



Late Pleistocene-Holocene mammalian body size change in Jordan's Azraq Basin: A case for climate driven species distribution shifts



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ABSTRACT

Mammalian body size diminution across the Late Pleistocene-Early Holocene transition in the southern Levant has been much researched, with special focus on gazelle in Levantine Mediterranean zones. Explanations of body size diminutions in those cases include temperature increase and anthropogenic factors. This study examines body size shifts in three mammalian taxa – *Gazella* (gazelle), *Lepus* (hare) and *Vulpes* (fox) – between 24,000–7500 cal BP, in the steppic Azraq Basin of northeast Jordan. Osteometrics derive from 19 archaeological sites through the Late Pleistocene-Early Holocene sequence. We use a ‘Z-score’ index of relative body size, and time-series analyses, to track body size shifts. All three taxa show relatively larger body size in the Late Pleistocene compared to the Early Holocene, with smallest Late Pleistocene sizes seen between 12,000–11,500 cal BP, during the Younger Dryas. While gazelles and hare recover size in our Early Holocene samples, they both show smaller sizes after 9000 cal BP. Similarity in size trends leads us to reject the influence of anthropogenic factors alone, in favour of ecological and climatic factors.

We attribute the sharp size decrease in gazelles in the Late Neolithic, 9000–7500 cal BP, to inter-specific size change, and the addition of a smaller Arabian species better adapted to the warmer arid post 8.2 kya conditions. Patterns for fox, albeit on small sample sizes, also hint at species turnover but in the Late Pleistocene. For hare, we track size decrease between the Late Pleistocene and Early Holocene as possible intra-specific diminution. Combined results argue for mammalian taxa experiencing complex responses to shifting ecological conditions in the Late Pleistocene-Early Holocene. Body size trends in the Azraq Basin appear counter to the expectations of Bergmann’s rule of thermoregulation. We propose instead that forage conditions, and resource availability and limitations are better fit drivers of mammalian body size adaptations and turnover (including species distribution shifts) in this semi-arid case study region.

1. Introduction

Alongside the global extinction of many large-bodied mammals during the Late Pleistocene and into the Holocene, a related trend is for *intra-specific* body-size shifts - mainly diminutions - in large mammals that survived as they adapted to new environments. Debate continues as to the relative roles of climate changes and increased human incursion into wildlife habitats as drivers for these within-species mammalian body-size changes (e.g. [McCain and King, 2014](#); [Smith et al., 2018](#)) since the factors influencing mammal body-size shifts are complex. In this paper we present new osteometric data for three mammalian taxa from a 17,000 year Late Pleistocene-Early Holocene sequence in Jordan to

demonstrate long-term body-size fluctuations. We then evaluate the palaeoecological drivers for the body-size shifts observed.

The extent to which Late Pleistocene and Early Holocene climatic shifts correlated, or even ‘forced’, major societal changes seen in archaeological evidence is subject to much debate for the southern Levant region (modern-day Jordan, Palestine, Israel, southern Lebanon and Syria). Some researchers propose that the Younger Dryas (c13,200–11,400 cal BP) triggered the local transition from hunting and gathering to agriculture ([Bar-Yosef, 2009](#); [Bar-Yosef and Belfer-Cohen, 2002](#); [Hillman et al., 2001](#)), while others find more continuity or complexity across the Late Pleistocene-Early Holocene divide (e.g. [Grosman et al., 2016](#); [Maher et al., 2011](#); [Richter et al., 2017](#)). Scholars also speculate as

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to how the 8.2 kya return to cold conditions impacted early farming societies in the Levant (e.g. Bar-Yosef, 2011, 2019) and whether Holocene aridification stimulated mobile pastoralism and population migrations (e.g. Gebel, 2009; Rollefson, 2009; but see Jones et al., 2019). These debates highlight the importance of understanding the effects of palaeoclimatic changes on human societies and resource bases. Assessment of palaeoenvironmental shifts are best made at local level, since it is evident that different localities (of southwest Asia, and especially the heterogeneous landscapes of the southern Levant) were impacted by global climatic shifts in varied ways (Hartman et al., 2016; Jones et al., 2019; Rambeau, 2010; Roberts et al., 2018; Rohling et al., 2019).

Our case-study is the Azraq Basin in north-east Jordan where local palaeoenvironmental conditions (e.g. Henton et al., 2018, 130, Table 1; Yeomans, 2018; Yeomans et al., 2024) are seen to differ from dominant southern Levantine models based on Mediterranean zone proxies. There are strong interests in understanding local palaeoecological conditions and shifts in the Azraq Basin: the area sustained the largest Early Epipalaeolithic sites (21,500–17,500 cal BP) anywhere in the Levant (Garrard and Byrd, 2013; Maher et al., 2012); sees permanent Late Epipalaeolithic settlement, counter to expectations (Richter et al., 2016); it witnesses some of the earliest nomadic livestock pastoralism known at c.9000 cal BP (Miller et al., 2019; Rollefson et al., 2014); and hosts high densities of desert ‘kite’ hunting structures, stimulating great interest in how they functioned. As a relatively arid Levantine zone, the Azraq Basin provides key insights into socio-economic shifts in prehistory. It is an ideal test-case for tracking ecological change since i) arid/semi-arid areas are more sensitive to environmental fluctuations (Asouti et al., 2015; Magaritz and Goodfriend, 1987), and ii) the Azraq Basin saw less anthropogenic resource pressure compared to better-watered Levantine zones (Martin et al., 2016; Yeomans et al., 2017b).

Previous zooarchaeological results from the Azraq Basin show broad-scale faunal turnover through the Late Pleistocene-Early Holocene (Martin et al., 2016; Yeomans et al., 2017b) with an Early Holocene disappearance of large game, an intensification of gazelle hunting and increased exploitation of fast small game (hare and fox). Gazelle dental isotope analyses show shifts in gazelle mobility between the Late Pleistocene and Early Holocene (Henton et al., 2017, 2018) further indicating changing ecological pressures. We now turn attention to body size changes in certain mammals through the sequence to further explore adaptive pressures.

In this paper, we examine zooarchaeological osteometric data from a time-sequence across the Late Pleistocene-Early Holocene transition, from c. 24,000–7500 cal BP. Samples derive from 19 archaeological sites in the present-day Jordan steppe-deserts (all except one in the Azraq Basin). The main focus is *Gazella* sp. (gazelle) which provides the largest data-set for metrical analysis, with inclusion of *Lepus* (hare) and *Vulpes* (fox) to a lesser extent.

Our aims are three-fold.

- 1) To present new data on mammalian body size trends from Jordanian Azraq Basin sites between 24,000 cal BP and 7500 cal BP;
- 2) To trace significant shifts in *Gazella* body-size within the sequence, and for *Lepus* and *Vulpes* where possible;

Table 1

Sample sizes of osteometric data used in analyses for this study for Z-score and LSI analyses, by taxon and period, showing absolute date range. Counts do not include osteometric ‘lengths’, and thus differ from SI Tables 3, 4, 5.

Period	Age cal BP	Gazella	Lepus	Vulpes
Late Neolithic	9000–7000	481	72	7
PPNB	10500–9000	140	88	7
Late Epipalaeolithic	14500–11500	1026	34	12
Middle Epipalaeolithic	17500–14500	25	0	0
Early Epipalaeolithic	21500–17500	1382	156	90
Initial Epipalaeolithic	24000–21500	80	0	0

- 3) To evaluate mammalian body size changes alongside published models of southern Levantine palaeoenvironmental change (from speleothem and lake level evidence) and published geomorphological evidence for local Azraq Basin environmental conditions (see section 6.3), to assess wildlife adaptations.

2. Mammalian body size adaptations

2.1. Body size adaptations in prehistory

Pleistocene mammalian body size decline within species has long been noted across continents. Examples include both herbivores and carnivores becoming smaller-bodied in warmer Late Glacial conditions, leading some to attribute the phenomenon to Bergmann’s rule (1968, 245–8) which relates body size to thermoregulation (e.g. Forsten, 1993; Guthrie, 2003; Harris and Mundel, 1974; Jensen, 1991; Klein and Scott, 1989; Kurtén, 1968; 1973; Klein and Scott, 1989; Seymour, 1993). Trends are not universal, and Kurten (1968) suggested factors other than temperature are at play. Whether size ‘diminution’ represents *intraspecific* or *inter-specific* character displacement is also not always clear (Forsten, 1993). Under ‘character displacement’ (following Brown and Wilson, 1956) a similar pattern could result from an ecological situation where two closely related species with overlapping ranges become more divergent morphologically.

Well-known global ‘islandisation’ case-studies – the trend of vertebrates displaying dwarfism in large species, and gigantism in smaller ones – while not directly applicable to our case study, deserve mention since they have greatly refined our understanding of body size shifts. There is general agreement that the mechanisms behind extreme evolutionary size changes on islands include the degree of isolation, specifics of colonization events, including resource limitations, with selective pressures also including the co-occurring predators and competitors (Lister, 1989, 1996; Lomolino, 2005; Lomolino et al., 2012, 2013; Palombo and Rozzi, 2013; van der Geer et al., 2018; van der Geer et al., 2013). While some authors believe the ‘Island Rule’ is relevant across mammalian orders (Lomolino et al., 2013), others argue for variation, such as Meiri et al. (2004) who find carnivores an exception. Regardless, the case of island mammals demonstrates the high plasticity of intra-specific body size which is subject to a suite of complex factors beyond climate and temperature change, all equally relevant to mainland terrestrial mammals. Islandisation studies also highlight the speed and extent to which selective pressures can lead to mammalian body size change (e.g. Lister, 1996; Lister, 1989, 539; Rozzi and Lomolino, 2017) with, for example, dwarf mammoths on Siberian Wrangel Island becoming c.30% smaller than mainland equivalents within c. 7000 years (Vartanyan et al., 1993), with others claiming even faster size reduction within feral cattle (Rozzi and Lomolino, 2017).

