The Development of Hominin Subsistence Strategies in the Eurasian Quaternary, a Review

Die Entwicklung menschlicher Subsistenzstrategien im Quartär Eurasiens: ein Überblick

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Abstract: *The introduction of meat to hominin diets was one of the most consequential shifts in human evolution. The eventual outcomes of habitual meat consumption, including larger brains, tool use, and greater social complexity, set in motion the series of events that has made life as we know it today possible. Food in general is an interesting topic because it exists at the intersection of biological necessity and cultural identity. Meat eating more specifically is important from an archaeological perspective because faunal materials often preserve at sites from all time periods. In this paper, I chronicle the development of meat-eating, especially as it occurred in Eurasia. I begin with the earliest hominins to leave Africa, and end with modern people in medieval Europe. This exercise is somewhat autobiographic*[1] *and focuses especially on examples I am familiar with or in which I have a particular interest. However, this review reveals several interesting and important points regarding the development of the human relationship with food, some of which we can see in the world today. The first is that the origins of modern meat acquisition strategies (i.e., hunting large, prime-aged adult animals) began in deep time, over 500,000 years ago. The second comes much later, after the appearance of modern humans. The success of* Homo sapiens *at the expense of our intelligent, well-adapted hominin cousins was at least, in part, related to our dietary flexibility and willingness to broaden our diets to encompass new foods and new ecological niches. This flexibility culminates in the third point, regarding the management and domestication of animals. With animal domestication, humans began a relationship with the environment that involved an unprecedented level of control and manipulation, which allowed us to increase our populations in ways unimaginable to foragers. This led to exponential growth in the diversity of subsistence strategies, which brings us to the final point, the cultural and social importance of meat today. When we look around the modern world, one of the most striking differences between cultures (and individuals!) is our food: what we consider edible, how we cook it, when we eat it. The central importance of food, in this case meat, reflects culture, religion, identity, and preference. This is true today, and we begin to see the recognizable origins of this diversity as early as the mid-Holocene.*

Keywords: *Eurasia, zooarchaeology, subsistence, meat, culture, identity*

Zusammenfassung: Die Einbeziehung von Fleischnahrung in die menschliche Ernährung bedeutete eine der folgenreichsten Veränderungen in der menschlichen Evolution. Die letztendlichen Folgen gewohnheitsmäßigen Fleischkonsums, darunter größere Gehirne, Werkzeuggebrauch und höhere gesellschaftliche Komplexität, setzten eine Reihe von Ereignissen in Gang, die das Leben, so wie wir es heute kennen, erst möglich machten. Nahrungsaufnahme im Allgemeinen ist ein interessantes Thema, weil es an der Schnittstelle von biologischer Notwendigkeit und kultureller Identität angesiedelt ist. Fleischkonsum im Besonderen ist aus archäologischer Sicht von Bedeutung, da auf Fundplätzen aus allen Zeitphasen Faunenmaterial häufig erhalten ist. Im vorliegenden Beitrag zeichne ich die zeitliche Entwicklung des Fleischverzehrs nach, wie sie vor allem in Eurasien zu beobachten ist. Ich beginne mit den frühesten

1 This paper began as the introduction to my 2018 habilitation, Hominin Subsistence Strategies in the Eurasian Quaternary at the University of Tübingen.

Homininen, die Afrika verlassen haben und schließe mit den modernen Menschen im mittelalterlichen Europa. Diese Vorgehensweise hat mit meinem eigenen Werdegang zu tun und ist besonders auf Beispiele fokussiert, mit denen ich vertraut bin oder an denen ich ein besonderes Interesse habe. Dabei legt dieser Überblick mehrere interessante und wichtige Schritte in Bezug auf die Entwicklung des Verhältnisses der Menschen zur Nahrung offen, von denen wir einige in der heutigen Welt beobachten können. Zunächst wird deutlich, dass die Ursprünge moderner Fleischbeschaffungsstrategien (d.h. die Jagd auf große, im besten Jagdalter befindliche erwachsene Tiere) bereits vor langer Zeit, im Altpaläolithikum vor über 500.000 Jahren, anzusetzen sind. So ist einer der wichtigsten Aspekte im späten Altpaläolithikum der direkte Beleg für die Jagd. Der älteste Hinweis ist ein geschlachteter Pferdekörper aus Boxgrove in England, der etwa 490.000-425.000 Jahre alt ist und eine Beschädigung in einem Schulterblatt aufweist, die von einem hölzernen Speer stammen könnte. Ein noch überzeugenderer Beleg für aktive Jagd sind die hölzernen Speere aus Schöningen in Niedersachsen, die in etwa 300.000 Jahre alten Schichten zusammen mit Dutzenden von Resten pleistozäner Mosbachpferde gefunden wurden.

Im Mittelpaläolithikum blieben die Neandertaler in der 'Raubtier'-Nische, die ihre altpaläolithischen Vorfahren eingenommen hatten. Dies schließt die regelmäßige Jagd auf große Huftiere und Zugang zur Megafauna durch entweder Jagd oder Aasfresserei ein. Einer der bemerkenswertesten Aspekte der mittelpaläolithischen Ernährung ist dabei ihre Beständigkeit. Änderungen in den Anteilen der gejagten Tierarten scheinen der umweltabhängigen Verfügbarkeit der Arten zu folgen. Die Kontinuität in der Ernährung erlaubte es den Neandertalern, in Eurasien über einen Zeitraum von mehr als 200.000 Jahren während mehrerer Phasen des Klimawechsels zu existieren. Allerdings könnte dieser Konservativismus letztlich eine Rolle beim Niedergang der Neandertaler gespielt haben.

Der zweite große Schritt erfolgte erst nach dem Erscheinen moderner Menschen. Der Erfolg von *Homo sapiens* auf Kosten unserer intelligenten, gut angepassten Vettern und Kusinen (vor allem der Neandertaler) stand mindestens teilweise in Verbindung mit unserer Flexibilität in der Ernährung und unserer Bereitschaft, unser Nahrungsspektrum zu erweitern, um neue Nahrungsmittel und neue ökologische Nischen einzubeziehen. Diese Flexibilität gipfelt in dem dritten Schritt, der durch die Haltung und Domestikation von Tieren gekennzeichnet ist. Mit der Tierdomestikation erreichten die Menschen ein Verhältnis zu ihrer Umwelt, das mit einem nie dagewesenen Maß an Kontrolle und Beeinflussung verbunden war. Dies ermöglichte es uns, unsere Bevölkerungszahlen in für Wildbeuter unvorstellbarer Weise zu vergrößern. Folge war ein exponentielles Wachstum bei der Diversität der Ernährungsstrategien, das uns zum letzten Punkt führt, nämlich der kulturellen und sozialen Bedeutung von Fleisch heutzutage. Wenn wir uns in der modernen Welt umsehen, wird durch unsere Ernährung einer der bemerkenswertesten Unterschiede zwischen Kulturen (und Individuen!) deutlich. Das betrifft die Fragen, was wir als essbar ansehen, wie wir es zubereiten und wann wir es essen. Die zentrale Bedeutung der Nahrung, in diesem Fall des Fleisches, spiegelt Kultur, Religion, Identität und Vorlieben wider. Dies gilt vor allem in heutiger Zeit, und wir beginnen, die Anfänge dieser Diversität bereits zu einem so frühen Zeitpunkt wie dem mittleren Holozän zu erkennen.

Schlagwörter: Eurasien, Archäozoologie, Ernährung, Fleisch, Kultur, Identität

Introduction

When we think about the history and evolution of humans and our closest hominin relatives, the vast majority of the story was written during the Quaternary Period (2.6 million years ago through present). This period witnessed the origins of toolmaking, expanding cognitive capacity, the development and maintenance of fire, the invention of art and music, plant and animal domestication, towns and cities, organized religion, market economies, the rise and fall of empires, the invention of vaccines, and space travel. In this span of time, humans have competed with other organisms and successfully adapted to a nearly impossible range of environmental circumstances to colonize all corners of the globe. At the heart of this success is a combination of flexibility, cultural complexity, and social cooperation unique to the human species. It is also true, however, that people have the same biological needs as other organisms – food, water, and shelter – and they must fulfill these needs in order to survive the day and pass on their genes.

Exploring the interplay between sociocultural factors and biological needs is central to understanding the evolutionary success of hominins. A particularly fruitful way to do this is to analyze hominin diets from a diachronic perspective. As omnivores, hominins have a wide range of options for sustenance, and foods from both plants and animals form a critical part of their subsistence base. For my work, I focus on the meat portion of hominin diets, for three major reasons: preservation, social and cognitive implications, and because meat-eating sets hominins apart from other primates. This is not to undercut the importance of botanical resources and vegetable input in the diets of hominins, and zooarchaeologists and archaeobotanists should collaborate whenever possible.

The first reason I focus on faunal materials is preservation. At archaeological sites, animal bones have higher rates of preservation as compared to other organic materials, due to bones containing both an organic and inorganic component (Lyman 1994; Reitz and Wing 2008). This is particularly the case in deep time, as excavators routinely recover faunal remains from Paleolithic sites, which is not necessarily the case with floral materials.

The second reason is the effect that meat eating has had on the development of the cognitive and social capacities of hominins. We know that the earliest stone tools, which are thought to be a marker of increasing cognitive ability, appear at or around the time of the earliest evidence for meat eating, 2.6-2.5 million years ago (Ma) (Semaw et al. 1997; de Heinzelin et al. 1999). Due to the resolution of the archaeological record, it is unclear if stone tools appeared before meat was routinely introduced into hominin diets or vice versa, but there seems to be some relationship between the appearances of the two behaviors. Consequently, many authors have hypothesized that the introduction of meat to the diets of early hominins helped drive an increase in brain size and complexity due to the long fatty acid chains found in animal tissue (Hayden 1981; Speth 1989; Eaton et al. 2002). Aiello and Wheeler (1995) further hypothesized that in later periods, the cooking of meat led to an additional increase in hominin brain size as cooking makes meat more digestible and reduces toxins. Beyond the cognitive benefits, the social aspects of meat acquisition are also important. The first meat-eating hominins were not formidable creatures, between 1.05 and 1.52 m tall and ca. 32-52 kg (Feldesman and Lundy 1988; McHenry 1992). Therefore, the routine acquisition of meat, whether achieved through scavenging or hunting, would have required some level of cooperation between members of a hominin group. Indeed, many modern social carnivores have high degrees of cooperation and social complexity, in particular wolves, hyenas, and lions.

My final reason for focusing on hominin meat eating is that, as we learn more about the capabilities of non-human primates (i.e., social complexity, ability to learn sign language, and tool making) and the ways in which they pass on these behaviors to their offspring in a form of cultural transmission, there are fewer and fewer behaviors that distinguish hominins from other primates (i.e., Whiten et al. 1999). Meat eating is one such behavior. It is true that baboons, bonobos, and chimpanzees occasionally engage in meat acquisition (e.g., Harding 1973; Hausfater 1976; Morris and Goodall 1977; Wrangham 1977; Surbeck and Hohmann 2008). However, this behavior occurs on an entirely different scale among non-human primates, both in frequency, and in the fact that non-human primates will not hunt prey larger than their own body size (McGrew 2001; Rose 2001; Stanford 2001). This is in stark contrast to the hominin lineage, and is a significant

behavior that likely set early hominins apart from the ancestors of modern apes and baboons.

In this review, I explore the evolution of hominin subsistence strategies through the Quaternary Period, with a focus on meat eating. This vast expanse of time covers several different hominin species, from foragers through modern market economies, yet many of the underlying hypotheses, methodologies, and interpretive frameworks are the same. Because they are biological organisms, the assumption is that hominins are trying not to starve to death, in order to survive and ultimately reproduce. Therefore, analysts can draw on a range of models from ecology and biology in order to predict and understand hominin decision making in the realm of subsistence. On some level, this is useful for the earliest meat-eating hominins through historical period *Homo sapiens*, yet as we move through time, we see an increase in the effects of additional sociocultural factors (i.e., population growth, technological innovations, religion, market pressures, status, and identity) that influence subsistence. I want to be explicit from the outset that work is not an attempt to find an underlying explanation for why people eat what they eat. Rather, I am seeking to highlight the diversity at the interplay between the biological need for food and the sociocultural factors that influence hominin subsistence strategies.

