

THESIS

QUANTIFYING LARGE MAMMAL EXTINCTION RATES AND SIZE-SELECTIVITY IN
EASTERN AFRICA: A TEST OF ANCIENT ANTHROPOGENIC EXTINCTION
HYPOTHESES

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ABSTRACT

QUANTIFYING LARGE MAMMAL EXTINCTION RATES AND SIZE-SELECTIVITY IN EASTERN AFRICA: A TEST OF ANCIENT ANTHROPOGENIC EXTINCTION HYPOTHESES

A fundamental focus of paleoanthropology is understanding the impact of ancient humans on their ecosystems. One critical way that humans change their ecosystems is by driving other species to extinction, and researchers have recently argued that this process began with the appearance of *Homo erectus*. These researchers hypothesize that with novel adaptations such as increased brain size, heightened carnivory, and innovative technology, *H. erectus* preferentially drove large mammals to extinction (i.e., size-selectivity) as early as ~2 million years ago (Ma). Size-selectivity of mammal extinctions in Plio-Pleistocene Africa has been examined previously, but no study has done so while adequately accounting for incomplete preservation and sampling in the fossil record. Here, we analyzed a published presence-absence dataset of mammal species from eastern Africa over the last six million years. We used capture-mark-recapture methods to estimate time-varying extinction rates as a function of body size, while controlling for size-biased sampling. This model allows for the quantification of size-selective extinctions through time and for a test of the hypothesis that elevated size-selectivity emerged with the appearance of *H. erectus* at 2 Ma. We found no increase in size-selective extinctions of large mammals at or after 2 Ma, and thus our results do not support the hypothesis that *H. erectus* drove size-selective extinctions in eastern Africa during the Plio-Pleistocene.

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CHAPTER 1 – INTRODUCTION

We are increasingly aware that humans impact ecosystems across spatiotemporal scales by changing biogeochemical cycles, hydrology, fire regimes, biodiversity, species introduction, land cover, and patterns of net primary production (e.g., Ellis, 2015). Given the ubiquity and potency of these changes, understanding how humans impact ecosystems is a critical undertaking of our time. Because humans have fundamentally altered ecosystems, some researchers argue that this period should be assigned a new geological epoch: the ‘Anthropocene’ (Crutzen, 2021). These arguments have raised questions about this history of human-environmental interactions.

Understanding the history of the human ability to fundamentally alter ecosystems is a key focus of paleoanthropology. Paleoanthropologists have sought an evolutionary ‘Holy Grail’ that ushered in the ability of hominins to change their environment, looking for a behavioral novelty or technological windfall. Traits including the use of tools, employment of fire, and the development of culture have all been investigated in this framework (Daniau et al., 2010; Laland et al., 2007; Olmstead & Walls, 2025; Thompson et al., 2021). While the question of *what* allowed hominins to drive change is significant, it cannot be answered without first understanding *when* hominins began altering ecosystems. Having a clear timeline of anthropogenic ecosystem change will equip us to investigate the hominin traits that facilitated this change. If we knew when hominins began fundamentally altering ecosystems, we could investigate the associated morphological, technological, or cultural adaptations that might have enabled them to do so.

Researchers have tried to estimate when humans began altering ecosystems. Some have conservatively pointed to the 18th century, arguing that industrialization, exponential population growth, and inventions such as the steam engine set the stage for the first significant anthropogenic impacts (Crutzen, 2021). These impacts included overfishing, water pollution, large-scale land-use change, and the widespread extinctions of species. Other researchers have refuted this timeline, arguing that the global colonization by *Homo sapiens* marked the first phase of transformation because this expansion coincided with critical changes such as species translocations and large-scale extinctions (Boivin et al., 2016). It is generally understood that *H. sapiens* were present in Africa by ~315 ka, had expanded across Eurasia by ~40 ka, and had reached the Americas by ~14 ka (Becerra-Valdivia & Higham, 2020; Hublin et al., 2017; Mellars, 2006). Some researchers have pushed the dawn of anthropogenic environmental transformation further back in time, citing the changes attributed to species such as *Homo neanderthalensis* (Roebroeks et al., 2021). Roebroeks and colleagues (2021) point to changes in landscape modification including reshaped vegetation structure and fire use. Perhaps most controversially, a group of researchers have argued that hominins impacting their ecosystems in a significant way dates as early as ~2 Ma (e.g., Faurby et al., 2020; Lewis & Werdelin, 2007; Lyons et al., 2004; Surovell et al., 2005). They make this argument based on patterns of large mammal extinctions, which will be discussed in detail in Chapter 2.

These researchers have asserted that as hominins underwent novel biological and cultural adaptations, they drove extinctions as far back as the early Pleistocene. These assertions are known generally as ancient anthropogenic extinction hypotheses and take two general forms (Faith et al., 2020). The first form argues that hominins drove large mammals to extinctions directly through hunting (e.g., Surovell et al., 2005). The second suggests that as members of the

genus *Homo* entered the carnivore guild, they outcompeted large carnivores and indirectly drove them to extinction (Werdelin & Lewis, 2013). While suggesting different patterns of anthropogenic extinction, these studies generally assert that *Homo erectus* was the first hominin capable of driving extinctions, given key adaptations and traits that separated it from earlier species such as *Homo habilis*. Example traits include a larger body size, larger home ranges, larger brain size, use of Acheulean stone tools, increased carnivory, and the potential use of fire (Antón et al., 2014; 2003). Additionally, these hypotheses focus on the size-selectivity of extinctions, i.e., the preferential extinction of larger-bodied herbivore and carnivore mammals. Researchers argue that because large mammals went extinct at rates unseen in the earlier fossil record, *H. erectus* must have driven their extinction (Lyons et al., 2004; Smith et al., 2018; Surovell et al., 2005).

The hypothesis that anthropogenic extinctions began with *H. erectus* has extensive implications for our understanding of human-environmental interactions. The idea that *H. erectus* drove mammals to extinction could indicate that their ability to hunt, outcompete carnivores, or alter landscapes rivaled that of *H. sapiens*, and raise questions about the social and technological advances necessary for this ability. This understanding could drastically extend the known temporal range of hominin top-down control because many currently accept the late Pleistocene as the origin of such control (Boivin et al., 2016). Given the potential implications of this hypothesis, it has been increasingly cited in fields beyond paleoanthropology such as conservation biology (e.g. Hoag & Svenning, 2017). Despite the increasing visibility of this hypothesis, it has yet to be robustly tested, and the attribution of extinctions to *H. erectus* requires much more extensive investigation before acceptance.

This is especially true because some of the studies that have tested this hypothesis have been criticized for not considering the context of long-term evolutionary or environmental change, and for not controlling for biases in the fossil record that arise from variable preservation or sampling effort (Faith et al., 2020). Failure to control biases in the fossil record leads to the underestimation of the true temporal range of taxa because incomplete sampling results in estimates of origination dates that are too late and extinction dates that are too early (Foote & Raup, 1996). This failure also leads to the underestimation of the spatial range of taxa, because sampling effort influences whether or not a taxon is recorded at a site or in a region (Wood & Smith, 2022). Estimated temporal and geographic ranges increase with sampling effort as fossils are found in additional geographic areas and time bins (Du et al., 2020; Signor & Lipps, 1982). Variable preservation can also lead to an underrepresentation of taxa in the fossil record based on, for example, a bias against preserving smaller-bodied organisms (Cooper et al., 2006; Miller et al. 2014). Given these biases, it is essential to control for variable fossil preservation and sampling effort when analyzing species diversity and spatiotemporal ranges and metrics based on these attributes (e.g., origination and extinction rates). Studies which investigate the role of *H. erectus* in mammal extinctions, such as Surovell et al. (2005), did not account for these biases, which undermines their conclusion that *H. erectus* influenced extinctions. Therefore, there is great need to test ancient anthropogenic extinction hypotheses while accounting for biases in the fossil record. Here, we test the hypothesis that anthropogenic extinctions began in eastern Africa with the appearance of *H. erectus* at 2 million years ago (Ma), while accounting for incomplete preservation and sampling of the fossil record.

To frame our study, we first predicted the patterns of mammal extinctions that would occur if they were caused by *H. erectus*. Extinctions would coincide temporally and spatially

with the currently oldest appearance of *H. erectus* in the fossil record: 2 Ma in eastern Africa (Hammond et al., 2021; Mussi et al., 2023). Accepting the idea that size-selectivity for large mammals is a unique anthropogenic signal, we expected to see larger mammals go extinct at higher rates than smaller mammals. Given these general predictions, we designated two scenarios that extinctions driven by the appearance of *H. erectus* might follow:

Scenario 1: The appearance of *H. erectus*, with novel adaptations and its emergence as a predator, pushed large mammals to extinction through direct (e.g. hunting large prey) or indirect means (e.g. competition with large carnivores for prey) at or immediately after 2 Ma. Extinction rates monotonically increase as a function of body size during this period, resulting in a spike of size-selective extinctions. After these extinctions, there were fewer large mammals, and size-selectivity return to background levels.

Scenario 2: *H. erectus* pushed larger mammals to extinction in a protracted manner, through direct or indirect means. Extinction rates monotonically increase as a function of body size, and size-selectivity is elevated from 2 Ma onwards, as opposed to exhibiting a temporally brief spike.

To assess if data from the fossil record support either scenario, we analyzed a published presence-absence dataset of mammal species from eastern Africa over the last six million years (Rowan et al., 2024). We used capture-mark-recapture models to estimate time-varying mammal extinction rates as a monotonic function of body mass (Liow & Nichols, 2010); a positive relationship between extinction rate and body mass would indicate size selectivity. We also account for variable fossil sampling and preservation rates by modeling species' detection rates as a function of body size, given previous studies showing size-biased preservation of mammals (e.g., Miller et al., 2014). Because our model allows us to estimate whether or not *H. erectus* was

precipitating extinctions biased against large mammals, this study gives us insight into the history of expanded ecological impacts in the evolutionary history of hominins. The rise of size-biased extinctions with the appearance of *H. erectus* would suggest that *H. erectus* was a significant force of change in its ecosystem and that the human ability to exert top-down controls on environments dated as far back as 2 Ma.

CHAPTER 2 – BACKGROUND

Our study aims to evaluate a model of mammal extinctions caused by *H. erectus* in the early Pleistocene in eastern Africa. With this research topic in mind, we first reviewed the late Pleistocene mammal extinctions. We do so because we want to highlight which extinction patterns are inferred to be anthropogenic, e.g., extinction bias against large animals and spatiotemporal overlap with humans. These patterns are cited in the ancient anthropogenic extinction literature as well, so it is important to understand them. We also review the late Pleistocene extinctions because they have well-developed hypotheses that have been extensively tested. These extinction hypotheses form the foundation of the ancient anthropogenic extinction hypotheses that we will test in our study. After covering the late Pleistocene extinctions, we will describe the climatic and ecological conditions in eastern Africa during the Plio-Pleistocene, to put mammal extinctions during this period in context. Finally, we will discuss our current understanding of *H. erectus* and synthesize the research on ancient anthropogenic extinction hypotheses.

2.1 The late Pleistocene mammal extinctions

The late Pleistocene (120 ka to 11.7 ka) was marked by striking global changes that included variable climatic oscillations and the colonization of five continents by *H. sapiens* (Perez & Prates, 2024). In addition to these changes, this period saw the extinction of many large terrestrial mammals from ecosystems across the globe. “Large animals” and “megafauna” are often used interchangeably in this literature to refer to animals with an adult body mass greater than 44 kg (Koch & Barnosky, 2006). We will use this definition when referring to large or megafaunal species. These extinctions happened relatively rapidly, with most species

disappearing in the period between 50 and 11 ka, and they reached five continents and a myriad of ecosystems and habitats. As a result, ecosystems that had once hosted a diversity of large herbivores and carnivores were left bereft of their largest inhabitants (Svenning et al., 2024). Critically, these extinctions also spelled the loss of ecosystem functions once filled by these large mammals, which included the alteration of the physical structure of habitats, nutrient and seed dispersal, and control of prey populations (Svenning et al., 2024).

2.1.2 Patterns of extinction

As mentioned before, extinction patterns during the late Pleistocene (120 to 11.7 ka) have been cited as evidence that humans were the extinction drivers. Specifically, researchers argue that the bias against large mammals and the spatiotemporal overlap of human populations with mammal extinctions are evidence of human activity. On a global scale, at least 97 genera of large mammals disappeared during the late Pleistocene, accounting for two-thirds of global large mammal genera (Martin & Steadman, 1999). Only 11 of 57 species of megaherbivores (> 1000 kg) survived until the present: three species of elephant, four species of rhinoceros, the common hippopotamus, the northern giraffe, and two bovines (Svenning et al., 2024). The continental patterns of these extinctions are summarized in Table 1 below.

Table 1: Continental patterns of mammal extinctions during the late Pleistocene (120 – 11.7 ka)

Continent	Extinction timing	Extinction losses	Examples of extinct taxa
Australia (Wroe et al., 2013)	~ 50 ka	• All species > 100 kg • 88 % genera > 44 kg • All browsers and carnivores > 44 kg • All families of marsupials > 44kg • All reptiles and birds > 44 kg	• <i>Genyornis</i> • Diprotodontids • Palorchestids, • Thylacolenids
Eurasia (Kahlke, 2007)	Warm adapted taxa: ~ 48.5 – 24.8 ka Cold-adapted taxa: ~ 14 ka onward	• 35 % genera > 44 kg	• Straight-tusked elephants • Hippopotamuses • Short-faced bears • Irish Deer • Callaboid horses
North America (Barnosky et al., 2004)	~ 20 ka	• All species > 1000 kg • 70 % species > 44 kg	• All members of Perissodactyla and Proboscidea • <i>Mammuthus</i> • <i>Mammut</i> • <i>Platygonus</i> • <i>Megalonyx</i> • <i>Nothrotheriops</i>
South America (Barnosky et al., 2004)	~ 20 ka	• All species > 320 kg • 83 % genera > 44 kg	• All members of Notoungulata, Proboscidea, and Litopterna
Africa (Faith, 2014; Svenning et al., 2024)	Intensified ~ 13 ka	• 21 % genera > 44 kg • 24 species > 5 kg	• <i>Palaeoloxodon iolensis</i> • <i>Pelorovis antiquus</i> • <i>Metridiochoerus compactus</i>

2.1.3 Extinction hypotheses

The patterns of extinctions detailed above, including their timing and selectivity, have been explained by a variety of hypotheses. As stated earlier, these hypotheses are important for us because they are now used to explain more ancient extinctions (i.e., pre-*H. sapiens*), including the extinctions that we evaluate, which will be explained later in greater detail below. First, we examine the extinction hypotheses which fall into three general categories: anthropogenic drivers, environmental drivers, and a combination of anthropogenic and environmental drivers (Stuart, 2015). Following that, we will discuss how anthropogenic hypotheses have been evaluated in the literature.

Anthropogenic hypotheses cover scenarios in which humans directly or indirectly drove animals to extinction. Perhaps the best-known model of direct anthropogenic extinction is the overkill hypothesis (Martin, 1966). This hypothesis posits that humans drove species to extinction when human hunting caused death rates to exceed birth rates in prey populations. Supporters of this model argue that overkill disproportionately impacted large species because large animals were the preferred prey of human hunters or because their life history made them vulnerable to population collapse (Brook & Bowman, 2005; Wolverton & Lyman, 2012). A ‘Blitzkrieg’ overkill scenario describes a rapid collapse of prey population after the sudden arrival of hominins with range expansion (Martin, 1995). A protracted overkill scenario describes losses in prey populations that were sustained after extended interactions with human hunters (Burney & Flannery, 2005). In Section 2.1.4, we will review seminal literature that cites direct anthropogenic extinction hypotheses.