2.2. Mammalian body size change in Levantine prehistory

For the southern Levant, Kurten’s early work (Kurtén, 1965) on the carnivores of the Palestine caves identified species at their largest in the late Glacial and dwarfing into the Early Holocene, which he interpreted as reflecting warmer conditions. Davis (1977) also found *Vulpes*, *Canis* and major ungulates at their maximum size in the Late Pleistocene, dwarfing in the Final Pleistocene (Natufian, c. 12,000 cal BP) which he attributed to temperature increase. He also identified a second Holocene size decrease in wolf, boar and aurochs attributed to domestication. Ducos and Kolska Horwitz (1997) undertook a wider regional study and found some ungulate taxa to change body size in relation to Late Pleistocene-Holocene climate shifts, interpreted as an adherence to Bergmann’s rule with additional impacts of grazing limitations. Their results are blurred, however, by the conflation of metrical data from diverse ecological regions.

For gazelles specifically, patterns are mixed. On the Levantine coastal plain, Bar-Oz and colleagues (2004) found no overall gazelle size

variation through time and no Late Pleistocene dwarfing. They attribute an apparent size increase in the Final Pleistocene to the selective hunting of larger males. Cope (1991) invoked similar ‘sex selection’ arguments to explain apparent gazelle dwarfing alongside increased size variation in the Final Pleistocene (but see Dayan and Simberloff, 1995 who refute the evidence). Other authors find gazelle size remaining stable across the Pleistocene-Holocene transition (Sapir-Hen et al., 2009) although osteometric sample sizes are sometimes limited. The apparent lack of size diminution in Early Holocene gazelles has been contrasted with goat, pig and cattle which all show diminutions which are argued to reflect domestication (Munro et al., 2018). Recent osteometric size tracking of gazelles between 24,000–9500 cal BP in Mediterranean zone Levant (Munro et al., 2022) finds little correlation with climate changes, but instead the authors link gazelle size fluctuations with increased anthropogenic presence, hunting pressure and impacts on landscapes.

Interpretation of mammalian body size shifts in southern Levantine prehistory are therefore varied. Results can vary even within the same species, some of which is attributable to the different ecological zones under study (noted by Munro et al., 2022, 11–12). Most authors assume mammal size shifts to represent *intra-specific* adaptations, with only a few scholars considering inter-specific character displacement (Dayan et al., 1989, 1991, 1992; Tchernov 1991, 1992; Tchernov et al., 1986). Work to date has focused exclusively on Mediterranean zones which have relatively high precipitation and rich vegetation which buffers herbivores from climatic fluctuations (Cordova, 2007; Rosen, 2007). Our Azraq Basin study is the first in a semi-arid zone.

3. Regional setting: the Azraq Basin

The osteometric data used in this study derives from a series of Late Pleistocene and Early Holocene zooarchaeological assemblages from sites in Jordan’s Azraq Basin (Fig. 1). The basin is a 12,000 km² inland drainage system in the steppe-desert of the north-east Jordan, encompassing diverse geological settings (Garrard and Byrd, 2013; Garrard et al. 1988). The west and southern areas are characterized by rolling limestone, chalk and marl hills; the north and north-east is covered by basaltic hills and boulder fields. Water drains into the Azraq Oasis at

500 m asl in the basin’s centre. While topographically varied, weather patterns are similar with hot dry summers and cool wet winters; temperatures currently range between –4 °C and 42 °C and rain falls in winter and early spring. The sites under examination fall into areas where precipitation is on a cline from c.200 mm in the north and west margins to less than 50 mm in the south and east. Vegetation is currently Irano-Turanian (wet steppe), with more arid Sudanian elements penetrating to the south and east (Nelson, 1973).

The Azraq Basin is a well-documented archaeological landscape seeing rich and mostly seasonal human occupation from the late Upper Palaeolithic through to the Late Neolithic and beyond (Betts, 1999; Betts et al., 1990; Betts et al. 2013; Byrd, 1988; Garrard et al., 1988; Garrard and Byrd, 2013, 1994, 1996; Maher et al., 2012; Richter et al., 2009; Richter et al., 2017; Maher et al., 2012; Rollefson et al., 2014). Nineteen archaeological sites provide data for the current study covering the period c. 25,000–7500 cal BP (Fig. 2). Some sites include more than one phase of occupation producing 25 distinct spatio-temporal assemblages with zooarchaeological samples (see Fig. 2).

Zooarchaeological assemblages are all published, and show a typical steppic faunal spectrum (Baird et al., 1992; Betts et al., 1990; Betts et al., 2013; Edwards, 2024; Garrard and Byrd, 2013; Garrard et al., 1988; Henton et al., 2017; Henton et al., 2018a; Henton et al., 2018b; Martin, 1998, 1999; Martin et al., 2013; Martin et al., 2010; Martin et al. 2016; Yeomans et al., 2017a; Yeomans et al. 2017b; Yeomans et al. 2019). Late Pleistocene assemblages were dominated by *Gazella* sp. – assumed to be *G. subgutturosa* on horncore morphology (Martin, 1998; Martin et al., 2016; Yeomans et al., 2017b) alongside lower numbers of small wild equids, probably onager (*Equus hemionus*), and aurochs (*Bos primigenius*), with hare (*Lepus* sp.) and fox (*Vulpes* sp.) increasing in the Holocene. Large ungulates (*Equus*, *Bos*) decrease dramatically in the Holocene, while gazelles continue throughout alongside introduced domestic sheep and goats from c. 9000 cal BP (Martin et al., 2016).

4. Materials and methods

4.1. Data selection

Only the bones of *Gazella* and *Lepus* provided large enough samples of osteometric data for detailed analyses (SI Tables 3 and 4 for raw data) while small samples of *Vulpes* metrics are included (SI Table 5). All gazelle, hare and fox osteometrics were taken using calipers on firmly identified postcranial skeletal elements following zooarchaeological standards (von den Driesch, 1976) to one tenth of a millimetre. Measurements were taken only on skeletally adult specimens (not unfused or juvenile elements which may not have attained maximum growth) and those with taphonomic/pathological alteration were excluded. Dental and cranial metrics were not employed in this study as they may not accurately reflect animal body size (Dayan et al., 1989, 1991, 1992; Lister, 1989).

In total our analysis comprised 7912 osteometric measurements of 3254 distinct gazelle elements, 764 measurements of 375 distinct hare elements, and 304 measurements of 122 distinct fox elements. Selected elements with osteometric data for gazelle only (e.g. used in Fig. 6 below) are shown in SI Table 6. Table 1 summarises osteometric sample sizes *discounting lengths* (following Meadow, 1999) for the three taxa by time-period; these form the samples for Z-score and LSI analyses, described below.

4.2. Analytical methods

We used statistical osteometric analysis to explore the variation in animal bone size within and between assemblages and to model size change through time. Three approaches were employed. In places, simple scatter plots and histograms were used to visualise the distribution of individual element-metrics. Second, we standardised and combined element-metrics for each taxon, to compare the relative skeletal

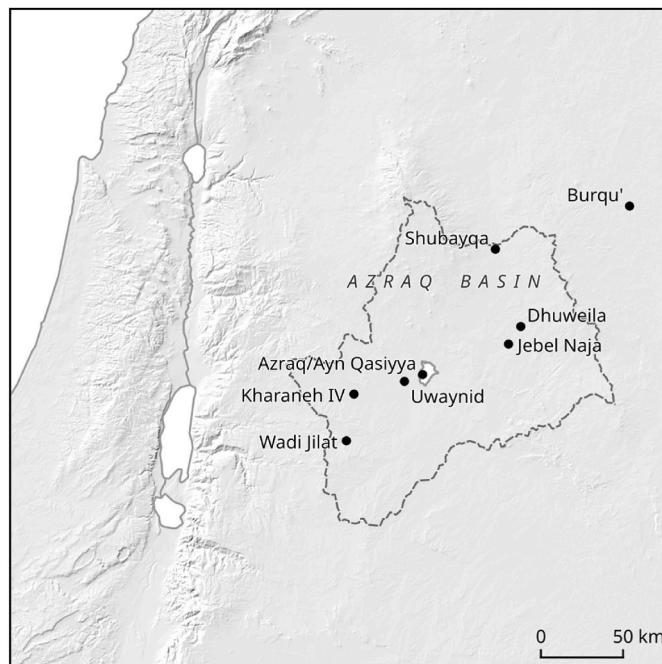


Fig. 1. Map of the Southern Levant showing the Azraq Basin in north-east Jordan (dashed line) and sites used in this study (see SI Table 1 for site coordinates). Note: there is often more than one site at locations shown.