Methodology and Theoretical Outlook

Methodology

One of the core goals of zooarchaeological research is to determine the representation of species in an archaeological assemblage, which can then be compared with other time periods, or other sites. In order to do this, faunal analysts rely primarily on measures of abundance, including the basic counting units NISP (number of identified specimens) and WISP (weight of identified specimens), as well as more derived measures such as MNE (minimum number of elements), MAU (minimal animal units), and MNI (minimum number of individuals) (Uerpmann 1973; Binford 1978; Grayson 1984; Lyman 1994; Stiner 2005a; Reitz and Wing 2008). The methods used vary by study, depending on the research questions and what is appropriate for a given time period and state of preservation. Beyond recording data on species and anatomical elements, zooarchaeologists collect information on tooth eruption and wear, epiphyseal fusion, nonhuman taphonomic damage (i.e., surface weathering and carnivore gnawing), and evidence of human behavior (i.e., cut marks, marrow processing, burning) (Behrensmeyer 1978; Stiner 1990; Lyman 1994; Fisher 1995; Villa et al. 2004).

Understanding the taphonomic history of a faunal assemblage is critical to reconstructing human subsistence strategies in the past. Distinguishing between different taphonomic processes is not only essential for determining the extent to which humans, animals, and weathering affected remains, it is also important for assessing whether or not any bone loss occurred, biasing the record. Density-mediated attrition is a well-known problem in zooarchaeology, and occurs because structurally weak elements and element portions are more susceptible to weathering processes than compact elements (Binford and Bertram 1977; Brain 1981; Davis 1987; Marean and Spencer 1991; Lyman 1994). Zooarchaeologists have developed several different techniques for evaluating

density-mediated attrition in an assemblage (i.e., Lyman 1985, 1994; Lam et al. 1999; Stiner 2005b), so it is generally possible to move beyond questions of preservation in order to evaluate human behavior.

Zooarchaeologists also borrow methodologically from biology and ecology. One area in particular is in the use of diversity indices, which measure the abundance and distribution of prey in an ecosystem or assemblage (Lyman 2008). A commonly used diversity index is the Inverse of Simpson's Index (1/D), which measures the extent to which a single species dominates an assemblage (Simpson 1949). Diversity indices are useful for comparing between different archaeological levels, or different sites within a region, and provide a link between the archaeological record and the natural environment. There are also other diversity measures used by zooarchaeologists, though Faith and Du (2018) recently determined that 1/D is particularly well-suited for archaeological assemblages.

Theoretical outlook

Beyond methodological examples, zooarchaeologists have drawn extensively on theoretical paradigms from the biological sciences. One of the most widely used theoretical paradigms in zooarchaeology is evolutionary ecology (see Bird and O'Connell 2006; Lupo 2007). Evolutionary ecology is an umbrella for multiple predictive models that are based on the assumption that foragers will optimize their food procurement and reproductive options in order to maximize their fitness (Pianka 2000). The most commonly applied evolutionary ecology models are the prey choice, patch choice, and central place foraging models (MacArthur and Pianka 1966; Orians and Pearson 1979; Schoener 1979; Stephens and Krebs 1986; Pianka 2000).

In the prey choice model, food items are ranked according to their return rate, which is a combination of caloric return and necessary energy expenditure. Foragers are only expected to pursue lower-ranked prey when high-ranked items are rare or absent in the environment (Emlen 1966; MacArthur and Pianka 1966; Stephens and Krebs 1986; Pianka 2000). In applying the prey choice model to human foragers, anthropologists have found that prey rank is closely connected to body size, with larger taxa having a higher ranking than small prey (Hames and Vickers 1982; Hawkes et al. 1982; Hill and Hawkes 1983; Simms 1987; Smith 1991; Kelly 1995; Broughton et al. 2011). Archaeologists have further refined these ideas when it comes to small game, pointing out that small, slow-moving animals have lower pursuit costs than small, fast-moving game, and are thus higher ranking (Stiner et al. 2000; Stiner 2001; Munro 2004; Steele and Klein 2009; Morin 2012). Additional configurations or technologies such as game drives or snares/nets can further change the equation and make small, fast-moving game more efficient to procure (Madsen and Kirkman 1988; Madsen and Schmitt 1998; Lupo and Schmitt 2002; Jones 2006). Archaeologists often apply prey choice models to questions involving resource depression and human hunting pressures (e.g., Grayson and Delpech 1998; Broughton 1999; Stiner et al. 1999, 2000; Cannon 2000; Stiner 2001, 2005a; Nagaoka 2002; Butler and Campbell 2004; Munro 2004; Speth 2004; Jones 2006; Speth and Clark 2006; Starkovich 2014a, 2012a).

Another widely used model is central place foraging theory, which attempts to understand how foragers choose where to collect food and how to transport it back to a home

base (Orians and Pearson 1979). Archaeological applications of central place foraging theory mostly seek to understand the field butchery and transport of ungulate prey by hominins (O'Connell et al. 1988, 1990; O'Connell and Marshall 1989; Broughton 1999; Cannon 2003; Nagaoka 2005; Faith and Gordon 2007; Faith et al. 2009). In general, as the distance between a kill and home base increases, foragers tend to transport higher-utility carcass portions back to the site. This model is particularly useful for site catchment and mobility studies.

The final evolutionary ecological model I will introduce is the patch choice model. The patch choice model has a similar premise as central place foraging theory, except it considers the way in which patches on a landscape are encountered and ranked, and how the return rate for a given patch drops once an organism begins foraging in it (Charnov 1976; Kelly 1995). A patch does not only have to be at the level of ecosystem; archaeologists have defined individual carcasses as patches, as foragers decide how intensively to process different tissues before moving on to the next carcass or kill (Burger et al. 2005; Nagaoka 2005). The patch choice model can, therefore, be used to address questions of resource intensification, as foragers tend to more intensively butcher a single carcass in times of resource stress or depletion (e.g., Potter 1995; Brink 1997; Broughton 1999; Stiner 2003; Munro and Bar-Oz 2005; Burger et al. 2005; Egeland and Byerly 2005; Nagaoka 2005; Starkovich 2014a).

In recent years, an alternative (but not mutually exclusive) paradigm to evolutionary ecology has emerged from the biological literature: niche construction theory (Lewontin 1982, 1983; Odling-Smee et al. 2003). Niche construction theory gives more agency to organisms in the evolutionary process, recognizing that they actively and unconsciously modify the niches of themselves and other organisms around them, which alters natural selection and influences evolution. In the natural world, examples of niche construction include nest and burrow manufacture, the spinning of webs, and the construction of pupal cases (Laland and O'Brien 2010). From this list, it is easy to imagine niche construction behaviors performed by hominins beyond the shelter creation behaviors of other animals. Consequently, zooarchaeologists have begun to apply niche construction theory to their work (i.e., Kuijt and Prentiss 2009; Broughton et al. 2010; Laland and O'Brien 2010; Dortch et al. 2014; Zeder 2016). This area of research has become particularly popular in time periods where humans are sedentary or have domesticated plants and animals, as people are very clearly modifying their environments and affecting the evolutionary trajectory of the organisms around them.

The theoretical paradigms reviewed here are not the only ones available to zooarchaeologists, nor do faunal analysts necessarily even need to work within theoretical frameworks. However, because major questions in zooarchaeology are based around evolutionary adaptations and human-environment interactions, it is helpful to have some ideas rooted in the natural sciences in order to understand hominins as both biological and cultural entities. With this methodological and theoretical background in place, I now turn to hominin subsistence strategies in the Eurasian Quaternary.

Lower and Middle Paleolithic

Hunting or scavenging? Making sense of an uncertain record

The earliest widely accepted evidence for hominin meat eating comes from Bouri, Ethiopia, 2.5 Ma (de Heinzelin et al. 1999; but see McPherron et al. 2010; Thompson et al. 2015). This is roughly contemporary with the earliest stone tools, found at Gona, Ethiopia 2.6-2.5 Ma (Semaw et al. 1997; but see Harmand et al. 2015). Regardless of older possible examples of meat consumption, by the Quaternary, hominins were eating meat, though it is unclear how often this behavior occurred. The question of which hominin species was responsible for the earliest faunal assemblages is also not yet known; some authors implicate *Australopithecus garhi,* while others argue for *Australopithecus afarensis* or *Homo habilis*, though the latter has a problematic taxonomic designation (McHenry 1992; de Heinzelin et al. 1999; McPherron et al. 2010). Because the focus of this review is on Eurasia, our discussion begins with *Homo erectus*, who left Africa roughly 1.8 Ma. By this time, African hominins had begun to gain access to meat, either through passive or power scavenging, or even occasional hunting (Bunn et al. 1980; Bunn 2007; Sahnouni et al. 2013; Bunn and Gurtov 2014). The small number of available sites from this phase makes it difficult to determine which meat procurement strategy hominins used most often, but like other carnivores and omnivores, it likely existed along a continuum that was not universal and changed depending on the circumstances (Starkovich and Conard in press).

By the time hominins entered Eurasia, archaeologists find increasing evidence for meat-eating. The earliest Eurasian examples come from Dminisi, Georgia, 1.77 Ma (Lordkipanidze et al. 2007), 'Ubeidiya, Israel, 1.4 Ma (Gaudzinski 2004), Sima del Elefante, Atapuerca, Spain, 1.22 Ma (Rodríguez et al. 2011; Huguet et al. 2013), and Vallonnet Cave, France between 1.07 and 0.99 Ma (Echassoux 2004). Researchers studying these sites agree that *Homo erectus* had early access to ungulate meat, based on the positioning of cut marks on long bone shafts. The rational is based on a series of experimental taphonomic and actualistic studies; if carnivores had heavily ravaged carcasses, the meat would have been stripped away from the mid-shaft, which would have rendered hominin efforts to remove meat pointless (see review in Starkovich and Conard in press; Domínguez-Rodrigo 1999). With the exception of Dmanisi, archaeologists argue that hominins hunted their prey (Gaudzinski 2004) or employed mixed hunting and scavenging strategies (Echassoux 2004; Huguet et al. 2013). Unfortunately, it is often difficult to distinguish between hunting and scavenging tactics at these early sites because the taphonomic evidence for the two behaviors is quite similar. It is important to note, however, that the bulk of the evidence from this time period indicates that hominins were relying on meat from medium- and large-bodied ungulates, and evidence for small game procurement is rare (but see Blasco et al. 2011).

After 1.0 Ma, the number of sites with evidence for meat procurement begins to increase as *Homo antecessor* appears in southern Europe (Bermúdez de Castro et al. 1997). At this time, faunal assemblages become larger so zooarchaeologists are able to apply a wider range of analytical techniques to the materials. Researchers continue to interpret sites as providing evidence for hunting or mixed hunting/scavenging strategies (Rabinovich et al. 2008; Martínez et al. 2010; Saladié et al. 2011; Huguet et al. 2013),

but larger datasets allow analysts to make more sophisticated conclusions regarding the nature of the record. For example, Saladié et al. (2011) pointed out that in the 780,000 BP (before present) layers at Gran Dolina, Atapuerca, whenever cut and carnivore bites are found on the same specimens, bites are always on top of cuts, which indicates that hominins had primary access to the carcasses. In 815,000-710,000 BP layers at Gesher Benot Ya'aqov, Rabinovich et al. (2008) interpreted repetitive butchery marks on ten fallow deer skeletons as evidence that hominins had the technical and communication skills to butcher prey carcasses in a standardized manner. At this point, we begin to see some glimmers of modernity in terms of meat acquisition strategies, but they are still few and far between, and say very little about the social structure and capabilities of hominin foragers.

