin, 2000), females are able to reproduce until the end of their lifespan, although there is a sharp drop in fecundity after 50 years with declining reproductive value from its peak at about 20 years.”
- Joshi et al. (2009): “The reproductive performance of the females falls off sharply by the time they are about 50 years of age”
- Lahdenperä et al. (2014):
  - “Here we use extensive demographic records on semi-captive Asian elephants (n = 1040)”
  - “We found that fertility decreased after age 50 in elephants, but the pattern differed from a total loss of fertility in menopausal women with many elephants continuing to reproduce at least until the age of 65 years. The probability of entering a non--re-pro-duc-tive state increased steadily in elephants from the earliest age of reproduction until age 65.”
  - “Post-reproductive lifespan reached 11–17 years in elephants”
  - “The complete, irreversible cessation of reproductive capacity seen in some long-lived social animals such as pilot and killer whales [14,43] and humans around age 50 is not perceivable in elephants.”

Conclusion: It is not worth to implement a menopause age for mammoths since there is no clear cut-off age. The model could be improved by adding a gradual decline in fertility with aging. That would need more investigation for the other species. We will await the results of the sensitivity analysis: If the reproduction rate is supremely important for the overall population density, we will consider implementing a non-constant and age-specific maximum reproduction rate.

C.2.2 Age of Physical Maturity

Mammoth

- Lister (1999):
  - “In *L. africana*, females have largely ceased growth in height by the age of 25, while males continue until around 45 (Laws et al. 1975: fig. 8.9). In *E. maximus,* female growth in height asymptotes in the mid-twenties, males in the mid-thirties (Sukumar et al. 1988: figs. 1 \& 2).”
  - “Haynes (1991) shows for *L. africana* that the various long-bone epiphyses fuse anything between 6 and 12 years later in males than females.”
- Altrichter and Mittermeier (2011): 37 years for *Elephas maximus*
- Larramendi (2015): “It is known for extant elephants that complete fusion of long bone epiphyses occurs late among males, around the age of 40, and this is also observed in woolly mammoths. However, in females this process is complete at an approximate age of 25 years (Roth 1984; Haynes 1991; Lister 1999; Lister and Stuart 2010).”
- Larramendi (2016): “Both sexes, however, seem to continue growing throughout their lives (see Laws 1966; Lindeque and van Jaarsveld 1993).”

Conclusion: Males: 35 to 45 years; - Females: 25 to 35 years

Steppe Bison

Nowak (1991): In plains bison, bison reach physical maturity at 6 and and females at 4 years of age.

Horse

- Nowak (1991): large breeds of domestic horse are not full-grown until 5 years of age
- Boyd and Houpt (1994, p. 188): "immature males (up to four years of age)"

Conclusion: 4 years until physical maturity for both mares and stallions.

C.2.3 Age of Reproductive Maturity

Mammoth

- Hanks (1972): "Females reached maturity at 14 years"
- Williamson (1976): African bush elephants in Wankie National Park first ovulated between 9 and 15 years of age (mean: 11 years).
- Whyte et al. (1998): "They have a mean age of first calving from 11 to 20 years old."
- Guthrie (2001) "There are hints of this in the reconstructed survivorship curves using molars from fossil Alaskan mammoths. Those curves show that mortality accelerates rapidly around 20 years of age, which may help us identify the social transitions into adulthood and the higher risks which accompany these life changes."
- Moss (2001): "In Amboseli, the youngest female to successfully conceive (resulting in a live birth) was 7 years old, but this was a rare event with a low probability. The median age of first conception was 12 years, which would be a more realistic age to use in modelling elephant population dynamics. While some females were able to commence reproduction relatively young, others were delayed for as much as 4 years."
- Joshi et al. (2009):
    - "In the Asian elephant, the young male may reach sexual maturity as early as 7 or 8 years [13] . The female cow reached of age for breeding when they are 12 to 14 years old and adult males get mature when they are 14 to 15 years old. Rare exceptions are also there in their mating processes [2]"
    - "Likewise, females may reach sexual maturity as early as 7 years of age under a high plane of nutrition, while sexual maturity could be delayed until 10 years or more if the animals are living in less productive marginal habitats."

Conclusion: Mammoth females reach reproductive maturity somewhere between 10 and 15 years of age.

Steppe Bison

- Asdell (1964): Puberty is reached with 2–3 years (plains bison).
- Nowak (1991): Sexual maturity reached at 2–4 years (plains bison).
- Green (1990): Reproductive age of *Bison bison* females: 3–18 years

Conclusion: 3 years

Horse

- Garrott et al. (1991, p. 647): "Recent reproductive studies, however, demonstrate that age of first foaling is usually 2–3 years"
- Boyd and Houpt (1994, p. 174): "Przewalski's mares are physiologically capable of conceiving as early as two years of age, however, most do not breed until the fourth year of life (Groves 1974)."

- Dawson and Hone (2012): “The age of first reproduction [in *Equus caballus*] is usually 3 years; however, fillies reproduce at the age of 2 when density is low and food is abundant (Berger 1986; Duncan 1992; Tatin et al. 2009).”
- Collins and Kasbohm (2017): “Free-roaming female horses typically have their first foals at 2–3 years of age, often produce foals in consecutive years, and remain reproductively active throughout their lives with only a small reduction in foaling rates in the oldest age classes (Speelman et al. 1944, Berger 1986, Siniff et al. 1986, Wolfe et al. 1989, Garrott et al. 1991)”

Conclusion: 3 years

C.2.4 Anabolism Coefficient (`k_fat`)

We use k_f for the efficiency to build up *fat* mass, k_p for building up *protein*, and k_g for buildung up *both* protein and fat.

- Moe et al. (1971):
  - “Data from this laboratory suggest that milk may be produced from body tissue reserves with an efficiency of 82 to 84% and that the body tissue reserves may be replenished in late lactation by deposition of body tissue with an efficiency equal to or exceeding that of milk production.”
  - “Metabolizable energy intake was measured by subtracting the energy lost as feces, urine, and methane from the intake of gross energy. Tissue energy is subject to the cumulative errors of measurement of ME, heat production, and milk energy and is associated with the largest error of determination of any of the measurements.”
  - “The 72.6% (1/1.378) from the tissue gain data or 74.7% (1/1.339) from the pooled data is significantly higher than the 58.7% which was obtained from the data of nonlactating animals in this laboratory (14).”
  - We understand that k_f is somewhere around 60% to 75%.
- Reid and Robb (1971):
  - “Recently Bull et al. (8) reported that the body composition and energetic efficiency of Southdown sheep fed four different diets were associated with sex. [...] However, of the metabolizable energy ingested above maintenance, the ewes retained 65.5% and the males stored 57.6%.”
  - This is a k_g value of 57.6 to 65.5%.
- Rattray et al. (1974):
  - “Fat synthesis required 10.2 ± 3.58 kcal ME per gram or 1.10 ± 0.38 kcal ME per kilocalorie of fat deposited.”
  - That translates to $k_f = 1.10^{-1} = 0.909$. That seems very high!
  - It also means that the anabolism coefficient is 42.68 $^{\mathrm{MJ}}/_{\mathrm{kg}}$. This seems very cheap!
  - We should not trust these numbers from the abstract without having read the fulltext article.
- Wallmo et al. (1977, p. 125): “According to Mautz et al. (1976) the net usable caloric yield from catabolized fat is about 6 $^{\mathrm{kcal}}/_{\mathrm{g}}$.” That translates to 25.1 $^{\mathrm{MJ}}/_{\mathrm{kg}}$ and is a lot less than the 39.5 $^{\mathrm{MJ}}/_{\mathrm{kg}}$ used by Illius and O’Connor (2000).
- Moe (1981):
  - “Using a linear function for maintenance ME (1683 + 8.1 LW for live weights (LW) between 20 and 90 kg), Thorbek (84) found partial efficiencies for protein and fat deposition of 43 and 77%.”

  - "Kielanowski and Kotarbinska (46) studied several exponents of body weight in describing relationships between ME intake or heat production and protein and fat gain in growing pigs. They found the exponent .734 fit best and used .75 for simplicity. Energy cost of protein deposition was 16 kcal ME/g, and cost of fat deposition was 13 kcal ME/g. Those estimates correspond to partial efficiencies of about 35 and 71%, respectively."
    - So fat is anabolised with about 54.4 MJ/kg. That is almost the exact value used by Illius and O'Connor (2000). But remember that pigs are generally more efficient in using metabolizable energy for fat (McDonald et al. 2010, p. 275).

- Robbins (1983, p. 296): "The NEC for de novo fat deposition in ruminants is virtually identical to that occurring in the simple-stomached animal (Reid et al. 1980)." We interpret that as an indicator that we can use the same anabolism coefficient k_f for both ruminants and hindgut fermenters.
- Blaxter (1989):
  - Table 12.1 on page 259 shows efficiency of utilization of metabolizable energy for deposition of fat and protein above maintance, i.e., k_{f+p} (also known as k_g for *growth*): Horse: 0.60; Ox: 0.50; Sheep: 0.50
  - Note that Illius and O'Connor (2000) using the 0.50 factor for *fat-only* growth is strictly speaking not legitimate because it includes protein synthesis. Since fat synthesis is more efficient, the factor is probably a bit higher.

- Minson (1990): Only k_g (here called k_f for growth) values that have digestibility already included. Without the original digestibility values, we don't have *our* k_f value.
- Jiang and Hudson (1992): Wapiti
  - "In our study, mobilization of body tissue provided 26 kJ/g during the winter pen trials but required 39 kJ/g to deposit on spring pasture."
    - These two figures seem to be very low.
  - "Thus, metabolizable energy was used for gain with an efficiency of 67%, a value consistent with estimates for red deer and domestic livestock on high-quality forages (Simpson et al. 1978)."
    - So $k_f = 0.67$

- McDonald et al. (2010, p. 275): "For ruminants, the efficiency of utilisation of ME for growth is generally lower than that for pigs, and it is also more variable, as shown in Table 11.7."
  - Table 11.6 (p. 275): k_f for pigs on normal diet is 0.74
  - That values in Table 11.7 (p. 276) are only for growth *and* fattening (k_g) of ruminants, and there are also no citations at all for the original studies.
    - Dried ryegrass (young): 0.52
    - Dried ryegrass (mature): 0.34
    - Meadow hay: 0.30
    - Lucerne hay: 0.52
    - Grass silage: 0.21 to 0.60
    - Wheat straw: 0.24
    - Dried grass (chopped): 0.31
    - Dried grass (pelleted): 0.46
  - The very low values in McDonald et al. (2010, p. 276) make us suspicious that there are other factors in the calculation that are not explained.

- Sibly et al. (2013, p. 155): "the total cost of synthesizing and storing one gram of fat is about 54 kJ (Pullar \& Webster 1977; Emmans 1994)." This seems in line with the value used by Illius and O'Connor (2000).

Conclusion: It seems very difficult to experimentally disentagle the efficiency for building up fat and for building up protein, k_f and k_p. So it seems advisable to use the range for either k_f or k_g for our parameter estimation, but to keep in mind that protein synthesis is generally a lot more expensive. Most figures we found are for ruminants, but since the few numbers for pigs and for horses don't seem to fall out of range too much, we don't think it's necessary to differentiate by digestion strategy. Therefore, we will use the same value for all HFTs. Most efficiency factors fall in the area of 0.5 to 0.7, so that be the range for our model.

C.2.5 Background Mortality

Mammoth

- Owen-Smith (1988):
  - "For African elephants at Manyara in Tanzania, annual mortality averaged 10% during the first year of life, thereafter declining to 3–4% , but about half of this mortality was related to hunting. At Amboseli in Kenya, where there was no hunting, calf mortality totalled 7.5% between birth and one year of age, and 15% by 2.5 years, in wet years. During dry years there was a sex difference in calf mortality: first year mortality among males averaged 25% compared with 10% among females, while 55% of males had died by 2.5 years compared with 30% of females." (p. 152f)
  - "Above 2.5 years, annual mortality rates [of elephants] drop to levels similar to those of adults." (p. 153)
  - "In Uganda, mortality among adult elephants was estimated to be 5–6% per annum, due mostly to shooting." (p. 153)
  - "At Tsavo in Kenya, annual mortality was 2–2.5% for prime females aged 15–40 years and for males up to 25 years of age; among older males mortality accelerated to 7.5% per annum, but probably incorporated past hunting." (p. 153)
  - "At Luangwa Valley in Zambia, the mean mortality rate of animals aged 10–50 years was 4.4% per annum." (p. 153)
  - "All of these estimates are based on the age structures found in shot samples, and thus assume a stationary population. They overestimate true mortality rate to the extent that these populations had been increasing rather than stationary (Douglas-Hamilton 1972; Hanks 1972; Laws 1969b, 1974; Laws, Parker \& Johnstone 1975; Lee \& Moss 1986)." (p. 153)
  - So summarize:
    - The mortality in the first year ("juveniles" in the Megafauna Model) is particularly high.
    - However, only after 2½ years, the mortality rates are similar to those of adults.
    - Adult mortality is about 5% maximum.
  - "Predation on calves by lions has been documented at Manyara in Tanzania and Kasungu in Malawi, but is probably more widespread. At Tsavo there is a record of a 7–8 year old elephant killed by lions (Douglas-Hamilton 1972; R. H. V. Bell personal communication)." (p. 153)
  - "Megaherbivores generally show low adult mortality rates from natural causes, of the order of 2–5% per annum. Male mortality rates may be somewhat higher due to fighting injuries" (p. 158)
  - "Predation by carnivores is a significant source of mortality among adults of all ungulate species up to and including the size of African buffalo. [...] Among elephants, rhinos and hippos, fighting among males and accidents such as becoming stuck in mud are the major source of mortality, apart from" hunting. (p. 159)
- Whyte et al. (1998): African elephants in Kruger park.

  - "[...] with between 2·5 and 5% of the population dying each year."
  - "The consistent increases in population when between 4 and 5% of the animals are killed makes 5% a reasonable estimate of the population's growth rate. A population growing at 5% annually, all females calving first in their 12th year and at 3·67 years thereafter, allows a back calculation of annual mortality of 1·5%."

- Moss (2001):

  - "Male elephants experienced higher rates of mortality than did females over the first 10 years of life; only 75% of male calves survived to age 10 years, while 84% of female calves reached this age."
  - "While 82% of female calves survived to the average age of first reproduction (14 years), only 39% of males survived to the age when they regularly enter musth (early 30s) and were likely to obtain significant numbers of matings (Poole \& Moss, 1981; Poole, 1987, 1989a,b)."

Conclusion: The model assumes constant mortality after completing the first year. This does not match the particular case of proboscideans because their vulnerable juvenile stage is longer and the senile stage is also longer.

Another complicating factor are the large Pleistocene predators. There is no way to say how much predation pressure was on mammoth calves (and perhaps even adults). We can only state that the total reproduction rate of mammoths must not have been exceeded by predation. However, even a high predation rate on juveniles might not threaten the viability of the overall population.

In order to consider the potential of high predation pressure on mammoth calves by groups of large Pleistocene carnivores we set a wide range of 5 to 30% annual juvenile mortality. Adult mortality could have been higher, too, with a strong carnivore guild. In some elephant adult mortality rates reported (7.5% in Tsavo, Owen-Smith 1988), human culling is also included, however. With its very low reproduction rate, we should consider a very low adult mortality, too. So, we choose a range of 1 to 8% for adult mortality.