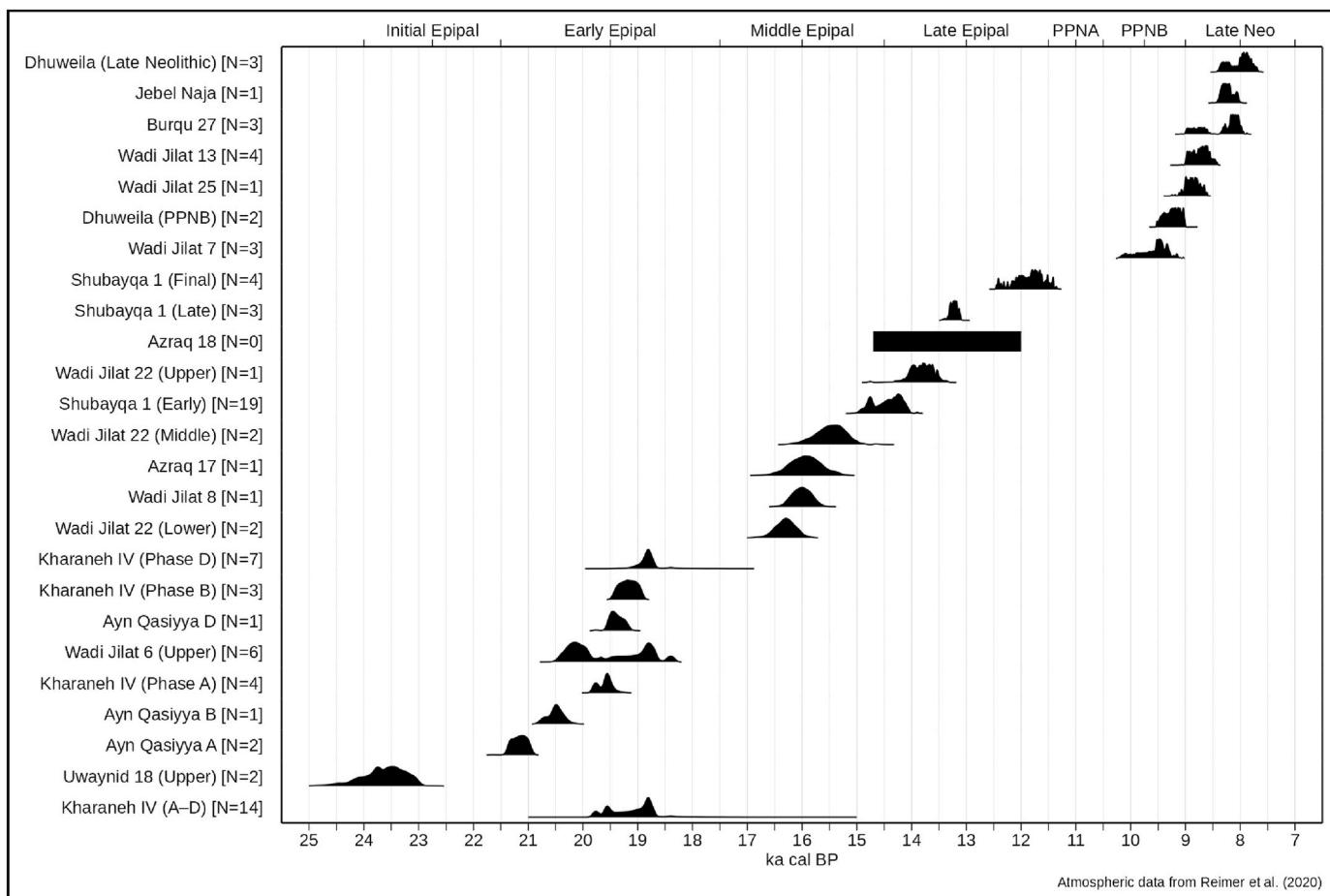


Fig. 2. Summed and calibrated radiocarbon dates for Azraq Basin/north-east Jordan assemblages used in analyses (calibration curve follows Reimer et al., 2020). Note that 'Kharaneh IV (A–D)' combines dates from all phases of the site and is used for zooarchaeological specimens not assigned to a phase; no radiocarbon dates are available for Azraq 18. (see SI Table 2 for radiocarbon information). (see Section 4.2.2 'Time series statistics' for details).

size of animals across the Azraq Basin assemblages using the maximum available data. Third, we conducted a time series analysis of relative bone size change on an absolute timescale using Monte Carlo simulation to account for the chronological uncertainty associated with radiocarbon dating. Postcranial skeletal element metrics (except long-bone lengths which we do not use) are a reliable indicator of body size (Scott, 1990); we therefore use the terms 'bone size' and 'body size' interchangeably. The main statistical analyses were performed in R version 4.3.3 (R Core Team, 2024).

4.2.1. Estimating relative body size from osteometric data

Raw osteometric data representing different elements and/or different measurements are not directly comparable, severely reducing the sample available for a given analysis and consequently its statistical power. As a result, zooarchaeologists frequently use a statistical transformation to *scale* or *standardise* individual element-metrics to make them comparable, based on the assumption that they all approximate the same underlying phenomenon (animal body size). Several approaches are available (see Meadow, 1999; Wolfhagen, 2020 for reviews), but in recent years the Log Standard Index or LSI (Uerpmann, 1979) has become the most frequently-used method (see Pozo et al., 2022). LSI is defined as $LSI = \frac{\log(x)}{\log(s)}$ or $LSI = \log\left(\frac{x}{s}\right)$ (the two forms are mathematically identical), where x is the unstandardised metric, and s is the corresponding measurement of a reference sample – the 'standard animal'. Typically, a modern specimen of the same species as the studied remains is used as the standard animal, though it can also be an 'internal' standard derived from the zooarchaeological assemblage itself

(Manning et al., 2015; Evin et al., 2023).

In our analysis, we encountered two limitations of the LSI method. First, only element-metrics where a corresponding measurement was made of the standard animal could be incorporated into the analysis, which excluded approximately 25% of our sample. Second, LSI does not take into account the variance of element-metrics. Previous authors have noted this limitation but considered it to have a negligible effect on the results of osteometric analysis (Meadow, 1999, 290–91). With the large dataset available to us, we observed significant differences in the variances of different element-metrics, which were preserved in their LSI-transformed distributions, and had the effect of 'muddying' the underlying trends in relative body size revealed in analyses.

We therefore used an alternative index of relative body size, the 'standard score' or 'Z-score'. This is the most common standardisation method in the wider statistical literature (Legendre and Legendre, 2012, 44) and has previously been applied to zooarchaeology, in a slightly modified form, as the 'Variability Size Index (VSI)' (Uerpmann, 1982). It is defined as $z = \frac{x-\mu}{\sigma}$, where x is the unstandardised metric, μ is the population mean, and σ is the population standard deviation. In this case the *population* referred to is all other metrics representing the same measurement of the same element. The standard score does not rely on an external reference sample, which allowed us to incorporate our entire dataset into the analysis. Dividing by the standard deviation also takes into account the fact that different element-metrics have different variances. Using the standard score in the analyses described below resulted in similarly-shaped overall trends compared with LSI, but with noticeably improved detail and precision, as expected from the increased

sample size and elimination of statistical noise resulting from variability between element-metrics.

Aside from this, using standard scores in osteometric analysis is functionally equivalent to using the LSI and raises many of the same methodological considerations. In particular, the presence of non-allometric variation between the archaeological populations being studied is problematic (Legendre and Legendre, 2012). This can be overcome by examining trends in individual skeletal elements as well as combined elements (Russell and Martin, 1995) and considering allometry when selecting element-metrics. Here, we follow the recommendations of Meadow (1999), including not using *length* measurements (see Table 1), with two exceptions.

1. We include the greatest length of the lateral side (GLl) of astragalus, alongside the breadth of the distal end (Bd). The astragalus is often the most frequently preserved skeletal element in the Azraq Basin assemblages (SI Table 6), with its compact structure making it less vulnerable to fragmentation. Studies on Bovidae (to which gazelles belong) find the astragalus to have general low intraspecific variability and low sexual dimorphism; Martinez and Sudre (1995) found its dimensions provide a good estimation of body mass and also observed a strong relationship between body mass and astragalus size in extant species of artiodactyls (using a length measurement equivalent to GLl as defined by von den Driesch, 1976; Martinez and Sudre, 1995, Fig. 6). Tsubamoto (2014) also found lateral length of astragalus to be a good predictor of body mass in mammals; it is therefore clearly a good indicator of overall body size which we are interested in for this study. For Levantine gazelles, two studies on *Gazella gazella* both find the astragalus Bd measurement to have low sexual dimorphism (Horwitz et al., 1990; Munro et al., 2011, see SI Table 6) but the latter suggests GLl displays more dimorphism, which needs to be borne in mind in our analyses below (see also Lebzon and Munro, 2022). Since the astragalus does not fuse but ossifies early, care was taken to check these elements were fully grown and adult, and did not display porosity or light weight (as young elements do) which would indicate they had not attained maximum adult size.
2. We include combined phalanges, even though measurements of anterior/posterior and medial/lateral phalanges vary. Again, they represent a large proportion of many of the Azraq assemblages, and including them increases the statistical robustness of our findings. To investigate whether their inclusion in the analysis significantly distorted our results, we compared the standardised distribution of phalanges to other elements, and the time series trend shown with and without their inclusion, finding no significant differences in the shape of either (SI Fig. 1).

We use kernel density estimate (KDE) plots to visualise the distribution of standardised relative body size across and between sites. A KDE plot is essentially a smoothed histogram (Beardah and Baxter, 1996) which estimates the underlying distribution of the data as a continuous function rather than a predefined set of frequency bins. Compared to histograms, this reduces the distorting effect of statistical noise/outliers and the analysts' choice of bin size. Kernel bandwidth selection was estimated automatically from the data.

4.2.2. Time series statistics

Time series analysis was used to assess changes in relative animal body size through time. The use of this with archaeological data is complicated by the fact that we rarely know the precise absolute date of the events data is collected from (Crema, 2011), e.g. the age of an archaeological occupation is not known with certainty. Conventional solutions to this problem include modelling time as a relative rather than absolute sequence or deriving a single midpoint estimate to use as the chronological predictor. However, both approaches sacrifice a significant amount of the chronological resolution otherwise available from absolute dating. In the case of mid-point estimates of radiocarbon dates,

it also risks producing spurious patterns, since it has been demonstrated that there is no good point estimate of the posterior probability distributions produced by radiocarbon calibration (Michczyński, 2007).