Cooperative hunting and niche partitioning

After 500,000 BP, there is a marked shift in hominin subsistence strategies (Starkovich and Conard in press). *Homo heidelbergensis* appeared slightly before this time in Europe, and after 500,000 BP, paleoanthropologists and geneticists document *H. neanderthalensis* and Denisovans in Eurasia, and *H. erectus* in Asia (Reich et al. 2010; Indriati et al. 2011; Stringer 2012). This phase also includes the transition from the Lower to Middle Paleolithic, which is more apparent in terms of changes in material culture than shifts in subsistence. Hominin diets were based largely on the meat from prime-aged adult ungulates, supplemented by small, sessile prey, and some amount of meat from megafauna. We see evidence for complex social behavior, such as communal hunting and meat sharing. Finally, we see the more regular incorporation of bone tools into hominin toolkits, such as soft hammer percussors, bone retouchers, and lissoirs.

One of the most important aspects of the late Lower Paleolithic record is the direct evidence for hunting. The oldest example of this is a butchered horse carcass (*Equus ferus*) from Boxgrove, England, which dates to ca. 490,000-425,000 BP, and has an impact mark on the scapula that might have come from a wooden spear (Roberts and Parfitt 1999; Smith 2012, 2013). An even more compelling example of hunting is Schöningen, Germany, which preserves at least ten wooden spears alongside the remains of dozens of large-bodied Pleistocene horses (*Equus mosbachensis*) in layers that date to ca. 300,000 BP (Thieme 1997; Voormolen 2008; Conard et al. 2015). Most archaeologists working at Schöningen agree that the site does not represent a single-kill scenario, but rather is the result of multiple smaller hunting events along with a natural accumulation of background faunas (Musil 2007; Voormolen 2008; Conard et al. 2015; Julien et al. 2015b; Kuitems et al. 2015, but see van Kolfschoten 2014). Regardless of the exact formation model, the manufacture of wooden spears as well as the ambush of a single taxon repeatedly in the same location shows advanced cognition in terms of planning depth. Similarly, the ability to kill multiple large ungulates at a time indicates the coordination of several hominin individuals, which would have involved social and linguistic sophistication not typically ascribed to hominins before this time (Conard et al. 2015). Further evidence for cooperative hunting and planning depth comes from 400,000 BP layers at Gran Dolina, Atapuerca (Rodríguez-Hidalgo et al. 2016, 2017). During this time, the site served as a natural trap that hominins used to drive and hunt bison. In total, the deposits contain at least 60 bison that were heavily butchered by hominin hunters. Age profiles indicate a

catastrophic mortality profile, meaning that an entire herd or group of bison was killed at once, and tooth microwear data suggest that there were two separate kill events, one in the late fall, and the other in the early spring.

In addition to communal hunting, there is evidence for meat sharing in the late Lower Paleolithic. At Qesem Cave, Israel, Stiner and colleagues (Stiner et al. 2009, 2011) analyzed the "orderly" and "disorderly" nature of cut marks on bones butchered by hominins occupying the site between 400,000 and 200,000 BP. The authors found that the Lower Paleolithic cut marks were less "orderly" as compared to Middle and Upper Paleolithic assemblages, which they interpreted as reflecting a situation involving less organized meat provisioning, where hominins would transport portions of a carcass to the site and everyone would have access to it. We conducted a similar study at Schöningen, though the situation is somewhat different from Qesem Cave, as the former represents a kill site and the latter is a habitation site (Starkovich and Conard 2015). At Schöningen, we found more "disorderly" cut marks on long bones, even compared to Qesem Cave, but we found a difference in orderliness when we compared different regions of the body. Specifically, cut marks on ribs and vertebra were more "orderly" compared to those on long bones, which we interpret as having to do with the logistics of butchering large carcasses, where it is easier to manipulate limb bones as compared to the trunk of the animal (Starkovich and Conard 2015).

Another critical aspect of the late Lower Paleolithic is that this period seems to be when hominins crystalized their role in the predator guild (Starkovich and Conard in press). In particular, hominins began to specialize in the hunting of prime-aged adult ungulates. This is in contrast to cursorial predators that hunt the weakest members of a group (e.g., old and young), and ambush predators that exploit members of a group at random, which results in death assemblages that reflect the living structure of a particular herd (Stiner 1990, 1994, 2002). Archaeological assemblages that contain a large number of prime-aged adults, in addition to some juveniles, become common in the late Lower Paleolithic (Moigne and Barsky 1999; Moncel et al. 2005; Voormolen 2008; Stiner et al. 2009, 2011; Blasco et al. 2013a, 2014; Rodríguez-Hidalgo et al. 2015), and continue into the Middle Paleolithic (e.g., Stiner 1994, 2005a, Gaudzinski 1995, 2004; Hoffecker 1999; Gaudzinski and Roebroeks 2000; Cabrera et al. 2004; Adler et al. 2006; Gaudzinski-Windheuser and Niven 2009; Gaudzinski-Windheuser and Roebroeks 2011; Starkovich 2017; Kitagawa et al. 2018). There is also at least one instance of prime-dominant hunting before the late Lower Paleolithic, 780,000 BP at Gran Dolina, Atapuerca (Saladié et al. 2011), but it seems to become the norm after about 500,000 BP.

The late Lower Paleolithic is also the period during which we begin to see increased evidence for the hominin exploitation of megafauna, such as proboscideans. The most convincing examples of this are from numerous lakeshore deposits, often in the Mediterranean region, such as Revadim Quarry, Israel, Áridos 2, Spain, La Polledrara di Cecanibbio and Castel di Guido, Italy, Marathousa I, Greece, and Boxgrove, England, where archaeologists have recovered megafauna bones that preserve cut marks from stone tools (Boschian and Saccà 2010; Yravedra et al. 2010; Anzidei et al. 2012; Rabinovich et al. 2012; Saccà 2012; Smith 2015; Konidaris et al. 2018; Tourloukis and Harvati 2018). These remains are difficult to interpret, however, and it is unclear if hominins hunted or scavenged the animals.

A final aspect of the period after 500,000 BP is the more routine incorporation of bone into hominin toolkits. One example of this is bone bifaces, which archaeologists have identified in Germany (Mania and Mania 2003), Italy (Segre and Ascenzi 1984; Anzidei and Cerilli 2001; Boschian and Saccà 2010; Anzidei et al. 2012; Saccà 2012), Hungary (Kretzoi and Dobosi 1990; Dobosi 2003), and Israel (Marder et al. 2006; Rabinovich et al. 2012). These artifacts from Eurasia date to between 500,000 and 300,000 BP (Beyene et al. 2013). Other bone tools that emerge at around 500,000 BP are percussors and bones used as hammers (Stout et al. 2014). Archaeologists have found a particularly large and diverse bone toolkit at Schöningen. This includes over 80 tools from the Spear Horizon (the area of the site that preserves the wooden spears and dozens of horse carcasses), such as horse metapodial hammers, percussors (alternatively called bone retouchers) and anvils. Analysts interpret these tools as being used for bone marrow extraction (e.g., hammers) and lithic manufacture (e.g., percussors and anvils) (van Kolfschoten et al. 2015). One retoucher in particular was manufactured on a humerus from a saber-toothed cat (*Homotherium latidens*) (Fig. 1; Serangeli et al. 2015). Julien et al. (2015a) document additional bone tools from a different locality at Schöningen, including bone retouchers, percussors, possible anvils, and lissoirs (or smoothers).

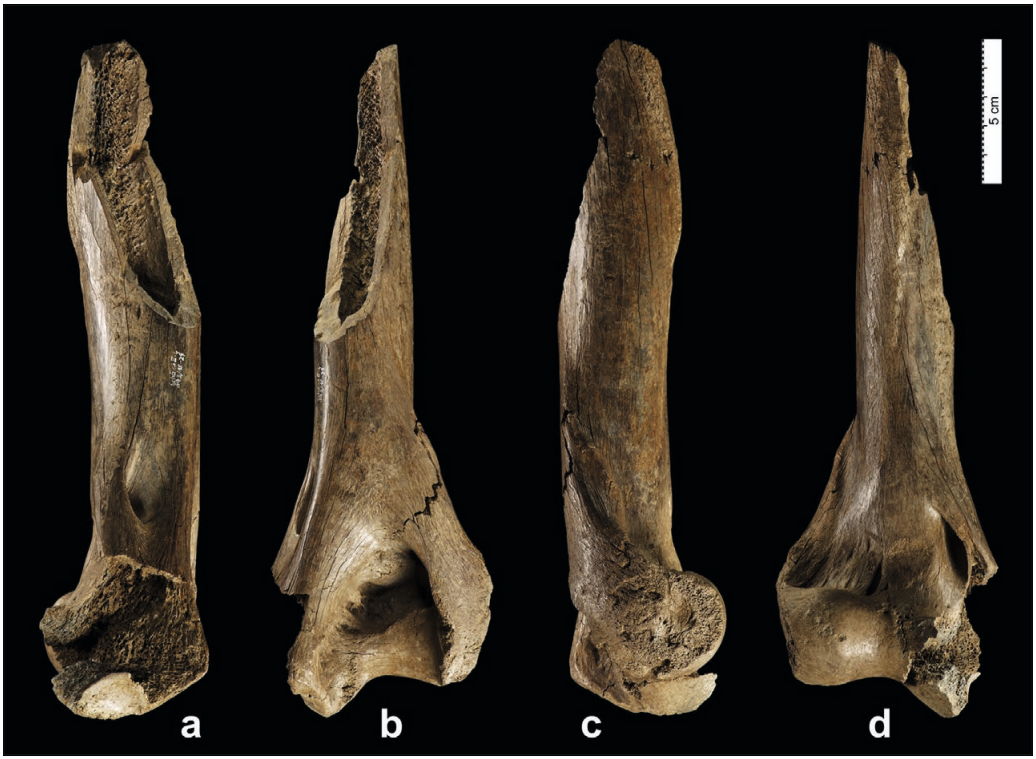

Fig. 1: Schöningen, Germany. Lower Paleolithic saber-toothed cat humerus used as a retoucher, ca. 320,000-300,000 BP. Photo: Volker Minkus; from Serangeli et al. 2015.

Abb. 1: *Schöningen, Deutschland. Als Retuscheur verwendeter Oberarmknochen einer altpaläolithischen, ca. 320.000-300.000 Jahre alten Säbelzahnkatze. Foto: Volker Minkus; nach Serangeli et al. 2015.*

By the Middle Paleolithic, Neanderthals continued in the predatory niche established by their late Lower Paleolithic ancestors. This included the routine hunting of large ungulates and access to megafauna through either hunting or scavenging (Gaudzinski 1995; Speth and Tchernov 1998; Conard and Prindiville 2000; Gaudzinski and Roebroeks 2000; Conard and Niven 2001; Stiner 2005a, 2009; Miracle 2005; Adler et al. 2006; Speth and Clark 2006; Costamagno et al. 2006; Yeshurun et al. 2007; Shea and Sisk 2010; Morin 2012; Niven et al., 2012; Rendu et al. 2012; Blasco et al. 2013b; Ready 2013), along with the collection of small, easy-to-catch prey such as tortoises and marine shellfish (Stiner et al. 2000; Stiner 2001, 2009; Speth and Tchernov 2002; Blasco 2008; Starkovich 2009, 2014a, 2017; Darlas and Psathi 2016). Zooarchaeological evidence supports this pattern, and the importance of large game in Neanderthal diets is also supported by isotopic studies (e.g., Bocherens et al. 1999; Richards et al. 2000; Bocherens 2011; Ecker et al. 2013). There is occasional evidence for Neanderthals exploiting small, fast-moving prey such as birds or leporids (Blasco and Fernández Peris 2009, 2012; Peresani et al. 2011; Cochard et al. 2012; Blasco et al. 2013b; Starkovich 2017), though this behavior seems to be an exception as opposed to the rule. Neanderthals continued to use bone as a raw material; we find both retouchers and lissoirs at Middle Paleolithic sites (e.g., Taute 1965; Baffier and Julien 1990; d'Errico et al. 1998; Daujeard et al. 2012, 2014; Soressi et al. 2013; Abrams et al. 2014; Toniato et al. 2018).