Steppe Bison and Horse

- Siniff et al. (1986), feral horses in Nevada: "Foal mortality ranged from 2% to 33%."
- Gates and Larter (1990): Mackenzie wood bison

  - "Adult survival (≥ 1 year) and calf survival were estimated by successive approximation from a model based on a life table analysis technique described by Taylor and Carley (1988)." (p. 232)
  - "Calves were the most common cohort found in wolf kills, with annual mortality from all causes estimated at 45%. Adult survival, estimated from life table analysis, is apparently very high." (p. 236)

- Turner Jr. et al. (1992), predation rates on feral horses: "The mean first-year survival rate estimated from the differential incidence of foals and yearlings in successive years was 0.27, which was less than one-third of the foal survival rate reported for other feral horse populations."
- Carbyn et al. (1993, p. 224): "...wolves in Wood Buffalo National Park killed 14% to 40% of calves and 27% to 62% of adults that died each year"
- Turner Jr. and Morrison (2001): feral horses in California and Nevada

  - "The average number of foals killed each year by mountain lions was ... 45.1% of foals produced."
  - "Adult survivorship averaged 0.92, ranging from a low of 0.81 ... to a high of 1.0"

- Dawson and Hone (2012): Wild horses
  - Table 5 (p. 103) shows estimated survival rates for the wild horses by age and sex.
    - Males and females don't differ very much.
    - Juvenile (0–2 years) survival has large 95% confidence intervals, but the means are around 80 to 90%.
  - "Wild horse populations in the Australian Alps showed dynamics and demography consistent with patterns of large mammalian herbivores – low density (2.0–6.4 horses per square kilometre), low annual population rates of increase (l = 1.03–1.09), low annual fecundity (0.21–0.31), high annual adult survival (0.91) and lower juvenile survival (0.63–0.76)." (p. 105)
  - "Annual adult survival was at the low end of the range reported in other studies and juvenile survival and fecundity were similar to other studies. However, the exceptions were the very low rates of survival of 0- to 1-year-olds (0.27) (Turner Jr. et al. 1992) and (<0.12) (Greger \& Romney 1999) where mountain lions preyed on young horses." (p. 106)
- Collins and Kasbohm (2017): "mortality rates for free-roaming horses are low as or lower than other similarly sized, native mammals (Berger 1986); annual survival estimates for adult horses have ranged from 70–80% (Wolfe 1980) to 95% and higher (National Research Council 1980, Berger 1986, Garrott and Taylor 1990)."

Conclusion: Pleistocene predation rates are obviously unknown, but we can surmise a strong carnivore guild. It's difficult to guess whether horse or steppe bison may have experienced higher mortality rates. The numbers for modern bison and feral horses have a high overlap. For simplicity, we set annual background mortality for both steppe bison and horse to the same values: 30% for the first year (juveniles) and 10% for adults.

C.2.6 Body Fat at Birth

- Widdowson (1950): Table 1 shows that human newborn (n=6) have 16.1% fat in their *live* weight. So the percentage of empty body mass must be even higher.
- Ringberg et al. (1981, p. 1041): "The hide and the hooves were removed and the carcass was eviscerated. The head was removed above the first cervical vertabra and the remaining carcass was weighed (carcass weight). The internal organs were dissected and weighed. The carcass was divided sagitallly into haves and the left half of the carcass was ground *in toto.* Representative samples were analyzed for water by freeze-drying and for fat content by the Folch chloroform-methanol extraction method (Christie 1973)."
  - Table 3 (p. 1043): "Chemical composition of reindeer carcasses. Mean (standard deviation)
    - Age=0–6 days; N=4; Body weight=4.4 (1.1) kg; Fat = 4.4 (1.0) %
    - That makes a range of about 2.4 to 6.4%.
- Hudson and White (1985, p. 224): White-tailed deer, sheep, cattle, horse are born very lean with body fat of 3–5%
- Oftedal et al. (1993):
  - "Newborn and young cubs that died in captivity and a litter of three cubs abandoned shortly after birth in the wild were used for compositional studies. Since ambient temperatures were below freezing and cubs succumbed quickly, it was assumed that cubs had not mobilized more than small amounts of nutrients from body stores."
  - "Table 1 shows that mean cub weight in eight litters ranged from 325 to 432 g at 0–2 d postpartum, equivalent to only 3.0–5.0 g/kg maternal weight. The entire litter averaged 12 g/kg maternal weight."

        - We are very surprised how small the cubs are.
    - “Newborn cubs also contained (g/kg empty body wt) fat 9.2, protein 120 and ash 25.”
        - That is 0.92% body fat in the empty body. The standard error is SE=2.77 g/kg, which gives with n=10 samples a range of 0.83 to 1.01%.
        - We don’t know how Kuzawa (1998) arrive at 2.3% body fat…
- Gerhart et al. (1996, p. 137): “Here, we define body mass (BM) as total mass less antlers, conceptа, and incidental blood loss; ingesta-free body mass (IFBM) as BM less alimentary contents”
    - Table 2 (page 139) shows fat as mean percentage ±SE of ingesta-free body mass:
        - Fetuses: n=5, 2.01 ±0.19
        - Dead newborns: n=4, 1.20 ±0.2 → 0.80 to 1.60
        - Live newborns: n=10, 2.4 ±0.2 → 1.78 to 3.03
- Pawłowski (1998, p. 67ff):
    - “The amount of fat in human newborns is also al peculiar trait among primates. The percentage of fat tissue which constitutes 10–15% of body mass of human newborn is similar to mammals living in arctic conditions, and not to a mammal living in Africa (Forbes, 1987).”
    - “When the weight of subcutaneous fat increases, the body temperature regulation range shifts to a lower temperature (Kawashima, 1993). The cutaneous temperature is lower and the difference between ambient and body temperature decreases. It reduces the heat loss from the body. Intensive increase of the subcutaneous fat tissue (SFT) is observed in the last 10 weeks of prenatal life (Forbes, 1987). During the first year the amount of fat tissue increases also dramatically acquiring 20–25% of body mass at the end of this period of life (Baker 1992). The increase in fat tissue is threefold more than for muscles weight.”
- Kuzawa (1998):
    - “Studies of domesticated and wild species reveal that most mammals, including nonhuman primates (Schultz, 1969; Lewis et al., 1983), do not begin to deposit white fat until after birth (Adolph and Heggeness, 1971).” (p. 178)
    - “Studies of common domesticates such as rats, pigs, and sheep and wild species such as black bear reveal that these species do not begin to deposit significant fat stores until the onset of suckling and are thus born lean, with roughly 1–4% of body weight as fat (Spray and Widdowson, 1950; Adolph and Heggeness, 1971).” (p. 181)
    - “Pond and Ramsay (1992) have previously shown that fat mass in specific depots scales to body size in adult mammals, and we have extended a similar analysis to mammalian neonates in Figure 2 using data from Table 1. The limitations of this analysis must be emphasized, as the data on neonatal body composition are sparse, […] The best-fitting equation reveals that fat mass at birth scales to birth weight with an exponent of 1.12, suggesting that larger-bodied species tend, on average, to have a slightly greater percentage fat mass at birth.” (p. 181)
    - “Cold-climate species such as musk ox, caribou, reindeer, walrus, and various species of seal are born with massive [brown adipose tissue] depots and higher metabolic expenditure but little if any subcutaneous [white adipose tissue] (Blix and Steen, 1979; Blix et al., 1984).” (p. 183)

Table S16. Measurements of body fat at birth

Species	%fat at birth	Birth weight	Source
Human	15.0	3 kg	Widdowson (1950)
Reindeer	4.4	4.4 kg	Ringberg et al. (1981)
Lamb	3.0	—	McCance and Widdowson (1977)
Calf	2.8	—	McCance and Widdowson (1977)
Foal	2.6	—	McCance and Widdowson (1977)
Black bear	2.3	394 g	Oftedal et al. (1993)
Caribou	1.8	5.65 kg	Gerhart et al. (1996)
Pig	1.3	84 g	Manners and McCree (1963)

Source: Kuzawa (1998, Tab. 1, p. 181)
Note: we don't know what the fat percentages refer to: total live weight or empty body?

Conclusion: Neonates of wild large herbivores are invariably lean. We did not find any chemical analysis of newborn elephants, unfortunately. However, we also didn't find a mention of elephant babies being surprisingly fatty (like humans for example). To differentiate between HFTs is difficult at this point.

The allometric regression presented in Kuzawa (1998) is in our eyes too uncertain to be useful. The sample size is extremely low, the body mass range is also small, the meaning of "%fat" is not standardized, the variance within each data point is high, and the samples are not taxonomically independent. That larger-bodied species should have a greater percentage fat mass at birth could or could not be. It seems safe to at least assume that it is not smaller.

It was mentioned (Pawłowski 1998, p. 67) that Arctic species have more body fat at birth. This should apply to Pleistocene species, too. However, the neonate empty-body fat percentages in *Rangifer* show a wide range: about 1 to 6.5%. We could choose this as a range for the sensitivity analysis, too.

There is a problem, however: The current model does not consider lactation, and the neonates cannot accumulate enough fat. We suspect that there is a cut-off point below which the body fat at birth is too low that neonates could survive. Therefore we set the range from **1% to 99% of maximum fat** for the sensitivity analysis to find this cut-off point. The next step might be to implement a special energy gain for juveniles during the time they would nurse in order to mimic lactation.

C.2.7 Body Fat Gross Energy

- Blaxter and Rook (1953):
  - "The heat of combustion of fat, 9.5 Cal./g appears to come from a compilation of early German results by Atwater (1895) and by Fries (1907), the values for cattle showing a variation of from 9357 to 9686 Cal/kg."
    - 9.5 Cal./g = 39.748 MJ/kg
  - "In human beings, Cathcart \& Cuthbertson (1931) and Cuthbertson (1933) have shown that the calorific value of fat can vary from 8880 to 9523 Cal/kg depending on the source of the material. Such variations are very significant in terms of energy storage."
  - Table 3: Cattle depositional fat observed average in this study: 9250 Cal/kg = 38.70 MJ/kg
- Robbins et al. (1974):
  - "The caloric value of the body fat and protein were estimated by regressing the dry, ash-free heat-of-combustion on the dry, ash-free protein and fat content of each carcass sample (Reid et al., 1968)."
  - "The estimated caloric content of the body protein (5.413 kcal/g) and fat (9.490 kcal/g) were similar to values in sheep and cattle (Blaxter and Rook, 1953; Paladines et al., 1964; Reid et al., 1968; Jagusch, Norton and Walker, 1970; Drew, 1971)."

  - 9.490 kcal/g = 39.70 MJ/kg

- Price and White (1985): "Therefore, the energy content of gain could be calculated from fattening curves appropriate to the level of fatness and from the energy content of protein (2.65 KJ/g) and fat (39.71 KJ/g).[87, 98, 101]"
- Blaxter (1989, p. 52): "For example, in sheep the enthalpy of combustion of the ether extracted (crude) fat is 39.1 kJ/g and of fat-free organic matter 23.2 kJ/g. For cattle the corresponding values are 39.5 kJ/g and 23.0 kJ/g, respectively (Agricultural Research Council 1980)."
  - When Illius and O'Connor (2000) used 39.5 MJ net energy gain from one kg of fat, they assumed 100% efficiency of using the gross energy of fat. Is that justified?
  - Illius and O'Connor (2000) quote Blaxter (1989) that it costs 54.6 MJ net energy to anabolize one kilogram of fat. Consecutively, Pachzelt et al. (2013) and Dangal et al. (2017) use the same value. However, we don't find that figure in the original Blaxter (1989) book. A full-text search for "54" in Google Books does not show any results either. Searching for "54.6" through Google Scholar within those publications that cite Blaxter (1989) did only show the above-mentioned publications. So we conclude that Illius and O'Connor (2000) has derived that value from Blaxter (1989), as follows:
  - We can derive the net energy requirement for anabolizing fat tissue by comparing k_m (efficiency of utilizing metabolizable energy for maintenance requirements) with k_f (efficiency for producing fat). The gross energy of fat tissue is about 39 MJ/kg (p. 52). The *metabolizable energy* (ME) required for building 1 kg of fat is therefore $ME = 39\,MJ/k_f$. The model calculates with *net energy*: $NE = ME \times k_m$. Through substitution we derive the net energy for anabolizing 1 kg of fat as $NE = 39\,MJ \times k_m/k_f$. Inserting $k_m = 0.70$ and $k_f = 0.50$ for oxen (p. 259) yields a value of 54.6 MJ/kg, the mysterious value used by Illius and O'Connor (2000)!

- Hyvönen (1996):
  - "In energy calculations 1 g of net fat corresponds to 9 kcal or 38 kJ."
  - "Most often the total fat of food is converted to energy using the energy value 9 kcal/g of triglycerides for the calculation."
  - "From the literature (Krishnamoorthy et al., 1979; Miles et al., 1984) we found that the energy value 9 kcal/g is an average value for triglycerides."
  - That is 4.184×9 kcal/g $= 37.656$ MJ/kg.

Conclusion: The gross energy appears to be remarkably constant. It doesn't vary between herbivore species. A range of 38.0 to to 40.0 MJ/kg will serve the sensitivity analysis.

C.2.8 Body Fat Maximum

- Wikipedia (2019-12-31) says that suet has a 94% fat content and a caloric value of 35.73 MJ/kg. However, not all body fat of large herbivores is in the form of suet. Other fat depots might have a higher water content.
- Reid et al. (1955): Compilation of cattle "whole empty body" composition data from literature.
  - Table 1, all cattle (n=256): mean fat = 14.2%; range = 1.8 to 44.6%
  - 44.6% is apparently quite an outlier and comes from a male beef cattle.
  - The female range is 3.3 to 29.2%. The 30% are probably more realistic.

- Ledger (1968): Seminal study on body composition of many samples of wild large mammals. Unfortunately it is not available online anywhere.
- Baker (1969):

  - Table 2: Lipid (crude fat) content of *human* adipose tissue varies between 35.9 and 78.9 percent.
  - Fat content is higher and water content lower in older individuals.

- Reid and Robb (1971):
  - "The data employed to study the nature of body composition in dairy cattle were obtained by various workers as the result of direct chemical analysis of the whole, empty (i.e., ingesta-free) body."
  - "The fat concentrations in the whole, empty body at the times of slaughter were: 20.6% in the baseline cow, and 29.2 and 27.2% in the two fattened cows."
  - "Earlier, Moulton (34) had conducted a similar experiment with steers. [...] At the end of the fattening periods, the steers contained 29.7 and 41.2% of fat in the EBW."
  - "Recently Bull et al. (8) reported that the body composition and energetic efficiency of Southdown sheep fed four different diets were associated with sex. [...] For the same EBW range, body fat varied from 17.5 to 33.6% in rams and from 23.0 to 43.2% in ewes."
  - So the ether-extracted lipid content of ingesta-free body in fattened cattle and sheep is about 30 to 40 %. How much would that be of the live weight? And is all that available as energy reserve?

- Weiner (1973): Roe deer in Poland
  - "The empty body weight, used in all further calculations, corresponded to the weight of the whole body with skin, head, viscera and legs, but without intestinal tract and antlers." (p. 210)
  - "Fat represents the most variable constituent of body dry weight. The share of ether extract in dry mass ranges from 13.1 to 26.8% (Table 5, column 4)." (p. 213)
    - Average: 12.4% ±4.4 (SD); maximum: 26.8%
    - Since these are *dry matter* percentages, they need to be multiplied with the water fraction (average 64.3 ±3.4). So the *average* lipid content in the fresh ingesta-free (but furred) body is around 8%. The *maximum* content is $26.8\% \times 64.2\% = 17.2\%$.
  - "Øritsland (1970) found in the reindeer (Rangifer tarandus platyrhynchos, Vrolik) an even higher fat reserve, amounting to 14% of its biomass." (p. 218)

- Robbins et al. (1974): Unfortunately no usable fat percentages.
- Reimers et al. (1982):
  - "The amount of ingesta was subtracted from the body weight to determine the ingesta-free body weight. [...] Total lipid in the homogenates was extracted by the chloroform-methanol procedure (Christie 1973)"
  - "At the end of the growing season, the fat content in the ingesta-free body was very high (27–40%) in Svalbard reindeer."
  - "At the end of winter the weight decrease of Svalbard reindeer was close to 50%. The loss of ... fat from the body was estimated at ... 76.3% ... Animals that had starved to death showed an additional weight loss of 8% and a nearly complete loss of fat."
  - "The decrease in body fat continued under prolonged starvation and animals that had died of starvation had the lowest fat content (0.6 ± 0.1%)."
  - "Maximum body fat concentration in the Svalbard reindeer (28.7–40.1%) was higher than in the two domestic reindeer yearlings (4.5 ± 0.2%) and also higher than reported in literature for other cervid species; e.g., less than 20% in deer (Robbins et al. 1974) and less than 11% in roe deer (Weiner 1973). However, the maximum value (40.1%) was lower or comparable to maximum values in pigs (61.5%) and sheep (46.6%) (Reid et al. 1968) and cattle (44.6%) (Reid et al. 1955)." (p. 1818)
    - These values are all crude fat of ingesta- and blood-free body mass, we assume.

    - We don't have access to Reid et al. (1968). Robbins et al. (1974) don't give absolute values in their paper. The value of 44.6% in Reid et al. (1955) is probably pretty extreme.
  - We conclude that it is reasonable to assume that when the ingesta-free body is completely fat-depleted, the animal will die of starvation. So this assumption by Illius and O'Connor (2000) is correct.