Indirect anthropogenic drivers include land alteration leading to the loss or fragmentation of critical habitat, the introduction by humans of novel predators including domesticated dogs, and the introduction of novel diseases that drove animals to extinction (Braje & Erlandson, 2013;

Fiedel, 2005). Another indirect driver is the arrival of humans in novel environments and subsequent competition with large predators for prey, ultimately driving those predators to extinction (Barton et al., 2016).

Environmental extinction hypotheses discount the effects of humans altogether. Proposed environmental drivers include habitat loss due to climatic changes and catastrophic events such as megadrought or rapid cooling (Burney & Flannery, 2005). It has also been proposed that climatic changes caused a disruption in coevolutionary relationships between plants and herbivores, severe enough to drive those herbivores to extinction (Burney & Flannery, 2005).

Some researchers are dissatisfied with the attribution of late Pleistocene extinctions to humans or environmental changes separately and have proposed a model of combined human impacts and environmental change (Owen-Smith, 1987). One scenario includes the loss of keystone megaherbivores, where human-driven megaherbivore extinction led to significant ecosystem dysfunction, which caused the extinction of other species in the ecosystem (Owen-Smith, 1987). Some have proposed predator avoidance as a mechanism, in which human hunting drove prey populations to resort to areas of refuge that could not support their populations (Koch & Barnosky, 2006).

2.1.4 Seminal studies on late Pleistocene extinctions

Each extinction hypothesis has various champions and evidence cited in its support. Here, we focus on the evidence used to support anthropogenic extinction hypotheses because this is most relevant for our research. Many researchers who implicate humans in the late Pleistocene extinctions primarily use the size-biased nature of the extinctions as evidence for human involvement. They assert that the extinction bias against large mammals was unprecedented in the Cenozoic mammal record, pointing to a novel extinction driver (human activity) (Lyons et

al., 2004; Smith et al., 2018). Smith et al. (2018) analyzed the global mammal fossil record and quantified size selectivity in extinctions over the late Pleistocene and compared this to size selectivity over the entire Cenozoic. Their results revealed a pattern of disproportionate large mammal extinction in the late Pleistocene, unlike any observed over the Cenozoic and argued that humans were responsible for this unique pattern of size-selectivity. They cited ethnographic and zooarchaeological research that found preference for large mammals in human hunting (Surovell & Waguespack, 2009) and argued that this human prey preference and overkill drove large mammal extinctions over the last 125 ka.

Another way that researchers connect human activity to the size-biased nature of the late Pleistocene extinctions is by analyzing the difference between mammal body-size distributions before and after human colonization. Lyons et al. (2004) compared body-size distributions before and after the estimated arrival of humans and found that mammals that survived after human colonization were significantly smaller than those that went extinct. They argue that this was due to overkill, but the estimated timing of human arrival used in this and similar studies raises questions about their conclusions. Lyons et al. (2004) designate the following time frames as “before human colonization”: 46 ka in Australia, 15 ka for the Americas, and 15 ka for Africa. Recent discoveries and research have changed our understanding of human arrival, and we now know that *H. sapiens* was in Africa at 315 ka (Hublin et al., 2017), in Australia as early as 65 ka (Clarkson et al., 2017), and likely arrived in the Americas before 15 ka (Bennett et al., 2021). These updated dates for human occupation make it critical to reevaluate body size distribution comparisons with the new dates in mind.

Some researchers who support an anthropogenic model focus on patterns of the extinctions beyond the size-biased pattern. For example, Svenning et al. (2024) argued that any

anthropogenic or environmental mechanism of late Quaternary extinctions would have to account for its global and asynchronous nature. They argued that while the late Pleistocene saw major climatic shifts, these changes were no more severe than earlier changes and failed to explain the extinctions, and because the expansion of *H. sapiens* was truly unique to the late Pleistocene, this was the key driver. The authors also cited human prey preference for large animals (Pitulko et al., 2016) and supported an overkill model of extinction. Koch & Barnosky (2006) also rejected extinction models based solely on environmental factors, reasoning that there was no evidence that the last glacial-interglacial transition was different enough from previous transitions to precipitate the extinction of animals who had survived earlier times. They also argued that there was no evidence to suggest that habitats favored by large animals disappeared in a systematic way. They supported models that combined direct and indirect human impacts, including overkill, competition with carnivores for prey leading to carnivore collapse, and habitat alteration.

Above, we addressed the global mammal extinctions during late Pleistocene extinctions and their related extinction hypotheses. While these extinction patterns and hypotheses are relevant for this study because they are cited in ancient anthropogenic extinction literature, the extinctions themselves are not the extinctions of interest for our study. We are interested in regional extinctions in eastern Africa ~2 Ma because this is the area and time period where some of the earliest *H. erectus* fossils are currently found (Hammond et al., 2021; Mussi et al., 2023). Accordingly, we will now transition to talking about ecological changes in eastern Africa. We decided to include the last six million years to better contextualize the extinctions of interest around ~ 2 Ma. We will first detail climatic and ecological change, then address mammal

turnover, which includes originations and extinctions of interest, before finally reviewing the ancient anthropogenic extinction literature.

2.2 Eastern Africa over the last six million years

This was a time of significant change in eastern Africa: drivers on a variety of scales interacted to shape climatic cycles, faunal turnover, and vegetation change (deMenocal, 1995, 2004; Faith et al., 2024). A widespread expansion of grasslands swept the face of the continent, faunal lineages expanded and disappeared, and hominins diversified and spread (Faith et al., 2024).

2.2.1 Climate change

As discussed earlier, climate change has long been cited as a driver of large-scale mammal extinctions, and this is no different for eastern Africa over the last six million year (e.g., Vrba, 1988). Multiple processes interacting over different spatiotemporal scales have influenced major climate changes in this region. Orbital-scale precession created a monsoonal climate in eastern Africa prior to 2.8 Ma (deMenocal, 2004). After 2.8 Ma, marine proxies record a smaller-scale driver that interacted with the monsoonal climate: high-latitude glacial periods at 2.8 Ma, 1.7 Ma, and 1.0 Ma, which coincided with more arid, cool, and variable climates (deMenocal, 2004). Overall, the marine sediment record documented recurring humid-arid climate cycles on a continental scale over the last five million years, superimposed on a long-term increase in overall aridity (deMenocal, 2004). Terrestrial paleoclimatic proxies tell a seemingly contradictory tale: lake sediments suggest that eastern Africa had large, fluctuating lakes during this period, indicative of wetter and seasonal regional conditions (Trauth et al., 2009).

2.2.2 Vegetation change

Climate change precipitated changes in the vegetation of eastern Africa during the last six million years (Levin, 2015). Some researchers have implicated vegetation change in the

extinction of mammals during this period rather than hominins (Bibi & Cantalapiedra, 2023; Faith et al., 2018).

The Pliocene began as a warm period approximately 5.3 Ma (Wara et al., 2005), with rainforests potentially reaching into areas of eastern Africa (Williamson, 1985). After 3.5 Ma, temperatures dropped and aridification periods led to the formation of diverse mosaic environments, with gradients of forests and grassy floodplains (Wynn, 2004). Arid-adapted plants such as shrubs, heath, and grasses expanded and diversified after 3 Ma (deMenocal, 2004). The expansion of C₄ grasslands was one of the key continental changes in Africa during the late Cenozoic (Levin, 2015). While some localities in Africa had abundant C₄ grasslands in the Early Miocene (Peppe et al., 2023), it was not until the late Pliocene and the early Pleistocene that majority grassland ecosystems were established in eastern Africa (Cerling et al., 1988). Pedogenic carbonate evidence from the Turkana and Olduvai basins suggest a replacement of woodland by open savannah grasslands between 3-1 Ma, with marked increase in grasslands at 1.8 and 1.2 Ma (Cerling et al., 1988; Levin, 2015; Levin et al., 2004).

2.2.3 Mammal turnover

Before synthesizing mammal turnover, it is important to note biases in the mammal fossil record. Much of the known fossil record from Plio-Pleistocene eastern Africa originates from limited areas in the East African Rift System, which represents only a tiny fraction of the eastern African region and the continent (Barr & Wood, 2024). Additionally, there is an incomplete sampling of regions and sites within the rift which is due in part to differential fossil preservation and sampling effort (Faith et al., 2021). The nature of the incomplete fossil record necessarily means that the spatial and temporal ranges of taxa are always underestimated. First appearance datums (FAD) are younger than true origination dates and last appearance datums (LAD) are

older than true extinction dates, and observed geographic ranges are smaller than their true counterparts (Foote & Raup, 1996). Therefore, while drawing conclusions about turnover during this time, this potential bias should be kept in mind.

There have been a few clear patterns of mammal turnover in eastern Africa over the last six million years. First, there was long-term change in megaherbivore diversity over the last 7 Ma, with a steady decline beginning ~4.6 Ma (Faith et al., 2018). Second, since ~3 Ma, there was a decline in species endemism and beta diversity levels, which measures how compositionally distinct communities are among sites (Rowan et al., 2024). Endemic losses were mainly found in browsers, frugivores, and taxa over 1000 kg (Rowan et al., 2024). Data from the Afar, Turkana Basin, and the Southern Rift of southern Kenya and northern Tanzania revealed an overall loss of mixed feeders and browsers after ~3 Ma and an increase in taxonomic richness of grazers (Reed, 1997). This loss of mixed feeders and the increasing number of grazing species shared between sites drove beta diversity down (Rowan et al., 2024).

The transition towards more shared grazing species coincided with the regional expansion of C4 grasslands and the loss of woodlands (Rowan et al., 2024). Some researchers argue that the expansion of grasslands can account for the taxonomic richness of grazers and that the loss of woodlands that browsers and frugivores depended on drove their extinction (Vrba, 1988). Complicating the close association between expanding grasslands and increasing taxonomic richness in grazers is the sharp decline of nonruminant grazers, including hindgut fermenters like suids and equids at 1 Ma despite evidence for growing grasslands at this time (Faith et al., 2019). Ruminant grazers expanded during this time, especially the family Bovidae, a highly diverse and flexible group. Members of Bovidae associated with open and grassy environments including Alcelaphini and Antilopini expanded the most (Faith et al., 2024).

The mammal turnover trends most relevant for studies on ancient anthropogenic extinction hypotheses will be referred to in the context of the studies themselves. After providing a background on some of the trends in climate, environmental change, and mammal turnover in eastern Africa during our study period, we turn now to the ancient hominin in question.

2.3 *Homo erectus*

H. erectus has a relatively well-known fossil record, but our understanding of this species is constantly being molded and shaped by new discoveries and changing interpretations. The current perception of *H. erectus* is sometimes different than the perception of the species presented in ancient anthropogenic extinction literature. Given this, we will discuss our current understanding of *H. erectus* and how the interpretation of the species in ancient anthropogenic literature aligns with this understanding.

H. erectus appeared in eastern Africa approximately 2 Ma alongside contemporaneous hominin species including *Homo habilis* and *Paranthropus boisei*. Two of the earliest appearances of *H. erectus* in the fossil record were an infant mandible from Melka Kunture dated at ~ 2 Ma and a partial occipital bone from East Turkana dated at ~ 1.9 Ma (Hammond et al., 2021). After its appearance in eastern Africa, it quickly dispersed into western and eastern Asia (Anton, 2003).

The ancient anthropogenic extinction hypothesis literature presents a relatively simple picture of *H. erectus*. First, *H. erectus* is described as a hominin with marked change in cranial and postcranial morphology including larger relative brain sizes, larger bodies, and dedicated bipedal locomotion (Aiello & Wells, 2002; Surovell et al., 2005). It is also understood to signal a significant shift in hominins from an herbivorous diet to a diet of increased carnivory (Anton et al., 2014). The increase in carnivory is interpreted to result from hunting or kleptoparasitism in

the form of confrontational scavenging (Lewis & Werdelin, 2007). Finally, the species is described as the first hominin with complex cultures and a marked advance in technology which is understood to be related to the hunting and butchering of prey animals (Lyons et al., 2004).

New studies of *H. erectus* morphology present a more complicated view of its cranial adaptations. In general, *H. erectus* crania have been described with a low and angulated vault shape, moderate postorbital constriction, continuous and thickened supraorbital tori, and a sagittal keel (Anton, 2003). Though larger brain sizes are often associated with this species, cranial capacities showed significant variation. The range had been understood to be $\sim 725 \text{ cm}^3$ in eastern Africa to $\sim 1250 \text{ cm}^3$ in China and Indonesia (Anton, 2003; Wood, 2001), but recently published crania have changed this range. A 1.5 million-year-old cranium attributed to *H. erectus* from the Afar has an estimated cranial capacity of $\sim 598 \text{ cm}^3$ (Bruner et al., 2023). D4500 from Dmanisi, Georgia is attributed to *H. erectus* at $\sim 1.8 \text{ Ma}$ and has a cranial capacity of just $\sim 550 \text{ cm}^3$ (Rightmire et al., 2017). These cranial capacities are within the range of earlier species such as *Homo habilis* and could suggest that the difference in brain size between emerging *H. erectus* and earlier species such as *H. habilis* was more subtle than previously believed and not the milestone that is referenced in ancient anthropogenic extinction literature.

The ancient anthropogenic extinction literature relies on the idea that increased carnivory appeared with *H. erectus*. This increased carnivory has been cited as a driver of a larger brain, body, and reorganized gut (e.g. Milton, 1999), but recent literature argues that an increase in carnivory did not appear at 2 Ma. Barr et al. (2022) analyzed bone modifications in the zooarchaeological record of eastern Africa from 2.6 to 1.2 Ma. By using species richness as a proxy for sampling effort, they demonstrated that greater sampling effort resulted in the observed heightened appearance of carnivory. After controlling for sampling effort, they found bursts of

heightened carnivory, but no consistent, sustained increase after the first appearance of *H. erectus* at 2 Ma. These results did not exclude an increase of carnivory over the complete temporal range of *H. erectus*, but they suggest that increased carnivory could not be tied to its appearance at 2 Ma.

The ancient anthropogenic extinction literature also cites novelties in culture and technology with the appearance of *H. erectus* at 2 Ma. Recent literature has generally affirmed the temporal connection between the appearance of *H. erectus* and the appearance of the Acheulean industry. For example, the infant mandible from Melka Kunture dated at ~ 2 Ma was found in close proximity to a ~1.95 Ma layer which contains some of the earliest known Acheulean tools (Mussi et al., 2023). Younger Acheulean sites such as at Konso in Ethiopia and Kokiselei in Kenya dated at ~1.7 Ma are also interpreted to be *H. erectus* sites and support the idea that technological change emerged near the appearance of *H. erectus* in eastern Africa (Asfaw et al., 1992, 1992; Diez-Martín et al., 2015). While the Acheulean industry can generally be associated with early *H. erectus*, whether these tools can be confidently tied to carnivory and the processing of meat is still an open debate. Researchers such as Toth & Schick (2017) have argued that there is a connection. They cite experimental studies of Acheulean technology and argue that the production of hand axes and cleavers were used for large-mammal carcass butchery. Dominguez-Rodrigo & Pickering (2017) also argue that this industry marked an intensification of carnivory in hominins at ~2 Ma. While these studies support Acheulean tools as butchery tools, the interpretation of these tools as projectiles used directly for hunting is controversial and has little support (Samson, 2006).

Our understanding of *H. erectus* is constantly changing, but it is clear that the interpretation of this species presented in some of the ancient anthropogenic extinction literature

is an oversimplified or outdated view of this diverse and complex species. It is important to keep the current and complex understanding of *H. erectus* in mind while evaluating ancient anthropogenic extinction hypotheses.