One of the most striking aspects of the Middle Paleolithic subsistence record is its stability (Stiner 2013). Changes in species representation seems to follow environmental availability (i.e., Starkovich et al. in prep.; Discamps et al. 2011; Morin 2012; Blasco et al. 2013b). In some instances, we see subtle markers of resource intensification, such as an increase in bone marrow processing, the hunting of juvenile ungulates, or the diminution of tortoises and shellfish which indicate increased harvesting pressures (Stiner et al. 2000; Speth and Tchernov 2002; Speth 2004; Starkovich 2017). Despite this, the real legacy of Neanderthals is their dietary consistency, which allowed them to flourish in Eurasia for over 200,000 years through various cycles of climate change. This conservatism might have ultimately played a role in their downfall, as Neanderthals were eventually outcompeted by modern humans that expanded throughout Eurasia after 50,000 BP.

Upper Paleolithic and Mesolithic

Diversification

The oldest Eurasian hominin thought to be culturally modern is from Manot Cave in Israel, and dates to between 60,200 and 49,200 BP (Hershkovitz et al. 2015). The age of the remains, which comes from uranium-thorium dating a crust on a human skull, is somewhat controversial, though other authors have argued that modern hominins entered Eurasia between 60,000 and 40,000 cal BP (Hublin 2012, 2015; Douka et al. 2014). Anatomically modern humans made earlier forays into southwestern Asia, such as at Skhul and Qafzeh (Shea 2008), though their cultural modernity is debatable and they do not appear to have spread westward at this time. After 50,000 cal BP, there are a number of stone tool industries in Eurasia that mark the transition from the Middle to Upper Paleolithic (e.g., Szeletian, Uluzzian, Châtelperronian), though there is little consensus whether they were manufactured by modern humans or Neanderthals, and this

debate is beyond the scope of the current review. The earliest stone tool industry that is widely accepted as having been made by modern humans is the Aurignacian, which has its oldest dates at Geißenklösterle in southern Germany, starting between 43,410 and 41,860 cal BP (Higham et al. 2012).

On a fundamental level, Upper Paleolithic diets were similar to Neanderthal and even late Lower Paleolithic subsistence strategies; whenever possible, humans hunted large-bodied, prime-aged adult ungulates (e.g., Straus 1987; Enloe 1997, 2003; Gamble, 1997; Grayson and Delpech 2002, 2003; Costamagno 2003; Phoca-Cosmetatou 2003; Münzel and Conard 2004; Adler et al. 2006; Niven 2006, 2007; Bar-Oz et al. 2008; Barth et al. 2009; Kuhn et al. 2009; Discamps et al. 2011; Napierala 2011; Stiner and Munro 2011; Morin 2012; Starkovich 2012b, 2017; Boger et al. 2014; Kandel et al. 2017; Morin and Soulier 2017; Kitagawa et al. 2018; Starkovich et al. in prep.). In some regions, the exploitation of mammoths was also important (Münzel 2001; Péan 2001; Svoboda et al. 2005; Bosch et al. 2012; Fladerer et al. 2014; Shipman 2015; Wilczyński et al. 2015), though as with previous phases, it is not well-established whether megafauna was hunted or scavenged. At the same time, Upper Paleolithic hominins were much more flexible in their use of low-return resources, which includes small, fast-moving game, and more intensive carcass processing. Many researchers interpret this shift as reflecting human population growth (Stiner 2009; Langlais et al. 2012; Starkovich 2014a). There are also changes in site use that point to demographic growth on a regional scale, with larger groups in residence, or people spending more time at a particular site. We see instances of within-group sharing and an expansion of technologies to include bone points, in addition to snares, nets and traps. By the Upper Paleolithic, flexibility and local diversification was key to the success of modern humans.

One of the clearest shifts in the dietary repertoire of Upper Paleolithic humans is the inclusion of small, fast-moving prey types such as leporids, birds, and fish. This is particularly the case in the Mediterranean Basin (Stiner et al. 2000, 2012; Stiner 2001; Aura Tortosa et al. 2002; Cochard and Brugal 2004; Atici 2009a; Jones 2009; Kuhn et al. 2009; Stiner and Munro 2011; Langlais et al. 2012; Lloveras et al. 2016; Starkovich 2017; Starkovich and Ntinou 2017; Starkovich et al. 2018a), but in recent years analysts have also identified the trend in Central Europe (Conard et al. 2013; Boger et al. 2014; Starkovich et al. in prep.). As mentioned above, there are a few examples of Neanderthals eating low-return prey, but it becomes much more common in the Upper Paleolithic. This is likely a combination of several factors: harvesting pressures on high-return animals such as ungulates, tortoises, and marine mollusks; the introduction of cordage technologies that would have made small, fast game more efficient to hunt; and possibly even the beginning of gender roles and the division of labor, where certain members of the group focused on different aspects of the foraging pursuit (Stiner et al. 2000; Soffer et al. 2000b; Kuhn and Stiner 2006; Starkovich 2017).

Another factor that influenced forager subsistence strategies has to do with the ways in which humans occupied sites starting in the Upper Paleolithic. There was not a monolithic shift across Eurasia, but in some places sites or even entire regions were occupied more intensively as of the Aurignacian (Conard et al. 2006; Conard 2011; Mellars and French 2011; Dogandžić and McPherron 2013; Miller 2015; Starkovich 2017). In other areas, intensively occupied sites appeared later, in the Gravettian or after the Last

Glacial Maximum (LGM) (Svoboda 2007; Stiner and Munro 2011). One result of this was, as larger groups of people occupied a site or spent more time in one place, they butchered carcasses more thoroughly. For example, at Klissoura Cave 1, Greece, we see more intensive marrow processing during phases of increased occupation intensity (Starkovich 2014a, 2017). There is also more evidence for heat-in-liquid bone grease rendering, when foragers crush vertebra and spongy long bone epiphyses and boil them in water to liberate the fat (Manne et al. 2006; Manne and Bicho 2009; but see Costamagno 2013 for the Middle Paleolithic). Similarly, there is evidence in some cases that hominins transported carcass portions based on marrow or grease content, as opposed to simply for their meat (i.e., Niven 2007; Morin 2012; Starkovich 2014a, 2017). It is important to note that season of occupation might have also influenced hominin carcass and processing patterns, though these behaviors are rarely documented before the Upper Paleolithic.

Increased time in residence has implications for issues of site maintenance, and the use of bone for construction materials. Recently, archaeologists have begun to find evidence for the maintenance of space by Neanderthals, evidenced by frequencies of burned bone and the distribution of burning across bone tissue types, coupled with geoarchaeological evidence for the scooping and dumping of combustion features. With the exception of Pech de l'Azé, which dates to ca. 100,000 BP (Dibble et al. 2009), most examples of this behavior are from late Middle Paleolithic sites, after 55,000 BP (Yravedra and Uzquiano 2013; Gabucio et al. 2014; Starkovich et al. 2018a). Bone burning as part of a site maintenance strategy continues in the Upper Paleolithic (Bosch et al. 2012), when people were spending more time at individual sites, and were burning organic materials in order to keep pests and carnivores at bay. Another rather spectacular example of increased residence time and the use of bone is in the mammoth huts found in Eastern Europe and on the Russian Plain (Kozłowski et al. 1974; Soffer 1985, 2003; Pidoplichko 1998; Iakovleva and Djindjian 2001; but see Demay et al. 2012 for a Middle Paleolithic example). Most of these dwellings date to the Gravettian or Epigravettian, and archaeologists have documented over 70 such structures (Shipman 2015). This degree of construction is an extreme example of spending more time at a single site, but highlights the diversity that is found in the Upper Paleolithic.

Beyond the use of bone for construction materials, we see a fluorescence in the use of bone for tools, including points, retouchers, lissoirs, for manufacturing rope, and as fuel (Taute 1965; Leroy-Prost 1975; Costamagno et al. 2003; Schiegl et al. 2003; Ploux and Soriano 2004; Théry-Parisot et al. 2005; Tejero et al. 2012; Lacarrière et al. 2015; Tejero and Grimaldi 2015; Yeshurun et al. 2018; Toniato et al. 2018). Upper Paleolithic humans also used bone and ivory as raw materials for a number of symbolic artifacts: carved bone beads, perforated teeth, anthropomorphic and zoomorphic figures, and musical instruments (Fig. 2; Soffer et al. 2000a; Kuhn et al. 2001; Conard 2003; White 2007; Conard et al. 2009; Beutelspacher and Kind 2012; Stiner 2014; Wolf 2015). Indeed, considering the adaptive success of Neanderthals and their predecessors, particularly in terms of subsistence strategies, the explosion of cultural symbolism is one of the few factors archaeologists can point to as distinguishing modern humans from other hominins, and it likely reflects a particular kind of symbolic thinking that facilitated social cohesion, and led to an adaptive advantage for modern humans (Conard et al. 2009).

Fig. 2: Hohle Fels, Germany. Aurignacian-aged small ivory figurine of a *Löwenmensch*. Height: 2.6 cm. Photo: Hildegard Jensen, © Universität Tübingen.

Abb. 2: *Hohle Fels, Deutschland. Aurignacienzeitliche Elfenbeinfigur eines kleinen Löwenmenschen. Höhe: 2,6 cm. Foto: Hildegard Jensen, © Universität Tübingen.*

Intensification and broad-based economies

Following the LGM, forager diets continued with the trend of diversification and resource intensification reached even greater levels. In southwest Asia, the Upper Paleolithic transitioned into the Epipaleolithic, while in Europe it gave way to the Mesolithic. Both time periods are broadly similar, in the sense that they represent the end of the Pleistocene and beginning of the Holocene, and are marked by an increase in sedentism alongside a continuation of foraging economies. The dating of this phase is offset from east to west because its end is defined by the Neolithic, which began at different times across Eurasia. In southwest Asia, the Epipaleolithic dates to roughly 23,000 to 11,500 BP, while the Mesolithic dates to between ca. 10,000 and 8,000 BP in southeastern Europe and ca. 10,000 and 5,500 BP in northwestern Europe (Stutz et al. 2009; Maher et al. 2012). Another significant point about this period is that, as the glaciers

retreated following the LGM, northern Europe was available for colonization by humans and other organisms. Across Eurasia, Mesolithic and Epipaleolithic foragers continued hunting large game when it was available (Noe-Nygaard 1974; Jochim 1998; Bar-Oz et al. 1999; Prummel et al. 2002; Ellis et al. 2003; Richter and Noe-Nygaard 2003; Bar-Oz 2004; Munro 2004; Magnell 2005; Meshveliani et al. 2007; Atici 2009a, b; Starkovich and Stiner 2009; Martin et al. 2010; Napierala 2011; Prummel and Niekus 2011; Stiner and Munro 2011; Arbuckle and Erek 2012; Munro et al. 2016). They also expanded their diets into new patches, both in terms of ecosystems on the landscape and by more intensively exploiting prey already part of their dietary repertoire. It becomes difficult to track the wide range of variation in subsistence strategies at this time, so I will focus on two of the most important shifts: the use of aquatic resources in the European Mesolithic, both at inland and coastal sites, and the increase in sedentism and intensified butchery patterns in the Epipaleolithic of southwest Asia, which eventually culminated in the domestication of plants and animals.