- Lindstedt and Boyce (1985), citing Calder (1984):
  - "Pitts and Bullard (1968) measured total fat stores as a function of body size in a variety of mammals from North and South America." The publication of Pitts and Bullard (1968) is not available online anywhere.
  - "As a consequence, the magnitude of stored fat becomes a greater fraction of body mass as size increases among mammals. Calder (1984) reexamined their data , regressing the mass of body fat (M_f, kg) in eutherian terrestrial mammals only against total body mass (M_b, kg), and found the same pattern: $M_f = 0.075 M_b^{1.19}$, (R² = 0.97, N=54). The 95% confidence interval of the slope extends from 1.13 to 1.25."
    - from the original (Calder 1996, p. 51): "... comparison with the allometry of total body fat, as extracted with ethyl ether from carcasses of wild mammals collected in alaska, virginia, and brazil, and taken from published reports on four domestic species, including men (pitts and bullard, 1968). we have excluded cetaceans and marsupials from the regression, for consistency with other equations for terrestrial eutherian mammals: ..."
  - The *fraction* is then $0.075 \times M_b^{1.19}/M_b = 0.075 \times M_b^{0.19}$
  - Let's play with that formula for mammoth body masses, i.e., 1000 kg for small females to 6000 kg for large males:
    - $0.075 \times 1000^{0.19} = 28\%$
    - $0.075 \times 6000^{0.19} = 39\%$
    - Those values are very reasonable!

- Torbit et al. (1985): "Estimates of body composition measured in this study are similar to those reported for white-tailed deer (*O. virginianus*) by Robbins et al. (1974). Also, as those authors noted, deer apparently contain proportionally more protein and less fat than do domestic sheep and cattle (Reid et al. 1955, Reid et al. 1968, Garret et al. during Searle et al. 1972)." We don't fully understand their analysis and how they measured fat.
- Depperschmidt et al. (1987), chemical analysis of 14 winter-starved, female pronghorns in Wyoming; hair-free and ingesta-free body was ground and analysed: "Chemical analysis confirmed that very little fat (mean = 2.1%) remained in study animals. These pronghorn had catabolized all nonessential fat and only essential phopholipids remained. However, efficiencey of laboratory chemical procedures used to solubilize and recover lipids decline when fat concentrations are less than 4% (Torbit et al. 1985a); thus fat concentrations presented here are not definitive."
- Body (1988): Lipid content in adipose (fat) tissue.
- Torbit et al. (1988): "[Kidney fat index] predictibility of [total body fat] is unreliable at very low fat levels." This study also hints on protein catabolism to meet energy requirements.
- White et al. (1989, p. 1130): "At calving, the fat level is 40–58 kg, which represents 30% of empty body weight, a very high reserve in wild ruminants. However, this is lower than the extreme fat reserve of 44% reported for Svalbard reindeer by Reimers et al. (1982). It is possible that our muskoxen may not have been fattening to their full potential; ..."
- Renecker and Samuel (1991, p. 746): "Seasonally, wild mule deer experience periods of extreme environmental conditions that limit accessibility and availability of food resources. This restriction on intake has resulted in weight loss of 20–22% in mature mule deer (Wood

et al. 1962) and up to 32% in fawns at the time of death (Baker 1976). Davenport (1939) suggested that mature white-tailed deer could safely lose 30% of their weight during winter and survive; however, survival would depend upon peak autumn weight and body size." So the *weight* loss until death is only about 20 to 30 percent. This means that the maximum amount of lipids used for energy mobilization must be even less.

- Parker et al. (1993), nine free-ranging Sitka black-tailed deer (*Odocoileus hemionus sitkensis*): "During winter, animals used 70 – 82% of their body fat and 10 – 15% of their protein reserves."
  - cited by Parker et al. (1996): deer lost up to 30% of their total body weight in winter
- Turner et al. (1993, p. 171): "We assume that the ungulates die at 70% of their lean bodyweight (e.g., Wallmo et al., 1977). Going into the winter, a moose has 23% of its body mass in fat, and a mule deer 10%. We assumed that our generic ungulate had 20% of its bodyweight in fat going into the winter." No citation for the moose. We don't know what the number refers to.
  - And Wallmo et al. (1977, p. 125) say: "Nagy (1974) and his students, found that mule deer died of starvation when they had lost approximately 30% of their pre-starvation weight, but they persisted 6 weeks or more without food." Nagy (1974) is not available anywhere online, though.
- Bunn and Ezzo (1993), carcass and offal fat of African ungulates from Ledger (1968): "Through literature searches we have compiled seasonal fat data on adult males and females of a number of ungulates [...]. In each case adult males and females deviate in their accumulations and depletions during the year and in their levels of fat (i.e., fat as a percentage of total body weight; females tend to have higher levels). [...] Torbit et al. (1985) found that during severe winters deer are known to lose as much as 70% of their body fat without starving to death; this appears to accompany about a 30% loss in body weight, a threshold from which deer can recover rapidly."
- Prothero (1995):
  - "Pond and Mattacks (1986) concluded that percent fat is approximately independent of body weight (i.e., total fat varies as about the first power of body weight), over the weight range from about 11 g (bat) to 650 kg (camel)." (p. 633)
    - But Pond \& Mattachs (1986) dissected adipose tissue and didn't dissolve lipids chemically. So their data are not what we need for our model.
  - "For mammals generally, including aerial, land and aquatic mammals, over a wide weight range, fat varies as the 1.094–1.146 power of body weight." (p. 638)
  - "On the present evidence, bone scales as the 1.073–1.133 power, and fat scales as the 1.146 power of body weight, in mammals generally. [...] The large mean scatter (73%) around the regression line for the pooled fat data implies that predictions of fat content from body weight alone may be substantially in error." (p. 639)
  - Since Prothero (1995) includes *all* mammals and Calder (1996) specifically restricts his analysis to eutherian terrestrial mammals, we believe Calder (1996) more.
- Kojola and Helle (1996): back fat depth in reindeer; not useful.
- Parker et al. (1996) Body fat cycles in free-ranging Sitka black-tailed deer in Alaska. But they just re-use the field data from Parker et al. (1993).
- Hyvönen (1996): "The terms ether extract, crude fat, total fat and total lipids are used interchangeably in compositional analysis of food."
- Hilderbrand et al. (1999, p. 1625), adult female brown bears in Alaska: "Body composition was estimated by means of isotopic dilution and (or) bioelectrical-impedance analysis (Farley and Robbins 1994; Hilderbrand et al. 1998)."

    - Around 20% body fat in spring and summer and around 35% in fall.
    - We don't know if the isotopic dilution and impedance methods reflect ingesta-free lipid content, so we dismiss these data.

- Illius and Gordon (1999), sheep: "The maximum fat mass attainable at any body size by Soay sheep (F_{max}) was estimated from the data of McClelland et al. (1976) to be $a \times W^2\ kg$, where a is 0.0099 for females and 0.0079 for males."
- Illius and O'Connor (2000), cattle:
    - Maximum fat mass for adults: 30% of adult body mass, citing Ledger (1968)
    - Maximum fat mass for other age classes: 15%, 20%, and 25% of *adult* body mass. (We don't know how that would translate to percentage of actual, pre-adult body mass because only aduld body mass is given in the article.)
- Guthrie (2001): "Northern male ungulates today characteristically add 20% of body fat beyond lean winter values." Not helpful because he doesn't specify what the fraction refers to.
- Peltier et al. (2003): "We studied responses of eight castrated male muskoxen to a diet of grass hay [...] Animals gained body mass in spring (239±39 kg) as body fat content increased from 26% to 38% of ingesta-free mass in winter without changes in lean mass and protein."
- Couturier et al. (2009): Seasonal body fat dynamics in caribou in Canada. Body fat was in the range of 5 to 10 percent in fall. Their total body fat is based on kidney fat with regressions from Huot (1989). Huot's body fat values seem all very low. We are not sure what "body fat" means in that publication...
- Ben-Dor et al. (2011): For *Elephas antiquus* they calculate 4.1% fat of live weight, based on buffalo, the largest animal mentioned by Ledger (1968). It is not corrected for higher fat fraction in bigger animals. This approach is not convincing. They don't specify what they mean with "fat", and they don't discuss the changing fraction of ingesta and hair of the live weight.

Conclusion: The regressions from Calder (1996) and Prothero (1995) are not very helpful, we believe, because they are not specifically for *maximum* body fat. Moreover, as Prothero (1995) notes, the error around the regression line is pretty high.

The fat, even the maximum, concentration in wild ungulates appears to be generally lower than in domestic animals. We don't think there are any body fat analyses published for elephants. The maximum fat values vary so widely that we have little hope of specifying them for Pleistocene animals any more precise than with a wide range.

The lowest maximum value of pure lipid in ingesta- and hair-free body of wild large herbivores might be around 20%. The highest is measured in reindeer and about 40%. This is probably a reasonable maximum for Pleistocene animals, too. Only domestic animals have higher values.

C.2.9 Body Fat Spread

- Weiner (1973):
    - "8 individuals of Capreolus capreolus, killed in winter 1971 and 1972 in Southern Poland" (astract)
    - "The empty body weight, used in all further calculations, corresponded to the weight of the whole body with skin, head, viscera and legs, but without intestinal tract and antlers." (p. 210)
    - Table 5 (p. 214): "Computed gross body composition of the whole roe deer, in per cent."
        - Dry weight composition in percent for 8 animals:
            - 21.3, 26.8, 23.8, 13.1, 23.5, 18.4, 21.8

      - Mean = 21.2%; SD=4.4.
    - If we take 30% as maximum fat, this SD = 4.8% of maximum fat.
- Reimers et al. (1982): Table 1 (p. 1814): "Body composition in reindeer from Svalbard and mainland Norway. Animals have been grouped according to fat content in the ingesta-free body." We will give the fat in ingesta-free body weight (IFBW) as a fraction of maximum fat content (40%).
  - Svalbard animals, late summer: 0.7885, 0.696, 1.000 ⇒ SD = 15.6%
  - Svalbard medium-fat animals, late winter: 0.546, 0.260 ⇒ SD = 20.2%
  - Svalbard low-fat animals, late winter: 0.260, 0.322, 0.249, 0.321 ⇒ SD = 3.8%
  - Svalbard animals dead from starvation in late winter: 0.013, 0.015 ⇒ SD = 0.1%
  - Domestic reindeer, mainland Norway: 0.115, 0.110 ⇒ SD = 0.4%
- Illius and O'Connor (2000) cite Ledger (1968) for a standard deviation in body fat of 12.5% of maximum fat mass. Unfortunately, we don't have access to Ledger (1968), but we know that their body composition data set is across many different species from different continents and times. We doubt that it is a suitable to estimate the diversity of body fat values within one population or cohort.
- Couturier et al. (2009): Table 4 (p. 372) summarizes different body fat percentages reported for reindeer as "mean±SE (N)". The SE (standard error of the mean) can be converted to SD (standard deviation) by multiplying with the square root of the sample count (N). The SD we calculate is the result of dividing by 40%, the maximum body fat fraction of reindeer.
  - George 1983–1984: 5.1±0.7 (15) ⇒ SD = 6.8%
  - George 1985–1986: 8.4±0.3 (27) ⇒ SD = 3.9%
  - George 1986–1987: 8.4±0.3 (16) ⇒ SD = 3.0%
  - George 2001–2002: 6.9±0.3 (14) ⇒ SD = 2.8%
  - Beverly: 10.8±0.1 (195) ⇒ SD = 3.5%
  - Central Arctic: 7.2±2.2 (3) ⇒ SD = 9.5%

Conclusion: If we were to quantify the standard deviation of body fat based on field data, we really need a big sample of animals from one population or, even better, one cohort. The values from Weiner (1973), Reimers et al. (1982), and Couturier et al. (2009) give some idea of the magnitude of SD. It ranges roughly between 0 and 15% maximum body fat (the 20% value in the data of Reimers et al. (1982) is an outlier with only N=2).

Standard deviation is, obviously, not constant, but depends on the mean body fat. The lower the mean, the smaller the spread. Since the parameter is only used for starvation mortality, it is only effective in the lower range of body fat. In this light it would be appropriate to define it rather lower than higher.

The model of calculating mortality based on a normal distribution of body fat within one cohort, is not ideal all together. We believe that it neither reflects reality nor can it be parameterized based on field data. If this parameter appears to be very influential based on the sensitivity analysis, we will think about a different mortality model.

Even though most literature values for SD are lower than 10%, we want to include the 12.5% from Illius and O'Connor (2000), too. Therefore we choose a range of 0 to 15%.

C.2.10 Body Mass of Adults

Mammoth

- Roth (1990, p. 153ff):
  - "The variability of body masses determined for living elephants sets an upper limit to the precision with which mass can meaningfully be estimated from a fossil. The variation described below represents the maximum percentages I was able to obtain from

  a survey of the literature. The mass of an individual elephant varies in the course of a single day. An elephant can take in 100 liters of water in a single bout, and thereby, with one drink, increase its mass by 100 kg, which is approximately 3.5% of the body mass of an average-size mature animal (Sikes 1971: 51). Stomach fill can account for up to 6% of live mass in African elephants (Buss 1961; Laws, Parker, and Johnstone 1975:172). Benedict (1936:107) reported that in one animal 12% of body mass was feces plus fluid from the intestine and body cavity; in another individual, intestinal contents accounted for 7% of body mass (…). In the most extreme situations, therefore, short-term fluctuations in the mass of an elephant are unlikely to exceed 15%."
  - "By far the greatest source of variation in body masses associated with a particular skeletal dimension are differences between individuals in body form and physical condition. Within Uganda, Laws et al. (1975:189) found Mkomasi elephants to be 9–13% heavier than Murchison Falls Park South elephants of the same shoulder height. Masses of the lighter population were taken at a favorable time of year (toward the end of the rains), and so the actual difference is probably underestimated by these figures. As Figure 9.2 illustrates, wild African and captive Asian elephants of the same shoulder height can differ in mass by as much as 100% or even 200% (that is a factor of 2 or 3)."

- Nowak (1991):
  - *Loxodonta africana* males: 5150 kg; females: 2950 kg
  - That makes males 74% bigger than females (or females smaller by a factor of 0.57).
- Lister and Stuart (2010): equations to use for *M. primigenius* (♀/♂)
- Larramendi (2016)
  - Body mass based on volumetric method.
  - European *M. primigenius* was larger than North Siberian specimens: Europeans larger than 6 t on average, Siberians about the size of extant Asian elephants.
  - Extremely large specimens might be erroneously identified as *M. primigenius*. The *M. primigenius fraasi* from Steinheim with ~9.5 tonnes might have just been a very large *M. primigenius* or a *M. trogontherii*.
  - "Most of the published extinct proboscidean shoulder heights in the bibliography, which are generally based on incorrectly mounted skeletons or on erroneus percentages of the bones related to the shoulder heights, are concluded to be inaccurate"
  - Average body mass for woolly mammoth: ~6 tonnes
  - "African bush male elephants are on average 23% taller than females, and Asian elephant males are only about 15% taller than females."
  - This makes an African male (6 tonnes) about twice as heavy as a female (3 tonnes). That also matches roughly how 23% greater shoulder height converts to volume increase: $1.23^3 = 1.86 \approx 2$

Conclusion: Since the sensitivity analysis and our research focus on Beringia and Eurasia, we will not include the extraordinarily big specimens from Europe. So we will use a range from extant Asian elephants (2 t) to average European specimens (6 t) for males (Larramendi 2016) and scale it for females with a factor of 0.5 to 0.57.

Steppe Bison

- Guthrie (1968, Tab. 1) lists *Bison priscus* with 500 kg (interior Alaska).
- Belovsky (1986): modern bison average 686 kg (both sexes)
- Hudson and Frank (1987): modern bison average 636 kg (both sexes)
- Stuart (1991, Tab. 3) list northern Eurasian *Bison priscus* with 1000 kg, but without a reference.