2.4 Ancient anthropogenic extinction hypotheses

Recently, researchers have posed a new framework to address extinctions in Africa and Eurasia during the early Pleistocene: *ancient* anthropogenic extinction (Faith et al., 2020).

‘Ancient’ has yet to be precisely defined under this framework but generally refers to hominins before *H. sapiens* (Lyons et al., 2004; Surovell et al., 2005). The hominin most often implicated by supporters of ancient anthropogenic extinction models is *H. erectus* (Lewis & Werdelin, 2007; Lyons et al., 2004; Surovell et al., 2005). *H. erectus* has been cited as the first hominin with a suite of adaptations that make it a reasonable candidate for an extinction driver: large body size, longer life history, fully terrestrial, new stone tool industry, and substantial meat consumption (Antón et al., 2014).

Ancient hominin extinction hypotheses take two general forms: one casting hominins as direct drivers of large mammal demise through overkill, and the other implicating the entrance of *H. erectus* into the carnivore guild as an indirect driver (Faith et al., 2020). Here, we synthesize studies that have addressed ancient anthropogenic extinction hypotheses, as well as the evidence cited to support or refute these hypotheses.

2.4.1 Ancient anthropogenic extinction literature

Some researchers argue that *H. erectus* directly drove large mammals to extinction by overkill and cite proboscidean extinctions in eastern Africa as evidence to support this claim. Lyons et al. (2004) argued that the late Pleistocene extinctions in Africa were less severe than on other continents because *H. erectus* had already driven size-biased extinctions earlier in time.

They pointed to 10 species of proboscideans that went extinct between the early and middle Pleistocene and argued that these species were victims of *H. erectus* as its culture, technology, and hunting prowess emerged. Surovell et al. (2005) also argued that *H. erectus* could have been responsible for proboscidean extinctions as early as 1 Ma highlighting the extinction of *Deinotherium* and *Elephas*. They reasoned that these extinctions coincided with archeological evidence of butchery. Weakening the argument of this study and of Lyons et al. (2004) was the subsequent demonstration that African proboscidean diversity had been steadily declining since the late Miocene, and that several species cited as potential victims of *H. erectus* went extinct before its appearance (Sanders, 2011).

Other researchers argue that *H. erectus* drove large carnivores to extinction by outcompeting them for prey. Lewis & Werdelin (2007) found that large carnivore species richness declined between 3.0 Ma and 0.9 Ma and that extinction rates increased conspicuously after 1.8 Ma. They argued that the anti-predator strategies of *H. erectus* and its hunting prowess could have contributed to depressed origination rates and increased extinction rates in carnivores. Werdelin & Lewis (2013) found that the large carnivore guild (> 21.5 kg) lost 99 percent of its functional richness after 3.5 Ma. They argued that emerging hominin hunting and competition reduced carnivore functional richness, and discounted climatic and ecological changes as drivers. However, neither of these studies accounted for variable sampling effort in their analysis of richness and taxonomic rates, which raises question about these proposed associations. Fortelius et al. (2016) found a spike in extinction rates for carnivores between 2 Ma to 2.2 Ma that was unmatched in the non-carnivoran record and suggested that the emergence of technologically advanced hominins triggered a trophic cascade which decimated the carnivoran community. Faurby et al. (2020) reported that carnivoran extinction rates corresponded with hominin brain

size increase. They suggested that earlier hominin traits like kleptoparasitism and scavenging enabled hominins to compete predators as early as 4 Ma. Closer to 2 Ma, more sophisticated tools, high population density, more reliance on animal protein, and enhanced cognition enabled hominins to outcompete predators through hunting.

Some researchers reject the idea that *H. erectus* was driving size-biased extinctions during this time. Faith et al. (2018) analyzed trends in eastern African megaherbivore community richness in relation to hominin evolution and found that megaherbivore diversity began declining ~ 4.6 Ma, which significantly predates hominins capable of top-down control (e.g. reducing the abundance of prey species through hunting). They argued that the expansion of C₄ grassland was the main driver of megaherbivore richness decline, given the temporal link between these two records and the fact that the majority of megaherbivore species incorporated browse in their diet (Faith et al., 2020). Bibi & Cantalapiedra (2023) analyzed body mass and mass-abundance distributions for African large mammal communities since the late Miocene. Their results support a model of extinction where vegetation change resulted in larger body sizes being less efficient when converting energy to biomass. They report the decline of megafauna beginning at ~ 4 Ma, which predated any hominin that could have feasibly exerted top-down control and refuted ancient anthropogenic extinction hypotheses on this basis.

CHAPTER 3 – MATERIALS AND METHODS

3.1 Data collection

To test the hypothesis that elevated extinction rates for large mammal species began with the appearance of *H. erectus*, we analyzed patterns in the eastern African mammal record over the last six million years of hominin evolution. ‘Eastern Africa’ is here defined as present-day Ethiopia, Kenya, and Tanzania (Fig. 1). All fossil record data and body mass estimates analyzed in this study were collected from published literature (Bibi & Cantalapiedra, 2023; Lariviere & Calzada, 2001; Grohé et al., 2022; IUCN, 2015; Jones et al., 2009; Larivière, 2001; Smith et al., 2004; Palmqvist et al., 2002; Rowan et al., 2024; Sillero-Zubiri et al., 2004).

3.1.1 Presence-absence data

We collected presence-absence data from a dataset of mammal species published by Rowan et al. (2024). Rowan et al. (2024) included mammal species belonging to the orders Artiodactyla, Carnivora, Hyracoidea, Perissodactyla, Primates, Proboscidea, and Tubulidentata. This dataset included 341 species of large mammal species from 95 fossil units of eastern Africa, spanning the last six million years. We created a species-by-time matrix from this presence-absence dataset (Table 2), using R code adapted from Cohen et al. (2022).

Each row in our species-by-time matrix represented one species, and each column represented one time bin. We binned the fossil units into 12 bins of 500,000 years each. For each element in our matrix, we denoted the presence or absence of each species for each time bin with

a 1 and 0, respectively. Each time bin had an average of approximately 58 species present. The number of species in each time bin is represented in Figure 2.

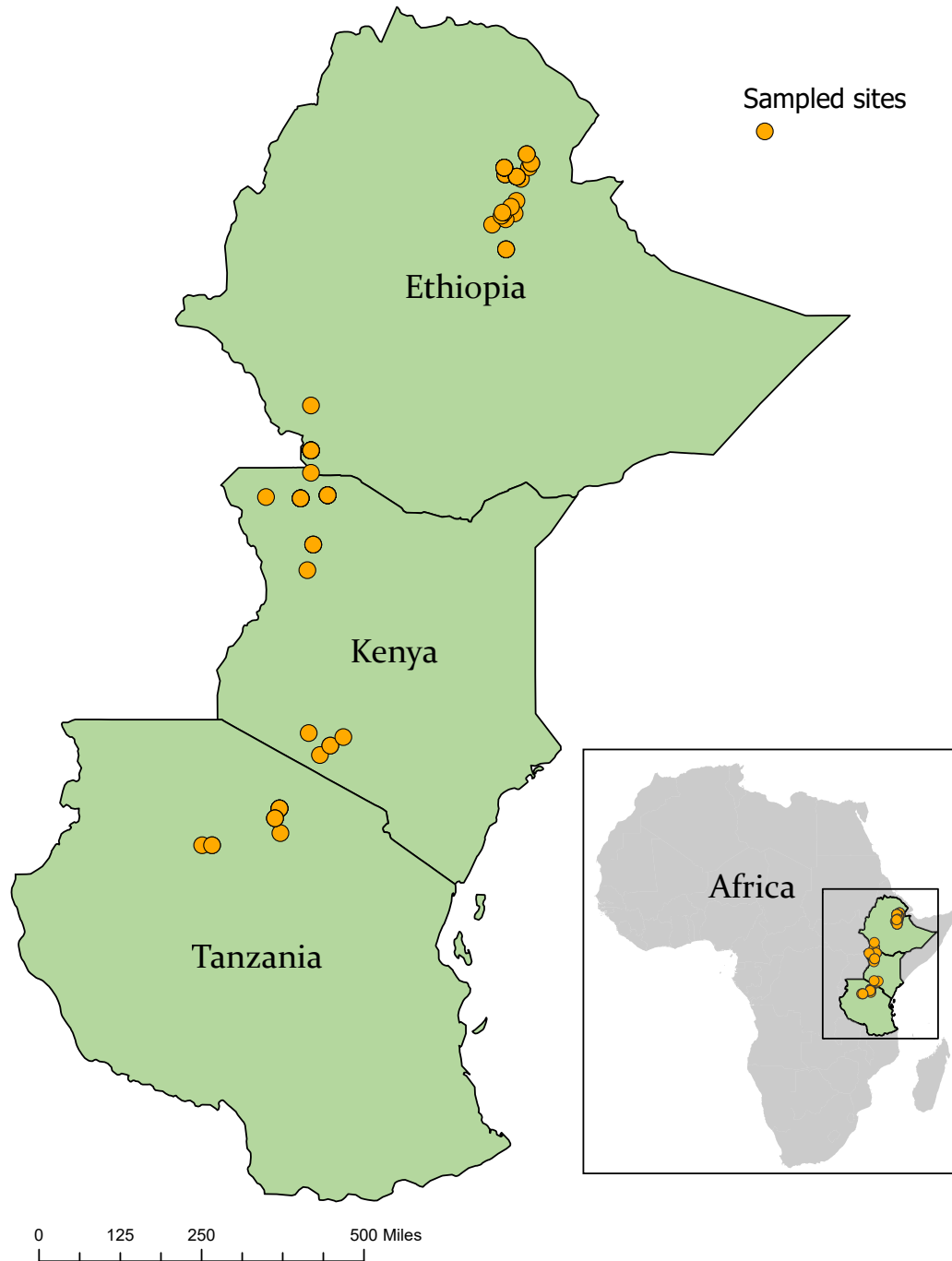


Figure 1: A map of the sites included in the Rowan et al. (2024) presence-absence data (ArcGIS Hub).

Table 2: A sample of the species-by-time matrix that we created from the Rowan et al. (2024) presence-absence data

Species	5.5-6 Ma	5-5.5 Ma	4.5-5 Ma	4-4.5 Ma	3.5-4 Ma	3-3.5 Ma	2.5-3 Ma	2-2.5 Ma	1.5-2 Ma	1-1.5 Ma	0.5-1 Ma	0.0- 0.5 Ma
<i>Aepyceros shungurae</i>	0	0	0	0	1	1	1	1	0	0	0	0
<i>Herpestes ichneumon</i>	0	0	0	0	1	0	0	0	0	0	1	0
<i>Oryx beisa</i>	0	0	0	0	0	0	0	0	0	0	1	1

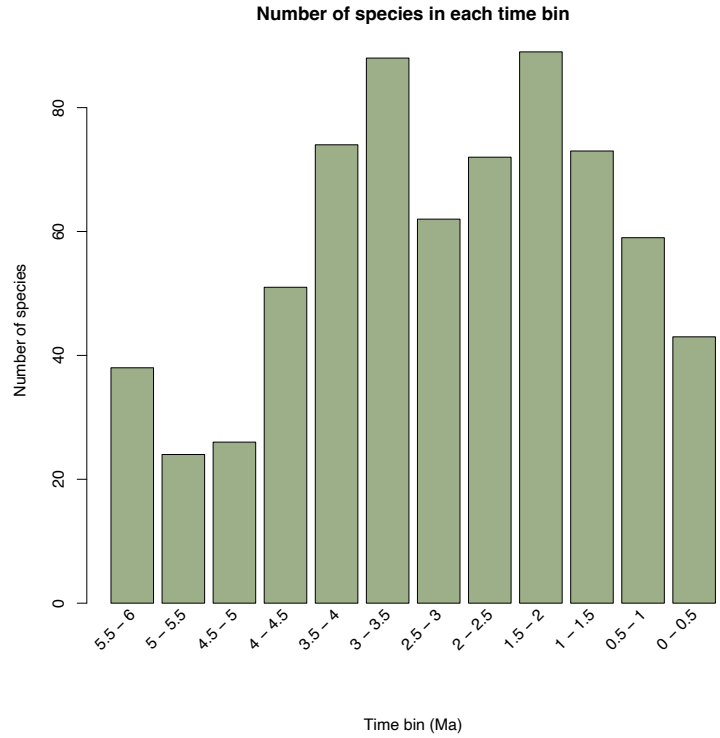


Figure 2: A bar plot representing the total number of species in each time bin

3.1.2 Body mass estimates

We collected body mass estimates for the species included in our species-by-time matrix from published data (Bibi & Cantalapiedra, 2023; Lariviere & Calzada, 2001; Grohé et al., 2022; IUCN, 2015; Jones et al., 2009; Larivière, 2001; Smith et al., 2004; Palmqvist et al., 2002; Sillero-Zubiri et al.). We collected approximately eight percent of the body mass estimates from the Macroecological Database of Mammalian Body Mass (MOM) (Smith et al., 2004). The MOM dataset included estimates for extant and extinct taxa, including members of Artiodactyla, Carnivora, Hydracoidea, Perissodactyla, Primates, Proboscidea, and Tubulidentata (Smith et al., 2004). We collected approximately eighty percent of estimates from the Mammal Dental Metric Dataset (Bibi & Cantalapiedra, 2023). The Mammal Dental Metric Dataset included dental metrics of extinct and extant African and Arabian large herbivorous mammals, including Artiodactyla, Perissodactyla, Proboscidea, and Primates (Bibi & Cantalapiedra, 2023).

This dataset incorporated body mass estimates of extant animals from the Pantheria database (Jones et al., 2009). Body mass estimates for extinct taxa were made using a fit of average species body mass to tooth length of extant taxa (Bibi & Cantalapiedra, 2023). Bibi and Cantalapiedra developed three prediction fits for making body mass estimates. The single fit method analyzed all taxa together, irrespective of taxonomic affiliation. The order-level fit was more taxon-specific and allowed varying allometric relationships between clades. The third fit included order-level fits for Artiodactyla, Perissodactyla, and Primates, but used single fits for Proboscidea. The authors noted that their results were not affected by changing the approach. We used the order-level and single-fit for Proboscidea body mass estimates for this study.

3.1.3 Excluded data

The original Rowan et al. (2024) dataset included 341 species. We excluded eight species from our species-by-time matrix because they had no presence data. We collected species-level

mass estimates for 182 of the remaining species. For 97 extinct species without species-level estimates, we used the average body mass estimate of extinct congeners. In situations where body mass estimates could not be found for the species or for genus members, the species was excluded from our dataset; this affected 54 species. Our resulting species-by-time matrix included 279 species, representing approximately 82 percent of the species included by Rowan et al. (2024).

3.2 The modeling framework

Our goal was to understand how body mass affected extinction probability through time. Because we also wanted to account for sampling and preservation biases in the fossil record—by estimating detection probability—we employed capture-mark-recapture (CMR) methods, specifically the Cormack-Jolly-Seber (CJS) model, implemented in a Bayesian framework. Detection probability under the CMR framework can be interpreted as the proportion of taxa detected out of the total number of taxa inferred to be extant during that time bin (Liow & Nichols, 2010). This will be explained in greater detail below.

3.2.1 Understanding CMR methods

CMR is a flexible model of inference used in a variety of disciplines including human demography, life-history, community ecology, and paleoecology (Lindberg, 2012). At its core, this framework is designed to tackle a fundamental issue in all of these disciplines: the issue of incomplete observations, which can bias quantities of interest (Liow & Nichols, 2010). For example, paleoecologists cannot sample all taxa of interest due to incomplete fossil preservation and limited fieldwork, which in turn can bias estimates of origination and extinction dates of taxa (Faith et al., 2021). CMR accounts for biases in such data by modeling the ecological processes

of interest to researchers *and* the biasing processes that give rise to the data (e.g., taphonomic processes) (Liow & Nichols, 2010).