In the Mediterranean region of Europe, there was an intensification of marine resources in the late Upper Paleolithic, which becomes more pronounced in the Mesolithic. As with other trends discussed in this review, the phenomenon did not manifest the same way in all regions, but is reflected by the more widespread inclusion of fish in the diet, the formation of large coastal shell middens, and settlement patterns that shifted toward the sea. In a pan-Mediterranean review, Colonese et al. (2011) found that marine mollusk use increased during the Mesolithic. The authors concluded that marine resources were important dietary supplements, but typically served as buffers in times of stress, or accompanied intensification efforts. In southern Greece, certain inland sites that had been prominently occupied during the Paleolithic were abandoned by the Mesolithic; simultaneously, coastal sites experienced an increase in occupation intensity and fishing as sea levels rose and the shore moved closer (Payne 1975; Rose 1995; Stiner and Munro 2011; Stiner et al. 2012; Starkovich et al. 2018b). Foragers occupying Greek islands relied heavily on fish and marine mollusks (Mylona 2003; Powell 2003; Trantalidou 2010). At Franchthi Cave, people fished for deep water tuna by the end of the Mesolithic, which would have required the building of boats. In the same phase, archaeologists find evidence for obsidian brought from the island of Melos (Perlès 1987, 1999), which indicates a larger maritime strategy had come into play.

On the Croatian coast, people intensively exploited large schools of mackerel in the Mesolithic, and increased coastal fishing of other taxa across this phase (Rainsford et al. 2014). Researchers document a similar pattern in coastal Italian and Spanish sites, where several isotope studies track an overall increase in fish and shellfish use across the Mesolithic, and in some cases the year-round use of shellfish (Garcia Guixé et al. 2006; Mannino et al. 2007, 2011, 2012). In Portugal, shell middens become common in the Mesolithic (Bicho et al. 2010), and in some instances foragers were selecting their settlement locations based on close proximity to marine shellfish and freshwater ecosystems (van der Schriek et al. 2007). Dean and colleagues (Dean and Carvalho 2011; Dean et al. 2012) found evidence for shellfish diminution and a shift to lower-ranked shellfish taxa from the Mesolithic to Neolithic of southern Portugal, which they argued might indicate populations were already stressed before the introduction of agriculture, which caused them to adopt the new economic system more quickly. It is important to note that despite the increased importance in marine resources in the Mediterranean

Mesolithic, considerable subsistence variation continued to exist even in regions where aquatic resource use was common (Galanidou 2011; Guiry et al. 2015).

Archaeologists find a similar increase in aquatic resource use at inland European sites and in the north, as foragers fished in local lakes and rivers, and the North and Baltic seas. Fishing was an important part of Mesolithic economies in Denmark; people exploited a variety of taxa in water near their settlements, but would also fish open waters (Enghoff et al. 2007; Pickard and Bonsall 2007). Isotope studies indicate that marine fish were the primary source of protein in the Danish Middle and Late Mesolithic (Fischer 2007). This was the case at both coastal and inland sites, which Fischer et al. (2007) interpreted as high seasonal mobility. In Belgium, Crombé et al. (2011) found higher mobility in the Early Mesolithic as compared to the Middle and Late, when people settled along rivers. Hartz et al. (2007) reviewed a large number of sites from northern Germany and southern Scandinavia. They point to a reliance on fish in addition to marine mammals such as seals. The British Isles similarly preserve evidence for heavy marine resource use in the Mesolithic, for example shell middens on the Isle of Portland, which have evidence of shellfish diminution across the phase, indicative of harvesting pressures (Mannino and Thomas 2001).

Dupont et al. (2009) synthesized data from Mesolithic sites in Brittany in northwestern France. Zooarchaeological and isotope information provide parallel lines of evidence that humans included ample marine protein in their diets from aquatic mammals, birds, fish, and mollusks. Further inland, analysts studying bone isotopes find Mesolithic foragers exploiting freshwater ecosystems (Naito et al. 2013). In a zooarchaeological study of inland sites from France, Switzerland, Germany, and Luxembourg, Bridault (1997) found an increase in fish from the Late Paleolithic to Mesolithic. Jochim (1998) reported similar findings from southern Germany. At La Vergne (France), which is 60-80 km inland, isotopes from human burials show mostly terrestrial diets with a slight contribution of marine resources (Schulting et al. 2008). This is also the case at inland sites in eastern Iberia, 30-50 km from the sea (Salazar-García et al. 2014). Finally, in the Iron Gates region of Eastern Europe, several isotope and faunal studies indicate a heavy reliance on riverine resources in the Mesolithic (Dinu 2010; Nehlich et al. 2010), particularly toward the beginning of the phase (Bonsall et al. 1997).

The second shift in subsistence strategies I would like to highlight occurred in the Epipaleolithic of southwestern Asia. A large amount of research from this period comes from the Levant, where the Early and Middle Epipaleolithic did not differ significantly from the Upper Paleolithic in terms of hunting strategies. Ungulates were the most common prey type, especially gazelles or fallow deer, depending on the environment (Maher et al. 2012). This is true at sites in Israel (Bar-Oz et al. 1999; Stiner et al. 2000; Bar-Oz and Dayan 2003; Munro 2004, 2009; Shimelmitz et al. 2018) as well as Jordan (Maher et al. 2001, 2012; Martin et al. 2010; Samei et al. 2016).

The end of the Epipaleolithic in the Levant is marked by the Natufian, a particularly well-studied cultural complex in the region. By the Natufian, there was an increase in sedentism, evidenced by stone housing, cemeteries, and non-mobile bedrock and groundstone features (Garrod 1957; Henry 1991; Valla 1995; Bar-Yosef 1998; Belfer-Cohen and Bar-Yosef 2000; Byrd 2005; Goring-Morris and Belfer-Cohen 2008). Many markers of intensification and diversification of meat resources are apparent at this time. Compared

to earlier phases of the Epipaleolithic, frequencies of large game declined. Fallow deer was replaced by gazelles, and proportions of birds, lagomorphs, and fish increased (Davis et al. 1988; Davis 1991; Pichon 1991; Stiner et al. 1999, 2000; Stiner and Munro 2002; Bar-Oz 2004; Munro 2004, 2009; Yeshurun et al. 2014; Yeomans and Richter 2018). At El-Wad Terrace in Israel, foragers also exploited squamates, mole rats, and mollusks and fish from the Mediterranean, even though the sea was 8-12 km away (Valla et al. 1986; Yeshurun et al. 2009; Bar-Yosef Mayer and Zohar 2010; Weissbrod et al. 2012). In terms of age profile data, starting in the Early Natufian, foragers preferentially targeted male gazelles (Cope 1991; Bar-Oz et al. 2004), and at the same time stopped avoiding small-bodied gazelle fawns, as had been the case in the pre-Natufian Epipaleolithic (Davis 1983, 2005; Bar-Oz 2004; Munro 2004, 2009). The inclusion of fawns into Natufian diets indicates a willingness by foragers to take part in non-sustainable hunting practices, even for a low-yield food item. Archaeologists also document intensified carcass processing, with even low-utility gazelle phalanges being opened for marrow in the Natufian (Munro 2004, 2009).

Taken together, the dietary changes found in the Natufian contrast with the earlier Epipaleolithic and are thought to reflect population packing and resource pressure from increased sedentism (Bar-Oz 2004; Munro 2004, 2009; Davis 2005; Stutz et al. 2009; Yeshurun and Bar-Oz 2018). Even within the Natufian, many authors see a behavioral and cultural shift from the Early (15,000-13,700/13,000 cal BP) to Late (13,700/13,000-11,700) phases (Yeshurun et al. 2014), with the former being marked by sedentism and intensification, and the latter characterized as a return to more mobile lifeways (Garrod 1957; Henry 1991; Valla 1995; Belfer-Cohen and Bar-Yosef 2000; Bar-Yosef and Belfer-Cohen 2002; Grosman 2003; Munro 2004). Recently, Yeshurun et al. (2014) challenged this assertion. The authors pointed out that at El-Wad Terrace, and more regionally, the most significant shifts occurred from the Epipaleolithic to the Natufian, not within the Natufian. Furthermore, while they agree that there is evidence that site occupation intensity decreased in the Late Natufian, many hunting and carcass processing tactics were similar to those found in the Early Natufian.

Overall, the evidence indicates that important shifts in subsistence occurred both with the onset of and within the Natufian in the Levant, and these changes did not necessarily look the same at all sites. Similar kinds of evidence are found at Epipaleolithic sites elsewhere in the Levant. Napierala (2011) documented the importance of large game, including gazelles, caprines, and equids, from a series of sites in Syria. He noted that the only significant change in species representation occurred at Baaz Rockshelter, where hares and tortoises comprise a significant part of the Natufian assemblage as compared to the Upper Paleolithic (Napierala et al. 2017). In Anatolia, Atici (2009a, 2009b, 2014) examined Epipaleolithic faunal assemblages from Karain B and Özküzini, which together span from ca. 20,000 to 13,500 cal BP. Before 13,900 cal BP, foragers primarily hunted prime-aged caprines and fallow deer. For the final centuries of the sequences, human diets widened to include additional ungulate taxa (e.g., roe deer and wild boar), as well as tortoises, hares, and partridges. Hunters also captured more juvenile caprines in this later phase. Atici (2009a, 2009b) interpreted these trends as a shift in site use, from temporary hunting camps to multi-season, more intensively occupied sites. Other sites in Turkey point to ungulate hunting and occasional small game use, and fairly high levels of mobility even in the middle and later phases of the Epipaleolithic (Arbuckle and Erek

2012; Baird et al. 2013). At Komishan Cave in Iran, Mashkour et al. (2016) cite gazelle hunting alongside the use of birds, marine resources, and carnivores toward the end of the Epipaleolithic.

Across Eurasia, the terminal Pleistocene witnessed a considerable degree of intensification and diversification of meat resources. Critically, these dietary shifts occurred alongside a decrease in mobility patterns and increasing complexity among foragers, especially in southwest Asia. Larger populations spending more time in one place served to further stress local resources, setting the stage for the management and eventual domestication of plants and animals.

Domestication and the Origins of Agriculture

Sedentism and domestication

Following the rapid intensification and diversification in meat acquisition strategies across Eurasia at the end of the Pleistocene, animal management and eventual domestication began in southwest Asia. Generalized ideas regarding the domestication of plants and animals suggest that it occurred in a relatively restricted geographic region of southwest Asia, in the Fertile Crescent, before spreading into adjacent areas of Asia, Europe, and Africa as part of a so-called "Neolithic package" (see Çilingiroğlu 2005) It is worth noting that the animals we associate with the Neolithic (i.e., sheep, goats, pigs, and cattle) were not the first domesticates. Rather, there is evidence that dogs were domesticated as early as 33,000 cal BP in Siberia (Ovodov et al. 2011; Druzhkova et al. 2013), and there might have been multiple domestication events during the Upper Paleolithic at several locations across Eurasia (Savolainen et al. 2002; Pionnier-Capitan et al. 2011; Germonpré et al. 2012; Napierala and Uerpmann 2012; Thalmann et al. 2013; Skoglund et al. 2015). However, despite their importance as hunting partners and occasional food items, dogs did not have the economic significance as domesticated ungulates. Regarding ungulates, archaeologists now know that domestication occurred in multiple areas, including the Levant, Anatolia, and the Zagros (e.g., Rosenberg 1999; Hauptmann 2002; Özdogan 2002; Larson et al. 2005; Pedrosa et al. 2005; Zeder 2011; Arbuckle 2014).