Table S17. Literature values for woolly mammoth adult body mass

Reference	Body Mass	Comment
Alroy (2001)	3174 kg	no reference
Bliss and Richards (1982)	2230 kg	
Guthrie (1968)	3000 kg	Interior Alaska
Johnson (2002)	5000 kg	citing Stuart (1991)
Mann et al. (2013)	3000 kg	Alaska
Matheus (2003)	4900 kg	male
Matheus (2003)	2700 kg	female
Smith et al. (2003)	5500 kg	global average, no reference
Stuart (1991)	5000 kg	northern Eurasia, no reference

- Lambert and Holling (1998, Tab. 1) list Pleistocene *Bison* sp. with 1025 kg (northern Florida).
- Alroy (2001) uses 522.8 kg for *Bison priscus*
- Johnson (2002) lists *Bison priscus* with 1000 kg.
- Smith et al. (2003) list *Bison priscus* with 900 kg as a global average.
- Matheus (2003, p. 85): "… steppe bison may have been 15–20% larger than either modern plains (*Bison bison bison*) or wood bison (*Bison bison athabascae*). Nowak (1991) listed a size range of 350–1000 kg for modern plains bison, with an average weight around 450 kg for females and 750 kg for males. Carbyn et al. (1993) estimated the average weight of modern male and female wood bison to be 625 kg and 450 kg, respectively. Adding 15–20% to the average weight of modern bison (≈ 550 kg, combined for males and females), yields 633–660 kg. Considering these data, I will use a weight of 650 kg for *Bison priscus* in this model."
- Altrichter and Mittermeier (2011): 360–544 kg (♀) and 460–988 kg (♂) for plains bison.

Conclusion: Following Matheus (2003), we scale from modern bison with an increase 20%. Considering the cited data for modern bison that yields about 800 kg for male steppe bison and 550 kg for females.

Horse

- Guthrie (1968, Tab. 1): 290 kg for Pleistocene *Equus caballus* in Interior Alaska. As Matheus (2003, p. 93) points out, this was before two distinct size classes were recognized in eastern Beringia.
- Bliss and Richards (1982): 150 kg for a Pleistocene horse.
- Stuart (1991, p. 482) equate the Holocene *Equus ferus* with Przewalski's horse/tarpan in Northern Eurasia and list it with 360 kg body mass.
- Alroy (2001): 6 Pleistocene *Equus* species, ranging from 306 to 574 kg.
- Smith et al. (2003): 11 Pleistocene *Equus* species, ranging from 250 kg to 574 kg.
- Matheus (2003, p. 93): "Modern domestic and feral horses have a considerable size range, often averaging 350–500 kg, but some may approach 1000 kg. Their large size in general is a product of domestication. Primitive wild caballines such as the tarpan and Przewalski's horse are smaller and stockier and weigh 200–300 kg; Ponies, such as the Shetland are about 150–175 kg (Nowak 1991). Since the small caballine of Beringia was, on average, a little larger than a Shetland (Guthrie 1984a), I will assign it a weight of 175 kg."
- Altrichter and Mittermeier (2011): 200–300 kg for extant Przewalski's horse. Nowak (1991) have the same range.
- Zimov et al. (2012, p. 39) assign to Pleistocene horses a body weight of 400 kg (as recent Yakutian horse).
- Mann et al. (2013, Tab. 1) use 290 kg for Pleistocene horses in Alaska, without reference.

Conclusion: A value of 300 kg seems to be within most of the ranges from the literature.

C.2.11 Body Mass at Birth

- Owen-Smith (1988):
  - “For large herbivores, neonate mass increases as a function of maternal mass to the power 0.79 (Fig. 10.4). […] Thus megaherbivores produce somewhat smaller offspring than expected from the trend among other African” ungulates.” (p. 191)
  - Figure 10.4 (p. 191): “Neonate mass in relation to maternal mass for mainly African large herbivores.”
    - all species: BM(kg) = $0.23 \times M^{0.79}$ (SE(b) = 0.031 , R² = 0.96, N = 27, P = < 0.0001).
    - The elephant lies directly on the regression line for all species.
  - “Martin \& MacLarnon (1985) refine the analysis further by taking into account grade differences between precocial and altricial species. They found neonatal mass to be related to $M^{0.91}$ for mammals with precocial young in general; while for artiodactyls alone neonatal mass is related to $M^{0.89}$ However, the overall best fit value for the exponent relating neonate mass to maternal mass is 0.80. This agrees closely with the value of 0.79 that I obtained for all large herbivores in Fig. 10.4.” (p. 192)
  - Table 10.2 (p. 193): African elephant: maternal weight is 2800 kg, and neonate mass is 120 kg.
    - That matches almost exactly the formula of Fig. 10.4: $0.23 \times 2800^{0.79} = 121.6$.
- Nowak (1991):
  - birth weight of domestic horses: ca. 45 kg.
  - birth weight of *Bison bison*: 15–30 kg; adult female: 450 kg
- Huntington et al. (2019), citing Gogan et al. (2005): “Gogan et al. (2005) collected fetal weights and crown-to-rump length from 300 bison fetuses from Yellowstone National Park over several years. … They estimated birth average weights of 22.5 kg for females and 27 kg for males.”

Conclusion: The formula of Owen-Smith (1988) with an allometric exponent of 0.79 has been parameterized for a range of herbivores and has a good fit. We will use it to derive the neonate body mass for all HFTs from the corresponding female adult body mass. For the sensitivity analysis, the relationship between adult and neonate body mass is constant then.

- Pleistocene horse from domestic horse (adult: 400 kg, newborn: 45 kg, Nowak 1991): $45\,kg \times 400^{-0.79} \times 300\,kg^{0.79} = 36\,kg$
- Steppe bison: $22\,kg \times 450^{-0.79} \times 550^{0.79} = 26\,kg$
- Woolly mammoth with the unchanged formula from Owen-Smith (1988): $0.23 \times 2200^{0.79} = 100\,kg$

C.2.12 Breeding Season

- Blix et al. (1984, p. 443): “The muskoxen, a native of Greenland and the Canadian North West Territories, give birth in late April–May when ambient temperature frequently drops to –35°C (Tener 1965).”
- Carbyn et al. (1993, p. 122): “In fact, conception, and hence calving, [in wood bison] can occur at any time; newborn calves have been seen during every month of the year in Wood Buffalo National Park. The regular calving season starts as early as April, but calving probably peaks during late May and early June. Some cows are still visibly pregnant in mid June (L. Carbyn, field observation).”
- Boyd and Houpt (1994, p. 175): “Although births [of Przewalski’s horses] have been observed in all months of the year (Mohr 1971), more than 75% of all foals born in 1988 were born between April and July in the northern hemisphere (Volf 1989).”

- Turner Jr. and Morrison (2001): “Foaling [of feral horses in California/Nevada] began in mid-April and >80% was completed by mid-July.”
- Guthrie (2001): “Assuming a rough 22 month gestation time, as in most living proboscidians, that would have dictated a rut time of sometime near late July to early August — well past the northern summer’s nutrient-caloric peak. Thus, bulls and cows (especially those without calves) would have had time to recover from winter debilitation. This late summer rut would have allowed both sexes to lay down significant fat reserves. For gravid females these future reserves would have been critical because they had to nurse young during the following winter (unlike any other northern ungulate today)”
- Reimers (2002): Reindeer herdes in Norway calved in May.
- Joshi et al. (2009): “cow elephants have an oestrus cycle of 20–27 days with a mean of 22 days”
- Hogg et al. (2017): bighorn sheep and pronghorn
    - “despite nearly identical climate and similar vegetative habitat, plasticity was expressed in fundamentally different ways in the study species. Variation in bighorn birth date was primarily due to plasticity in breeding date, whereas variation in pronghorn birth date was primarily due to variation in gestation duration.” (abstract)
    - “Bighorn mothers appeared to use stored energy to subsidize the cost of birth prior to the local environmental optimum in an energy- mediated competition with other females to minimize birth order rank. Pronghorn mothers, committed to high levels of energy allocation to offspring and subject therefore to frequent energy deficiency, timed birth conservatively to more closely match peak reproductive expenditure with peak energy income at the local environmental optimum.” (abstract)
    - “Synchrony in bighorn birth was relatively moderate (Appendix S1: Fig. S3). Eighty-one percent of all births fell within 10 d of the annual median. […] Pronghorn birth was more synchronous; 91% of all births fell within 10 d of the annual median (Appendix S1: Fig. S4).” (p. 9)
    - Is there any way to tell how elephants and mammoths time their birth?
    - “Although variation in vertebrate phenology relative to the mean or to an assumed optimum date is frequently measured (see English et al. 2012 for a recent review of ungulates) and sometimes modeled (Lenarz and Conley 1982, Price et al. 1988, Rowe et al. 1994), and although the fitness consequences of variation in birth date have been rigorously examined in a few ungulate species (Wilson et al. 2005, Plard et al. 2014, 2015), surprisingly little is known about the ecological conditions associated with fitness optima in ungulates. Environmental models of [optimal birth date] are typically verbal and take the form ‘birth should be timed to match peak reproductive expenditure with maximum food quality and abundance’ (Bunnell 1982, Thompson and Turner 1982, Bronson 1989, Ticer et al. 2000). We show that this is not necessarily the case and that species with similar opportunities for energy income and similar post-birth peaks in reproductive expenditure may differ markedly in [optimal birth date] and environmental conditions at birth.” (p. 2)
    - “What combination defines the optimal match of birth date to plant phenology? In lieu of direct measurements of maternal energy income, we argue that an index of NPP is a suitable surrogate. Such indices estimate the abundance of new plant tissue produced per unit time and as such integrate quality and abundance in a reasonable way.” (p. 18)
        - Now this is a good confirmation of the approach by Pachzelt et al. (2013). We are also thinking about implementing this instead of the current prescribed static breeding period. But that will be explored if the breeding period is really an influential parameter.
    - “The advantage of early birth for NBR [National Bison Range] mothers was related to

  predation on neonates. [...] ewes were engaged in an energy-based competition to escape (precede) the functional response of a predator guild keyed to the appearance of bighorn lambs specifically and/or ungulate neonates generally. [...] Early lambs in populations subject to severe winters can (alternatively or additionally) benefit from an extended first growth season and improved first winter survival (Festa-Bianchet 1988a, Feder et al. 2008).”
  - “plastic responses for the components of birth date were generally on the order of 10 d or less in both species”

- Bonnet et al. (2019)
  - “In a wild population of red deer, average parturition date has advanced by nearly 2 weeks in 4 decades.”
  - “adaptive evolution likely played a role in the shift towards earlier parturition dates.”
  - “In a population of red deer (*Cervus elaphus*, Linnaeus 1758) on the Isle of Rum, Northwest Scotland, parturition date has advanced at a rate of 4.2 days per decade since 1980, a change that has been linked to temperatures and other weather conditions in the year preceding parturition, especially around the time of conception”
  - “our different analyses all point towards a role of selection in advancing parturition date.”

Conclusion: We expect that the influence of breeding date will be small with a constant field metabolic rate. This would change if cost of pregnancy and lactation were explicitly represented.

The start of the breeding period is really dependent on whether the species is a capital or an income breeder; for the Pleistocene species we can only conjecture. Spring onset might be very different in the grid cells that we are planning to use for the sensitivity analysis. For these reasons we select a wide and non-species-specific range for the breeding season somewhere around spring: from March 15th to May 15th. In Julian days: 75 to 136.

The length of the breeding period is species-specific (Hogg et al. 2017). From a simulator’s perspective one might ask if it matters at all or whether having all births occur on one date would make a difference. It would be computationally easier. So we will vary the parameter between 1 and (an arbitrary) 30 days.

C.2.13 Catabolism Efficiency

- Corbett et al. (1990, p. 26): “Animals will intermittently experience periods of feed shortage, especially in a pastoral system of production, when they have to use energy from catabolism of body fat and protein for maintenance or survival. In section 1.4.9 it is recommended that the energy content of 1 kg liveweight loss by non-lactating animals of any particular liveweight should be taken to be the same as the energy content of 1 kg liveweight gain made at the same liveweight by animals of the same breed and sex. The energy from liveweight loss will not be used with 100% efficiency, but there is little information on its use for maintenance. Marston (1948) assessed the energy costs of 20% of total energy provided, that is an efficiency of 0.8, and a similar value, 0.79, is implied in the report by Flatt et al. (1965); k_m (body energy) = 0.80 is adopted.”
- Illius and O’Connor (2000) assume 100% efficiency in converting from body fat gross energy to net energy.
- Armstrong and Robertson (2000): “When a sheep is not eating, and E_i is equal to 0, k_m in eq. 3a is replaced by k_f, the net efficiency of catabolising body fat for maintenance, which is set to 0.8 (SCA 1990).” The citation “SCA (1990)” is equal to Corbett et al. (1990)
  - k_f usually denotes the efficiency of converting metabolizable energy from forage to

body fat. They seem to use it for converting body fat energy to net energy. The formulas are just very hard to understand…

- McCue (2010): Not read yet, but perhaps useful.

Conclusion: The parameter seems to be insufficiently studied. The 80% from Corbett et al. (1990) apply to both fat and protein mobilization, and protein is certainly less efficiently catabolized than fat. A 100% efficiency will not exist. We think 70 to 90% is a reasonable estimate for all HFTs.

C.2.14 Efficiency of Hindgut Digestion

- Illius and Gordon (1992): "In one of the few studies to compare ruminants and hindgut fermenters of similar body weights, Johnson et al. (1982) observed that the ratio of horse to cattle DM intake averaged 1.73 (cf. 1.84 and 2.03 by Foose (1982) and the model, respectively); the ratio of digestibility was 0.89 (cf. 0.84 and 0.93 by Foose (1982) and the model);"
  - Illius and O'Connor (2000): 0.93
  - Foose (1982): 0.84
  - Johnson et al. (1982): 0.89

Conclusion: For horse and mammoth, we will just take the minimum and maximum of the values: 0.84 to 0.89.

C.2.15 Empty Body Fraction

- Gill (1968): Gut capacity in *Bison bison*. "The ratio of the weight of the total alimentary tract with the digesta to the body weight (Table 5) amounts to 0.12:1, both in the adult »Pluvius II« and in one year old »Pud«."
- Robbins et al. (1974): White-tailed deer. "The ingesta-free body weight averaged 90.31 ± 2.19% (range = 86.05 to 95.15%) of the live weight (figure 1). The estimated dry weight of the hair on the entire carcass increased curvilinearly with increasing body weight (figure 2)."
- Parra (1978, p. 207f.): "Parra (1973) has reviewed the values of [gastro-intestinal tract] content in herbivores and folivores (Table 1). Most of the original determinants of gut capacity were obtained by filling the gut with water to a certain pressure. Warner and Flatt (1965) have discussed the errors involved with this technique. There are considerable differences within species and within herbivore taxa, but the differences within species and within herbivore taxa, but the differences do not indicate any specific tendency in gut capacity for animals of comparable size with foregut versus hindgut fermentation strategies. […] There were no major differences in gut capacity (Figure 1) or fermentation contents (Figure 2) between herbivores with foregut fermentation and with hindgut fermentation. This conclusion should not be extrapolated beyond the values studied and should be approached with caution, since they represent *wet* gut contents from animals of different stages of maturity and physiological conditions. For both ruminant and nonruminant herbivores, as size increases, the relative capacity of the gut, as percent [body weight], will also increase (Table 2)."
  - Figure 1 (p. 208): "Log-log plot of values shown in Table 1 for total capacity of the gut (kg) and body weight (Kg) exponential equations relating total capacity of the gut (Y) and body weight (W)."
    - All herbivores: $Y = 0.0936W^{1.0768}$
    - Ruminant: $Y = 0.0896W^{1.0475}$
    - Non-ruminant: $Y = 0.1020W^{1.0799}$

  - Table 1 (p. 207): “Wet contents of gastro intestinal tract (G.I.T.). The values shown correspond to gut fill of animals fed roughage as the main component of their diet sacrificed within 6 hours after the last feeding … Source: Parra. R., 1973”
    - 36 values from foregut fermenters, 12 values from hindgut fermenters.
    - Many values are from Ledger (1968)
    - The cattle data are for body weight between 273 and 546 kg. Surprisingly, the 273 kg datum has the highest proportion of digesta. The cattle digesta fractions range from 13.1 to 23.9%. The mean is 17.82. The lowest value is 0.73 of the mean, and the highest value is 1.34 of the mean.
    - Only two values for sheep: 12.1% and 19.1%. That is a mean of 15.6. The lower value is 0.77 of the mean, and the higher value is 1.22 of the mean. That is comparable to the cattle data.

- Reimers et al. (1982):
  - Table 1: The fraction of ingesta-free body weight of total body weight (no antlers, blood, and fetus) in reindeer is between 71 and 83%. The fawns are in the middle. So we assume there are no tremendeous age-related differences in ingesta fraction to consider.
  - “Blood and antleres made up on the average 5.4 ± 2.3% of the live body weight.”
  - Reimers et al. (1982) observe in starved (i.e., ±fat-free) reindeer carcasses that the structural body mass (no fat, no ingesta, no blood, no antlers) is around 80% of live weight (Tab. 2). On average the gut contents were 21.7 ± 4.6% of total body weight, which is higher than in roe deer (12.7%) and white-tailed deer (9.7%) (p. 1818).