We collected published radiocarbon dates for each site in our analysis (Fig. 2; SI Table 2), grouping dates by site-phase where available and where the zooarchaeological assemblage was also recorded by phase. Dates were calibrated using the IntCal20 curve (Reimer et al., 2020) and summed per site or site-phase using the method implemented in the R package 'rcarbon' (Crema and Bevan, 2020; Timpson et al., 2014). Radiocarbon dates were not available for one site (Azraq 18) which we therefore modelled as a uniform distribution based on a typo-chronological estimate of its age (14.7–12.0 ka cal BP, Garrard and Byrd, 2013, p. 103). The resulting summed, calibrated distributions necessarily combine information on both the occupation length of the site and the uncertainty associated with the dating, though we acknowledge that this conflation is less than ideal and does limit the utility of the resulting statistic (Carleton and Groucutt, 2020; Carleton, 2020). To incorporate this information into the time series analysis, we used a Monte Carlo simulation-based approach where each specimen was assigned an age randomly sampled from the chronological probability distribution associated with its assemblage (following Crema, 2011). For the analyses presented in Figs. 3, 4 and 7 this simulation was repeated 10,000 times to construct an envelope of possible time series.

With this data, we estimated the central trend in body size change through time using regression analysis, constructing a generalised additive model (GAM) of relative body size against specimen age over every iteration of the simulation, using the R package 'mgcv' (Wood, 2011). We further estimated the trend in the range of relative body size using an additive quantile regression on the 10% and 90% percentiles of the simulated envelope using the R package 'quanteg' (Koenker, 2023). This helps highlight that while the trend in mean body size through time is robust, the effect is relatively subtle in the context of the natural variation in body size observed in the animal populations.

5. Results and discussion

5.1. Gazelle body size trends through time

Relative body size trends for *Gazella* between c.24,000–7500 cal BP in the Azraq Basin can be gauged in Fig. 3 which uses osteometrics of all postcranial skeletal elements together, scaled using the Z-score method. Only breadth measurements are used, with the exception of astragalus GLl (greatest length of lateral side) for reasons explained above.

Despite all appropriate osteometrics being included in Fig. 3 and sample sizes maximized, some periods still have small samples, indicated where there is wide fluctuation in the 10% and 90% quantile lines, such as between 17,000–15,000 cal BP. For this time-range, trends should be treated with caution. Discounting that period, Fig. 3 shows relatively stable gazelle body size through the Last Glacial Maximum and post-glacial period until c.15,000–14,500 cal BP (mean $Z = 0.27 \pm 0.81$) where a slight size decline is seen. Smallest body sizes in the long Late Pleistocene sequence are between c.12,500–11,500 cal BP (mean $Z = -0.55 \pm 0.71$), shown by the regression line. In the Early Holocene, from c.11,000 cal BP, gazelle body size increases although not to Late Pleistocene sizes (mean $Z = -0.24 \pm 0.89$), while from 9000 cal BP until the end of our sequence at 7500 cal BP we see a steep and steady body size decline (mean $Z = -0.79 \pm 1.10$). Alongside this trend are apparent variations in measurement ranges within the sequence, shown by the 10% and 90% in Fig. 3, which are discussed below (5.2).

Combining osteometrics of all skeletal elements, as in Fig. 3, can blur patterns. We therefore also examine trends for the single best-represented element which provided measurements, the astragalus. Metrical trends are shown for two dimensions: GLl, the Greatest Length of the lateral side (Fig. 4 upper) and Bd, Breadth of the Distal end (Fig. 4 lower). As explained above (4.2 Analytical Methods) astragalus bone breadths are good reflections of body weight, while GLl is well attested

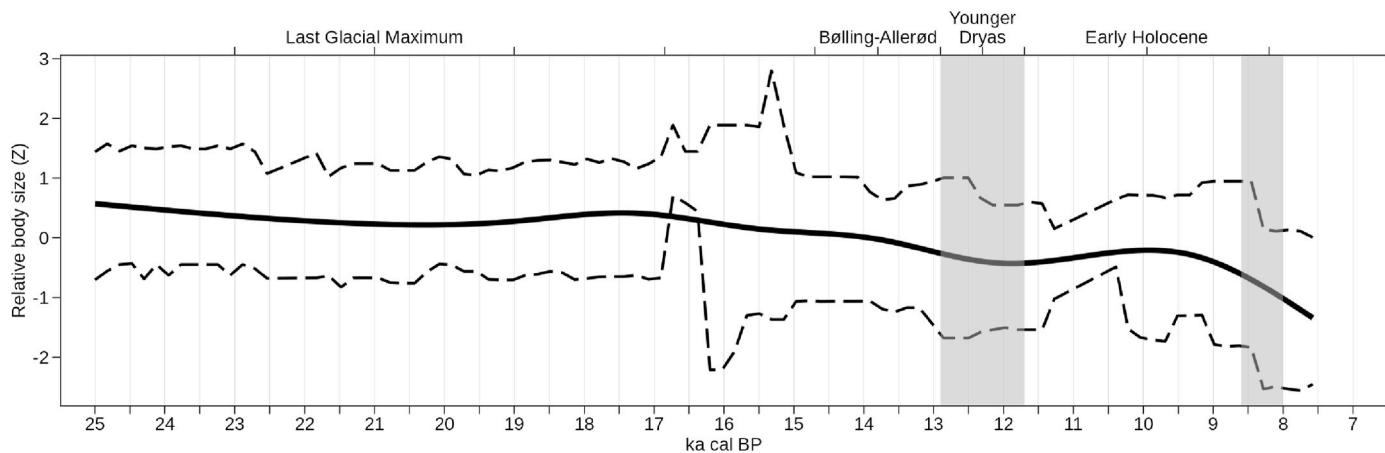


Fig. 3. Relative body size (Z) of gazelle through time, using all postcranial skeletal elements (breadth measurements only + astrag GLI). Dashed lines show the 10% and 90% quantiles; solid black line is the regression. Shaded areas indicate the Younger Dryas (left) and 8.2 ka climate events (right).

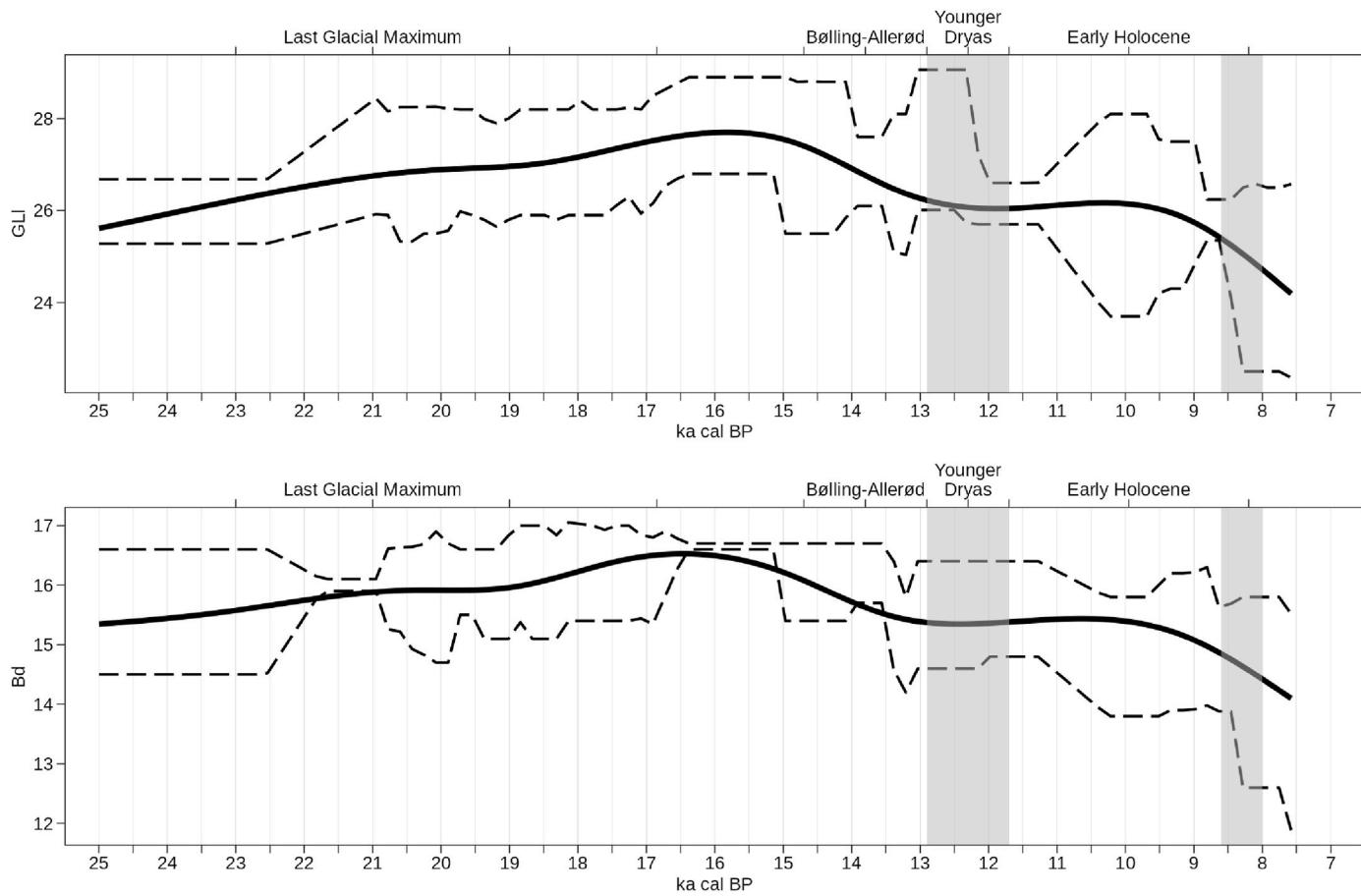


Fig. 4. Relative body size (Z) of gazelle through time, using only astragalus GLI (upper) and Bd (lower). Dashed lines show the 10% and 90% quantiles; solid black line is the regression. Shaded areas indicate the Younger Dryas (left) and 8.2 ka climate events (right).

to correlate with body mass in bovids. Astragalus metrics are a sub-set of those in Fig. 3 and sample sizes thus smaller, meaning trends prior to 21,000 cal BP and between 17,000–15,000 cal BP should be treated with caution. The benefit of using single element metrics is that inter-dependence issues are reduced (when elements could potentially derive from the same individual), and that non-allometric variation, which can occur when using different skeletal elements, is eliminated.