Current evidence indicates that domestication occurred after the formation of sedentary villages, as opposed to agriculture driving a decrease in mobility and tying people to specific locations on the landscape. In the Natufian examples outlined above, increasingly sedentary groups with higher population densities lived in stone houses, buried their dead in cemeteries, and intensified their food resources by ca. 15,000 cal BP (Garrod 1957; Henry 1991; Valla 1995; Bar-Yosef 1998; Belfer-Cohen and Bar-Yosef 2000; Bar-Oz 2004; Munro 2004, 2009; Byrd 2005; Davis 2005; Goring-Morris and Belfer-Cohen 2008; Stutz et al. 2009; Yeshurun and Bar-Oz 2018), nearly 5,000 years before the earliest domesticates in the region. In Anatolia, at Hallan Çemi Tepesi, foragers built and occupied a large tell over the course of nearly 600 years (ca. 11,700-11,270 cal BP) (Higham et al. 2007). The site is a fully settled village, and while there is some possible pig management or proto-domestication, there is no evidence for the domestication of other ungulates or plants, indicating that sedentism did not rely on food production (Rosenberg et al. 1995, 1998; Rosenberg and Redding 1998, 2000; Savard et al. 2006; Starkovich

and Stiner 2009). At Aşıklı Höyük, sedentary foragers hunted ungulates, including ovicaprids, starting before 11,000 cal BP, and later transitioned to the intensive hunting of sheep and subsequent penning and management of the animals by 10,200 cal BP (Stiner et al. 2014). A similar situation is apparent at Chogha Golan, a large tell in the foothills of the Zagros Mountains of Iran, which was occupied from 12,000 to 9,600 cal BP (Conard and Zeidi 2013). At Chogha Golan, foragers hunted ungulates and fished in the local river, in addition to gathering small-seeded grasses and other wild grains (Riehl et al. 2015; Starkovich et al. 2016). Analysts identified morphologically domesticated emmer wheat in 9,800 cal BP deposits at the site (Riehl et al. 2013, 2015). The faunal sample is currently not large enough to address the question of animal domestication at Chogha Golan (Starkovich et al. 2016), though the importance of gazelles until midway through the sequence (ca. 10,000 cal BP) indicates that if domesticated animals were used at the site, it most likely occurred after this time.

Animal domestication appears in regions where humans had a long history of hunting wild progenitors of Neolithic domesticates. This often makes it difficult to pinpoint the shift from hunting, to managing or penning wild animals, to full domestications. Researchers rely on some combination of morphology, size, culling patterns, isotope values that reflect whether animals were foddered, and geoarchaeological evidence for penning to determine where on the continuum between hunting and domestication zooarchaeological remains lie. Sheep were the first domesticated ungulate. Archaeologists have documented evidence for sheep management at multiple locations in Turkey as well as Syria starting between about 10,500 and 10,200 cal BP (Hongo et al. 2005; Peters et al. 2005; Lösch et al. 2006; Helmer and Gourichon 2008; Grupe and Peters 2011; Stiner et al. 2014, but see Helmer 2008 for possible earlier evidence). Domestic sheep are found in Turkey by about 9,500 cal BP (von den Driesch and Peters 2001), and they appear abruptly at sites in Syria, Israel, and Jordan at roughly the same time (Clutton-Brock 1979; Helmer et al. 1999; Horwitz et al. 1999; Legge and Rowley-Conwy 2000; Wasse 2002). The sudden appearance of sheep at the latter set of sites indicates that they were introduced from elsewhere, and were not domesticated *in situ*. By 9,000 cal BP, domestic sheep are found at sites in the Zagros, and in eastern Jordan (Stampfli 1983; Becker 1991; Horwitz et al. 1999; Martin 1999; Zeder 2008).

Management or proto-domestication of goats appears around 10,000 cal BP, shortly after domesticated sheep appear. As is the case with sheep, there is early evidence for goat management in multiple regions, including Turkey, Syria, Iran, and Jordan (Hole et al. 1969; Hecker 1982; Ducos 1993; Buitenhuis 1997; Zeder and Hesse 2000; Hongo et al. 2005; Makarewicz and Tuross 2012; Peters et al. 2013). Archaeologists find additional evidence across southwest Asia, including the appearance of morphologically domesticated goats in ecosystems where wild goats were not native, in the subsequent millennium (Helmer et al. 1999; Saña Segui 2000; Wasse 2002; Helmer 2008; Saña and Tornero 2008; Arbuckle 2014).

The evidence for cattle domestication is more sparse than that for caprines, but seems to point to Syria, southwestern Turkey, and northern Iraq for its origins (Helmer et al. 2005; Bollongino et al. 2012; Arbuckle 2014). There are some instances of possible cattle management in the region between ca. 10,500 and 10,000 cal BP, though for the most part this interpretation relies on changes in sexual dimorphism and body size reductions

in cattle populations (Helmer et al. 2005; Helmer and Gourichon 2008; but see Hongo et al., 2009 for isotopic evidence for foddering by 10,300 cal BP). Morphologically domesticated cattle appear after 8,500 cal BP in Israel, the Jordan Valley, and in Anatolia; at several sites in Turkey their appearance is abrupt, indicating that cattle were introduced from elsewhere (Horwitz et al. 1999; Horwitz and Ducos 2005; Arbuckle and Makarewicz 2009; Marom and Bar-Oz 2009, 2013; Twiss and Russell 2009; Arbuckle 2013). Finally, domesticated cattle appear in the Zagros region of Iran after 8,000 cal. BP (Hole et al. 1969).

The origins of pig domestication are similarly patchy, and because of their different social and nutritional characteristics (i.e., not travelling in herds and being omnivorous), early management might have taken a different form compared to the bovids. Researchers have proposed that pig management can involve penning and foddering, or alternatively, the free range management of males and/or females (Redding and Rosenberg 1998; Albarella et al. 2007; Hadjikoumis 2012). Possible pig management appears in Anatolia by ca. 10,000 cal BP, or even earlier (Rosenberg and Redding 1998; Hongo et al. 2004; Helmer and Gourichon 2008; but see Starkovich and Stiner 2009). Archaeologists find increasingly convincing evidence after 9,500 cal BP, based on a combination of the appearance of smaller individuals, juvenile culling patterns, and evidence for foddering (Churchill and Smith 2000; Ervynck et al. 2001; Peters et al. 2005; Lösch et al. 2006; Helmer 2008; Helmer and Gourichon 2008; Grupe and Peters 2011). Pig management appears even later, after 9,000 cal BP in Lebanon, Jordan, and Israel (Helmer 1994; Horwitz et al. 1999; Haber and Dayan 2004; Marom and Bar-Oz 2013; Makarewicz 2016), and finally reached Central Anatolia and the Zagros after 8,000 cal BP (Flannery 1983; Martin et al. 2002; Zeder 2008; Arbuckle 2013; Price and Arbuckle 2015).

In addition to the realization that domestication occurred only after the appearance of sedentism and increasing complexity, archaeologists now know that the Neolithic did not arise and spread as some kind of package that included a set suite of domesticated plant and animal species. Rather, the domestication of individual taxa arose independently at multiple locations in southwestern Asia, then spread in a spatially and temporally heterogeneous manner (Asouti and Fuller 2012; Fuller et al. 2012; Riehl et al. 2013, 2015; Arbuckle 2014; Arbuckle et al. 2014; Starkovich et al. 2016). Arbuckle (2014) notes that before 10,000 cal BP, there were only five sites that preserve evidence for the full suite of domesticated ungulates, and they are geographically spread between Turkey, Syria, and Cyprus. This, along with the wide expanse of locations with early dates for domesticates, further supports the idea that domestication originated in multiple locations at once (Peters et al. 2005; Dietrich et al. 2012; Arbuckle 2014). Furthermore, initially, management, and/or domestication occurred at a rather low-level, until sheep and goat herding became more intensive at around 9,500 cal BP. Pig and cattle husbandry followed nearly a millennium later, and Arbuckle (2014) points out that all four domesticated taxa had not fully spread across southwest Asia until ca. 8,000-7,000 cal BP.

Archaeologists are not entirely certain why people first domesticated plants and animals. Since the origins of animal management and domestication occurred in multiple regions at different times, it is unlikely that the same reason accounts for the origins of domestication in all cases. The most widespread model to explain the beginning of domestication is that a combination of human population growth, sedentism and resource

intensification led to the depression of wild resources and the subsequent management and adoption of domesticates (Flannery 1969; Tchernov 1991, 1993; Alvard and Kuznar 2001; Munro 2003, 2004; Davis 2005). This explanation is typically based on research from the Levant and as such is particularly well-suited to that region. Additional models have arisen as zooarchaeologists have conducted more work elsewhere in southwest Asia. A second model links domestication to systems of ritualized hunting and/or feasting (Rosenberg 1999; Helmer et al. 2004; Peters and Schmidt 2004; Russell and Meece 2005; Hayden 2009; Arbuckle 2015). Recently, Arbuckle (2015) conducted an analysis of data from over a hundred sites in southwest Asia. He found that, outside of the Levant, ungulates (especially caprines) experienced only a mild depression in the phases directly preceding animal domestication, and were actually fairly abundant. Following other authors that highlight the social importance of hunting, Arbuckle (2015) argued that domestication occurred only after the economic benefits of herding outweighed the social benefits of hunting. He also postulated that the reason sheep and goats were the first domesticated ungulates is that they are small-bodied and might therefore afforded hunters less prestige than wild pigs and cattle. A final model recently proposed by scholars involves niche construction by humans. This partially comes out of the recent application of niche construction theory to the study of the origins of domestication, where the social and cultural systems of humans are credited with perpetuating behaviors that restructured the ecological relationships between humans and certain taxa (Zeder 2015, 2016). However, it is also similar to earlier work done by Marom and Bar-Oz (2009), in which they predicted that agricultural areas attracted more wild ungulates, in particular pigs and cattle, to fields to graze. This led to more encounters between animals and humans, which led to the eventual management and domestication of certain species.

Neolithic hunting and the Secondary Products Revolution

Once the set of Neolithic plant and animal domesticates was in place, it spread westward into Europe. This movement was fairly rapid; domesticates reached Cyprus and Crete by 10,500 and 9,000 cal BP, respectively (Efstratiou et al. 2004; Vigne et al. 2009, 2011, 2012) and were in southern Greece by 9,000 cal BP (Munro and Stiner 2015). Neolithic lifeways then followed two separate routes into Central and Western Europe, one along the margins of the Mediterranean Basin, the other up the Danube and Elbe river systems (Zeder 2017). Domesticates reached the northern Balkans and southeastern Italy by 8,000 cal BP (Chapman and Müller 1990; Biagi 2003; Skeates 2003; Legge and Moore 2011; Bonsall et al. 2013; Krauß et al. 2014) and spread through Italy and southern France within the next three hundred years (Guilaine 2006; Guilaine et al. 2007; Rowley-Conwy et al. 2013). The Neolithic appeared throughout Iberia between 7,700 and 7,300 cal BP (Zilhão 2001, 2003) and in the Paris Basin by 7,000 cal BP (Manning et al. 2013). Finally, domesticates reached northern Europe at 6,200 cal BP (Arias 1999; Rowley-Conwy 2011, 2013) and the British Isles by 5,800 cal BP (Tresset 2003; Sheridan 2010).

The character of the Mesolithic to Neolithic transition varies from place to place. Caprine herding was adopted more readily in the Mediterranean Basin, while much of Central Europe relied more heavily on cattle. In many regions, including the northern Balkans, Italy, France, and central Germany, Neolithic economies seem to have been incorporated

into existing Mesolithic lifeways, and hunting and fishing continued to be part of the subsistence pursuit (Geddes 1984; Bonsall et al. 1997; Döhle 1997; Scarre 2003; Tresset 2003; Benecke 2006a; Tresset and Vigne 2007; Arbogast and Jeunesse 2013; Çakırlar 2013; Rowley-Conwy et al. 2013). In the Iberian Peninsula, indigenous Mesolithic populations largely inhabited the interior of the region, so Neolithic migrants tended to settle on the coast, subsisting primarily on domesticates (Zilhão 2001, 2003; Dean and Carvalho 2011; Dean et al. 2012). This resulted in long Mesolithic holdouts in the interior, with Neolithic lifeways adopted centuries after they were found on the coasts and in southern France (Arias 1999, 2007; Zilhão 2001; Peña-Chocarro et al. 2005). In parts of Central Europe, hunting was uncommon following the adoption of the Neolithic (Manning et al. 2013). In the north, where the Neolithic was adopted the latest, Mesolithic communities continued to hunt and exploit coastal resources for ca. 1,500 years, even while they were in contact with their Neolithic neighbors to the south (Rowley-Conwy 1999, 2003, 2013; Noe-Nygaard et al. 2005; Fischer 2007; Fischer et al. 2007; Scheu et al. 2008).