- Clauss et al. (2005): Autopsy of an African elephant (♀, 3140 kg).
  - “The total [gastro-intestinal tract] contents amounted to 542 kg or 17.3% of BM.”
  - citing Parra (1978): gut contents (kg) in herbivores in general equals $0.0936 \times BM^{1.0768}$
    - Applying the formula yields 17.3%. Wow, that matches exactly the measurement to one decimal point!
  - “These calculations indicate that the equation for hindgut fermenters, based mostly on small species, might overestimate the total [gastro-intestinal tract] contents if applied to larger species and that the general herbivore equation is probably more adequate.” (p. 294)
  - “In conclusion, the necropsy of this captive individual suggests that the capacity of the [gastro-intestinal tract] of elephants does not deviate from the interspecific average.”

Conclusion: For mammoth, we use the ingesta fraction of 17.3% from Clauss et al. (2005). We consider this an average value and use the spread from the cattle and sheep data in Parra (1978) to define a range. We say that we go 25% below and 25% above the mean. For the mammoth, this gives a range of 13.0 to 18.6% ingesta weight, which translates to 81 to 87% empty body fraction. The values for horse and bison will probably also lie in this range.

C.2.16 Gestation Length

Mammoth

- Hanks (1972): “22-month gestation period”
- Whyte et al. (1998) “Gestation is 22 months”
- Guthrie (2001): “Assuming a rough 22 month gestation time, as in most living proboscidians”
- Joshi et al. (2009): “The gestation period in Asian elephants varies from 18 to 23 months”

Conclusion: A 22-month gestation period for *Loxodonta africana* seems to be widely accepted. For the sake of a parameter range, we choose 18 to 23 months (as in the Asian elephant).

Steppe Bison

- Asdell (1964): Gestation period of *Bison bison* is 9 months.
- Nowak (1991): Gestation period averages 285 days in *B. bison*. That is ca. 9½ months.
- Carbyn et al. (1993, p. 122): “Female bison are pelyestrous, with an estrous cycle of about three weeks (Fuller 1966); their gestation period is about 285 days (Halloran 1968).”

Conclusion: 9 months

Horse

- Asdell (1964): Duration of gestation in domestic horses extremely variable, breed averages range from 329–345 days (standard deviation usually about 9.5 days).
- Turner Jr. and Kirkpatrick (1986, p. 251): “The length of gestation [of feral horses] is approximately 340 days [=11⅓ months] and, unlike other characteristics of reproduction is uniform across herds and individuals.”
- Boyd and Houpt (1994, p. 174): “A typical gestation [of Przewalski’s horses] lasts approximately eleven months with a reported range of 46 to 50 weeks (Veselovsky and Volf 1965, Mohr 1971, Groves 1974, Summers et al. 1987, Monfort et al. 1991). This variability in pregnancy length is not unusual in the domestic mare and it is not uncommon to observe variations in gestation length between 327 to greater than 357 days (Roberts 1986).”

Conclusion: 11 months

C.2.17 Lifespan

Mammoth

- Owen-Smith (1988, p. 154): “Life tables for African elephants show a steep rise in annual mortality after an estimated age of 50 years, associated with a decrease in the grinding area of the teeth. However, no captive African elephant has survived longer than about 44 years. For Asian elephants potential longevity in captivity is typically 50–60 years, with a maximum age of 67 years recorded. Hence it is estimated that African elephants in the wild have a potential lifespan of 55–60 years (Laws 1966).”
- Whyte et al. (1998): “Like humans, female elephants have a life span of ~60 years”
- Moss (2001): “Maximum lifespan for females was over 65 years; for males it was close to 60.”
- Zimov et al. (2012): 80 years
- Larramendi (2016): 60 years, based on 6 tons body mass and allometric formula from Blueweiss et al. (1978)

Conclusion: Lifespan range: 60–80 years

Steppe Bison

- Nowak (1991): Wild individuals of plains bison are known to have lived about 20 years; max. potential longevity 40 years in captivity.
- Green and Rothstein (1991) summarizing Green (1990) (plains bison): “Age-specific fecundity … declined … to 0 by age 20”

Conclusion: We use a lifespan of 20 years, similar to plains bison.

Horse

- Turner Jr. and Kirkpatrick (1986, p. 251): “Reports of feral horse lifespan in the early 1970’s frequently gave 15–18 years as a maximum. However, as the number of horses studied has increased dramatically in the past 10 years and age assessment technique has improved,

the lifespan has been found to be 18–25 years, with only a small number of horses, usually lone males, reaching 25.”
- Nowak (1991), domestic horse: Females can potentially produce one foal every year from age 2 to 22 years. Few horses live past their twenties, though maximum known longevity is about 50 years.
- Boyd and Houpt (1994, p. 174): “[Przewalski’s mares] generally remain fertile until about twenty years of age”
- Collins and Kasbohm (2017)
    - “Between 2008 and 2014, we captured 1,873 individual feral horses.” (p. 292)
    - “An equine veterinarian estimated the age of each captured horse using teeth characteristics. … Estimated ages of captured horses ranged … to 30 years old for males and 26 years old for females.” (p. 290)

Conclusion: We use a lifespan of 22 years.

C.2.18 Maximum Anabolism Rate

- Truscott et al. (1983) probably has the required information for fattening rates, but we don’t have access to the article.
- White et al. (1989), three sexually mature female muskoxen (*Ovibos moschatus*): “Almost all annual gains in body weight and body fat occurred during the 6- to 8-week rutting period from mid-August to mid-October.”
- Carstens et al. (1991): growing steers and their different body components. We are interested in the maximum anabolism of fat for adults and juveniles (i.e., fattening) not so much in body growth. However, the cited studies in Table 7 and the text below (p. 3258) might contain useful data.

Conclusion: At this early stage of model development, it does not seem fruitful to limit the rate of fat gain. In the short growing season, the grazers will have to gain fat as fast as possible and will also be adapted to this. The data we found don’t give a clear direction either.

C.2.19 Maximum Daily Intake

- Hobbs (1989): mule deer. “maximum daily intake is set at 1.7% of the inital body mass (BW_{in}, in kg) of adult does (Alldredge et al. 1974, Baker and Hobbs 1987) and at 2.9% of the body mass of fawns (Alldredge et al. 1974).” That is $0.1115\,kg \times 195.7^{-0.25}\,kg^{-0.75-0.25} = 2.98\%$
- Romney and Gill (2000) note that daily dry matter intake also depends on the digestibility of the forage: “However, relationships between fibre measured using neutral detergent solution (NDF) and dry matter (DM) intake (DMI) are not always consistent.”

Bison

- Typical values for cows range between 2 and 4%.
- Minson (1990): Daily intake for beef cattle (Minson and McDonald 1987):

$$I = (1.185 + 0.00454\,W - 0.0000026\,W^2 + 0.315\,G)^2,$$

  where I = intake (kg DM/day), W = liveweight (kg), and G = growth (kg/day)
- Galbraith et al. (1998) have measured 111.5 g kg$^{-0.75}$ ad libitum dry-matter intake for *Bison bison* (n=5) of a mean body weight of 195.7 kg.
- Clauss, Schwarm, et al. (2007, Appendix Tab. 2), citing Schaefer et al. (1978): *Bison bison*, weighing 279 kg consumed 78.8 g DM/kg$^{0.75}$ per day, which is 1.9% of live weight.
- Kuzyk (2008, p. 58): dry-matter intake per metabolic weight for *Bison bison* (n=5 408 kg): 114.8±22.5 g kg$^{-0.75}$. As fraction of body mass: 2.5±0.5 (values are means ±1 SE)

- Huntington et al. (2019): From a wide range of studies on bison they cite average daily intake in the range of 1.8% to 3.6%, but nothing higher.

Conclusion: We will use 3.6% the highest value we found for bison (Huntington et al. 2019), which represents an upper limit.

Horse

- Wolter et al. (1976): 6 male ponies (188–206 kg) had a voluntary intake of max. 4.87 kg DM/day, which is ca. 2.5% of body mass.
- Pagan et al. (1998): 4 thoroughbred geldings (age: 5–8 years; body mass: 508 kg). Voluntary dry-matter intake, fed with alafalfa and grass: 9.12 kg DM/day, which is ca. 1.8%.
- Pearson et al. (2001): Four adult Welsch-cross ponies (mean weight 250 kg) had an *ad libitum* dry-matter intake of 3.86% of live weight when fed with alfalfa.

Conclusion: Since we are looking at the *maximum* daily dry-matter feed intake, we round up the highest figure (Pearson et al. 2001) to 4% of body mass.

Mammoth

- Clauss, Frey, et al. (2003), feeding trials with captive Asian elephants:
  - "The growing bull (animal no. 1) had a significantly higher intake than the other elephants (Table 4; $p < 0.001$)." (p. 164)
  - "The results of this study are generally in accord with corresponding literature data (Table 7). High intakes in that data set were achieved by growing animals (Monfort and Monfort, 1979; Spala et al., 1990), which compares well with the intake observed in elephant no. 1 from this study. The highest intake record, however, stems from Bhashkaran Nair and Ananthasubramaniam (1979) who fed their elephants on palm leaves only; the exceptionally high digestibility coefficients of that study raised doubts about its compatibility with the other studies." (p. 166)
  - "The only other data set that compared both elephant species, albeit with a much lower number of animals (Foose, 1982), found a similar intake of grass hay between the species" (p. 169)
- Christiansen (2004, p. 534): "Assessed feeding rates of wild elephants often leads to very high estimates in comparison with both their predicted energy needs and their food consumption in captivity. Feeding rates of wild bull African elephants are often assessed to be as high as 300 kg, and around 150 kg for cows (Laws \& Parker, 1968; Laws, 1970a, b; Guy, 1975 (citing 170 kg day^{-1} for bulls); Laws et al., 1975). In Asian elephant bulls, feeding rates of 150 kg day^{-1} have been assessed (Vancuylenberg, 1977). Observations on captive elephants support the notion of exaggerated feeding rates being ascribed to wild elephants, probably because the daily feeding cycle of 12–14 h day^{-1} (Guy, 1975, see also table 2, p. 4) or even 17–19 h day^{-1} (Vancuylenberg, 1977) involves long periods of low-intensity feeding (see also Guy, 1976). If indeed the exaggerated values were true, one would have to wonder how, if at all, fossil proboscideans could sustain body sizes sometimes far exceeding those of extant elephant, unless they fed on substantially more nutritious items. For this reason alone, the above values appear suspect."
- Clauss, Schwarm, et al. (2007): (*cf.* Tab. S18)
  - "The absolute dry matter intake (aDMI, per day) in mammals was shown to scale between $BM^{0.84}$ and $BM^{0.72}$ in 12 herbivorous and 12 carnivorous species, respectively (Bourlière, 1975), and organic matter intake in 26 ungulate species from Foose (1982) scaled to $BM^{0.77}$." Bourlière (1975) does not say anything about the intake scaling. The citation must be a mistake. Foose (1982) is not available online.

  - “As predicted, this data collection supports the general assumption that aDMI scales to $\mathrm{BM}^{0.75}$ in herbivorous mammals.”
  - “Figure 3: Correlation of body mass (BM) and absolute dry matter intake (DMI, measured as kg per day). Data from Appendix Table 2. The overall allometric regression equation is $y = 0.047x^{0.76}$.”

- Boult (2018, p. 115): “Maximum ingestion rate scaling coefficient ($\mathrm{maxIR}_{\mathrm{scaling}}$): Maximum ingestion rates estimated by Lindsay (1994) were converted to kg day^{-1} assuming elephants feed for 16 hours a day (Lindsay, 2011). Given the average asymptotic mass of 4690 and 2740 kg for males and females, respectively (Lee and Moss, 1995), the allometric equation describing maximum ingestion rate (Equation B.1a) can be rearranged, giving an estimate of the scaling coefficient at 0.27 for males and 0.24 for females. A single mean value of 0.255 is used in the model.”

Table S18. Selected data on maximum daily dry-matter intake (DMI as percent of body mass) of elephants and corresponding values allometrically scaled for a hypothetical 6 t mammoth

Source	Species	Body Mass	Sex	%DMI	for 6 t with $M^{3/4}$	for 6 t with $M^{2/3}$
Clauss, Löhlein, et al. (2003)	Asian	888 kg	♂	(2.13–2.57)[*]	1.59%	1.36%
Clauss, Löhlein, et al. (2003)	Asian	1067 kg	♀	1.42–1.90	1.23%	1.07%
Clauss, Löhlein, et al. (2003)	Asian	2200 kg	♀	(1.13–1.37)[†]	1.07%	0.98%
Clauss, Löhlein, et al. (2003)	Asian	3217 kg	♀	1.25–1.51	1.29%	1.23%
Clauss, Löhlein, et al. (2003)	Asian	3177 kg	♀	1.17–1.42	1.21%	1.15%
Clauss, Löhlein, et al. (2003)	Asian	4013 kg	♀	1.28–1.49	1.35%	1.30%
Monford & Monford (1979)	African	504 kg	?	1.81	0.97%	0.79%
Meissner et al. (1990)	African	4500 kg	?	1.38	1.28%	1.25%
Foose (1982)	African	2873 kg	?	1.19–1.25	1.04%	0.98%
Hackenberger (1987)	African	2660 kg	?	1.7	1.39%	1.30%
Roehrs et al. (1989)	African	1320 kg	?	1.47	1.01%	0.89%
Hackenb. & Atkinson (1982)	African	2367 kg	?	1.58	1.25%	1.16%
Spala et al. (1990)	African	622 kg	?	1.73	0.98%	0.81%
Kozaki et al. (1991)	African	4900 kg	?	1.27	1.21%	1.19%
Bhashkaran Nair & Anath. (1979)	Asian	1555 kg	?	(4.43)[‡]	3.16%	2.82%
Benedict (1936)	Asian	3550 kg	?	1.29	1.13%	1.08%
Hackenb. & Atkinson (1982)	Asian	2813 kg	?	1.03	0.85%	0.80%
Hackenberger (1987)	Asian	2502 kg	?	1.30	1.04%	0.97%
Foose (1982)	Asian	3402 kg	?	1.12	0.97%	0.93%

Source: Clauss, Frey, et al. (2003, Tab. 1, 4, and 7)

Note: Calculation for mammoth values: An allometric relationship for (absolute) daily dry-matter intake: $DMI_{\text{abs.}} = a \times BM^{b}$. The exponent b equals the intraspecific metabolic exponent and varies between ⅔ and ¾. The *relative* daily dry-matter intake is then: $DMI_{\text{rel.}} = a \times BM^{-1/3}$ or $DMI_{\text{rel.}} = a \times BM^{-1/4}$. The coefficient a is can be calculated for each datum in the table as $a = DMI_{\text{rel.}} \times BM^{(1-b)}$.

[*] This young bull has an extremely high intake because he is in a growth spurt; the datum is excluded.

[†] This animals has data for only 2 out of 5 feeding trials is excluded.

[‡] This animal has an extremely high intake because they only fed palm leaves; the datum is excluded.

Conclusion: The extrapolated fractional DMI values for an example 6 t mammoth in the table (Tab. S18) show roughly a range between 0.8 and 1.5% (including both ⅔ and ¾ power scaling). Extrapolating to 2000 kg (the lower range of male adult mammoth body mass) yields a range between 1.1 and 1.9%. Because the mammoth body mass range is so wide, it is not ideal to use only *one* parameter range of fractional DMI. However, this is the first round of sensitivity analysis, so it is okay to cover a wider range. Therefore we conclude to apply a maximum daily intake fraction range of 1.0–2.0% to *all* possible adult body masses for mammoth.