In neoecology, these methods are the most common statistical methods used to investigate survival in animal populations, estimating survival and capture-recapture probabilities (Kéry & Schaub, 2012). In these survival studies, a subset of a population of animals is captured, marked, and released. After a set time interval passes, a new subset of this population is captured, marked, and released. As this process is repeated, an individual's capture history is recorded, and survival and detection probabilities can be estimated for the population.

This process and its related concepts can be modified to accommodate the fossil record (Liow & Nichols, 2010). While neoecological survival studies are based on the capture, marking, and recapture of individuals through time, paleoecological studies are based on the detection or non-detection of fossil taxa at different geological ages. Inferences are typically made at the taxonomic level (e.g., species) rather than the individual level (Liow & Nichols, 2010). The first detection of a fossil taxon in time is analogous with the first capture and marking of a live animal. Rather than being 'marked', the fossil taxon is detected and recorded. A fossil detection history replaces the individual recapture history of neoecological studies. While neoecological models measure births and deaths of individuals, paleoecological studies consider origination and extinction of taxa (Liow & Nichols, 2010).

Assumptions for neoecological CMR studies can likewise be modified for the fossil record (Liow & Nichols, 2010). These include the assumption that marked individuals are representative of the population of interest, individuals are identified without error, and the fate of a marked animal is independent of the fate of another marked animal (Kéry & Schaub, 2012). In paleoecological systems, a detected taxon is assumed to be representative of the larger fossil

assemblage and identified without error (e.g., the taxon is identified correctly), and the extinction of one taxon has no bearing on the extinction of other taxa. The violation of these assumptions can bias parameter estimations (Kéry & Schaub, 2012). Assumptions not directly related to the fossil record include the stipulation that markers do not affect the behavior or survival of the marked individuals, and that markers are not lost or misidentified (Lindberg, 2012).

The application of CMR methods to the fossil record can be explained with a hypothetical scenario for clarity (Fig. 3). Imagine that a sampling area of interest includes fossil units which capture a temporal range that is divided into equal bins: Bin 1, Bin 2, Bin 3, Bin 4 and Bin 5. Bin 1 is the oldest bin and Bin 5 is the youngest. For simplicity, the species present in this time and sampling area are known only as a species of zebra, monkey, and giraffe. We record the detection history for our three species of interest, starting with the zebra.

	Time Bin 1	Time Bin 2	Time Bin 3	Time Bin 4	Time Bin 5	
	Detected 1	Not detected 0	Not detected 0	Detected 1	Not detected 0	 Detected in this time bin
	Detected 1	Detected 1	Not detected 0	Detected 1	Detected 1	 Inferred to be a false absence: interpreted as extant
	Detected 1	Not detected 0	Detected 1	Not detected 0	Not detected 0	 Inferred to be true absence: interpreted as extinct
	Bin 1 detection probability: 3/3 = 1.0	Bin 2 detection probability: 1/3 = 0.33	Bin 3 detection probability: 1/3 = 0.33	Bin 4 detection probability: 2/2 = 1.0	Bin 5 detection probability: 1/1 = 1/0	Bin detection probability = $\frac{\text{Number detected}}{\text{Number inferred extant}}$

Figure 3: A graphic representing how CMR is applied to the fossil record

The zebra is first detected during Bin 1, and its detection is denoted with a '1'. This detection is assumed to be true, meaning that the species was identified without error. The zebra is not detected during Bin 2 or 3, and its apparent absences are denoted with a '0'. These apparent absences could represent true or false absences. A true absence would mean that the zebra was not present at the study site during Bin 2 or 3. A false absence would mean that the zebra was present but not detected. False absences are due to a number of factors including poor preservation conditions or low sampling intensity (Blasco-Moreno et al., 2019). The zebra is detected during Bin 4, and its detection is denoted with a '1'. We allow the detection during Bin 1 and 4 to inform the status of the apparent absences at Bin 2 and 3: we assume that the zebra was indeed present during Bin 2 and 3 and that these apparent absences are false absences. We can make this assumption based on our sampling area (i.e., eastern Africa): with a large sampling area, it is more parsimonious to assume that the zebra was present but not detected in Bin 2 and 3 than to assume the entire species dispersed out of the sampling area after Bin 1 and returned en masse in Bin 4.

We record the detection histories for the monkey and the giraffe in like manner. The combined detection histories of the zebra, monkey, and giraffe allow us to calculate detection probabilities for each time bin, which equals the number of taxa detected in that bin divided by the number of taxa inferred to be extant in that bin. With this, we can estimate survival and extinction probabilities for these taxa, while accounting for detection bias.

The CMR framework includes an expansive group of models, from which we chose the open-population model known as the CJS model (Kéry & Schaub, 2012).

3.2.2 Understanding the CJS model

The CJS model belongs to a class of open-population CMR models that condition on the first detection of a taxon (i.e., only processes after first detection are modeled) (Kéry & Schaub, 2012). It estimates survival probability (ϕ) and detection probability (p), where ϕ is the probability that a taxon survives from one time period to the next, while p is the probability that an individual was recorded, given that it was present at a given time period. Since we were interested in extinction rather than survival, we modified the CJS model to estimate extinction probability (ε), defined as one minus survival probability, or $\varepsilon = 1 - \phi$.

The CJS model for this study was designed using state-space likelihood, which can be generally described in the following way (the model is formally specified below). The binary state of a fossil species is extant or extinct. Species i is first detected at time t (Kéry & Schaub, 2012). It may survive until $t + 1$ with probability ϕ_t or it may go extinct between the time bins with probability ε_t , where $\varepsilon_t = 1 - \phi_t$. If species i is extant at $t + 1$, it may survive until $t + 2$ with probability ϕ_{t+1} or go extinct with probability ε_{t+1} . This process continues until the species is extinct or until the last time bin of the study (Kéry & Schaub, 2012). The observation process is conditional on this state process, giving the state-space model a hierarchical structure. If species i is extant at t , it will be detected with probability p_t , i.e., the detection probability (Kéry & Schaub, 2012). Once the species is extinct, it will not be detected in the fossil record in later time bins.

The CJS model can be fit using a frequentist or Bayesian framework; we use the latter (Kéry & Schaub, 2012).

3.2.3 Understanding Bayesian analysis

We leveraged Bayesian analysis to tackle a key issue in our study: we wanted to make inferences about unobserved process based on the observed data (Hobbs & Hooten, 2015). A central tenet of Bayesian inference is its treatment of observed and unobserved quantities. Under this framework, observed quantities (i.e., data) are treated as fixed. Unobserved quantities including model parameters, latent states, and missing data are treated as random variables (Hobbs & Hooten, 2015). We wanted to learn about unobserved quantities including extinction probability, detection probability, and the true state of a species, so we treated them as random variables. In accordance with Bayesian inference, the behavior of these random variables was governed by probability distributions (Hobbs & Hooten, 2015).

Bayesian analysis uses three rules of probability to reveal the characteristics of these probability distributions: the rule of conditional probability, the rule of total probability, and the chain rule of probability (Hobbs & Hooten, 2015). The basis of Bayesian analysis is Bayes' Theorem which can be derived with the three rules of probability. Bayes' Theorem states that the probability of the parameters given the data (the posterior distribution) is equal to the joint probability of the parameters and the data, divided by the marginal distribution of the data (Hobbs & Hooten, 2015). The marginal distribution serves as a normalizing constant to ensure that the posterior distribution integrates to 1. The joint distribution is comprised of the likelihood and the prior distributions of unobserved quantities. The likelihood and priors used in our CJS model will be discussed later.

3.3 The model

To analyze extinction probability as a function of species' body mass for a given time bin, we built a CJS model in a Bayesian hierarchical framework. Code for the CJS model was

adapted from Kéry & Schaub (2012). A Bayesian network or directed acyclic graph specifies how the joint distribution of our model was factored into conditional distributions (Hobbs & Hooten, 2015). Our Bayesian network and all symbol definitions used in our model are included below (Table 4) (Fig. 4).

Table 3: Symbol definitions, adapted in part from Liow & Nichols (2010).

Symbol	Definition
i	individual species
t	time bin
f_i	the time of first detection for species i
n	total number of species
T	total number of time bins
x_i	mass of species i ; the covariate which was log10-transformed and centered
$y_{i,t}$	observation for species i at time t (observed = 1/not observed = 0)
p_i	probability of detecting species i (does not vary through time)
$\varepsilon_{i,t}$	probability that species i goes extinct between t and the next time bin $t + 1$
$\phi_{i,t}$	probability of species i surviving between t and the next time bin $t + 1$
$z_{i,t}$	true state of species i at t (extant = 1/extinct = 0)
α_0	baseline odds of detection when $x_i = 0$ (mean log10 body mass), or intercept
α_1	effect of increasing body mass on detection probability, or slope
$\beta_{0,t}$	baseline odds of extinction when $x_i = 0$ (mean log10 body mass), or intercept
$\beta_{1,t}$	effect of increasing body mass on extinction probability, or slope
μ_0	mean of $\beta_{0,t}$ across time bins
σ_0^2	variance of $\beta_{0,t}$ across time bins
μ_1	mean of $\beta_{1,t}$ across time bins
σ_1^2	variance of $\beta_{1,t}$ across time bins

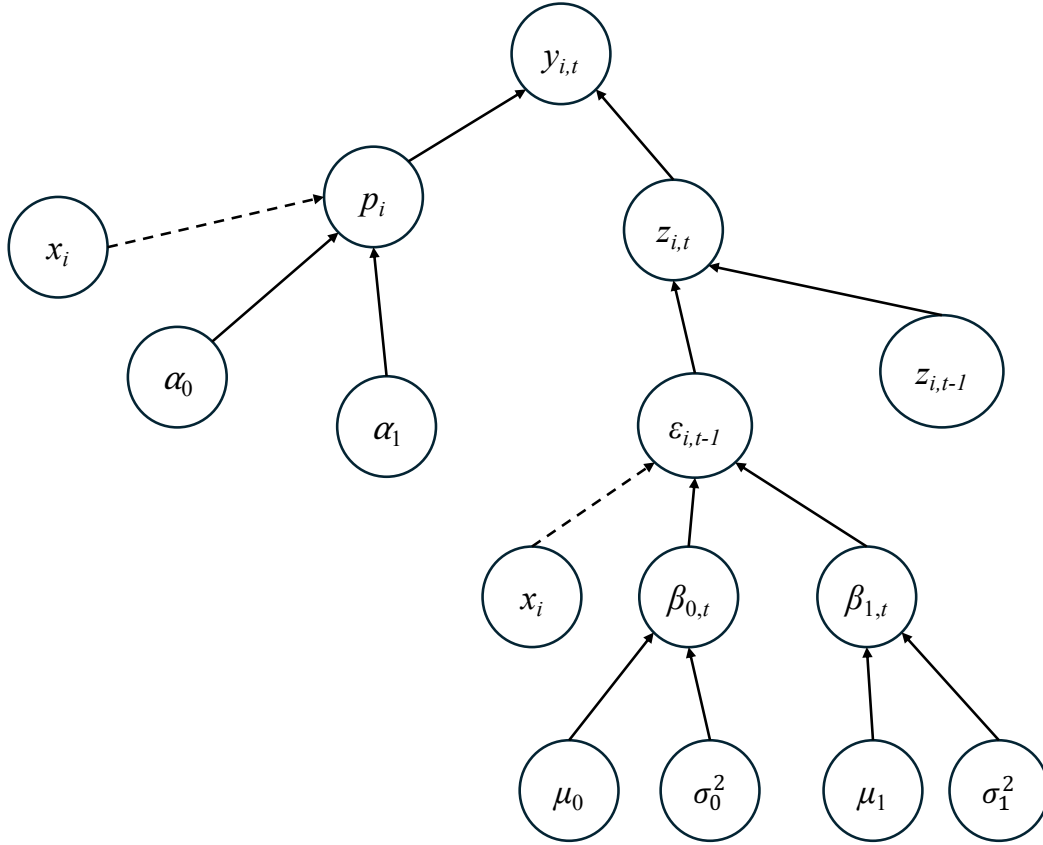


Figure 4: The Bayesian network for our model

We modeled the true state ($z_{i,t}$), observed data ($y_{i,t}$), detection process (p_i), and extinction process ($\epsilon_{i,t}$). Because a species going extinct and being detected can occur only when it is extant, the model conditions on the first detection of a species (when it is first known to be extant), which was noted and indexed as f_i (Kéry & Schaub, 2012). We then defined the state and the observation processes. The state process describes whether a species was extant or extinct ($z_{i,t} = 1$ and $z_{i,t} = 0$, respectively). The state of any species at its first detection is, by definition, extant:

$$z_{i,f_i} = 1 \quad (1)$$

The state of a species after first detection is conditional on its survival probability ($\phi_{i,t-1}$) and its true state ($z_{i,t-1}$) at the time step before. The state process was modeled as a Bernoulli trial and is defined by the equation below (Kéry & Schaub, 2012):

$$z_{i,t} \sim \text{Bernoulli}(z_{i,t-1}\phi_{i,t-1}) \quad \text{for } i = 1, \dots, n \quad (2)$$

$$\text{for } t = f_i + 1, \dots, T$$

Thus, if a species was extinct in the previous time bin ($z_{i,t-1} = 0$), the Bernoulli probability is zero, ensuring that the species is extinct in the current time bin ($z_{i,t} = 0$), as well as all time bins going forward. If the species was extant in the previous time bin ($z_{i,t-1} = 1$), the Bernoulli probability is the survival probability ($\phi_{i,t-1}$), meaning that the species remains extant in the current time bin ($z_{i,t} = 1$) with probability equal to the survival probability.

Next, we defined the observation process. The observation of a species in a time bin was conditional on the true state of the species during that time bin and its detection probability (Kéry & Schaub, 2011). The observation process was modeled with Bernoulli trials and is defined by the following equation (Kéry & Schaub, 2012):

$$y_{i,t} \sim \text{Bernoulli}(z_{i,t}p_i) \quad (3)$$

As a result, any species that was extinct during time t ($z_{i,t} = 0$) results in a Bernoulli probability that equals zero, meaning that the species will not be detected in the current time bin ($y_{i,t} = 0$) and all future time bins (the true state, $z_{i,t}$, equals zero for all future time bins following the logic in the previous paragraph). If the species was extant ($z_{i,t} = 1$), the Bernoulli probability is the

detection probability (p_i), meaning the species will be detected ($y_{i,t} = 1$) with probability equal to the detection probability.

Equations 1–3 represent the state and observation process. After defining these processes, we modeled the extinction and detection process as a function of body mass.

3.3.1 Extinction probability as a function of body mass

We modeled the probability of a species going extinct during a time bin as a logistic regression function of body mass. Body mass for all species was log10 transformed and then centered before fitting the model. The extinction process is defined by the equation below:

$$\begin{aligned} \text{logit}(\varepsilon_{i,t}) &= \beta_{0,t} + \beta_{1,t}x_i & \text{for } t = f_i, \dots, T - 1 \\ \varepsilon_{i,t} &= 1 - \phi_{i,t} \end{aligned} \quad (4)$$

Estimating intercepts ($\beta_{0,t}$) and slopes ($\beta_{1,t}$) independently for each time bin as fixed effects would have resulted in an overparameterized model that was at high risk of overfitting the data. Instead, we modeled time as a random effect, wherein the intercepts are drawn from a normal distribution with mean, μ_0 , and variance, σ_0^2 , and slopes are sampled from a normal distribution with mean, μ_1 , and variance, σ_1^2 :

$$\begin{aligned} \beta_{0,t} &\sim \text{Normal}(\mu_0, \sigma_0^2) \\ \beta_{1,t} &\sim \text{Normal}(\mu_1, \sigma_1^2) \end{aligned} \quad (5)$$

This random effects strategy not only makes our model less complex but also leverages the phenomenon of “borrowing strength” or “shrinkage”, where, e.g., intercepts estimated for

time bins with fewer species are informed by and made more precise by data from time bins with more species (Hobbs & Hooten, 2015).