Beyond the importance of domesticates for their meat, the Neolithic also brought about the Secondary Products Revolution. The Secondary Products Revolution was first proposed by Sherratt (1981, 1983) and argues that, millennia after the domestication of cattle, sheep, goats, and pigs, people began to use their secondary products (e.g., milk, wool/hair, and labor). Significantly, people can use secondary products without killing the animal, enhancing the economic benefit of domesticates. Under this model, the use of secondary products and their supporting technologies then spread from southwest Asia into Europe, East Asia, and Africa, in a similar way that the Neolithic had spread after its initial development. Current evidence from zooarchaeology and the analysis of lipids on ceramics confirms the importance of secondary products. However, the data indicate that the use of secondary products actually began in a similar way as the use of domesticates: at multiple places through time, and in some cases accompanied the earliest animal husbandry (Greenfield 1988, 2005, 2010; Vigne and Helmer 2007; Marciniak 2011; Çakırlar 2012; Greenfield and Arnold 2015).

Religion, Identity, and Socioeconomics

Animals and religion

Before the Neolithic, hints of the importance of animals as part of religion or ritual customs come from the famous Magdalenian and Aurignacian French and Spanish cave paintings, in addition to animal figurines from southern Germany that date to between 35,000 and 40,000 cal BP (Valladas et al. 2001; Conard 2003, 2009; Kind et al. 2014). For the most part, these images represent economically important taxa, such as large ungulates or megafauna, though sites like Chauvet Cave preserve images of large carnivores, and figurines from Hohle Fels and Vogelherd include representations of birds, fish, and even hedgehogs (Conard 2003; Conard et al. 2013). It is tempting to tie Upper Paleolithic imagery to religious practices, but the argument is difficult to substantiate in deep time for the majority of the representations. Starting in the Neolithic, we begin to see an increase in examples of animals being incorporated in religious practices.

Some of the earliest examples of the ritual or religious significance of animals comes from sites such as Göbekli Tepe and Çatal Höyük in Turkey. Göbekli Tepe dates to between ca. 9,200 and 8,700 cal BP and preserves monumental architecture with representations of animals such as snakes, foxes, wild boars, cranes, aurochs, and wild sheep, among others (Fig. 3; Peters and Schmidt 2004). Çatalhöyük dates to ca. 9,100-8,000 cal BP and contains dozens of animals depicted in paintings, reliefs, and as whole bones built into or hanging on walls (Russell and Meece 2005; Bayliss et al. 2015). Analysts have argued for ritual feasting millennia earlier (11,700-11,270 cal BP) at Hallan Çemi Tepesi, where an alignment of three sheep crania was found in a central activity area associated with communal events (Hayden 1995, 2009; Rosenberg and Redding 2000). Archaeologists find similar examples of animals in imagery at Chalcolithic sites in southwestern Asia (i.e., Epstein 1985; Schmandt-Besserat 1997; McMahon 2009). These cases provide strong support for the idea that animals were part of human rituals and religion throughout much of the Holocene, though the nature of such practices is difficult to fully understand.

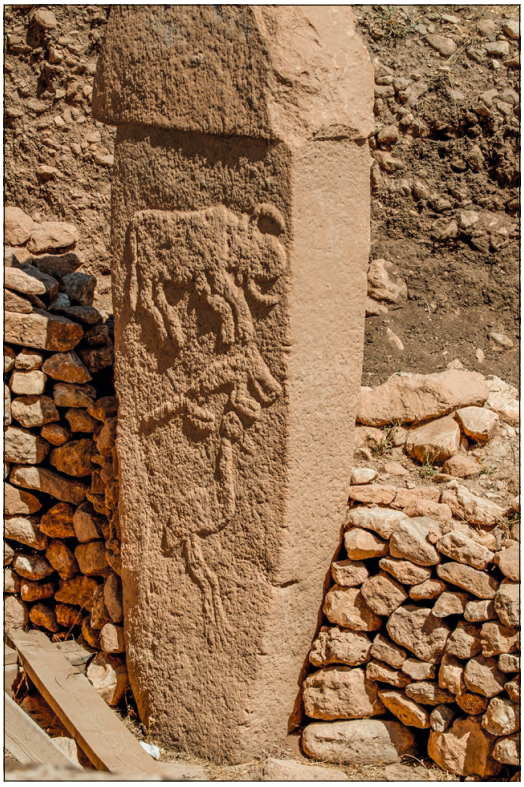

Fig. 3: Göbekli Tepe, Turkey. Neolithic pillar depicting cattle, a canid, and a bird (top to bottom). Photo: Teomancimit (Own work) [CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0)], from Wikimedia Commons.

Abb. 3: *Göbekli Tepe, Türkei. Neolithischer Pfeiler mit der Darstellung eines Rindes, eines Caniden und eines Vogels (von oben nach unten). Foto: Teomancimit (Own work) [CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0)], von Wikimedia Commons.*

As we move into more recent times, especially after the development of writing, it becomes easier to interpret the ritual or religious use of animals. Again, there are many examples to illustrate this point, but I will focus on the pig taboo in the Old Testament as it relates to ancient Palestine, and the ritual sacrifice of animals, or *thysia*, in the Bronze Age through Classical period of Greece.

The Old Testament defines a number of unclean animals that should not be eaten: bats, camels, ferrets, hares, mice, moles, pigs, snails, weasels, and several species of bird, reptile, and amphibian. Pigs, despite being domesticates with a long history of use in southwest Asia, are excluded because they are not ruminants:

And the swine, though he divide the hoof, and be clovenfooted, yet he cheweth not the cud; he is unclean to you. (Leviticus 11:7, King James Version).

And the swine, because it divideth the hoof, yet cheweth not the cud, it is unclean unto you: ye shall not eat of their flesh, nor touch their dead carcase. (Deuteronomy 14:8, King James Version).

Scholars have proposed several hypotheses to explain the origin of the pig taboo in Judaism, including the behavioral characteristics of pigs, their ecological requirements, the relationship between pig consumption and social/economic status, political decisions, and the pastoral history of a culture (Harris 1985; Lobban, Jr. 1994; Zeder 1998; Grigson 2007).

In the past, archaeologists attempted to assign cultural affiliations based on the presence or absence of pigs at sites in ancient Palestine, with the assumption that by Iron Age I (1130-950 BCE, before common era), pigs would be present at Philistine sites and absent from Canaanite/Israeli sites (Hesse 1990; Finkelstein 1996; Hesse and Wapnish 1997). In a recent study of 78 archaeological assemblages with refined chronologies, Sapir-Hen et al. (2013) found a more complex situation. While pigs are indeed common at Iron Age I Philistine urban sites, they are largely absent in rural settings. Instead, the authors found a larger distinction at Iron Age IIA-B (950-680 BCE) sites, depending on if sites were in the Kingdom of Israel or the Kingdom of Judah. In the Northern Kingdom (Israel), pigs are consumed, while they are absent to the south (Judah). The authors attributed this difference to dense human populations in Israel which restricted pastoral grazing land and caused people to turn to pigs. Sapir-Hen et al. (2013) pointed out that the authors of the bible included the pig taboo even though pigs were already rarely eaten in most of the region. They hypothesized that the taboo might have emerged in the highlands in order to distinguish between pastoralists and the lowland Philistines. Alternatively, it might have been used as a cultural codification to integrate the Israelites who moved to the south after the North Kingdom collapsed in 720 BCE (Sapir-Hen et al. 2013).

Beyond the avoidance of certain species, animals were (and still are) an important part of rituals in many eastern Mediterranean cultures. The Greek writer Homer described the ritual of *thysia*, where people led sheep, goats, cattle, and occasionally pigs, to a sacred space such as an altar or temple, where they were sacrificed:

Then, when they had prayed and had sprinkled the barley grains, they first drew back the victims' heads and cut their throats, and flayed them; and they cut out the thigh-pieces and covered them with a double layer of fat, and laid raw flesh thereon. These they burned

on billets of wood stripped of leaves, and the inner parts they pierced with spits, and held them over the flame of Hephaestus. But when the thigh-pieces were wholly burned and they had tasted the inner parts, they cut up the rest and spitted it, and roasted it carefully, and drew all off the spits. Then, when they had ceased from their labour and had made ready the meal, they feasted, nor did their hearts lack aught of the equal feast. (Homer, Iliad 2:420).

Though Homer was writing in the 8th century BCE, when *thysia* was practiced in Greece, the events mentioned in the *Iliad* took place during the Trojan War (1260-1180 BCE), in the Bronze Age. This begs the question as to whether Homer was simply ascribing a contemporary ritual to the past to make it more relatable to his readers, or if the origins of the practice actually occurred in antiquity.

In Greek mythology, the gods were sated by the smell of the sacrificed, burning animal thighs. Priest would often burn tails for divination purposes, reading meaning into the twisting and curling of the tail (van Straten 1988). In addition to textual descriptions, iconographic depictions of these rituals are found in murals as well as on pottery (Fig. 4; Detienne 1977; Jameson 1988; Marinatos 1988; Durand 1989; Bergquist 1993; van Straten 1994; Ekroth 2011).

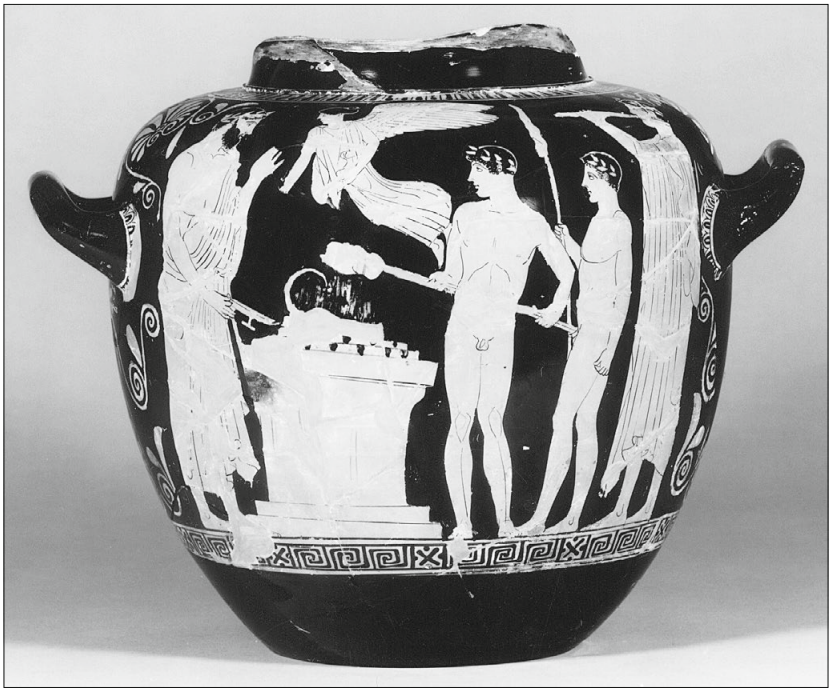

Fig. 4: Fifth Century (440-430) BCE Attic red-figured stamnos depicting the ritual burning of a piece of an animal on an altar with special observation of its tail. Polygnotos. London, British Museum E 455. Photo © Trustees of the British Museum. From Bundrick 2014.