C.2.20 Metabolic Rate

BMR = Basal metabolic rate; FMR = Field metabolic rate

- Benedict (1938, p. 102ff): "A post-absorptive elephant is inconceivable. [...] Many elephants have a custom of swaying the entire body from side to side, the so-called weavers, and it was deemed useless to make metabolism measurements on that type of animal, so the whole survey was delayed many years until a non-weaving elephant was available. It is frankly admitted that the corrections applied to the measurements obtained on the elephant were imperfectly establised, that in reducing the measured metabolism about 25 per cent (to correct for the increase due to standing and to ingestion of food) we probably have erred on the side of too small a reduction, and that the true basal metabolism of the elephant is somewhat lower than the value reported in the earlier publication. (Benedict 1936) [...] The basal total heat production of this 3672-kg. elephant is therefore stated, with reserve, to be 49,000 calories per 24 hours, and the potential errors in this value are clearly recognized."
  - That is BMR = 205 MJ/day.
- Kleiber (1961) as cited by Lindstedt and Boyce (1985, p. 874):
  - $BMR = 3.67 \times M^{0.75}$ in W
  - $BMR = 0.317 \times M^{0.75}$ in MJ/day (R²=0.97, N=54)
  - That would be 159 MJ/day for a 4 t mammoth.
- Farlow (1976): correlation of intake and body mass, but only energy intake and not mass intake.
- Christopherson et al. (1979): BMR of two bison calves (male/female, ca. 6–17 months) measured at controlled temperatures (10, 0, −30°C) in gas exchange chambers. Measurements range from 499±34 to 934±185 kJ $\mathrm{kg}^{-0.75}$ day^{-1} (mean±SE). The mean of all bison measurements is 697.
  - Extrapolating that to an adult male steppe bison (800 kg): $BMR = 800^{0.75} \times 697\ \mathrm{kJ/day} = 105\ \mathrm{MJ/day}$
  - For adult female steppe bison (550 kg): $BMR = 550^{0.75} \times 697\ \mathrm{kJ/day} = 79\ \mathrm{MJ/day}$
- Taylor et al. (1981), used by Illius and O'Connor (2000).
  - Cited by Illius and Gordon (1999): $BMR = 0.3 \times M \times M_{adult}^{-0.27}$ in MJ/day
    - That is in W: $BMR = 0.3 \times 10^6/(60 \times 60 \times 24) \times M \times M_{adult}^{-0.27} = 3.47 \times M \times M_{ad}^{-0.27}$
    - For an adult: $BMR = 3.47 \times M^{0.73}$ in W.
    - For a 4 t mammoth that would be 127 MJ/day – less than the MBR by Kleiber (1961).
  - Note that Illius and O'Connor (2000) use 0.4 instead of 0.3: $FMR = 0.4 \times M \times M_{ad}^{-0.27}$, but they don't give a reason. That would already be 170 MJ/day for a 4 t mammoth.
- McBride et al. (1985): BMR of 6 winter-acclimatized mature Quarter Horse geldings (467–564 kg, averaging 513 kg) measured with gas face masks
  - "a minimal metabolic rate of 431–447 kJ·100 $\mathrm{kg}^{-1}\cdot\mathrm{h}^{-1}$ was measured at temperatures ranging from +10 to −10 °C."

  - “Previous studies have reported resting metabolic rates varying from 469 to 533 kJ$\cdot$100 kg$^{-1}\cdot$h^{-1} in two pony mares (Winchester 1943), from 466 to 480 kJ$\cdot$100 kg$^{-1}\cdot$h^{-1} in two geldings (Wooden et al. 1970). from 544 to 628 kJ$\cdot$100 kg$^{-1}\cdot$h^{-1} in 44 mixed yearlings and 2-yr-olds (Magidov et al. 1962), from 494 to 632 kJ$\cdot$100 kg$^{-1}\cdot$h^{-1} in five Orlov trotters × heavy draught crossbreds (Nadal’jak 1962a) and from 502 to 582 kJ$\cdot$100 kg$^{-1}\cdot$h^{-1} in 2O heavy draught stal- lions (Nadal’jak 1962b) . National Research Council estimates based on a ME equivalency of 9O% DE (Hoffman et al. 1967), predict ME intake required for maintenance of a 500-kg mature horse of 515 kJ$\cdot$100 kg$^{-1}\cdot$h^{-1}(NAS-NRC 1978)”
  - We wonder why the authors are not using metabolic weight.

- Elgar and Harvey (1987) cite Eisenberg (1981) for basal metabolic rate of *Elephas maximus* with 2730 kg and 0.15 O_2/g/h. We suppose the value comes originally from Benedict (1938). With the coefficient of 20.1 $^{J}\!/_{ml\,O_2}$ from Langman et al. (1995) this is a BMR of 198 $^{MJ}\!/_{day}$.
- Peterson et al. (1990):
  - “Sustained metabolic rates (SusMR) are time-averaged metabolic rates that are measured in free-ranging animals maintaining constant body mass over periods long enough that metabolism is fueled by food intake rather than by transient depletion of energy reserves.”
  - “For all species, the ratio of SusMR to RMR, which we term sustained metabolic scope, is less than 7; most values fall between 1.5 and 5.”
  - This is a good benchmark for an energy model. If the energy model yields total expenditures too far above BMR, it must be wrong.

- Jiang and Hudson (1992): Energy expenditure of Wapiti.
  - “Metabolizable energy requirements for maintenance of live weight were 572 kJ/$W^{0.75}$ for penned wapiti in winter and 936 kJ/$W^{0.75}$ for wapiti on summer pasture.”
  - “Ecological maintenance (energy for energy equilibrium of free existence) is therefore about 1.6 times physiological maintenance, in agreement with energy expenditures of free-ranging wapiti estimated by heart rate (Pauls et al. 1981).”

- Cuyler and Øritsland (1993): Svalbard reindeer; FMR about 1.5 times higher than Kleiber’s BMR, during winter.
- Nagy (1994):
  - “it seems likely that other sources of variation, such as season, sex, age, ambient temperature, daily behaviour pattern and food availability may have large effects on FMR that are not accounted for in this analysis.”
  - “The data set used in this analysis consisted of FMR values, all measured with doubly labelled water, for 61 species of mammals, including 44 species of eutherians and 17 species of rnetatherians. The data for 23 species of eutherians and 13 species of metatherians available in 1987 are summarised by Nagy (1987). That analysis included regression calculations that incorporate several data points per species for some species, where cohorts within those species differed significantly among themselves. For this paper, only a single mean value for each species was used in regression calculations.” (p. 44)
    - The magnitude of within-species variation might be key to define a parameter range for our purpose.
  - “Linear least-squares regression analyses were used to evaluate allometric relationships.” (p. 44)
  - “The regression equation for the eutherian data is $kJ\ day^{-1} = 4.63\ g^{0.762}$ (r = 0.986, r^2= 0.972, 95% CI of slope = 0·722–0·803, 95% CI of intercept = 3·59–5·97)” (p. 44)

        - The 95% confidence interval of the intercept is 78% to 129% of the mean (4.63). For the example 4 t mammoth that is 497 MJ/day.
    - "Knowledge of body mass and taxonomic infraclass allows prediction of FMR to within about ± 40% (coefficient of variation for '% of predicted FMR' values) for eutherians," (p. 49)
        - The "% of predicted FMR" values are in Table 2 and Figure 2. The coefficient of variation is the standard deviation divided by the sample mean. Approximately 96% of the samples occur within ±2 standard deviations of the mean. So, we could define a ±80% range around the value predicted by the allometric regression. That is a lot of uncertainty!
    - "Such variation is exemplified by [double-labeled water] studies done throughout a year (summarised by Nagy 1993), which reveal an annual variation in FMR of springbok antelope from 92% of predicted FMR in the dry season, to 194% in the wet season, to as high as 269% of predicted FMR by males in rut (K. A. Nagy and M. H. Knight, unpublished data)." (p. 50)

- Langman et al. (1995):
    - "We measured the oxygen consumption of three young African elephants (mean mass 1542 kg). [...] The rate of energy expenditure was calculated from the rate of oxygen consumption using an energetic equivalent of $20.1\ J\ ml^{-1}\ O_2$."
        - They do not give a source for the conversion coefficient. Nagy et al. (1999, p. 259) use 21.7 kJ per liter of CO_2.
    - "The mean rate of energy expenditure of standing elephants was 0.915±0.068 W/kg (S.E.M.). This value is similar to that reported by Benedict (1938) more than 50 years ago."
    - For the mean body mass, the resting metabolic rate is 1411 W = 122 MJ/day. That's about right.

- Galbraith et al. (1998) derive 659 to 694 kJ $\mathrm{kg}^{-0.75}$ d^{-1} BMR for bison, but the values are lower in winter (608–617) than in spring (711–771).
- Lovegrove (2000): "Nearctic and Palearctic mammals had higher basal rates than their Afrotropical, Australasian, Indomalayan, and Neotropical counterparts."
- Owen-Smith (2002) just uses double the BMR to approximate FMR.
- Christiansen (2004, p. 534): "An Asian elephant of 3833 kg consumed 268 litres of oxygen h^{-1} (Eckert et al., 1988), or 6342 litres day^{-1}, providing that the basal metabolism was constant throughout the day, which is unlikely, as it should be lower during sleep. Assuming a respiratory quotient of around 0.8, as in most animals (Eckert et al., 1988; see also Zubay, 1989), this implies a BMR of 30874 kcal day^{-1}, 90% of the predicted BMR of 34100 kcal day^{-1} ($70\times\mathrm{Mass}^{0.75}$; see McNab, 1974), in accordance with the above. The actual caloric intake will depend on the composition of the food and assimilation rates, which in elephants are rather low because of the poor degree of mastication and short intestines, resulting in very nutritious dung filled with discernible food remains (Benedict, 1936; Laws et al., 1975). The digestive efficiency of the Asian elephant has been found to be around 40% (Benedict, 1936), considerably below the assimilation rates of cattle, horses and sheep (Benedict, 1936), deer (Drodz \& Osiecki, 1973), rodents and lizards (Drodz, 1975; Karasov \& Diamond, 1985) and cats (Golley et al., 1965)."
    - The Asian elephant is close to the 4 t mammoth example. The BMR of 34100 kcal/day equals 129.2 MJ/day. That gives a good baseline.
    - 268 l O_2/h = 268000 ml O_2/h = 0.069919 ml O_2/h/g. That is by a factor of 10 smaller than the oxygen consumptions given in Elgar and Harvey (1987). How can that be?

- Savage et al. (2004): *Elephas maximus*: BM = 3672 kg; BMR = 2336.5 W = 202 MJ/kg. This value is a lot greater than the one calculated by Christiansen (2004)! Datum from Heusner (1991), who in turn cites Benedict (1938).
- Anderson and Jetz (2005):
  - For mammals (n=111): $FMR = 0.68M^{0.72}$ (FMR in kJ/day and mass in g)
  - With independent contrast analysis: $FMR = 0.68M^{0.73}$
  - For an example 4 t mammoth that would be 38.5 MJ/day and 44.9, respectively. That is too low by a factor of about 10. Something must be wrong.
- Nagy (2005):
  - "All FMR values (kJ day^{-1}) are means for a single species (from one or several studies averaged), with only one value per species being used. [...] Mammal data are for a variety of seasons"
  - FMR for mammals (kJ/day) with M in gram = $4.820 \times M^{0.734}$ (N=79, r²=0.950) (p. 1662). That is 338 MJ/day. Now this is a realistic result.
  - "The residual variation in FMR that is not explained by body mass is substantial, amounting to up to a sixfold range (ratio of maximum:minimum) in mass-adjusted values of kJ day^{-1} (Nagy and Obst, 1991; Nagy, 1994). This means that, if FMR is predicted for a species on the basis of its Class and body mass alone, by using one of the linear equations reported above, the result can misrepresent the actual FMR of that species by as much as ±70% (that is, the real FMR may be as low as 30% of predicted or as high as 170% of predicted)."
  - "Thus, there is little support for the generalization that allometric slopes for FMR can be well represented by the value of 0.75 ..."
  - But Figure 2 shows that BMR and FMR exponents are really close for mammals (N=79), without a "significant" difference.
    - "BMR slopes (or SMR slopes for reptiles) are from Kleiber (1975; for mammals, eutherians), Hayssen and Lacy (1985; mammals, eutherians, marsupials)" [Fig. 2]
  - "Predictive equations, all based on body mass as the most important variable, are available for daily FMR (Nagy et al., 1999) and daily food requirements (Nagy, 2001) of terrestrial vertebrates."
  - "However, on a seasonal and annual basis, animals consume additional food, which provides the substances for growth and reproduction, and this additional food is not accounted for in the predictive equations that are currently available."
- Arnold et al. (2006): FMR of Przewalski horse
  - "Substantial changes in metabolic rate from summer to winter have been reported for several wild Artiodactyla (reviewed in Arnold et al., 2004). Here, we demonstrate for the first time a similar seasonal adaptation in a perissodactyl species. Metabolic rate of Przewalski horses living under close to natural conditions varied considerably over the year, as indicated by a twofold change in mean daily f_H. A change in f_H is the cardiovascular system's main response to varying oxygen demand and therefore represents a reliable index of energy turnover rates (Butler et al., 2004)."
  - "Earlier reports regarding a similar reduction [like in hibernators] in BMR in ungulates during winter were initially refuted on experimental grounds, but found new support with the discovery of nocturnal hypometabolism in *Cervus elaphus* during winter (Arnold et al., 2004)."
  - "reproduction in spring apparently increased daily mean f_H considerably during the most energetically demanding weeks around foaling."
  - "During a typical day in December, 56% of all available two-minute data sets represented resting behaviour, but at the beginning of June only 3% of the data sets had

  - an activity level 10%, which was typical for uninterrupted lying or standing motionless (Kuntz et al., 2006)."
  - "Thus, considerably higher [heat increment] is to be expected during summer. Therefore, the argument that higher metabolic rate of large herbivores during the summer months just reflects the intense use of abundantly available protein-rich food and the cost of building up body energy stores rests on solid grounds (Jiang and Hudson, 1993; Mautz et al., 1992; Mesteig et al., 2000; Nilssen et al., 1984b; Pekins et al., 1992; Worden and Pekins, 1995)."

- White et al. (2007, p. 321): "Our analysis of 127 exponents suggests that there is no single true allometric exponent relating metabolic rate to body mass and no universal metabolic allometry. […] For example, examination of patterns of FMR variation in mammals might reasonably make use of a ¾ exponent, because mammalian FMR scales with an exponent not significantly different from 0.75 (Nagy et al. 1999, Savage et al. 2004, Nagy 2005)."
- Clauss, Schwarm, et al. (2007): "White and Seymour (2005) convincingly demonstrate that an increase of the exponent from 0.68 towards 0.75 is an effect of the inclusion of data from large herbivores in the data set: large herbivores can hardly be assessed for metabolic rate in a post-absorptive state due to the presence of an active microbial fauna in their gut, even after a prolonged fast. […] The results of White and Seymour (2005) have enormous relevance for the discussion about the determinants of metabolic rate. However, for the purpose of our study, which is concerned with digestive physiology in herbivores, including large ones, their results emphasize that we should expect food intake – which is a function of the metabolic unit of the herbivore and its symbiotic microbes – to scale to $BM^{0.75}$ in an interspecific comparison."
- Isaac and Carbone (2010): Not helpful for our question since it only looks at resting metabolic rate and statistical analysis regarding the allometric exponent.
- Brown and Sibly (2012, Fig. 2.4): FMR is about 3 times higher than BMR. Maximal metabolism is about 10 times BMR.
- Hudson et al. (2013):
  - "Of the much smaller collection of empirical studies that have investigated body mass dependence of FMR, all but one have used species-averaged data. These studies have found that b is close to ⅔ for birds, close to **¾ for mammals** and close to 8/9 for reptiles (Nagy, Girard \& Brown 1999; Savage et al.'s 2004b; Anderson \& Jetz 2005; Nagy 2005)."
  - "Our mean-slope results do not support theories that predict b≈¾, at least not for mammals."
  - "Our results were consistent with ¾ as a central exponent value for birds but not for mammals; results were consistent with ⅔ for both birds and mammals. These findings contradict previous studies that examined species-average mammalian FMR data and found *b* close to ¾ (Nagy, Girard \& Brown 1999; Savage et al. 2004b; Nagy 2005)."

- Sibly et al. (2013, p. 153f): "Animal physiologists distinguish basal or resting metabolic rate (BMR), the rate of metabolism of an inactive, starving animal measured over a relatively short period of time, typically minutes (McNab 1997), from the rate of metabolism in the field (FMR), which is of the order of three times BMR (Peterson, Nagy \& Diamond 1990; Brown \& Sibly 2012). […] So far we have considered the interspecific scaling of metabolic rate. There has been some debate as to whether the same scaling rules apply intraspecifically. This is expected if metabolic rate is determined by mechanistic constraints as many believe, and we suggest this be assumed in a minimum model. However, there is a suggestion that juveniles of large species have higher metabolic rates than same-size adults of smaller species (Makarieva, Gorshkov \& Li 2009)."

  - In our model, the interspecific metabolic scaling is also used intraspecifically and in ontogenetic growth. So it's good to see more elaborate models making the same assumption.
  - This article is very interesting, but for our first approach – using only total FMR – it is not helpful because it deals with the different components of FMR only.