3.3.2 Detection probability as a function of body mass

Our model accounts for incomplete fossil preservation and sampling by explicitly estimating detection probability for each species. Given studies that note taphonomic biases against smaller-sized mammals (e.g., Miller et al., 2014), we modeled detection probability as a logistic regression function with body mass as a covariate; body mass was log10-transformed and centered as before. Detection probability was allowed to vary by species, but not by time, and is defined as:

$$\text{logit}(p_i) = \alpha_0 + \alpha_1 x_i \quad (6)$$

3.3.3 Prior distributions for our parameters

We designated flat prior distributions for our σ_0^2 , σ_1^2 , μ_0 , μ_1 , α_0 , and α_1 parameters (Hobbs & Hooten, 2015). We assigned a normal distribution with a mean of 0 and a variance of 2.7 for α_0 and α_1 , which has been shown to provide a flat prior on p_i , given the logit transformation (Northrup & Gerber, 2018) (Equation 7).

$$\alpha_0 \sim \text{Normal}(0, 2.7) \quad (7)$$

$$\alpha_1 \sim \text{Normal}(0, 2.7)$$

We assigned uniform distributions with a minimum of zero and a maximum of 3.3 for the square-root of variance σ_0 and σ_1 (Equation 8).

$$\sigma_0 \sim \text{Uniform}(0, 3.3) \quad (8)$$

$$\sigma_1 \sim \text{Uniform}(0, 3.3)$$

We assigned a normal distribution with a mean of 0 and a variance of 25 for μ_0 and μ_1 (Equation 9).

$$\mu_0 \sim \text{Normal}(0, 25) \quad (9)$$

$$\mu_1 \sim \text{Normal}(0, 25)$$

We chose these hyperparameter values for σ_0 , σ_1 , μ_0 , and μ_1 , following a series of prior predictive simulations (McElreath, 2020). This process will be described in greater length in Section 3.4.

3.3.4 Probability distribution statement

The probability distribution statement below (Equations 10–11) illustrates the relationships outlined by the directed acyclic graph (Fig. 4). In accordance with Bayes' theorem, the posterior distribution is proportional to the likelihood distribution multiplied by the prior distributions. The likelihood and priors together make up the joint distribution (Equation 10), which is factored into conditional distributions (Equation 11).

$$\begin{aligned} & [\mathbf{p}, \mathbf{E}, \mathbf{Z}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\mu}, \boldsymbol{\sigma}^2 \mid \mathbf{Y}] \propto \\ & \left(\prod_{i=1}^n \prod_{t=f_i+1}^T [y_{i,t} \mid z_{i,t}, p_i] [z_{i,t} \mid z_{i,t-1}, \phi_{i,t-1}] [\beta_{0,t-1} \mid \mu_0, \sigma_0^2] [\beta_{1,t-1} \mid \mu_1, \sigma_1^2] \right) \\ & \times [\alpha_0][\alpha_1][\mu_0][\mu_1][\sigma_0^2][\sigma_1^2] \end{aligned} \quad (10)$$

$$\begin{aligned} & [\mathbf{p}, \mathbf{E}, \mathbf{Z}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\mu}, \boldsymbol{\sigma}^2 \mid \mathbf{Y}] \propto \\ & \left(\prod_{i=1}^n \prod_{t=f_i+1}^T \text{Bernoulli}(y_{i,t} \mid z_{i,t} p_i) \text{Bernoulli}(z_{i,t} \mid z_{i,t-1} \phi_{i,t-1}) \text{Normal}(\beta_{0,t-1} \mid \mu_0, \sigma_0^2) \text{Normal}(\beta_{1,t-1} \mid \mu_1, \sigma_1^2) \right) \\ & \times \text{Normal}(\alpha_0 \mid 0, 2.7) \text{Normal}(\alpha_1 \mid 0, 2.7) \text{Normal}(\mu_0 \mid 0, 25) \text{Normal}(\mu_1 \mid 0, 25) \end{aligned} \quad (11)$$

$$\times \text{Uniform}(\sigma_0 \mid 0, 3.3) \text{Uniform}(\sigma_1 \mid 0, 3.3)$$

$$\text{where } z_{i,f_i} = 1$$

$$\text{and } p_i = \frac{e^{\alpha_0 + \alpha_1 x_i}}{1 + e^{\alpha_0 + \alpha_1 x_i}}$$

$$\text{and } 1 - \phi_{i,t-1} = \varepsilon_{i,t-1} = \frac{e^{\beta_{0,t-1} + \beta_{1,t-1} x_i}}{1 + e^{\beta_{0,t-1} + \beta_{1,t-1} x_i}}$$

For our Markov chain Monte Carlo (MCMC) settings, we designated 3 chains of 10,000 iterations each. We set burn-in at 5,000, indicating the number of initial iterations that are discarded before the chain was saved (Hobbs & Hooten, 2015).

3.4 Prior predictive simulations

We conducted prior predictive simulations to ensure that we chose reasonable hyperparameter values for our prior distributions. These simulations are useful because it is difficult to predict what effects our chosen priors will have on unknown quantities at higher levels of our hierarchical model (McElreath, 2020). We first drew a random value for our μ and σ parameters from their assigned distributions. We then plugged these draws into the normal distributions assigned to β and drew a value for β_0 and β_1 . The β draws were then plugged into our logistic regression equation for extinction probability along with simulated body mass estimates. These steps were repeated for 100 iterations, and each simulated extinction probability was plotted against body mass. We plotted all 100 iterations together to see if our selected prior distributions allowed for a wide variety of relationships between extinction probability as a function of body mass (Fig. 5).

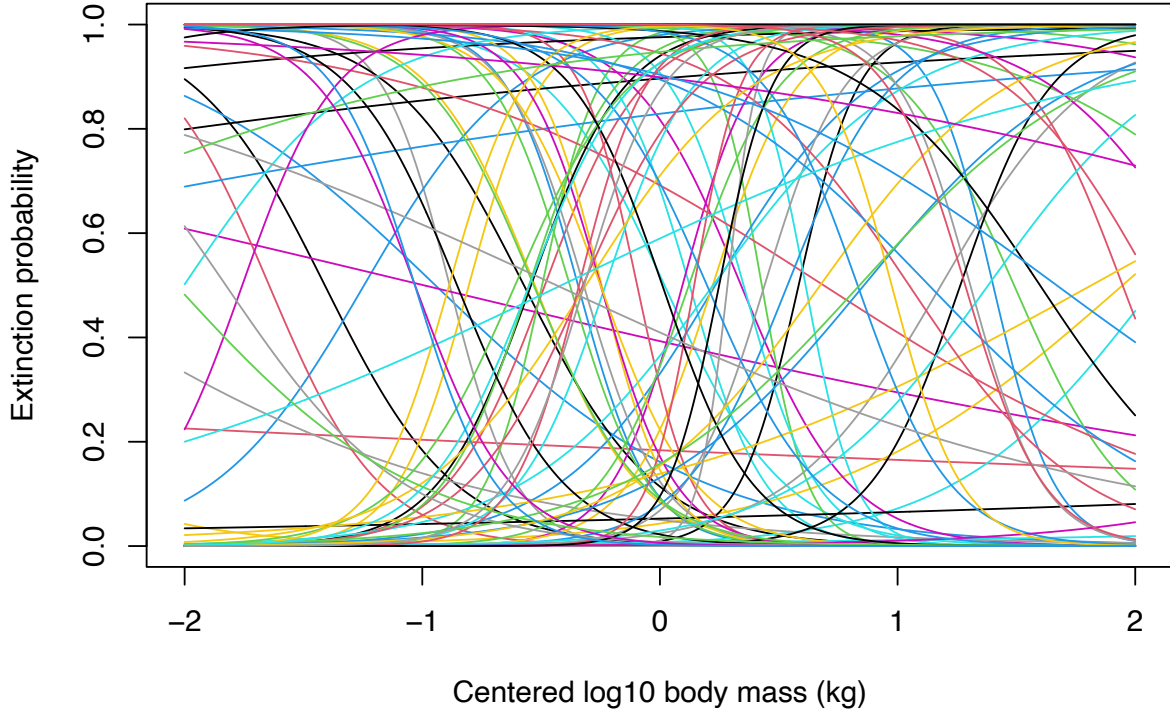


Figure 5: Prior predictive simulations, illustrating simulated relationships between extinction probability and body mass for our chosen prior distributions for μ and σ (100 iterations, wherein each color is a different iteration)

Our plot shows a variety of logistic function shapes, indicating that our choice of prior distributions results in a vague prior for the relationship between extinction probability and body mass (i.e., vague priors for $\beta_{0,t}$ and $\beta_{1,t}$). As a result, we are confident that our specified prior distributions are reasonable.

3.5 Data simulations

We wanted to check if our model was mathematically specified and coded correctly. First, we created an empty species-by-time matrix with dimensions identical to our observed species-by-time matrix: 12 time bins and 279 species. Then, we assigned a high detection probability of 0.82 and a high survival probability of 0.88. Using these set parameters, we simulated detection

histories for each species and filled our species-by-time matrix. We fit our model to this simulated dataset and found that our model could recover the prespecified parameter values, so we were confident that our model was accurately specified and coded.

3.6 Software

The model was fit using the Just Another Gibbs Sampler program (JAGS), which implements MCMC sampling using the Bayesian Analysis Using Gibbs Sampling (BUGS) language (Plummer, 2017). JAGS translates the joint distribution of Bayes' theorem into a specification of an MCMC sample (Hobbs & Hooten, 2015). It works by setting up proposal distributions, choosing values of tuning parameters, and returning the MCMC chain for each parameter. Inputs for JAGS include code for priors, the deterministic model, and the likelihood. JAGS was called from R using the 'R2jags' package. R version 4.5.2 and RStudio version 2026.01.1+403 were used for our analyses (R Core Team, 2026; Su & Yajima, 2008).

CHAPTER 4 – RESULTS

4.1 Model outputs

Our model allowed us to estimate species' extinction probability as a function of body mass through time, as well as detection probability as a function of body mass.

4.1.1 Extinction probability and size-selectivity

Extinction probability was modeled as a logistic regression, wherein β_0 represents the intercept. Since $\beta_{0,t}$ was allowed to vary through time, values were estimated for each time bin, where, for example, $\beta_{0,2}$ indicates the log-odds of extinction at mean log10 body mass going from time bin 2 to 3. This resulted in 11 values for β_0 . We exponentiated the log-odds estimates to convert to the odds scale and then converted from odds to probability for ease of interpretation (Fig. 6; Table 4). This represents the probability of extinction at species' mean log10 body mass for a given time bin, e.g., a value of 0.5 indicates that the probability of survival and extinction are equally likely.

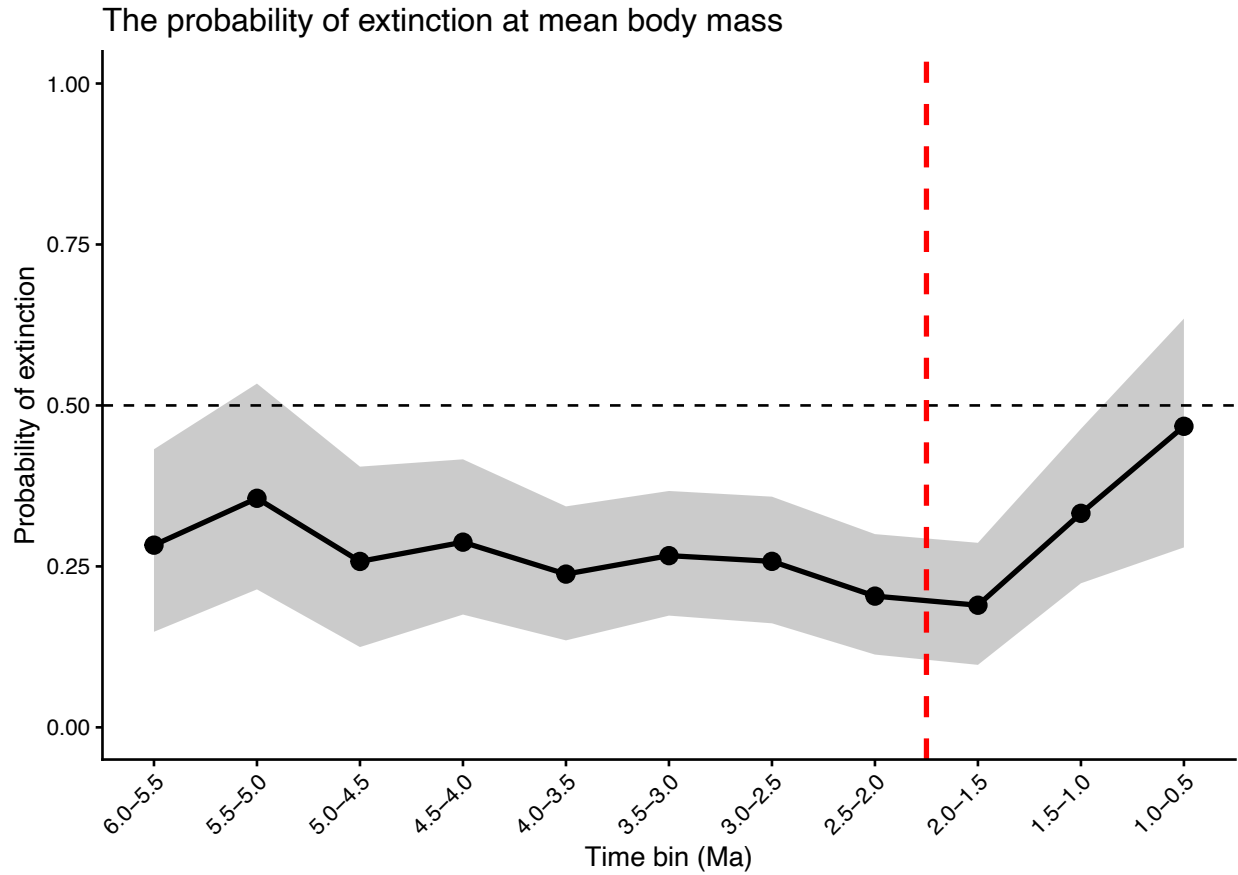


Figure 6: The log-odds intercept coefficients were converted to probability to represent the probability of extinction at species' mean log₁₀ body mass for each time bin. The gray shading represents the 95 percent credible interval, indicating that there is a 95 percent probability that the true parameter values fall in this region. The red dashed line represents approx. 2 Ma, the first appearance datum of *H. erectus*.

Table 4: The probability of extinction at species' mean log10 body mass for each time bin. Each $\beta_{0,t}$ is subset by the corresponding time bin number and then transformed into extinction probability, e.g., $\beta_{0,1}$ is the probability of extinction from 6.0 to 5.5 Ma.