Both astragalus plots in Fig. 4 show similar trends, unsurprising since they may represent different measurements of the same bone. Focusing

on periods with robust sample numbers, size variations clearly mirror those in Fig. 3 but are more pronounced: we see relatively large gazelle body sizes between 21,000–17,000 cal BP (mean GLI = 26.9 ± 0.9 mm; mean Bd = 15.9 ± 0.6 mm), some size decrease between 15,000–12,000/11,500 cal BP (mean GLI = 26.7 ± 1.2 mm; mean Bd = $15.6.0 \pm 0.7$ mm), with similar sizes for the c.12,500 cal BP point (mean GLI = 26.8 ± 1.2 mm; mean Bd = 15.6 ± 0.8 mm). Thereafter, size increases into the Early Holocene – again not reaching Late Pleistocene sizes – followed by a sharp decrease after 9000 cal BP (mean GLI = 24.9

± 1.5 mm; mean Bd = 14.5 ± 1.1 mm). One further observation is that astragalus GL1 (Fig. 4 upper) is less affected than Bd (lower) by small sample sizes, and does not display the very narrow quantile lines in places.

5.2. Gazelle size ranges and distributions

There are two main reasons for exploring taxon size ranges and distributions of osteometrics in zooarchaeological studies of wild fauna. One is to assess sex ratios represented by measurement data; the other is to gauge whether more than one species or breeding population is present. We also briefly consider whether observed gazelle size diminution may be a function of including measurements of juvenile elements (such as the astragalus which ossifies early), since juvenile proportions are known to increase in Neolithic assemblages (post 10,500 cal BP) (see section 6.2; Martin et al., 2016).

5.2.1. Sex ratios

Osteometric data is often used to examine the balance of adult male and female animals within assemblages, as represented by measurement ranges and distributions, on the assumption that males have larger body sizes than females in most wild mammals, with overlap expected. Wild goats, for example, have high degrees of sexual dimorphism which exhibits metrically (Zeder, 2001), as do other bovids such as bison in which most postcranial elements can be attributed to either male or female on the basis of their wide size difference (Speth, 1983). Sexual dimorphism can also be exhibited to different degrees across post-cranial skeletal elements (Lebenzon and Munro, 2022), with weight-bearing dimensions often reflecting greater size differences between males and females than non weight-bearing bones (e.g. Payne and Bull, 1988).

Here we ask whether the increases and decreases in gazelle size observed in Figs. 3 and 4 could be driven by shifts in sex-specific culling, as some authors have hypothesised for gazelle in the Levantine Epipalaeolithic (Cope, 1991, although see Dayan and Simberloff, 1995). In this scenario, larger gazelle body size would reflect more males in an assemblage, while smaller average body size would suggest a higher proportion of females. The preferential culling of male prey is not a well-attested human hunting practice (Collier and White, 1976) but is associated more with early herd management strategies where humans conserve female breeding livestock (although in this system, males are culled as juveniles and their bones would not therefore be measured). Targeted male culls have been observed both archaeologically and ethnographically, however (Noble and Crerar, 1993; Speth, 1983), so need consideration.

Gazelle size ranges and distributions for assemblages with more than 25 metrical datapoints are shown in Fig. 5, using all available osteometrics. The median line fluctuates slightly across Early and Middle Epipalaeolithic assemblages (from Uwaynid 18 Upper, median Z = 0.49, to Shubayqa 1 Early, median Z = -0.05), then shows reduction in the Late Epipalaeolithic at Shubayqa 1 Final. The Early Holocene (Wadi Jilat 7, median Z = -0.28) sees larger average gazelle sizes again, with the median reducing through time in each assemblage until the Late Neolithic at Dhuweila.

The only assemblages exhibiting bimodality in measurement distributions are Early Epipalaeolithic Kharaneh IV D and PPNB Wadi Jilat 7, and to a lesser degree PPNB Dhuweila. The large metrical sample from Kharaneh IV D shows roughly equal representation of larger (adult male?) and smaller (adult female?) animals. This pattern is not surprising since Kharaneh IV, as with all Azraq Basin assemblages, represents a long-term palimpsest of repeated seasons of human occupation and hunting activity (Garrard and Byrd, 2013; Maher et al., 2012; Martin et al., 2010; Muheisen, 1986, 1988; Richter et al., 2017). Any targeting of sex-specific gazelle herds would almost certainly get lost in the ‘noise’ of accumulated results of multiple hunting events. From

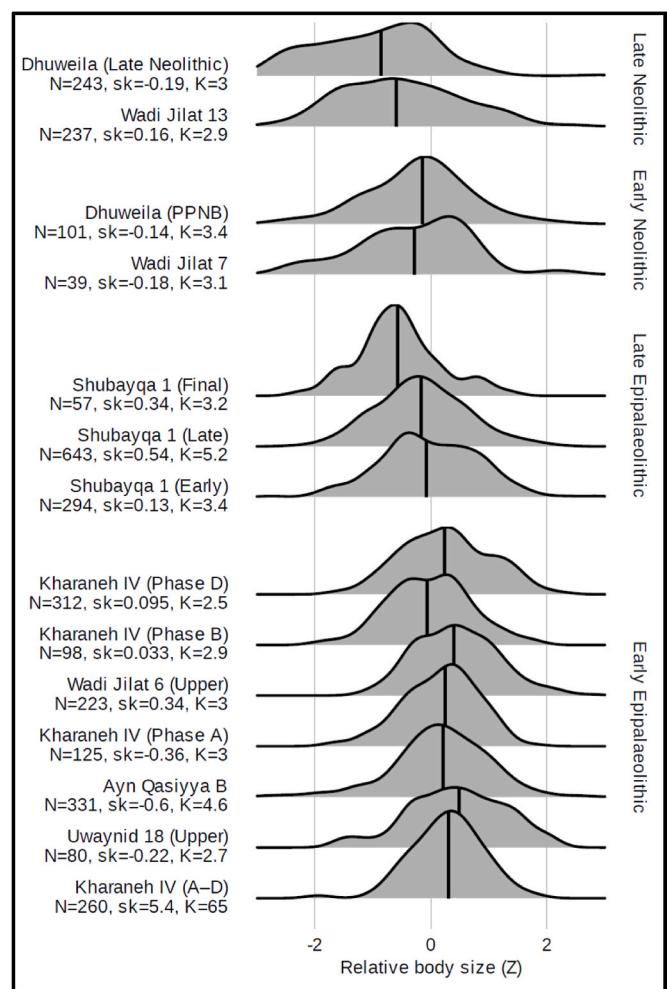


Fig. 5. Distributions of relative body size for gazelle (shown as Z with median values) for Azraq Basin assemblages, excluding sites with 25 or fewer measurements; plots use all available measurements; sites/assemblages are displayed oldest (bottom) to youngest (top). Sample size per assemblage is shown (N), alongside skew (sk) and kurtosis (K) measures.

Fig. 5 we therefore assume no strong sex-selection of either males or females at Kharaneh IV D, and by extension at any other Epipalaeolithic site, since they all show similar measurement ranges and distributions even if not bimodal, a conclusion supported by previous analyses (Martin et al., 2010).

A check is provided by plotting metrics of the scapula, a sexually dimorphic element. For Levantine gazelles, two studies of *Gazella gazella* skeletons (Horwitz et al., 1990; Munro et al. 2011) find relatively high dimorphism between males and females in scapula BG metric (see SI Table 6, %Dimorphism). We assume similar within-skeleton dimorphism across the *Gazella* genus: Wronsky and colleagues' (Wronski et al., 2010) analysis of inter-species sexual dimorphism in modern Middle Eastern gazelles found little variation in the postcranial skeleton. Scapula BG vs GLP measurements from the large sample from Early Epipalaeolithic Kharaneh IV (with fewer from Wadi Jilat 6 Upper) show two clusters (Fig. 6) convincingly corresponding to males and females, with overlap, confirming both sexes to be represented in Fig. 5. There are insufficient scapula measurements to plot the same for the Late Epipalaeolithic and Neolithic assemblages. Previous analyses, however, demonstrate that Dhuweila PPNB and Late Neolithic assemblages contain both males and females (Martin, 1998, 166), while Fig. 5 hints at slightly more males than females in the PPNB Wadi Jilat 7 and Dhuweila distributions.

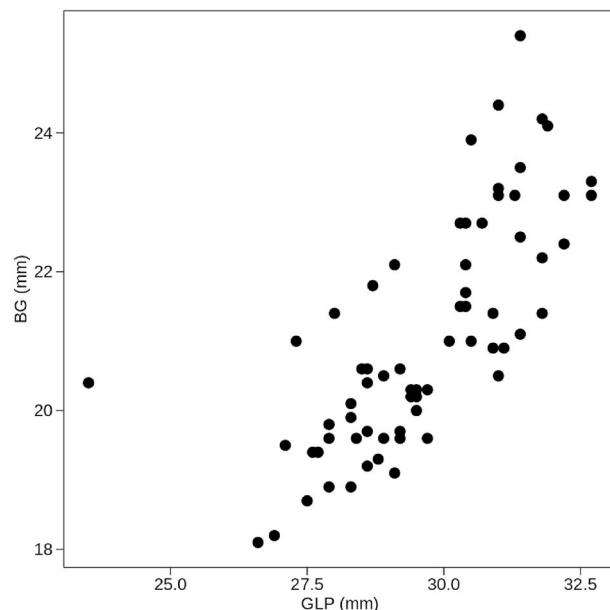


Fig. 6. Scatterplot of gazelle scapula BG vs GLP from Early Epipaleolithic Kharaneh IV (all phases).