Abb. 4: *Attischer rotfiguriger Stamnos aus dem 5. Jh. (440-430) v.Chr. mit der Darstellung einer rituellen Verbrennung eines Tierstückes auf einem Altar unter besonderer Beobachtung des Schwanzes. London, Britisches Museum E 455. Foto © Trustees of the British Museum; nach Bundrick 2014.*

For over a century, the earliest archaeological evidence of *thysia* came from Geometric (ca. 1100-800 BCE), Archaic (ca. 750-480 BCE), and Classical (ca. 510-323 BCE) period sanctuary sites (i.e., Reese 1984, 1989; Davis 1996; Bammer 1998; Vila 2000; Forstenpointner 2003; Benecke 2006b). These sites are generally characterized by heavily burned animal remains, in particular upper leg bones such as femurs or humeri, as well as caudal vertebrae from sheep, goats, and cattle (Ekroth 2014, 2017). Occasionally, there is evidence for a bias in the side of the animal that was offered to the gods, as in the case of Artemision at Ephesus (Forstenpointner 2003). Recently, archaeologists have noted some small assemblages of burned pig bones at Mycenaean sites (1600-1100 BCE), which seem to be part of a similar version or perhaps incipient form of the ritual (Isaakidou et al. 2002; Hamilakis and Konsolaki 2004; Cosmopoulos and Ruscillo 2014).

In 2007, excavators began working at the Arcadian sanctuary site of Mt. Lykaion in southern Greece (Romano and Voyatzis 2014). Their work uncovered a mountaintop with 1.5 meter-deep sediments that are entirely anthropogenic in origin, with bone and ash in the sand- and silt-sized sediment fractions (Mentzer et al. 2017). The site preserves millions of faunal remains, mostly thighs and tails from sheep or goats; a 2 meter x 2 meter excavation unit yielded 874 sheep/goat individuals (Starkovich 2014b). Direct radiocarbon dating on calcined bones indicates that, as Homer wrote, *thysia* did indeed begin in the Bronze Age at Mt. Lykaion, by 1739-1316 cal BCE, then fluoresced in the subsequent Geometric and Hellenistic periods, 1000-500 cal BCE (Starkovich et al. 2013). In addition to evidence for the early origin of *thysia*, work at Mt. Lykaion also established continuity of ritual activity in the sacrifice of animals, for over a thousand years of site use (Starkovich et al. 2013; Starkovich 2014b).

Identity and socioeconomic status

The final avenues of zooarchaeological research that I will review are identity and socioeconomic status. In both cases I focus on medieval Europe, where archaeologists have conducted considerable work on the two topics. Identity is partially an extension of religious practices; for many people, religion is as much about culture as it is about faith, and the two are often intertwined. For example, as mentioned above, the Old Testament provides a list of taboo foods that are avoided by people practicing Judaism. Even today, secular Jews living in Israel may adhere to the same set of taboos, either from a cultural avoidance, or because certain foods are unavailable or difficult to find. This also means that, through their subsistence practices, people can present one identity to the outside world, while they practice a different identity in the privacy of their own homes. This dichotomy came to a head during the late 15th century, as the Spanish and Portuguese inquisitions (and similar movements elsewhere in Europe) forced people to convert to Catholicism, and attempted to root out heretics from people who had previously converted. This left Jews, Muslims, pagans, and other religious minorities with few options: convert, or face expulsion, imprisonment, or even death.

This historical reality has sparked an area of research into the dietary practices of people living in medieval Iberia, in order to identify if people were living openly or privately as non-Catholics. Compared to Catholics, who have no food restrictions, Muslim and Jewish faunal assemblages should both lack pig remains. At Islamic sites there is some nuance; in certain periods there are small numbers of pigs (Davis 2006; Davis et al.

2008), which might be explained by the relaxation of pig taboos in the later Islamic phase (Grau-Sologestoa 2017). Iberian sites with Jewish inhabitants are more strict regarding the lack of pigs; in addition to a range of other taxa (see above), hind limbs and pelvises are also often missing (Armitage 1984; Insoll 1999; Valenzuela-Lamas et al. 2014). This is because it is forbidden to consume blood in Judaism, and the sciatic nerve and femoral artery are difficult to remove from the pelvis and femur without exposing the meat to blood (Valenzuela-Lamas et al. 2014). Jewish and Muslim dietary restrictions and the fallout from the inquisition also reached other parts of medieval Europe. For example, the Blauwhof, a noble 16th-17th century estate in Belgium, was occupied by a rich family of Portuguese merchants, the Ximenez family (Aluwé et al. 2015). In Portugal, the family had been Jewish until the late 15th century when they converted to Catholicism to avoid losing their business. Historical texts suggest that this conversion was quite public, and included donations to the Antwerp cathedral. An analysis of the faunal remains from the Blauwhof indicates that privately, the Ximenez family was indeed living as Catholics, eating pork, occasional hares, and consuming non-kosher hind limb elements (Aluwé et al. 2015). However, the Ximenez family held onto one important aspect of their identity: their Portuguese roots. This manifested in the consumption of more sheep and goat than was typical of a contemporary Belgian elite (Aluwé et al. 2015).

In terms of socioeconomic status, archaeologists have conducted much work on the relationship between food and status. Typically, wealthy or high-status individuals consume foods that are high-quality, expensive, and/or are particularly desirable in their respective cultures. There are several zooarchaeological markers of high-status diets in medieval Europe: high taxonomic diversity, the presence of wild game and birds, rare or expensive species, animals butchered before they reach adulthood, and body parts with high meat yields (Crabtree 1990; Ashby 2002; Grant 2002; Ervynck et al. 2003; Serjeantson 2009; Woolgar et al. 2009; Bartosiewicz et al. 2010; Kühtreiber 2010; Rehazek and Marti-Grädel 2010; Küchelmann 2012; Grau-Sologestoa 2017). Archaeologists have analyzed high-status diets based on a series of these traits in medieval Belgium, England, Germany, Spain, and Switzerland. Interestingly, many of these studies are based in economic theory that is tied very closely (or explicitly; i.e., Ervynck et al. 2003) to the evolutionary ecology models that began this review.

In Belgium, we find evidence of high socioeconomic status at the same estate with two distinct owners during two different time periods. In an earlier occupation of the site, called the Hof van Leugenhaeghe in the 14th-15th century, unknown owners subsisted on a range of high-status foods, including a diverse spectrum of wild ungulates, game birds, juvenile cattle, and pig skulls (Aluwé et al. 2016). In the 16th-17th centuries, after the construction of the Blauwhof on the property, the above-mentioned Ximenez family enjoyed the meatiest elements from sheep, goats, and cattle, in addition to juvenile ungulates, occasional hunted mammals, and a wide range of birds (Aluwé et al. 2015). In both instances, high status diets are supported by a range of markers found elsewhere in medieval European faunal assemblages. It is also important to note that status is best understood with supporting archaeological evidence, which in the case of the Hof van Leugenhaeghe/Blauwhof comes from ceramics and other artifacts, in addition to textual records marking the property as a noble estate.

Conclusions and Future Perspectives

The purpose of this review is to explore diachronic changes in hominin subsistence patterns in the Quaternary Period of Eurasia with a special focus on variation and complexity of the meat component of the diet. This is a vast topic, and I have barely scratched the surface of the diversity found in this phase. Furthermore, limiting the subject to Eurasia, in particular Europe and Southwest Asia, misses important developments that occurred in East Asia, Africa, Australia, and the Americas. Clearly, there are many more examples that could be highlighted in this work, but I have confined the review to areas in which I have personal experience or a special interest.

Food is cultural. Ask any American ex-pat who has searched their village to find a turkey in the days leading up to Thanksgiving, or a German abroad who has to come to terms with the fact that, outside of Europe, green asparagus is much easier to find than white. But food is also essential to life from a nutritional standpoint. The challenge for researchers interested in human adaptations and evolution is to find the intersection between external forces, such as climate change and the environmental availability of food resources, and human-driven factors, including population growth, technological change, social relationships, and cultural choice. As we move later in time, human-driven factors seem to become more significant than external forces.

There are several conclusions I would like to draw from this work that highlight the importance of subsistence strategies on human evolution and culture. The first is that the origins of what we think of as modern meat acquisition strategies began deep in time in Eurasia, before the appearance of *Homo sapiens* or even Neanderthals. These strategies are typified by the hunting of large, often prime-aged adult, ungulate prey, and seem to have been in place by at least 500,000 BP. The hominins that first moved to the top of the food chain do not appear to have had projectile hunting weaponry, which speaks to their social and communication capabilities, since they had the skills to dispatch multiple bison or horses in a single event. In any case, this behavioral pattern was in place by the time Neanderthals evolved, and long before modern humans made their permanent foray into Eurasia after 50,000 BP.

The second conclusion is that one of the major factors in the success of modern humans at the expense of Neanderthals and other Eurasian hominins is the dietary flexibility of *Homo sapiens*. Neanderthals and their predecessors occasionally caught and consumed small game. For the most part, this included slow-moving sessile taxa such as tortoises and shellfish, though there are a few examples of Middle Paleolithic hominins hunting leporids or birds. Modern humans, however, expanded their diets to the point that small, fast-moving prey were a ubiquitous and important dietary contribution in many regions. It is not entirely clear what drove this dietary expansion; possibilities include advancements in organic technologies (i.e., snares, nets, and traps), hunting pressures from population growth, the movement of certain segments of the population away from life-threating hunting situations and into other food acquisition roles, or extreme cultural conservatism by native Eurasian hominin populations. Whatever the driving force, the outcome was the success of modern humans at the expense of all other hominins.

A third conclusion from this work is in regards to the origins of animal management and domestication. With domestication, humans entered into an unprecedented level of

niche construction by controlling the range, habitat, and food of the animals on which they subsisted. This in turn gave people access not only to a steady food supply, but also a range of secondary products that could be utilized when the animal was still alive. Animal management and plant domestication expanded quickly out of its center of origin in southwest Asia, and put humans in a feedback loop of population growth that could only be sustained by food from domesticates, and agriculture that had to be managed by larger human populations. One contributing factor to this might have been younger weaning ages for children in agricultural societies, which reduced birth spacing and further drove population growth. Some unintended consequences of agriculture were large-scale environmental impacts from larger populations and a rise of zoonotic diseases, such as influenza and smallpox, which came from increased contact with animals among agriculturalists.

My final conclusion is that in the second half of the Holocene, we see a dramatic increase in the number of examples of the cultural, religious, and socioeconomic importance of meat. It is highly likely that meat held cultural significance before this time, but a combination of continued local cultural and ethnic diversification, economic stratification, organized religious behaviors, and written records, simply makes this kind of behavior more visible in later periods. In this phase we see the strong appearance of food taboos, not only in religion (i.e., the pig taboos of Jews and Muslims, or certain Christians not eating meat on Fridays), but also cultural taboos such as dogs and cats not being consumed in Western Europe. Cultures in the Eastern Mediterranean begin to regularly incorporate animals into their ritual and religious ceremonies, which is not so different from using grandma's recipe every year when making an Easter ham. Meat becomes a marker of identity, which includes socioeconomic status ("expensive" versus "cheap" cuts of meat or nobility controlling hunting grounds), religion, and ethnic background. In this prehistoric phase and into the historic period, meat eating takes on much of the significance and complexity we recognize today.

In closing, I would like to reiterate the potential that faunal remains have to provide insights about hominin behaviors in the past, almost to an extent not found with other lines of evidence, simply because of their ubiquity given favorable preservation circumstances (see also Steele 2015). This is partially because organisms have a biological need for food, and the successful acquisition of food impacts the abilities of an individual or population to pass on their genes to the next generation. But it is also because food is so integral to the cultural fabric of hominins, and it can also tell us about human demography and technological solutions to environmental problems. Furthermore, studies of subsistence can tell us both about day-to-day life in the past, in addition to special events and occasions in certain circumstances. Looking ahead, it is possible and even likely that the conclusions I drew in this work will be revised, refined, or outright disproven. However, it is certain that future contributions by faunal analysts will only continue to add to our understanding about the level of complexity and degree of diversity of hominin subsistence strategies during the Eurasian Quaternary.

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