<i>Parameter</i>	<i>Time bin (Ma)</i>	<i>Extinction probability</i>	<i>2.5%</i>	<i>97.5%</i>
$\beta_{0,1}$	6.0–5.5	0.28	0.15	0.43
$\beta_{0,2}$	5.5–5.0	0.36	0.21	0.53
$\beta_{0,3}$	5.0–4.5	0.25	0.12	0.40
$\beta_{0,4}$	4.5–4.0	0.29	0.17	0.42
$\beta_{0,5}$	4.0–3.5	0.23	0.14	0.34
$\beta_{0,6}$	3.5–3.0	0.27	0.17	0.37
$\beta_{0,7}$	3.0–2.5	0.26	0.16	0.36
$\beta_{0,8}$	2.5–2.0	0.20	0.11	0.30
$\beta_{0,9}$	2.0–1.5	0.19	0.10	0.29
$\beta_{0,10}$	1.5–1.0	0.33	0.22	0.46
$\beta_{0,11}$	1.0–0.5	0.46	0.28	0.63

All estimates range between 0.19 and 0.46, suggesting that survival was more likely than extinction for species at the mean log10 body mass over every time bin. The probability of extinction is stable from 5.0 Ma to 1.5 Ma, staying between 0.19 and 0.25. It reaches its lowest point of 0.19 between 2.0 and 1.5 Ma before a sharp increase between 1.5 and 0.5 Ma. The probability of extinction between 1.0 and 0.5 Ma reaches the highest point of 0.46, suggesting that extinction was nearly as likely as survival during this period for a species at the mean log10 body mass.

β_1 represents the slope or size-selectivity coefficient of the extinction regression model. Since $\beta_{1,t}$ was allowed to vary through time, values were estimated for each time bin, resulting in 11 values in β_1 . The slope indicates the effect of body mass on extinction probability in each time bin. We exponentiated the slope for interpretability to get the multiplicative change in odds of extinction as body mass increases by one order of magnitude (due to the log10 transformation of

body mass) (Fig. 7; Table 5). A $\beta_{1,t}$ value of 1 for a given time bin denotes no size-selectivity in extinctions. A value of 0.5, for example, indicates that the odds of extinction halve as body mass increases by one order of magnitude. A value of 2.0, on the other hand, means that the odds of extinction double as body mass increases by one order of magnitude. Put simply, $\beta_{1,t} < 1$ indicates that the odds of extinction decrease as body mass increases, whereas $\beta_{1,t} > 1$ means that the odds increase.

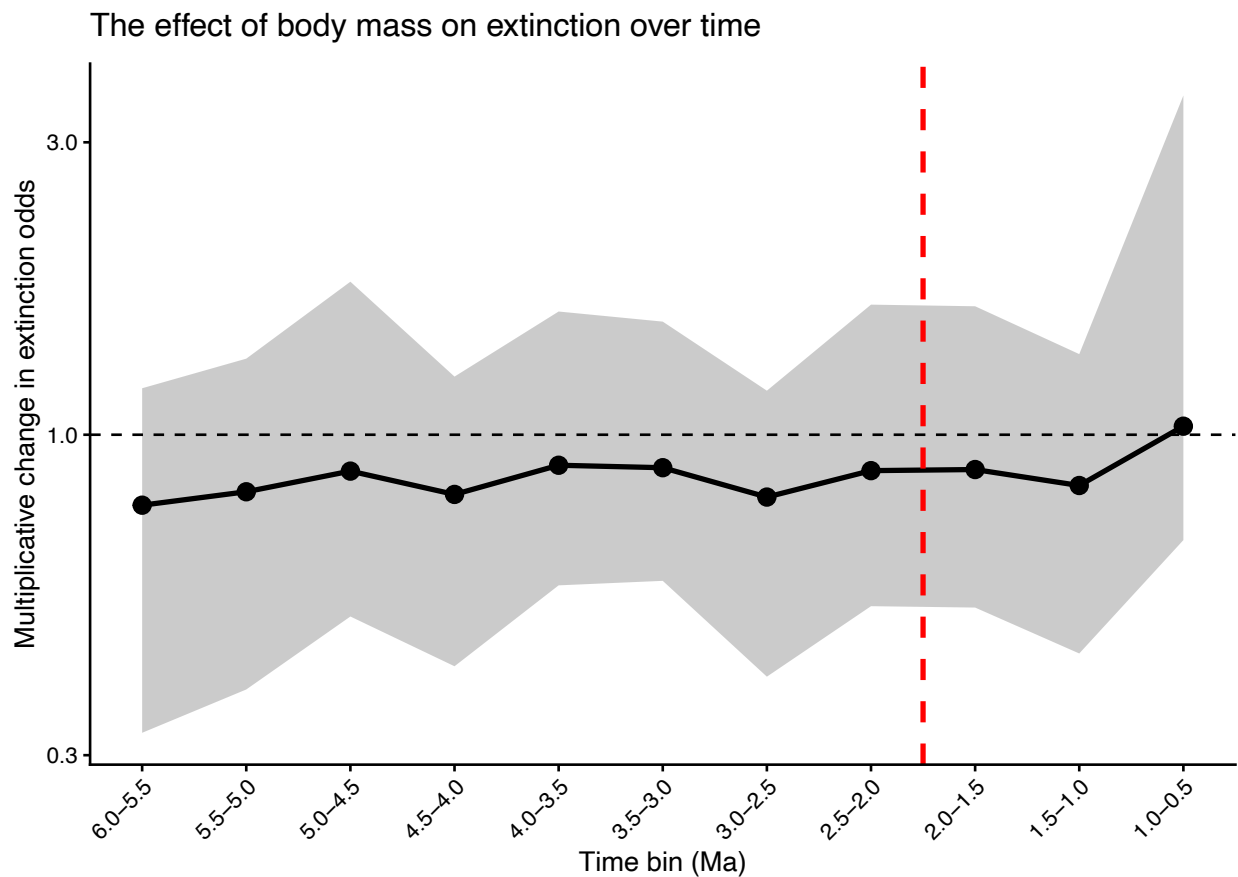


Figure 7: The log-odds slope coefficients were converted to the odds scale to represent in each time bin the multiplicative change in extinction odds as body mass increases by one order of magnitude. The 95 percent credible intervals are represented by the shaded polygon. The red dashed line represents approx. 2 Ma, the first appearance datum of *H. erectus*.

Table 5: The multiplicative change in extinction odds as body mass increases by one order of magnitude for every time bin.

<i>Parameter</i>	<i>Time bin (Ma)</i>	Multiplicative change in odds	2.5%	97.5%
$\beta_{1,1}$	6.0–5.5	0.76	0.33	1.19
$\beta_{1,2}$	5.5–5.0	0.81	0.39	1.33
$\beta_{1,3}$	5.0–4.5	0.94	0.51	1.78
$\beta_{1,4}$	4.5–4.0	0.80	0.42	1.24
$\beta_{1,5}$	4.0–3.5	0.94	0.57	1.59
$\beta_{1,6}$	3.5–3.0	0.93	0.58	1.52
$\beta_{1,7}$	3.0–2.5	0.79	0.40	1.18
$\beta_{1,8}$	2.5–2.0	0.92	0.53	1.63
$\beta_{1,9}$	2.0–1.5	0.93	0.52	1.62
$\beta_{1,10}$	1.5–1.0	0.84	0.44	1.35
$\beta_{1,11}$	1.0–0.5	1.30	0.67	3.58

Selectivity coefficients remained relatively stable from 6 Ma to 1 Ma, with values in the range between 0.72 and 0.81. These values below 1 suggest that smaller mammals had slightly greater odds of going extinct than larger mammals during this time period. Selectivity coefficients exceed one only during the 1.0–0.5 Ma time bin (1.16), indicating a slight size-selective bias against large mammals in extinctions during this period.

Given our focus on size-selectivity in extinction probabilities and leveraging the fact that Bayesian models produce posterior distributions that are true probability distributions (i.e., they integrate to one over their support), we can use our model results to estimate the probability that $\beta_{1,t}$ is positive (i.e., extinctions are size-selective) (Fig. 8; Table 6). A value of 0.5 for $\beta_{1,t}$ indicates that size-selective extinctions are just as likely to be positive as negative, i.e., it is equally likely that extinctions preferentially affect larger versus smaller mammals. $\beta_{1,t} > 0.5$ means that size-selectivity is more likely to be positive, i.e., extinction odds are higher for larger mammals.

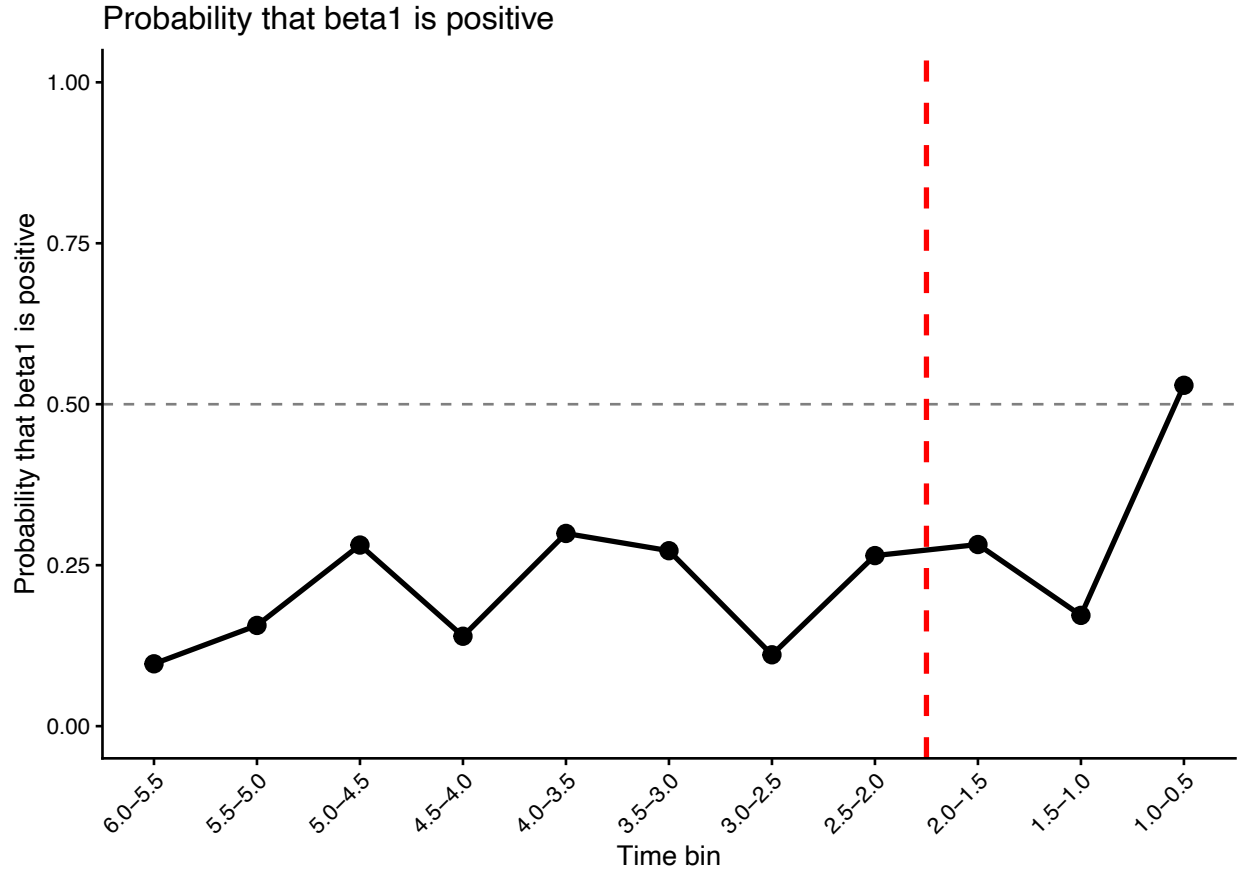


Figure 8: The probability that the selectivity coefficient, $\beta_{1,t}$, is greater than 0 for each time bin, i.e., the probability that extinctions are size-selective. The red dashed line represents approx. 2 Ma, the first appearance datum of *H. erectus*.

Table 6: The probability that the size-selectivity coefficient, $\beta_{1,t}$, is positive for each time bin.

<i>Time bin</i> (Ma)	Probability that $\beta_{1,t}$ is positive
6.0–5.5	0.10
5.5–5.0	0.16
5.0–4.5	0.28
4.5–4.0	0.14
4.0–3.5	0.30
3.5–3.0	0.27
3.0–2.5	0.11
2.5–2.0	0.26
2.0–1.5	0.28

1.5–1.0	0.17
1.0–0.5	0.53

The probability of $\beta_{1,t}$ being greater than 0 ranged from 0.10 to 0.53, indicating that the probability of extinction selecting for large mammals was relatively low for most of the time bins. The probability started at its lowest point of 0.10 in the time bin from 6.0 to 5.5 Ma and stayed relatively consistent between 6.0 and 1.0 Ma. It jumped to a high of 0.53 in the time bin from 1.0 to 0.5 Ma, indicating that there was a 53 percent chance that extinction selected for large mammals in this time bin.

4.1.2 Detection size-selectivity

Detection probability was modeled as a logistic regression, where α_0 represents the intercept and α_1 represents the slope or size-selectivity coefficient, and both are held constant through time (therefore, these are both scalars and not vectors). For ease of interpretation, we exponentiated these estimates to convert them from the log-odds to odds scale (Table 7).

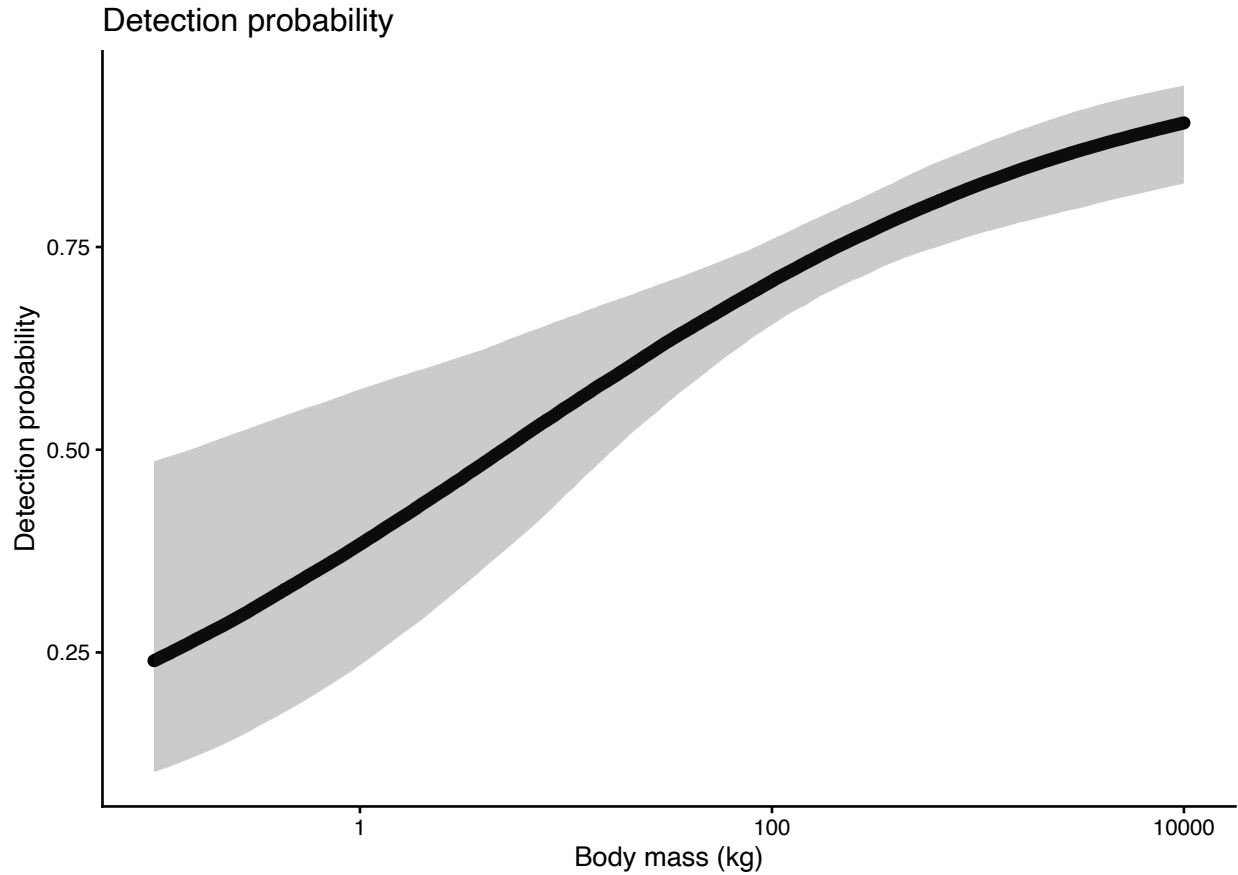


Figure 9: Plot of estimated detection probability as a function of body mass, given the estimated posterior distributions for α_0 and α_1

Table 7: Estimated parameter values for the detection probability logistic regression, presented in log-odds and odds scale.