In sum, we can rule out the possibility that size decreases observed between Late Epipalaeolithic and Late Neolithic gazelles are a function of biases in representation of sexes in the metrical samples, ie more males in the Late Pleistocene and more females in the Early Holocene. Both sexes, unsurprisingly, are present throughout, and while there may be fluctuations within assemblages, sex bias does not explain the gazelle body size decreases observed.

5.2.2. Possible inclusion of juvenile elements?

Gazelle age-at-death data from the Azraq Basin assemblages shows an increase in juveniles hunted at Neolithic sites (post 10,500 cal BP) (section 6.2; Martin et al., 2016). To ensure our metrical trends are not capturing a shift in age structure, especially since the astragalus ossifies early (but has no fusion areas), we were careful to measure only fully fused elements, and for astragali only those which appeared adult in morphology and were dense in texture (see 4.2.1). A check on whether astragalus metrics are affecting overall metrical trends can be seen in the comparison of Fig. 3 (all gazelle postcranial elements) with Fig. 4a/b (astragalus only). While Fig. 4 shows slightly more pronounced trends, both figures show the same smaller measurements from 9000 cal BP.

This comparison suggests it is highly unlikely that there is inadvertent inclusion of juvenile gazelle astragali in our metrical dataset which could impact the size trend. We also note that astragalus metrics form only 14% of the overall Neolithic (post 10,500 cal BP) metrical dataset used in Figs. 3 and 5. Other factors appear to be impacting size trends.

5.2.3. More than one species?

Three gazelle species are believed to have inhabited the southern Levant in recent times: *Gazella gazella* in Mediterranean parkland zones, *G. dorcas* in sandy desert habitats and *G. subgutturosa* in steppic environments (Harrison and Bates, 1991) with significant overlap in distributions. Genetic analyses on modern animals also demonstrate introgression between *G. subgutturosa* and *G. marica*, the Arabian sand gazelle (discussed in detail below, 6.4.2). Gazelle populations in the Azraq Basin were decimated mid-20th century before systematic wildlife surveys were undertaken (Nelson, 1973) making it unclear which species were present in modern times. For prehistoric periods under consideration here, horncore morphology suggests the presence of *G. subgutturosa* in Epipalaeolithic and Neolithic assemblages (at Kharaneh IV A, B, D; Uwaynid 18 Upper; Shubayqa 1; Dhuweila Late Neolithic; Martin, 1998; Martin et al., 2010; Yeomans et al., 2017b). *G. subgutturosa* fits expectations of the steppic grassland environments of the Azraq Basin, but there are no aDNA studies to date to confirm identification.

Throughout the Epipalaeolithic/Late Pleistocene, measurement ranges and distributions fit predictions for a single species (Fig. 5). Wider measurement ranges in Early Holocene sites, with flatter distributions in Late Neolithic assemblages (Wadi Jilat 13 and Dhuweila) raise questions about the cause of this change, which is accompanied by a stepped decrease in median and mean size. Two possibilities seem plausible: first, that a single gazelle species (e.g. *G. subgutturosa*) experienced an increase in body size range, and second that Late Neolithic samples represent more than one species.

The body size range of mammals is driven by complex factors, a prime one being the degree of sexual dimorphism in a breeding population. Pioneering observations on the relationship between social organization and ecology in ungulates (Geist, 1974; Jarman, 1974) stress how sexual dimorphism is part of ungulate adaptive behaviour. Jarman showed how the extent and manifestation of sexual dimorphism varied between antelope species in Africa depending on the specifics of forage habitats, group social organization and mating strategies (Jarman, 1974, 260–262). Geist (1974) proposed that in fluctuating forage habitats – such as those with highly seasonal forage availability or patchy resources - there is selection for large males in bovids, where larger body size increases reproductive success. In ungulates, sexual selection for males is now widely recognized as resulting from male-male

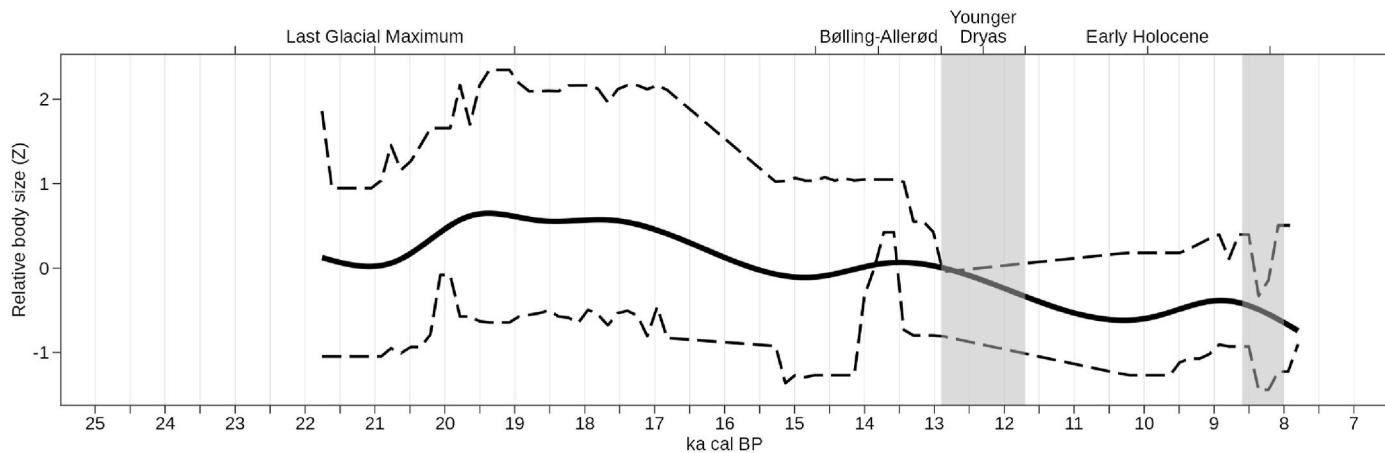


Fig. 7. Relative body size (Z) of hare (*Lepus* sp.) through time from eastern Jordan assemblages, using all skeletal elements. Dashed lines show the 10% and 90% quantiles; solid black line is the regression. Shaded areas indicate the Younger Dryas (left) and 8.2 ka climate events (right).

competition within breeding groups with polygamous mating strategies (as most bovids have, including gazelles, Martin, 2000) and particularly in open habitats (Clutton-Brock et al., 1982; Lindenfors et al., 2007; Loison et al., 1999; Pérez-Barbería et al., 2002). While the Azraq Basin is highly likely to have experienced environmental change and fluctuation between Late Pleistocene and Early Holocene (see below), Fig. 5 shows the wider body size range in the Holocene results from an increase in smaller metrics, driving the range and median downwards, not an increase in larger sizes which could be interpreted as males. This does not support expectations of increased sexual selection, with larger males and heightened dimorphism in the Holocene.

We should therefore consider whether Neolithic gazelle size ranges reflect the addition of another smaller species in assemblages. Neolithic size ranges do not see an overall shift downwards, indeed the larger body sizes see little change through time. The increased range is caused by the addition of smaller measurements, ie. smaller animals being incorporated into analyses. The flatter profiles seen for Wadi Jilat 13 and Dhuweila Late Neolithic support a suggestion of two overlapping size distributions with no clear unimodal or bimodal patterns. While it is impossible to confirm without palaeogenetic studies (or morphometric work on horn-cores which currently do not exist in sufficient numbers) we propose that Late Neolithic assemblages reflect the inclusion of two gazelle species, one larger – similar to that seen in the Late Pleistocene – and another smaller species. The smaller animals are suggested from the PPNB but are clearly apparent in the Late Neolithic.

5.3. Hare body size trends through time

Osteometric sample sizes are far smaller for hare (*Lepus* sp.) than gazelle (SI Table 4), and the period 17,500–14,500 cal BP lacks any datapoints at all so cannot be assessed. Despite this Fig. 7 shows shifts in hare body size through time from the Azraq Basin sites. All skeletal elements are combined in the Z-score analysis, which serves to dampen trends as with the gazelle analyses.

Overall hare size (the regression, Fig. 7) is largest at c.20,000–19,000 cal BP (mean $Z = 0.64 \pm 1.00$) decreasing slightly until 17,500 cal BP (mean $Z = 0.46 \pm 0.89$). Where we have Late Pleistocene samples (14,500–11,750 cal BP) hare appear smaller body size (mean $Z = 0.20 \pm 0.73$) and smaller again in the Early Holocene, with fluctuations. Within the Early Holocene, smaller body sizes are seen between 10,500–10,000 cal BP (mean $Z = -0.55 \pm 0.41$); body size increase is noted at 9000–8500 cal BP after which size decreases (mean $Z = -0.47 \pm 0.53$). The trend mirrors that for gazelle, although the Early Holocene size increase and decline occurs roughly a millennium later for hare.

Univariate and Bivariate plots of measurements of single skeletal elements show similar patterns, despite small samples. Hare calcaneum size (Fig. 8a) displays complete separation between larger Early Epipalaeolithic specimens (mean GL = 27.8 ± 1.7 mm; mean GB = 9.3 ± 0.6 mm) and smaller Neolithic examples (mean GL = 23.3 ± 1.0 mm; mean GB = 7.7 ± 0.5 mm), while Late Epipalaeolithic calcaneum metrics are too few to assess. Hare distal humerus measurements (Fig. 8b) appear to confirm the pattern that Neolithic specimens fall in the smaller part the larger Epipalaeolithic size range and indeed extend the lower part of the range downwards/smaller. Caution is needed with *Lepus* distal humerus metrics since Jones (2006) found this element to exhibit sexual dimorphism in a species of European wild lagomorph (with females larger than males). In general, however, Neolithic/Early Holocene hares in the Azraq Basin are clearly smaller on average than those seen prior to 17,500 cal BP. In addition, within the Early Holocene samples there is a suggestion of size decrease between the PPNB and Late Neolithic (Fig. 7).