- Brinkmann et al. (2016):
  - "FMR was determined for all experimental animals (N=10) for 2 weeks in summer (July) and winter (February) using the doubly labelled water (DLW) method (Lifson and McClintock, 1966; Speakman, 1997)."
  - "The FMR in summer across all animals ($63.4\,\text{MJ}\,\text{day}^{-1}$) was about three times higher than that in winter ($19.3\,\text{MJ}\,\text{day}^{-1}$; Brinkmann et al., 2014)."
  - "Similar reductions of metabolic rate under natural conditions in winter have also been reported for several wild ungulates (red deer, Cervus elaphus: Arnold et al., 2004; Przewalski horse, Equus ferus przewalskii: Arnold et al., 2006; moose, Alces alces: Renecker and Hudson, 1985; Alpine ibex, Capra ibex: Signer et al., 2011). [...] The three times higher FMR in summer versus winter may result from increased locomotor activity and altered BMR." (p. 2562)

Conclusion: First we thought that Nagy (2005) confirms the convenient ¾ power law for FMR in mammals, and that we could just use this exponent and only vary the intercept. A solid ¾ power law would also make it possible to define expenditure and intake "per metabolic weight" (per $BM^{0.75}$), as done in many older publications. However, Hudson et al. (2013) contradict the ¾ exponent and find a ⅔ exponent for FMR in mammals.

Unfortunately, we could not find any publication where FMR of elephants was measured. The BMR from Langman et al. (1995) for African elephant and from Elgar and Harvey (1987) for Asian elephant give a baseline.

Applying the formulas for FMR from the various publications to an example 4000 kg mammoth yields results between 338 MJ/day (Nagy 2005) and 497 MJ/day (Nagy 1994). We exclude the weirdly low values from the formula in Anderson and Jetz (2005). The BMR for an Asian elephant of about the same weight as deduced by Christiansen (2004) is 129 MJ/day. There is too much of a discrepancy here. We cannot use a formula to extrapolate FMR that gives us values of 2.6 to 3.9 times the BMR. A factor of 2.6 is already pretty high.

With FMR we need to extrapolate widely, there are only very few data, and those are very divergent even within species. We conclude that there is no point in using FMR formulas directly.

The allometric formulas for BMR are much more precise than the ones for FMR. We know that FMR is about 1.5 to 3 (or even 5) times higher than BMR (Peterson et al. 1990; Cuyler and Øritsland 1993; Owen-Smith 2002; Brown and Sibly 2012). So it would be most appropriate to define a parameter range for an allometric regression of BMR and multiply that result with a variable factor between 1.5 and 3.0.

We can scale the BMR from the measured value of 205 MJ/day for *Elephas maximus* (3672 kg) Benedict (1938). We don't know which scaling exponent to use, either ¾ or ⅔, but we will start with the classic ¾ power law:

$$BMR = 202\,\text{MJ/day} = a \times 2730^{0.75} \implies a = 0.53\,\text{MJ/day}$$

The value for an "average" 4 t mammoth bull in Table S14 is $0.53\,\text{MJ/day} \times 4000^{0.75} = 267\,\text{MJ/day}$. To extrapolate to the extreme body mass in our parameter range: For a 6 t mammoth bull that will be a BMR of 361 MJ/day and a FMR between 542 and 1083 MJ/day. If we preliminary assume a birth weight of 140 kg for mammoth, then the BMR for a newborn is 22 MJ/day and the FMR 32–65 MJ/day.

Using the ⅔ power law (Hudson et al. 2013), a = 1.03 MJ/day. The 6 t mammoth would have a BMR of 340 MJ/day and a FMR between 510 and 1020 MJ/day. For an adult that is almost no difference to the ¾ power law. However, for the 140 kg newborn that is a BMR of 28 MJ/day and a FMR of 42–83 MJ/day, and that might possibly make a difference.

This approach has led us to formulate the whole expenditure model like so (*cf.* Sec. B.3.3):

- The parameter BMR for an adult (male) is defined as an explicit number. We define it for males because they are usually heavier, so there won't be any implicit extrapolation within the model. Range: With an exponent between ⅔ and ¾ scale from (fixed) largest BMR measurement, the 202 MJ/day in *Elephas maximus* (2730 kg) (Heusner 1991).
- An allometric exponent for *ontogenetic/intraspecific* scaling is defined to derive from this user-defined BMR the appropriate values for females and young animals. Range: ⅔ to ¾
- The FMR is defined as a constant factor of BMR. Range: 1.5 to 3.0

For horses, BMR values measured by McBride et al. (1985) are about 440 $\mathrm{kJ \cdot 100\,kg^{-1} \cdot h^{-1}}$ for a body weight of 500 kg, which is 53 MJ/day. Scaled with a ¾-exponent to 300 kg that makes 36 MJ/day for the Pleistocene horse.

C.2.21 Metabolizable Energy Coefficient (ME/DE)

- Blaxter (1989), Table 12.1, p. 258: "Approximate values for species consuming average diets", Efficiency of metabolizable energy below maintenance: Pig: 0.85; Horse: 0.75; Ox: 0.70; Sheep: 0.70
- Givens et al. (1989) use DE/DE = 0.81.
- Minson (1990): Table 4.2 (p. 94): ME/DE ratio ranges from 0.77 to 0.83 for temperate grasses with a mean value of 0.80.
- Parker et al. (1996): "We used the following apparent metabolizable energy coefficients (Robbins 1993, p. 306): 81.8% for forbs, grasses, and sedges; 80.6% for shrubs and winter browse stems; and 76.4% for conifers. These values help to compensate for the effects of oils, terpenoids, phenols, and resins that analysis of tannin precipitating capacity does not incorporate towards the reduction of protein and dry-matter digestion."
- Galbraith et al. (1998): 0.82 for bison, 0.87 for wapiti, and 0.87 for white-tailed deer

Conclusion: We will round the range from Minson (1990) to 0.75–0.85, which has the mean of 0.80. This range contains all other values we have seen so far. Since the data are sparse, we will use the same values for all HFTs.

C.2.22 Net Energy Coefficient (`k_maintenance`)

- Robbins (1983): Table 13.9 shows maintenance net energy coefficients for wildlife:
  - Eland on hay and concentrates: 72.7% (Rogerson, 1968)
  - Moose on browse: 68.2% (Regelin et al., 1981)
  - White-tailed deer on browse: 63.9% (Robbins, 1973)
  - White-tailed deer on browse: 48.3% (Mautz et al., 1975)
  - Wildebeest on hay and concentrates: 70.8% (Rogerson, 1968)
- Schwartz and Thompson (1985, p. 30): "Net energy as a fraction of energy metabolized from forage depends on the productive state of the animal and net energy for maintenance is usually about 50 to 75% of metabolizable energy (Robbins 1983)."
- Givens et al. (1989) uses a ME:DE ratio of 0.81, and that is also cited in McDonald et al. (2010, p. 258).
- Minson (1990) has unfortunately only efficiencies for fattening.

Conclusion: We think a range of 60% to 85% should cover all possible values. We know that the coefficient might depend on the forage quality. If the model is highly sensitive to this value, we can incorporate this dependency later.

C.2.23 Reproduction Rate

Mammoth

- Hanks (1972):
  - "This study is based on 1236 elephant shot over the period from 1965 to 1969."
  - "The mean calving interval was estimated from the age-specific incidence of placental scars, as described by Laws (1967)."
  - "The mean calving interval was 3·5 to 4·0 years."
- Williamson (1976):
  - "Placental scar frequencies for 118 non-pregnant females were plotted against age (Fig. 4)."
  - "[...] giving a calving interval with a range of 3.9 to 4.7 years. [...] The slope of the line is an estimate of the mean calving interval (4.3 years)."
  - "The length of the lactational anoestrus [is] 25.9 months. This gives a calving interval of approximately 47.9 months (4 years) [assuming 22 months gestation period] which agrees fairly closely with the figure calculated from the incidence of placental scars."
- Owen-Smith (1988): [p. 144f] "For African elephants mean conception intervals vary between 3.3 and 5.5 years in various regions [...] Birth intervals of Asian elephant females are about 4 years both in the wild and in captivity. A minimum birth interval of 23 months was recorded following the death of a calf, but the shortest interval after a surviving calf is 36 months (Kurt 1974)."
- Whyte et al. (1998):
  - "the inter-calving interval can be as short as three years or as infrequent as nine years."
  - "A culled sample of 966 adult cows shows an almost exact equality in the numbers of those pregnant (484) and non-pregnant (482). This means that, on average, a cow is pregnant for half of her adult life. Thus the calving interval will be twice the gestation time of 22 months, i.e. 44 months or 3·67 years (Whyte, in prep.)"
  - "Calef (1988) suggests 8% as the theoretical maximum growth rate for elephants. We agree with Dobson (pers. comm.) that this seems to be far too high."
  - Unfortunately we don't have access to many publications referenced in Whyte et al. (1998).
- Moss (2001):
  - "The mean calving interval has been considered to be the single most important parameter inluencing the growth rate of an elephant population (Hanks \& McIntosh, 1973)."
  - "In Amboseli, females can produce another calf as quickly as 22 months (one gestation length) after a birth if the first calf dies or 27 months after the birth of a surviving calf. Overall, however, females tended to produce a calf once every 4.5 years."
  - "Shorter average calving intervals have been reported in other populations with known individuals. In the Addo population (Whitehouse \& Hall-Martin, 2000), mean calving intervals were 3.8 years."
- Joshi et al. (2009): "Reproductive performance was known to vary with age, season, locality, population density and plane of nutrition"
- El Adli et al. (2017): Growth patterns in 4–5 years interval in adult female mammoth tusks are interpreted as representing calving intervals.

- Fordham et al. (2022, Supplementary Methods, p. 8): “We fit a Ricker logistic function to a 13-year time series for African elephants (*Loxodonta africana*) in Tarangire National Park, Tanzania, from 1993 to 2005 (Foley \& Faust 2010). This time series was chosen because the population was in a state of rebound after heavy poaching prior to 1993 (Foley \& Faust 2010). This provided a mean estimate of Rmax (lambda) of 1.08 (at an annual time scale).” 8% maximum annual increase of total population roughly equals a maximum female reproduction rate of 0.16.

Conclusion: Minimum calving interval: 3.5 to 4.7 years. That translates to maximum annual reproduction rate for females as: 0.21 to 0.28.

Steppe Bison

- Vereshchagin and Baryshnikov (1982): “interrupted growth bands on horn sheaths recovered from permafrost in northeastern Siberia suggest that Bison priscus females typically brought forth 11 or 12 calves during a lifetime. […] the first calf is generally born only when the female reaches an age of two or three years”
- Gates and Larter (1990):
  - “Pregnancy was determined by two techniques. Autopsies were conducted on the 28 adult females (≥ 2 years old) culled in both winters. Assays of serum samples for pregnancy/specific protein B (PSPB) were used from 16 chemically immobilized adult female bison” (p. 232)
  - “Van Vuren and Bray (1986) calclulated a mean pregnancy rate of 0.79 within a range of 0.67–0.86 for five confined herds. The pregnancy rate of 0.70 for Mackenzie 2-year-old and older females was lower than that found in confined herds but was comparable to rates found in four other wild populations” (p. 235)
- Green and Rothstein (1991) summarizing Green (1990): “Age-specific fecundity was nearly maximal at age 3 (78%), remained over 75% through age 11 (except for age 10, with 74%), and then declined gradually to 0 by age 20; the maximum was 86%, at age 7. Although there was a general decline in fecundity during the typical reproductive lifespan (age 3–18 years), a plateau occurred between ages 3 and 11.”
- Carbyn et al. (1993, Tab. 20): Total pregnancy rates of wood bison in Wood Buffalo National Park, based on slaughter data, vary between 21.3 and 70.7% with an average of 47%.
- Bradley and Wilmshurst (2005) use a pregnancy rate of 75% for simulating wood bison in Canada.

Conclusion: Maximum pregnancy rates might lie between 70 and 80%. We choose 75% as a fixed value for the model.

Horse

- Asdell (1964): usually 1 young, twins usually aborted (0.5–1.5% twin births)
- Turner Jr. and Kirkpatrick (1986, p. 250): “Pregnancy rates [of feral horses] are highly variable both across years and among ranges, with a range of 35 to 85%, i.e. 35–85 pregnancies per 100 mature mares per year.”
- Siniff et al. (1986): 2 years of data on foaling and mortality rates in 2 wild horse populations in Nevada. Foaling rates were very variable with a maximum of 69% of mares foaling.
- Wolfe et al. (1989, p. 920), pregnancy rates in feral horse populations in Nevada, Oregon, and Wyoming: “The mean incidence of pregnancy among mares ≥ 2 years old in our entire samples from Nevada, Oregon, and Wyoming was 57.0, 61.0, and 81.4%, respectively”
- Dawson and Hone (2012): “In general, reproductive rates [of wild horses] are high, with 80–90% of the prime aged females foaling (Berger 1986; Garrot *et al.* 1991a; Duncan 1992).

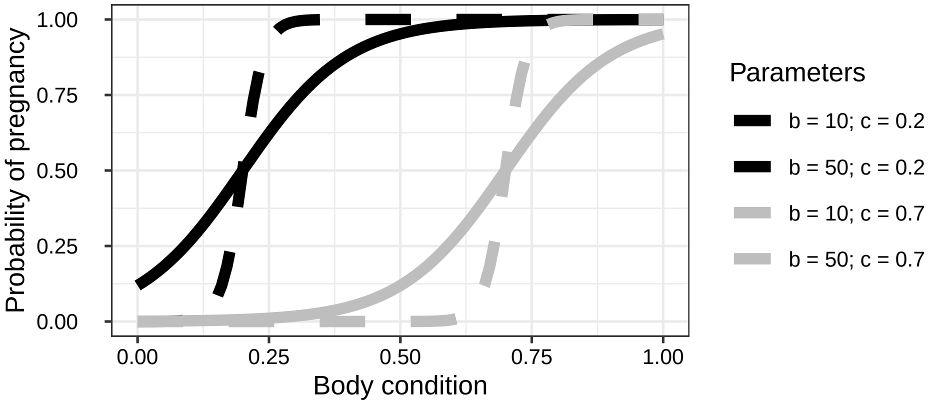

Figure S18. Extremes of the parameter ranges for logistic reproduction model. b is growth rate; c is midpoint value.

> Mares continue to have high foaling rates until the onset of senescence at 15–18 years of age (Garrott \& Taylor 1990; Garrott *et al.* 1991a; Grange *et al.* 2009)."

Conclusion: Since the model does not consider age-specific differences in foaling rate, the maximum reported numbers (90%) would be too high. 70% seems more appropriate.

C.2.24 Reproduction Trajectory

In some publications (e.g., Cook et al. 2004; Tollefson et al. 2010), the probability of pregnancy, as a dependent of percentage of total body fat, is expressed in a logistic function of this form:

$$y = \frac{e^{a+b\times x}}{x + e^{a+b\times x}}$$

This can be simplified to:

$$y = \frac{x}{x + e^{-(a+b\times x)}}$$

Illius and O'Connor (2000) show their breeding rate model in Formula (2). It has more variables, but comes down to the same formula as above. Instead of total body fat percentage they use **body condition,** which is defined as the ratio of current fat mass, FM, to the maximum fat mass, FM_{max} (*cf.* Fig. S13):

$$y = \frac{1}{1 + e^{-b(FM/FM_{max}-c)}}$$

The exponent makes the parameters b and c explicit. Parameter *c* is called the **midpoint** value of a generalized logistic function. It is the body condition at which 50% of females are pregnant. Parameter *b* is called **growth rate** and defines the slope of the curve — the softness of the threshold, one could say. Illius and O'Connor (2000) use a growth rate of 15 and a midpoint of 0.3, without further explanation.

- Frisch and McArthur (1974): Critical body fat hypothesis, which states that minimum body fat is required for onset of puberty and for estrous.
  - Bronson and Manning (1991) refutes this hypothesis, and we didn't find any supportive recent papers for it, either.
- White et al. (1989):
  - "The hypothesis that gains in body weight must be made before the rutting period to maximize conception rate was rejected."