Parameter	Log-odds	Odds	Probability
α_0	0.94	2.56	0.72
α_1	0.68	2.0	NA

The estimated parameter values indicate a positive relationship between detection probability and body mass (Table 7; Fig. 9). When transformed from the odds to probability scale, $\alpha_0 = 0.72$, indicating that when log10 body mass is at its average, a species' detection probability is 72 percent. The α_1 value of 2.0 on the odds scale means that as body mass increases by a factor of 10, the detection probability increases by a multiplier of 2x.

4.1.3 Parameter posteriors

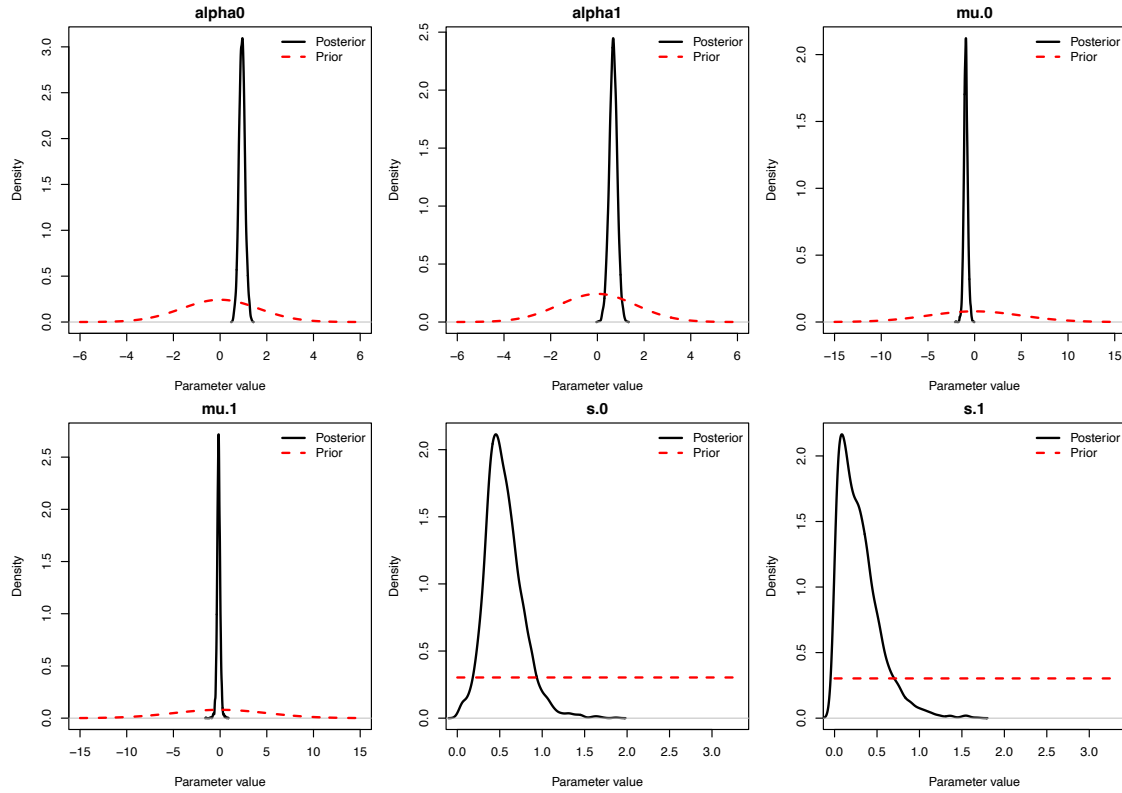


Figure 10: Density plots of estimated posterior distributions along with their prior distributions.

α_0 and α_1 are the detection probability regression intercept and slope, respectively. μ_0 is the regression intercept of extinction probability as a function of body mass, averaged over all time bins. The estimate for μ_1 is the extinction regression slope averaged across all time bins. σ_0 and σ_1 estimates indicate how much the intercept and slope varied across time bins, respectively. All parameters are presented on the log-odds scale.

By plotting the prior and posterior distributions together, we visualize how strongly our data shifted the posterior away from the prior (Fig. 10) (Hobbs & Hooten, 2015). Generally, our posteriors have shifted from their respective priors, indicating that our data had a strong influence on the posterior, the choice of prior distribution was not overly influential, and our model did not suffer from issues like non-identifiability (Gimenez et al., 2025). The μ_0 posterior estimate of -0.95 (on the log-odds scale) is the average intercept across all times bins for the

extinction probability as a function of body mass regression. The μ_1 estimate of -0.16 (on the log-odds scale) is the average extinction regression slope across all time bins, indicating extinction probability was higher for smaller mammals on average. The σ_0 estimate of 0.55 shows us that the extinction intercept was moderately variable across all time bins, and the σ_1 estimate of 0.29 shows us that that the extinction slope deviated even less across all time bins.

4.2 Model convergence

Gelman and Rubin diagnostics (Rhat) are the standard method for evaluating convergence of multiple MCMC chains (Gelman & Rubin, 1992). Rhat values indicate convergence if estimates approach 1 (Hobbs & Hooten, 2015). Values of more than 1.05 indicate the need for more iterations. Our Rhat values indicate that our chains converged well (Table 8).

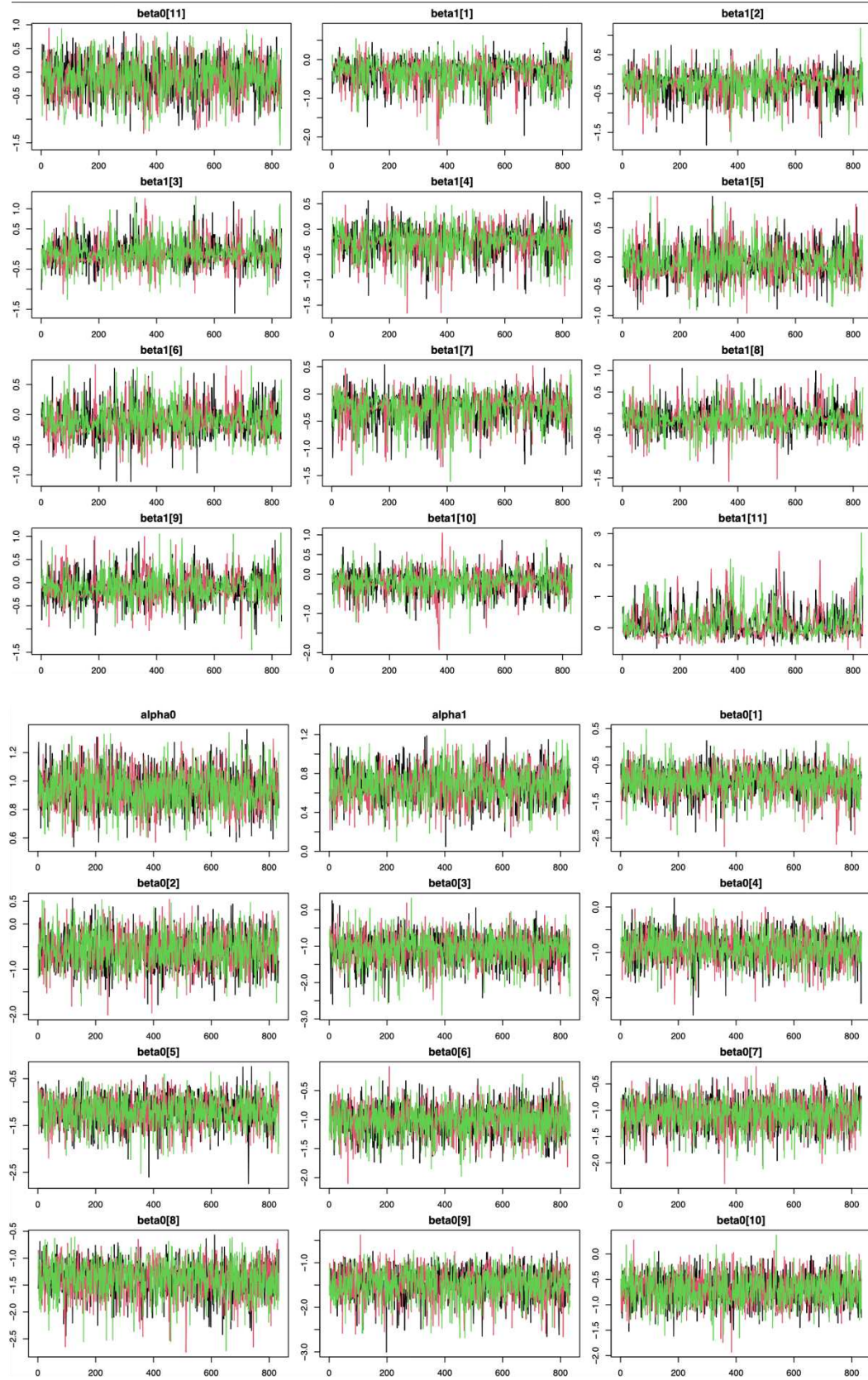
Effective sample size is related to the issue of autocorrelation in MCMC chains (Hobbs & Hooten, 2015). The effective sample size is an estimate of the number of independent samples drawn from the posterior distribution and is therefore smaller than the true sample size due to autocorrelation in a given MCMC chain. Small effective sample sizes indicate the need to increase the number of MCMC iterations for greater estimation accuracy (Hobbs & Hooten, 2015).

Table 8: Rhat values and effective sample sizes for model parameters

Parameter	Rhat values	Effective sample size
α_0	1	1662
α_1	1	1234
μ_0	1	2019
μ_1	1	1013
σ_0	1.01	1039
σ_1	1.01	237
$\beta_{0,1}$	1	2320
$\beta_{0,2}$	1	1964

$\beta_{0,3}$	1	2179
$\beta_{0,4}$	1	2063
$\beta_{0,5}$	1	1966
$\beta_{0,6}$	1	2125
$\beta_{0,7}$	1	2203
$\beta_{0,8}$	1	1822
$\beta_{0,9}$	1	1584
$\beta_{0,10}$	1	2355
$\beta_{0,11}$	1	1002
$\beta_{1,1}$	1	886
$\beta_{1,2}$	1	1597
$\beta_{1,3}$	1	1402
$\beta_{1,4}$	1	1296
$\beta_{1,5}$	1	1024
$\beta_{1,6}$	1	1243
$\beta_{1,7}$	1	921
$\beta_{1,8}$	1	1396
$\beta_{1,9}$	1.01	1261
$\beta_{1,10}$	1	1075
$\beta_{1,11}$	1	470

Trace plots show parameter estimates at each iteration in the MCMC chain over time (Hobbs & Hooten, 2015). Trace plots indicate convergence and good mixing when there is a horizontal band of overlapping chains, resembling a “fuzzy caterpillar”. Our trace plots indicate good convergence and mixing for our parameters (Fig. 11)



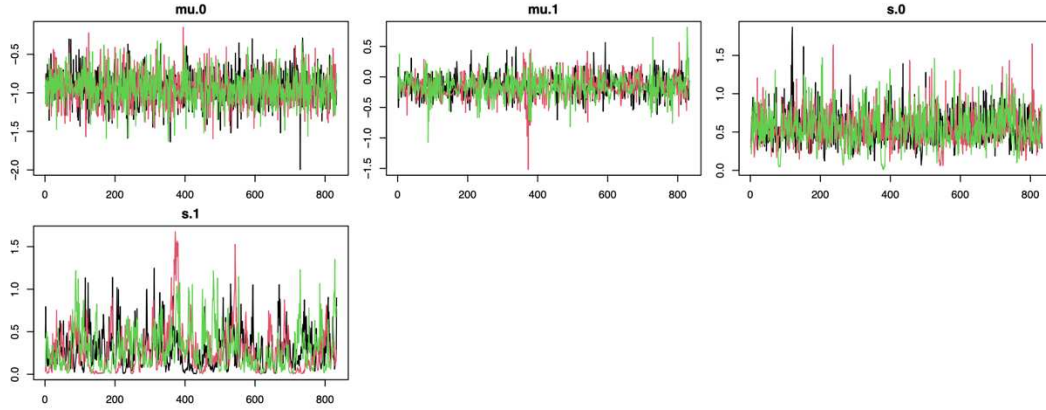


Figure 11: Trace plots show how our three MCMC chains converge. Good convergence happens when the chains overlap and mix, resembling a “fuzzy caterpillar”

4.3 Posterior predictive checks

To assess the fit of our model to data, we use posterior predictive checks, which evaluate whether our model can simulate new data that is similar to our original data, given the estimated posterior distributions of our parameters (Gelman et al., 2014; Hobbs & Hooten, 2015). Using our model and estimated posterior distributions, we simulated 1000 of species-by-time matrices. To evaluate whether there were any systematic deviations between observed and simulated data for each time bin, we summed the number of detections in each column for the simulated data and took the mean number of detections. We then compared this mean to the number of detections for each time bin in our observed data (Fig. 12). Our model was able to recover similar detection sums for each time bin. The most significant deviation was the underestimation

of detections in the time bin from 2 to 1.5 Ma.