The broad-scale Pleistocene-Holocene size diminution in hare is highly unlikely to reflect sex selection. Firstly, despite some noted skeletal element dimorphism (Jones, 2006) there is a lack of sexual dimorphism noted overall in hare body weights (Riga et al., 2001, contra Lu, 2000). If distal humerus metrics are dimorphic, the metrics in Fig. 8b

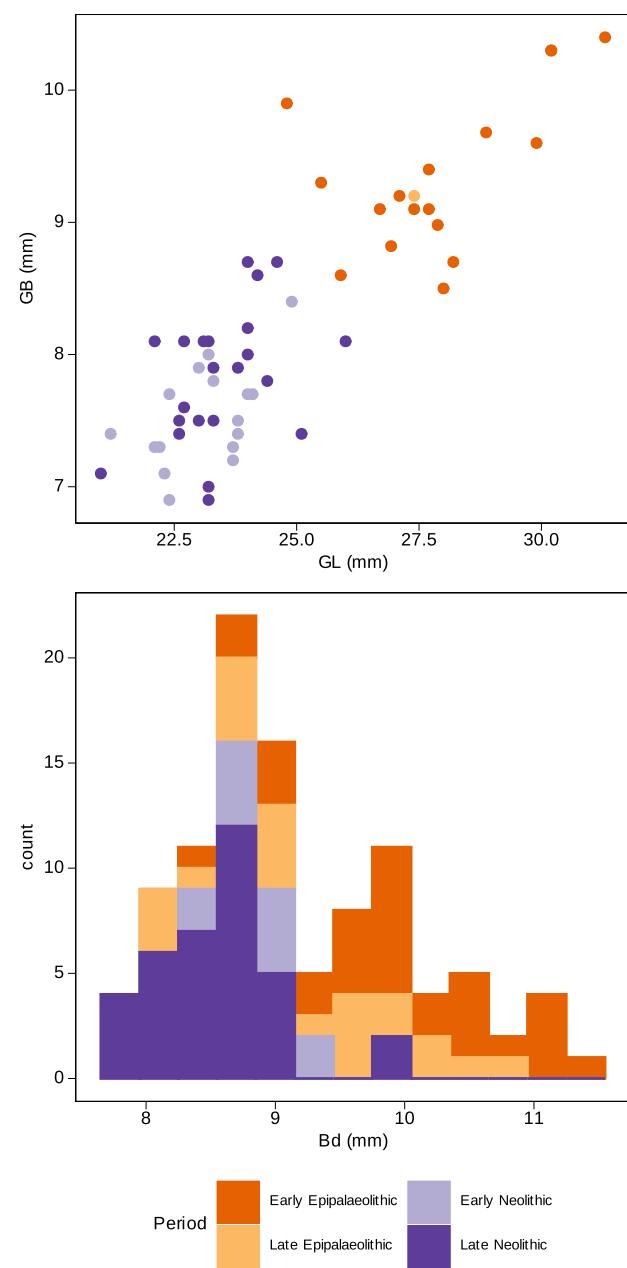


Fig. 8. a (above): Scatterplot of hare calcaneum, GL vs GB measurements (mms) from Early Epipalaeolithic, Late Epipalaeolithic, Early Neolithic/PPNB and Late Neolithic assemblages 8b (below): histogram of hare humerus Bd (mms) from Early Epipalaeolithic, Late Epipalaeolithic (Early and Late Natufian), PPNB and Late Neolithic assemblages.

show a bimodality suggesting two sizes/sexes are present. They also display a range shift in the Neolithic, not just a shift in distribution within the range, which could be interpreted as changes in sex selection. Secondly, it is an implausible human collection strategy that only one sex of hare was captured and deposited throughout the thousands of years of Late Pleistocene occupation, with the other sex solely targeted in the Early Holocene. If both sexes are represented throughout, other explanations are needed for the size decline observed. The complex issue of intra-species versus inter-species size variation in Middle Eastern hares, and potential drivers of size change, is discussed in sections 6.3 and 6.4.1 below.

5.4. Fox body size trends

Due to limited samples of *Vulpes* sp. osteometrics, they have been grouped into four broad time phases - Early Epipalaeolithic, Late Epipalaeolithic, PPNB and Neolithic - with no further temporal resolution.

Fig. 9 shows Early Epipalaeolithic foxes in the Azraq Basin to be overall larger in size (mean $Z = 0.12 \pm 0.91$) than Late Epipalaeolithic and Neolithic specimens (mean $Z = -0.55 \pm 0.65$, and mean $Z = -0.62 \pm 0.69$ respectively), and with a far wider metrical distribution. Late Epipalaeolithic and Neolithic measurements fall in the lower part of the Earlier Epipalaeolithic distribution, with narrower ranges which may be partly affected by small sample sizes. The size distributions of the Late Epipalaeolithic and Neolithic specimens completely overlap, but a shift between the Earlier Epipalaeolithic and the Late Epipalaeolithic/Neolithic can be observed, which may reflect the appearance of a new smaller species in the Later Pleistocene which survives into the Holocene, rather than body size diminution within a single species which would show more gradual adaptation through time.

5.5. Summary

Results show a broad trend for all three taxa - gazelle, hare and fox - for relatively larger body size in the Late Pleistocene than the Early Holocene. Within this, however, there is temporal and taxon-specific variation. While gazelle size in the Azraq Basin is relatively large from c.24,000 cal BP, they appear to increase in size at 17,000–15,000 cal BP (noting sample sizes are small) before declining to their smallest Late Pleistocene size between 12,000–11,500 cal BP. In the Early Holocene gazelle size is initially large, although not to Pleistocene levels, but starting at 9000 cal BP (Late Neolithic) there's a steep size decline. As argued above, we see this in part as resulting from the addition of a smaller gazelle population in assemblages, reducing mean size.

Hare size is also relatively large from 20,000–19,000 cal BP which is the earliest there are available samples, with mean size initially increasing at c. 13,000–12,000 cal BP, before decreasing towards the later Epipalaeolithic (Fig. 7). Hare size is relatively smaller in the Early

Holocene record, with a slight size increase at c. 10,500 cal BP before another decrease detectable between the PPNB and Late Neolithic (c.9000 cal BP) accompanied by narrower ranges in the latter.

Fox has far smaller samples but also shows relatively large sized animals in the Early Epipalaeolithic with smaller specimens in the Late Epipalaeolithic/Final Pleistocene which continue into the Early Holocene. We suggest the smaller Late Pleistocene fox specimens reflect a new species which survives into the Holocene.

6. Selective pressures on mammals in the Azraq Basin

6.1. Drivers of mammalian body size

The drivers of mammalian body size variation and change are complex (see section 2), with selective pressures including climate, thermoregulation, resource limitations, predators and competitors - the latter also including anthropogenic and livestock impacts on wildlife and forage. We also need to consider inter- and intra-specific mammalian change, since we argue above that some size diminutions noted (e.g. for gazelle and fox) reflect the presence of more than one population/species. Islandisation studies also provide key insights into skeletal allometric variation that accompanies mammalian dwarfism (e.g. Dayan et al., 1989; Klein, 1986; Lister, 1989, Table 1; Zeder and Lemoine, 2020) showing postcranial elements to track size better, which is why we focus on postcranial metrics.

The much invoked ‘Bergmann’s rule’ that animal size is linked to thermoregulation has been demonstrated to be far too simple an explanation for body size change. Many examples of modern mammals do not behave accordingly (e.g. Dayan et al., 1989; Lister, 2013; McNab, 1971) showing temperature regulation to be just one of the selective forces on body size. A suite of other factors such as phylogeny, migration ability and resource availability will also be at play (Blackburn et al., 1999). The specifics of mammal behaviour, such as flexibility in activity and feeding times, can also buffer the pressures of climate change on body size (McCain and King, 2014).

Seasonality, abundance and type of plant availability are increasingly found to be important factors determining herbivore growth (Guthrie, 2003; Lister, 2013). Lister suggests that “[u]nder this interpretation, the Pleistocene tundra-steppe is regarded as a richer habitat for many large herbivores (and hence carnivores) than the interglacial forests ...” (2013, 729). Indeed, Henry and colleagues’ (2023) recent analysis of body size determinants for a large number of terrestrial mammal species strongly favours the ‘resource availability hypothesis’ where body size shows strong correlation with grazing productivity. These authors reject Bergmann’s rule as an explanation for body size variation.

It is clear that a wide range of ecological and energetic concerns affect how terrestrial mammals respond to climate changes, which are likely to be highly specific and contextual (Fuller et al., 2016) rendering predictive models challenging (Mitchell et al., 2018). Nevertheless, broadscale trends are borne out in both modern and fossil terrestrial herbivore size, showing north-south size clines, with larger body sizes in more northern latitudes, and smaller body sizes more southerly (Rodríguez et al., 2008; Wright and Viner-Daniels, 2015), even within restricted north-south ranges (Zeder, 2001). We therefore consider selective pressures on gazelle, hare and fox from our Azraq Basin case-study, to attempt to understand the body size trends observed.