  - 3 female muskoxen, born wild, then kept in captivity.
  - "We do not conclude, however, that regain in body weight and body condition are not implicated in the control of conception rate in muskoxen. In female muskoxen, this regain in body weight and condition may be the controlling factor during the rut. A phenomenon known as flushing increases ovulation rate (Lindsay 1976) when ewes are given access to high-quality food during the estrous period. Recent studies show that if the upward dietary change is very marked, an increase in body weight does not necessarily occur (Lindsay 1976); flushing therefore involves both dynamic and static effects of body weight (Rattray 1977; Jöchle and Lamond 1980)." (p. 1130)
  - "We now hypothesize that if the late summer regain in body weight and fat is prevented it may suppress ovulation or conception. The latter effect could be envisaged in the wild, especially on high arctic islands and in Greenland where occasional early heavy snowfalls may severely limit food availability in September through November. Such an effect has been associated with low pregnancy rates in females and high overall winter mortality (Parker et al. 1975; Miller et al. 1977)." (p. 1130)
  - All the cited publications are not available to us.

- Bronson and Manning (1991):

  - "There is no doubt that ovulation can be regulated somehow in relation to whole-body energy balance and that fat stores are an important component of energy balance, but there is no reason to accord body fat a direct causal role in regulating ovulation." (abstract)
  - "The issue here is not one of correlation, however,; it is one of cause and effect." (p. 945)
  - "In larger animals, Armstrong and Britt [8] could find no relationship between back fat and estrous cycling in adult pigs whose food intake was manipulated. Similarly, Schwartz et al. [38] saw no relationship between body fat as measured by thickness of the abdominal skinfold and pubertal ovulation in rhesus monkeys fed high- versus low-fat diets. McShane et al. [39] and Bucholtz et al. [40] reduced the fat reserves of young heifers and ewe ambs, respectively, by administering growth hormone chronically and found no effect on the timing of puberty. Finally, Estienne et al. [41] could find no effect of lipid infusion on LH secretion in ewe lambs." (p. 947)
  - "If not fat, what is the agent that allows the activity of the GnRH [Gonadotropin-releasing hormone] pulse generator to be modulated by energy balance? Two candidates are currently receiving considerable attention: the metabolic fuels and insulin. In regard to the first, it is becoming well established now that ovulation is dependent upon the moment-to-moment availability of oxidizable metabolic fuels — glucose and fatty acid." (p. 948)

- Ropstad et al. (1991), 632 Reindeer calves slaughtered in November to January:

  - "The present data also support evidence that there is a lower limit for fat reserves beyond which pregnancy is not possible (10). Similar findings have been reported in humans (11 [Frisch \& McArthur, 1974]). In our material this limit was around 60 g perirenal fat."
  - "There was a rapid increase in the pregnancy rate with increasing dressed weight once the limit of 22 kg was exceeded."
  - Potentially we could try to convert the threshold of perirenal fat mass to empty weight body fat percentage.

- Wade and Schneider (1992):

  - "Although pregnancy is less affected by fuel availability, both lactational performance and maternal behaviors are highly responsive to the energy supply."

  - “Both ovulatory cycles and lactation are highly sensitive to food availability. However, in comparison to cycling and postpartum females, pregnant females show relatively modest responses to short-term food deprivation.” (p. 238)
  - “We are not aware of any evidence to suggest that cold, per se, has any effect on reproduction independent of its effects on energy metabolism (66).” (p. 241)
  - On page 246 strong arguments against the **lipostatic models of fertility.** There are some correlations between body fat and fertility, but definitively no causal link. Even correlations are not consistent. In summary: “a critical amount of body fat is neither necessary nor sufficient for normal ovulatory cycles” (p. 246)

- Crête and Huot (1993), as cited by Couturier et al. (2009): female caribou need a body fat threshold of 7.8% in the fall to become pregnant. Their body fat is based on kidney fat with a regression from (Huot 1989). We don’t know what Huot’s “body fat” is until we see the full-text article.

  - “By comparison, ovulation was observed only in animals that had accumulated over 7 kg of fat in November in a small herd of captive RGH females not exposed to a male during the breeding season (Crete et al. 1993). Fat deposition might continue during late autumn - early winter, but there is evidence that lean animals fail to reproduce, as pregnant females in March possessed, on average, 7.2 kg of fat reserves (range 3.7 - 10.1 kg; Huot 1989). Poor summer nutrition may have a direct influence not on ovulation but rather on gestation through breeding behaviour (Reimers 1983), effects on fertilization or implantation of the ovum, or spontaneous abortion.” (p. 2294)

- Gerhart (1995, p. 49f): “Previous studies indicate that a female must accumulate a critical amount of fat (Sadlier 1969; Frisch et al. 1973), reach a critical body weight (Kennedy and Mitra 1963; Frisch and Revelle 1970; Smith 1991), or achieve a minimum fat:lean ratio (Frisch and McArthur 1974) to achieve puberty or maintain ovulation. Reproductive data from *Rangifer tarandus* subspecies support the hypothesis that a critical body fat level or body weight must be reached for a female to conceive. Pregnant barren-ground caribou (*R.t. groenlandicus* and *R.t. grand*) were fatter in early winter than nonpregnant females (Dauphine 1976; Allaye-Chan 1991) and wild Norwegian reindeer (*R. t. tarandus*) with heavier autumn carcass weights were more likely to be pregnant (Reimers 1982). Pregnancy status for Peary caribou (*R.t. pearyi*) in late winter was highly correlated with both body weight and indices o f body fat (Thomas 1982). Most recently, parturition rate for Alaska barren-ground caribou (R . t. granti) has been correlated with autumn body weight (Cameron et al. 1993, Cameron and Ver Hoef 1994), and a body-fat threshold for ovulation has been reported for woodland caribou (R.t. caribou, Crete et al. 1993).”

  - Figure 11 on page 61 shows the relationship between body fat (FM) and probability of pregnancy (Π), and Table 9 on page 58 shows the numbers. The logistic formula is on page 53.
    - For 1990 and 1992: $\Pi = e^{-2.123+0.7345\times FM}/(1+e^{-2.123+0.7345\times FM})$
    - For 1991: $\Pi = e^{-2.123-1.841+0.7345\times FM}/(1+e^{-2.123-1.841+0.7345\times FM})$
  - “While body condition may not be an ultimate cause of differences of fertility, body condition is determined in part by whole body energy balance. Thus it is a useful correlate to fertility, particularly for population management and ecology (Bronson and Manning 1991).” (p. 69f)

- Robinson (1996, p. 30): “The effects of nutrition on embryo survival were reviewed by Robinson (1990) and more recently by Ashworth (1994).”
- Cameron (1997): not useful, only covers signal roles of glucose, insulin, and leptin.
- Adamczewski et al. (1998), 32 pregnant and 18 nonpregnant muskoxen:

- "There were no pregnant muskox cows with < 19% fat in the IFBM [ingesta-free body mass], and a 50% probability of pregnancy was associated with 22% fat in the IFBM [...] In caribou, the critical range of fatness for pregnancy in early winter was 5 to 9% fat in the IFBM (12). The pregnancy rate for range cattle varied most between 8.5 and 15% fat in the IFBM (39) and puberty in heifers occurred from 13 to 18% fat in the IFBM (51). Sheep showed an almost continuous increase in ovulation rate from 11 to 29% fat in the IFBM (10)." (p. 608)
  - "However, results of this study and those from captive muskoxen (49) suggest that condition exerts a greater influence on reproductive status than does recent nutrition." (p. 611)
  - "In keeping with a more liberal reproductive strategy, caribou do not need to be in exceptionally good condition to conceive (12). [...] As suggested by Klein (25) and Gunn (16), these differences imply a more tightly regulated relationship between food supply and reproduction in muskoxen than in caribou." (p. 612)
- Cook et al. (2001), elk (*Cervus elaphus nelsoni*):
  - "inadequate nutrition in summer and autumn reduce pregnancy rates by preventing estrus and ovulation rather than by inducing early-embryo mortality." (abstract)
  - "Early embryonic mortality has also been associated with inadequate nutrition. Although it has been documented in white-tailed deer, *Odocoileus virginianus* (Teer et al. 1965; Roseberry and Klimstra 1970), moose, *Alces alces* (Testa and Adams 1998), caribou, *Rangifer tarandus* (Russell et al. 1998), and domestic livestock (Ayalon 1978), our data did not reveal increased embryonic mortality in undernourished elk" (p. 850)
  - "Our data indicate that relatively severe DE [digestible energy] deficiencies are required to prevent pregnancy." (p. 851)
- Friggens (2003): fulltext not available
- McEvoy and Robinson (2003):
  - "Body energy balance and environmental signals interact to activate the gonadotrophin releasing hormone (GnRH) pulse generator in the brain and induce ovulation (reviewed by Adam \& Robinson, 1994). However, the mechanisms linking the pulse generator to energy balance remain unclear, even under controlled experimental conditions (Foster \& Nagatani, 1999; Adam, 2000). [...] In large mammals in natural habitats circannual rather than circadian fluctuations in energy balance predominate in determining whether or not to ovulate. Furthermore, where there is potential for more than a single ovulation, for example in domestic sheep, actual ovulations are positively correlated with accumulative energy balance as measured by body condition score (Doney et al. 1982). Within this overall relationship there are long- and short-term modifications. The long-term ones coincide with ovulatory ovarian follicles leaving the primordial pool (c. 6 months before ovulation in ewes) whereas short-term modifications result from improved energy balance for as little as 6 days before ovulation (see Robinson et al., 1999b)." (p. 45)
  - "Among farm animals, pigs and sheep exhibit an inverse relationship between feed intake in early pregnancy and circulating progesterone concentrations with, in both species, associated reductions in embryo survival (Robinson et al ., 1999a). This may be relevant to other species for, as pointed out by Leus \& McDonald (1997), endangered wild pigs kept in zoos invariably become obese with accompanying failure to reproduce." (p. 52)
    - The decline in reproductive performance for obese individuals is neglected in the model because obesity is not prevalent in the wild.
- Garrott et al. (2003), *Cervus elaphus*: "Reproductive rates remained essentially constant,

near their biological maxima (mean = 0.91, SE = 0.02). Annual recruitment was highly variable. Snowpack had a pronounced effect on recruitment (r2 = 0.91), the most severe snowpack conditions resulting in the virtual elimination of a juvenile cohort."

- Martin et al. (2004): no correlations with body fat
- Cook et al. (2004):
  - Figure 14 on page 25 shows pregnancy rate against body fat percentage:
    - 1997: $y = e^{-3.978+0.587\times x}/(1 + e^{-3.978+0.587\times x})$ That translates to $b = 0.587$ and $c = 3.978/0.587\ \% = 6.776\%$
    - 1996: $y = e^{-4.716+0.594\times x}/(1 + e^{-4.716+0.594\times x})$ That translates to $b = 0.594$ and $c = 7.939\%$.
  - Figure 36 on page 47 shows pregnancy–body fat correlations from other studies.
- Robinson et al. (2006): no correlations with body fat
- Friggens et al. (2010):
  - "What happens when the cow fails, or is failing, to accumulate the reserves she needs to safeguard reproduction? The seemingly logical answer to this question is that the cow should delay committing to further reproductive investment and this seems to be the case (Knight, 2001; Diskin et al., 2003) but how does the physiology of the cow 'know' that she has failed or is failing in energy terms? We have argued that the cow does this by 'monitoring' body fat mobilisation and body fatness (Friggens, 2003)." (p. 1199)
  - "The discovery of leptin, a hormone produced by the adipose cells that has been implicated in control of appetite (see Ingvartsen and Boisclair, 2001) that is also linked to reproductive function (Hoggard et al., 1998; Spicer, 2001), was an important step towards understanding the physiological significance of fat reserves. This is not meant to imply that leptin explains everything, far from it." (p. 1201f)
  - "Across species, there is a general consensus that thin individuals have depressed reproductive performance (Gunn et al., 1972; Frisch et al., 1977; Bronson, 1989; Woodroffe, 1995; Adamczewski et al., 1998), although whether body fatness is the direct cause has been questioned (Bronson and Manning, 1991; Wade et al., 1996)." (p. 1202)
  - "it seems increasingly clear that body fatness should be considered a factor that can modulate reproduction independently of body mobilisation." (p. 1203)
- Tollefson et al. (2010), captive mule deer:
  - "Poor nutrition or body condition in ungulates can adversely affect hypothalamic–pituitary function (Cupps 1991, Schillo 1992, Wade et al. 1996), delay puberty (Senger 1999), prevent ovulation (Tanaka et al. 2003), reduce pregnancy rates (Folk and Klimstra 1991, Mani et al. 1996, Tanaka et al. 2003), and reduce production of offspring (Adamczewski et al. 1998, Russell et al. 1998, Cook et al. 2004a, b). Low body fat reserves, especially in lactating animals, may also increase probability of terminating pregnancy shortly after breeding (Sosa et al. 2004)." (p. 974)
  - Figure 5a on page 981 shows probability of pregnancy against body fat (%) for captive mule deer (this study) and Cook et al. (2004), which is elk.
  - "Body fat was not a significant factor in the model for predicting pregnancy in our captive mule deer" (p. 981)
  - "However, mule deer seem to be able to conceive at lower fat levels than can elk. For example, captive and wild elk had only a 25% chance of becoming pregnant, whereas at 5% body fat, our captive mule deer had .75% chance of becoming pregnant (Cook et al. 2004a, b)." (p. 983)
- Vatankhah et al. (2012): only sheep body condition scores, no body fat percentage.
- Schneider et al. (2012):

  - "This review emphasizes the metabolic hypothesis: a sensory system monitors the availability of oxidizable metabolic fuels and orchestrates behavioral motivation to optimize reproductive success in environments where energy availability fluctuates or is unpredictable." (abstract)
  - "The metabolic hypothesis was diluted in the literature after the discovery that leptin, the protein product of the ob gene, decreased food intake and restored reproductive capabilities in obese, hyperphagic, infertile ob/ob mice" (p. 11)
  - "Leptin decreases food intake and stimulates reproductive process in a wide variety of species (reviewed by Schneider, 2000), but contrary to the lipostatic hypothesis, leptin acts on estrous cycles by modulating the intracellular availability of oxidizable fuels." (p. 11)
  - "The observed changes in behavior, hormones, and metabolic fuel partitioning are best understood within the metabolic hypothesis: A sensory system monitors the availability of oxidizable metabolic fuels and orchestrates behavioral motivation to optimize reproductive success in environments where energy availability fluctuates or is unpredictable. [...] There is now recognition that so-called lipostatic hormones, once thought to maintain a set point in body fat content, are actually modulators of metabolic fuel availability, more specifically, fuel oxidation, and synthesis." (p. 14)

- Cook et al. (2013):
  - Figure 12 on page 24 and Figure 14 on page 24 show pregnancy-to-body-fat curves. They are not modelled with a logistic curve, though.
  - "We seasonally measured body condition and reproduction in 21 elk herds in 5 western states." (p. 38)
  - "Probability of pregnancy was positively related to body fat in autumn but we found no evidence that winter or nutritional condition in early spring affected pregnancy rates the subsequent autumn." (p. 38)

- Boult (2018, p. 116): "Body fat threshold required for oestrus cycling($oest_{on}$): Temporal variation in conceptions of elephants suggests that they experience condition-dependent oestrus; few conceptions occurred in years when the maximum NDVI value (used as a proxy for vegetation abundance) was low which is suggestive of a physiological threshold under which elephants do not enter oestrus and conceive (Wittemyer, Rasmussen and Douglas-Hamilton, 2007). Estimates of this physiological threshold are not available for elephants but have received some attention in humans, and Bronson \& Manning (1991) suggest that 20% body fat is required for oestrus cycling. The proportion of body fat (M_{stor}; kg) in relation to total mass (M tot ; kg) required for oestrus cycling was therefore taken as 0.2."

Conclusion: The approach by Illius and O'Connor (2000) to use a logistic correlation between body condition at the time of mating and the number of offspring in the breeding season is good because it is common practice. The parameterization is very difficult for the following reasons:

1. Correlative field studies are rare.
2. The regressions don't always have good predictive value.
3. The absolute or relative body fat values from field studies are difficult to translate to the "body condition" of Illius and O'Connor (2000), i.e., fraction of maximum fat mass. That is because body fat is hard to measure in the first place, and the maximum fat mass is not defined.
4. Each large herbivore species has a unique response to body fat during mating season, depending on their reproductive strategy.

For all these reasons we see no way to apply the result of a particular field study to any of the Pleistocene HFTs. We can only conjecture that the animals must have followed a rather conservative reproduction strategy because they were rather long-lived (especially mammoths), and the winters were long. In the sensitivity analysis we will cover a wide parameter range: midpoint between 0.2 and 0.7 and growth rate between 10 and 50 (Fig. S18).

References for Appendix

Note that citations contained in quotations from other works (in Appendix C) are not listed here. In these cases please refer to the respective bibliography of the quoted publication.

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