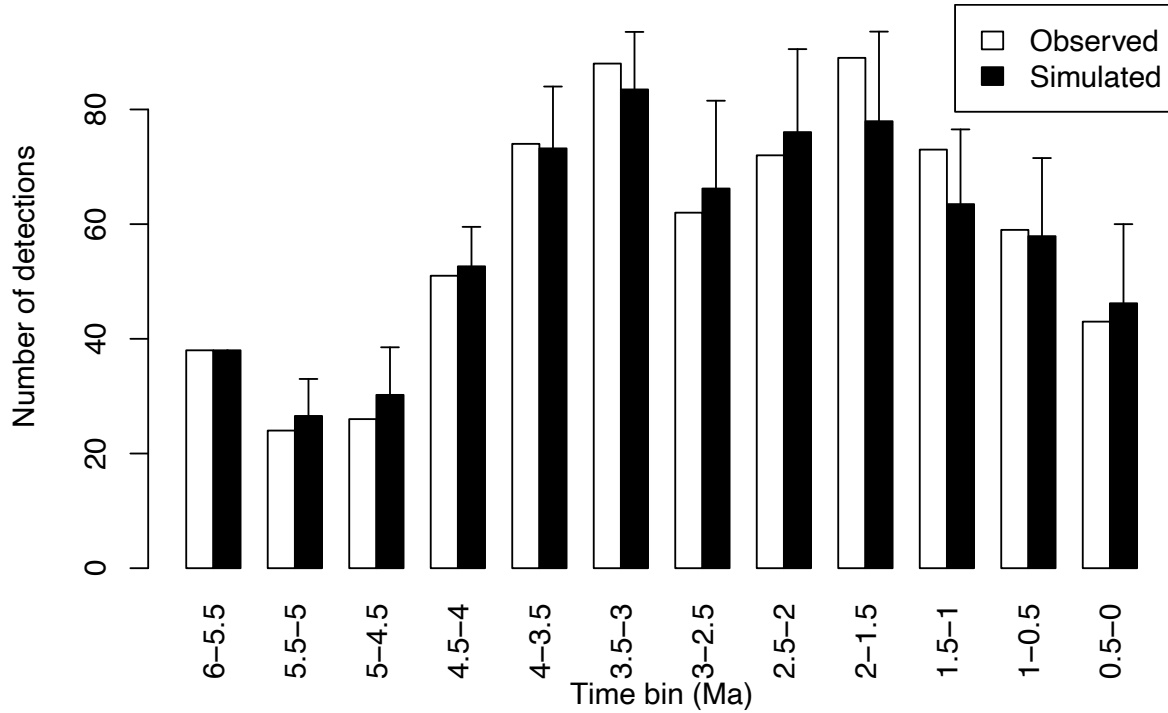


Figure 12: Posterior predictive checks, comparing the observed and average simulated number of detections per time bin

Additionally, we calculated a Bayesian p-value, using the total number of detections in the species-by-time matrix as the test statistic. A Bayesian p-value is calculated by estimating the probability that the test statistic from the simulated data is greater than the test statistic from our observed data (Hobbs & Hooten, 2015). Accordingly, we took the number of simulated datasets that had more detections than our original dataset and divided this number by the total number of simulated datasets to get a p-value of 0.43. Extreme values of 0.9 or 0.1 would indicate a poor fit, so our p-value tells us that there is sufficient goodness-of-fit.

CHAPTER 5 – DISCUSSION

We were interested in the origin of hominin top-down impacts on ecosystems. Because extinctions biased against large mammals are cited as an anthropogenic signal, we looked for this signal with the appearance of *H. erectus* in eastern Africa. We analyzed size-selectivity in eastern Africa mammal extinctions by modeling mammal extinction rates as a function of body mass, while controlling for variable fossil preservation and sampling rates. Variable preservation and sampling rates were accounted for by modeling species' detection rates as a function of body size.

5.1 Principal findings

Our major findings can be summed up as follows. First, body mass is a small-to-modest predictor of species' survival or extinction. When body mass increases by one order of magnitude, the multiplicative change in extinction odds hovers around 0.85 through time, indicating higher extinction probabilities for smaller mammals (Table 5, Fig. 7). More importantly, this effect goes in the *opposite* direction of size-selectivity predicted from the anthropogenic extinction literature. For each time bin, we calculated the probability that size-selectivity was in the expected direction against larger mammals and found that this probability is always low, fluctuating around 0.25 (Fig. 8). Second, we found that at all periods from 6.0 Ma to 0.5 Ma, average-sized species are more likely to survive than to go extinct (Table 4, Fig. 6). In fact, they are about three times as likely to survive until the next time bin than go extinct until 1.5 Ma onwards. From 1 to 0.5 Ma, these species become equally likely to survive and go extinct. Finally, body mass is a strong predictor of whether species are detected in the fossil

record: for an increase in body mass by one order of magnitude, the odds of detection double (Table 7, Fig. 9).

5.1.1 Extinction probability and selectivity

Our estimated extinction selectivity coefficients (β_1) suggest that extinction probability of mammals did not monotonically increase as a function of body size with or after the appearance of *H. erectus*. As detailed earlier, we predicted that extinctions precipitated by *H. erectus* would follow one of two scenarios, based on the idea of increased carnivory in *H. erectus*. We discuss our results here in relation to these predictions.

Scenario 1 envisioned emerging *H. erectus* as a catastrophic hunter, driving large mammals to extinction at its appearance 2 Ma, through overkill or by outcompeting large predators for prey. This scenario predicted a spike in selectivity for large animals at 2 Ma, followed by a return to background levels. We evaluated the time bins surrounding 2 Ma (i.e., 2.5–2.0 Ma and 2.0–1.5 Ma); by looking at 2.5–2.0 Ma, we can account for the possibility that *H. erectus* speciated before the current estimated first appearance datum at 2 Ma (Hammond et al., 2021; Mussi et al., 2023). Our results showed no spike in selectivity in the time bins surrounding 2 Ma. In fact, size-selectivity coefficients during this time period match those going back to 6 Ma.

This suggests that the speciation of *H. erectus* at 2 Ma in eastern Africa was not a significant or catastrophic moment for large mammal communities. If *H. erectus* was hunting at this time in eastern Africa, it had no significant impact on large mammal extinctions. Any morphological, technological, or behavioral adaptations unique to the emergence of *H. erectus* was not immediately a key driver of significant top-down impacts, at least as inferred from size-selective extinctions.

Scenario 2 envisioned *H. erectus* as a protracted driver of large mammal extinctions through overkill or competition with large carnivores. This scenario predicted a gradual increase in selectivity for large animals from 2 Ma onwards, but our results do not find such a pattern.

Our results do not allow us to comment on if *H. erectus* was hunting during this period. However, the results strongly discount the idea that size-selective hunting reached catastrophic levels at any point in the first million years of *H. erectus*' existence. There was a slight jump in size-selectivity in the period between 1.0 and 0.5 Ma. Since *H. erectus* persisted in eastern Africa until an estimated 0.9 Ma (Mori et al., 2020), it is perhaps possible that it adapted novel hunting strategies around this time, which weakly influenced large mammal extinctions. However, there is no significant archeological evidence to support this idea. This period broadly coincides with the loss of nonruminant grazers after 1 Ma mentioned by Faith et al. (2024) but because these grazers shared a different digestive strategy than the ruminant grazers that survived this period, it is more likely that this difference in strategy could explain these losses and the jump in probability of size-selection (Faith et al., 2024).

Though not the focus of our primary research questions, our model also enabled us to look at size-selectivity in extinctions as far back as 6 Ma, long before the appearance of *H. erectus*. Hominins appearing before *H. erectus* include *Homo habilis*, as well as members of the genera *Australopithecus* and *Ardipithecus*. There was no elevated size-selectivity between 6 and 2 Ma, which agrees with paleoanthropologists' notions that pre-*Homo* hominins were unable to exert top-down control in their communities (Bibi & Cantalapiedra, 2023; Faith et al., 2018).

Our model results also enabled us to see if we could connect size-selective extinctions to non-anthropogenic drivers. We anticipated that we might see elevated extinction rates for large mammals starting at ~4.6 Ma when Faith et al. (2018) reported a decreasing richness in

megaherbivores which they attributed to the expansion of C₄ grasslands. However, we observed no size selectivity for large mammals during this time period. One possible explanation for the discrepancy between Faith and colleagues' study and ours is that the decrease in megaherbivore richness from 4.6 Ma to the present is due to decreasing speciation rates, not increasing extinction rates.

5.1.2 Extinction estimates in context

Our extinction selectivity estimates were not unprecedented given results from past research on this topic. Smith et al. (2018) evaluated mammal extinctions on a global scale, estimating size-selectivity coefficients across the Cenozoic record. Their results over the last six million years show that extinction selectivity coefficients were consistently negative on the log-odds scale (Table 9), indicating size-selectivity against smaller mammals. It is intriguing that we found similar results, given the difference in spatial scale of analyses. Perhaps this suggests some external driver of extinctions against smaller mammals at the global scale that 'trickles down' and has a non-trivial effect at the smaller scale of eastern Africa. Or perhaps, there is some intrinsic ecological/evolutionary feature of smaller mammals that makes them more susceptible to extinction during this time period.

Table 9: Selectivity coefficients on the log-odds scale from Smith et al. (2018) and this study.

Time bin (Ma)	Smith et al. (2018) selectivity coefficients	This study's selectivity coefficients
2 – 1	-0.25	-0.32
3 – 2	-0.52	-0.39
4 – 3	-0.44	-0.20
5 – 4	-0.36	-0.36
6 – 5	-0.17	-0.57

Tomiya (2013) examined the extinctions of mammalian genera in the North American and Eurasian fossil record from 28 Ma to 1 Ma. They evaluated the duration of genera for mammals with body mass ranging seven orders of magnitude. In Eurasia, they found that large-bodied genera had higher extinction probabilities. In North America, however, they found no correlation between body size and extinction probabilities and concluded that size-biased generic extinctions were not a general feature of the North American mammal record in the Neogene. While we evaluated size-biased extinctions at the species rather than genus level, our results generally find that extinctions were biased towards smaller-bodied animals, which stands in contrast to the results of Tomiya (2013). This could be due to a number of factors including a difference of taxonomic or temporal scale, or that different ecological processes were operating in Africa compared to Eurasia and North America.

5.1.3 Detection selectivity

Our estimates of detection probability indicated a strong size-selective signal, increasing as a function of body mass. We can interpret this to mean that large-bodied mammals had a greater probability of overcoming the taphonomic barriers that any species must overcome to be recorded in the known fossil record. A mammal's remains must survive the transition from the living assemblage to the death assemblage, be buried, be preserved as a fossil, and finally must be sampled for it to be included in a species-by-time matrix (Behrensmeyer et al., 2000). Our estimated detection probability encompasses all these processes and cannot distinguish between them.

While our study estimates the probability of all these processes together, other studies have looked at specific parts of this multi-step process. For example, Miller et al. (2014)

analyzed the surface skeletal assemblage of mammal species at Amboseli National Park (Kenya) and estimated the probability of going from the living assemblage to the death assemblage as a function of body mass. By using this probability in conjunction with our probability of going from the living assemblage to being sampled as a fossil, one could hypothetically derive the probability of going from the death assemblage to being sampled in the fossil record, all as a function of body mass.

5.2 Study limitations

One of the limitations of this study was the constraints on available data. Body mass cannot be directly measured for any extinct taxa. Given this, all body mass values used for extinct taxa in this study are based on estimates. Any estimate of this kind has a degree of error associated with it. This error will be modeled and accounted for in the future, using our Bayesian framework. Additionally, error could have been introduced by our treatment of missing mass data. For species missing body mass estimates, we assigned the mass value of congeneric species. However, we can be reasonably confident that closely related species have similar body masses. In a study of body size across taxonomic hierarchies for terrestrial mammals, Smith et al. (2004) found that body mass for mammalian species over 18 grams were highly conserved within their genera. Within our Bayesian modeling framework, we can also assign greater uncertainty to those species' masses that are estimated using congener masses and see if our results are impacted in any significant way. Lastly, we can leverage Bayesian models' ability to handle missing data to specify informed distributions for the body masses of those species we had to remove from analyses, e.g., specify a distribution using species found in the same family (Hobbs & Hooten, 2025).

Bias might have been introduced into our study with the violation of the assumptions of the CJS model. As outlined earlier, CJS has a series of assumptions including that taxa are identified without error and are representative of the community at large. It is of course possible that there was a subset of the species included in the Rowan et al. (2024) dataset that were misidentified, which would introduce false negatives or positives. Regarding false negatives, because this was a presence-absence dataset, only one correctly identified specimen per species per time bin would be needed to ensure an accurate capture history. Given the large spatial extent of our study (i.e., eastern Africa) and the inclusion of many sites, we do not expect there to be many false negatives in our species-by-time matrix. False positives, on the other hand, would require misidentifying Species A as Species B. This would only be a problem if Species B was absent from the time bin of misidentification. While it is difficult to gauge the extent of this error, we cannot envision this error being systematically concentrated in certain species in certain time bins, i.e., this bias, if it exists, is most likely randomly distributed across species and time bins. If true, this error would not bias our results in any systematic way.

To test anthropogenic extinction hypotheses, we modeled extinction probability as a logistic function of body mass. While the literature is unclear what functional form size-selective extinctions should take, it is plausible that size-selectivity might manifest itself as a step function: low constant extinction probability below some body mass threshold, which jumps to a higher constant extinction probability at the mass threshold. While we did not explicitly model size-selectivity in this manner, our logistic regression should be able to detect size-selectivity following a step function, i.e., $\beta_{1,t}$ would still be estimated as greater than zero. Furthermore, if size-selectivity followed a step function in reality, this would create systematic deviations of data from model predictions that we do not detect in our posterior predictive checks.

5.3 Future directions

If we are interested in the role of *H. erectus* as an extinction driver, we could look beyond Africa to see if there were similar patterns in Eurasia (e.g., Surovell et al., 2005). Finding a different size-selective signal in Eurasia during the expansion of *H. erectus* could raise questions about the prey naivete hypothesis. This hypothesis argues that extinctions of large mammals happened on the frontiers of hominin range expansion, as large mammals encountered a new type of predator that they had not evolved defenses for (Brook & Bowman, 2002). Therefore, looking at regions where we estimate *H. erectus* first arrived in Eurasia (e.g., 1.8 Ma at Dmanisi) would be particularly significant. This is especially interesting, given that Tomiya (2013) found higher extinction probabilities in larger-bodied mammals in Eurasia.

As previously outlined, ancient anthropogenic extinction hypotheses take two general forms. The first postulates that ancient hominins drove large herbivores to extinction by overhunting (Surovell et al., 2005), and the second hypothesizes that hominins drove large carnivores to extinction by encroaching into the carnivore guild and competing with them for prey (Faurby et al., 2020; Lewis & Werdelin, 2007; Werdelin & Lewis, 2013). These hypotheses rely on vastly different predictions of hominin behavior at the time. Hunting large mammals such as proboscideans to extinction would require a completely different suite of behaviors. Large mammal hunts might rely on cooperative hunting, extensive planning, jump sites, or advanced tool use. Competing with large carnivores could indicate high-risk confrontational scavenging or adaptations for hunting prey animals. These two general hypotheses also make different predictions for extinction patterns. The first predicts that large herbivores would face the greatest extinction risk, while the second predicts greater risk in large carnivores. Our model is not designed to differentiate between these extinction patterns, but a future study could estimate

extinction risk for large herbivores and large carnivores separately, to differentiate between these patterns and make inferences about hominin behavior at this time.

5.4 Concluding remarks

This study is part of a larger effort to better account for biases when working with the fossil record in paleoanthropology. This is a persistent need in paleoanthropology. Faith et al. (2021) asserted that while techniques for dealing with biases in sampling are available, they have been inconsistently applied to hominin-related studies. Methods such as capture-mark-recapture models have been used to account for biases in the fossil record since 1983 (Nichols & Pollock 1983). A small collection of paleoanthropological studies has employed these capture-mark-recapture methods to study turnover. Cohen et al. (2022) used these methods to estimate time-varying speciation, extinction, and detection probabilities in a study of eastern African mammal turnover. However, these methods remain an underused tool in the field of paleoanthropology despite their clear advantages. Our study demonstrates how these methods can be employed to help answer questions in hominin evolution.

This study also demonstrates the importance of testing ancient anthropogenic extinction hypotheses. These hypotheses are being increasingly cited in literature beyond paleoanthropology, such as conservation biology and other fields (e.g. Hoag & Svenning, 2017), despite a lack of robust testing. As a result, these untested hypotheses are gradually being accepted as truth, which affects our understanding of the history of human top-down impacts and potentially influences conservation theory and practice (e.g., conservation paleobiology; Dietl et al., 2015). Our findings did not support anthropogenic extinction hypotheses, as applied to the appearance of *H. erectus*, and highlight the need to continue investigating the predictions made by these hypotheses for potential insight into the history of human-environmental interactions.

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