6.2. Anthropogenic factors

Recent work identifying gazelle body size diminution during the Late Pleistocene through to the Early Holocene in Mediterranean zone southern Levant makes a strong case for anthropogenic factors as drivers (Munro et al., 2022), including increased human population, landscape fragmentation and gazelle hunting pressure. Prior to the Late Pleistocene/Late Natufian, however, Munro et al. (2022) find body size to fairly

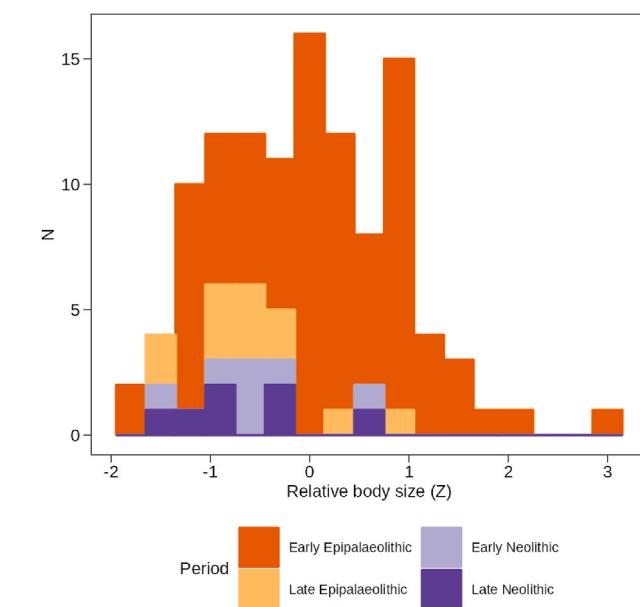


Fig. 9. Osteometrics of *Vulpes* sp. shown as relative body size (Z), for four time periods: Early Epipalaeolithic, Late Epipalaeolithic, PPNB and Late Neolithic. The X-axis shows the log mean for each measurement. Metrics ($n = 65$) are from Scapula BG, Humerus Bd, Radius Bp, Astragalus GL, Calcaneum GL, Tibia Bd (following von den Driesch, 1976) from Kharaneh IV, Wadi Jilat 6, Ayn Qasiyah B, Shubayqa 1, Wadi Jilat 7, Dhuweila, Wadi Jilat 13 and Wadi Jilat 25.

closely track environmental shifts, following Bergmannian expectations of larger size in cooler conditions.

Unlike the Levantine Mediterranean zone, the Azraq Basin does not show evidence for human pressures on landscapes or over-exploitation of animal or plant resources during the Late Pleistocene sequence (Martin et al., 2016; Yeomans et al., 2017b). Settlement is predominantly seasonal, with assumed high mobility, presenting a picture of relative ecological equilibrium. In the Early Holocene, however, the impacts on wildlife of expanding human settlement into the Azraq Basin and the north-east Jordan deserts from the late PPNB onwards (c. 9500 cal BP) needs consideration, particularly since these were pastoralist groups accompanied by domestic grazing livestock (Martin, 1999; Rollefson et al., 2014).

The scale of expanding pastoralism is currently difficult to gauge. Zooarchaeological assemblages from the PPNB and Late Neolithic (9000–7000 cal BP) remain dominated by hunted gazelle (some >90%, Martin et al., 2016), with domestic caprine stock constituting less than 20–30% (e.g. Betts et al., 2013; Martin, 1999). It's therefore clear that even if livestock was mainly kept 'on the hoof' it didn't replace wildlife, probably because all settlement evidence (e.g. temporary architecture, thin occupation deposits) points towards pastoralist grazing being seasonal and nomadic. All evidence to date (Betts et al., 2013; Rollefson et al., 2014; Wasse et al., 2024) suggests that pastoral activity and wildlife hunting coexisted in the same landscapes.

We need also to ask whether the well-studied desert 'kite' traps, of which some at least date to the Late PPNB and Late Neolithic (e.g. Abu-Azizeh et al., 2021; Betts and Burke, 2015; Grassard et al., 2022) exerted hunting pressure on gazelles which are believed to be their main target. If so, could this have driven the observed body size decreases? High juvenile counts of hunted taxa are often seen as zooarchaeological indicators of hunting pressure and hunting intensity (e.g. Munro, 2004 for Mediterranean zone Levantine gazelle), which drives animal populations to be dominated by younger age groups. Elsewhere we have presented gazelle cull pattern data for the Azraq Basin sites (Martin et al., 2016; Yeomans et al., 2017b), showing percentages of juveniles to indeed be higher in the Late Epipalaeolithic/Natufian and also PPNB/Late Neolithic than in the Earlier Epipalaeolithic. The high percentages in the Shubayqa Natufian (Yeomans et al., 2017b) are intriguing since kites or drive hunting is not so far evidenced from this period in eastern Jordan, and indeed Natufian period sites are scarce in this region, complicating a straightforward correlation between hunting pressure and high percentages of juveniles. Another factor influencing high juvenile counts may be the wetter and lusher Late Pleistocene and Early Holocene conditions (see 6.3 below) allowing for double birthing of gazelles, as they do in the Lower Galilee today (Barharav, 1974, 1983), meaning there are more juveniles within herds and populations. This may in part explain increased juvenile counts, both in the Azraq Basin landscape and archaeological assemblages, regardless of hunting intensity, and seems likely given i) the palaeoenvironmental data (6.3 below), and ii) the absence of Late Pleistocene/Natufian hunting traps to date.

Desert 'kite' traps can be assumed to have considerably increased hunting efficiency from the Late PPNB onwards (when some at least are dated to). Most kites and kite-chains, however, remain undated, and their wide morphological variation (Barge et al., 2023) suggests long chronological development and usage. We cannot therefore see a clear causal link between hunting traps and the gazelle size diminution we see in the Azraq Basin Neolithic gazelle metrics, although this is a key avenue for future research.

What we do know is that gazelles are well known for their reproductive resilience and adaptability (e.g. Svizzero, 2019) and we see no decline in their proportions in assemblages through the PPNB and Late Neolithic (Martin et al., 2016). The desert kite tradition indeed attests to their presence and abundance. It is widely believed that gazelle herds were not significantly in decline in the Azraq Basin until the late 19th century/20th century when they were hunted to local extinction with

firearms (Nelson, 1973). It's also notable that steppic/desert gazelle populations would have had the option of seasonal mobility/migrations, counter to the more territorial *G. gazella* populations of the Mediterranean zone Levant (Mendelssohn, 1974), an idea explored below.

In sum, we do not see the same landscape and hunting pressures in the Azraq Basin as the more densely and permanently populated Mediterranean zones. Pastoral expansion and the seasonal livestock grazing would certainly have had ecological impacts, but Neolithic pastoralism clearly did not lead to significant gazelle habitat loss (since sites show 60–90% gazelle throughout the period, Martin et al., 2016) as interpreted by Munro and colleagues (2022) for Mediterranean areas. Anthropogenic impacts, including kite hunting, are therefore not the sole or even prime cause of gazelle size diminution observed from 9000 cal BP in the Azraq Basin. That hares and foxes also decline in size over similar time periods hints at additional environmental and ecological drivers.

6.3. Levantine climate shifts and body size change

Palaeoclimatic models for Late Pleistocene-Early Holocene southern Levant derive from combined speleothem and lake level proxies (Bar-Matthews et al., 1999; Bartov et al., 2002; Hazan et al., 2005; Robinson et al., 2006) and generally relate to Mediterranean zone Levant. They present a picture of cold, dry conditions around the Late Glacial Maximum (from c. 24,000 cal BP) with gradual warming from c. 18,000 cal BP (interpreted from low Lisan lake levels). Geomorphological evidence from the Azraq Basin gives a mixed picture for the LGM: there's evidence for cool aridity in some areas, but around the main Early Epipalaeolithic archaeological sites there's evidence for year-round standing water and marshland (Hunt and Garrard, 2013; Jones and Richter 2017). These would be ideal conditions for dry steppe grasslands with shrubs mixed with wetland marshes, and would be highly favourable to herbivores. There is also evidence of warming from c. 18,000 cal BP (Colledge, 2001; Richter et al., 2013) which would increase vegetation productivity, alongside local drying. Each of our study taxa – gazelle, hare and fox – show relatively large body size during the LGM period. Our data is poor for the 17,000–15,000 cal BP time-range when there is evidence for warming in the Azraq Basin, especially for hare and fox, but gazelle body size shows an increase in this period. The evidence suggests that warmer wetter postglacial environments increased forage productivity, under which relatively larger gazelle body size would reflect lusher wet-steppe conditions. We can speculate that large hare body size was underpinned by similar favourable forage conditions, and there was good nutrient availability for foxes too.

The later Pleistocene (14,500–11,500 cal BP) in the southern Levant is characterized initially by warm and moist conditions of the Bølling-Allerød, coinciding with the Early Natufian, followed by the Younger Dryas cold phase at c. 13,200–11,400 cal BP during the Final Natufian cultural phase (Bar-Matthews et al., 1999; Bartov et al., 2002; Hazan et al., 2005; Robinson et al., 2006). Azraq Basin climate signatures are varied at this time: geomorphological evidence dating to 14,000–11,500 cal BP from Azraq and Wadi Jilat shows local marsh disappearance (Hunt and Garrard, 2013) suggesting relative aridity. The sequence at Shubayqa 1 in the northerly Azraq Basin, on the major flow of the Wadi Rajil, provides resolution into Early to Final Natufian resource availability. Here, Yeomans and colleagues (2024) find continued wetland bird exploitation in the Final Natufian (12,083–11,807 cal BP) – ie. evidence for standing water – albeit diminished from the Early Natufian phase.

Cooler drier conditions are likely to have limited vegetation growth in the Younger-Dryas period of the Late Pleistocene, and it's notable that our results show gazelle to be at their smallest Late Pleistocene size in this 13,000–11,500 cal BP period (see Figs. 3 and 4 and especially 5 – Shubayqa 1 Final phase).

Azraq Basin hares also decrease in size in the Later Epipalaeolithic (Figs. 7 and 8b) from larger average sizes in the Earlier Epipalaeolithic, a

pattern also hinted at for the limited fox metrical samples (Fig. 9). For hare (Fig. 7) there's a trend for larger body size during the warmer, wetter conditions of the Bølling-Allerød/early Natufian, and decreasing size during from 13,200–11,400 cal BP during the Younger Dryas cold phase/Final Natufian. As with gazelle, hare size and probably fox, appear to correlate with potential decreasing nutrient availability (in this case limited by lower precipitation and temperature).

We should note an absence of metrical data in our sequence for the earliest part of the Holocene (11,500–10,500 cal BP, see Fig. 2), equivalent to the Levantine PPNA which is considered cool and arid, due to a lack of sites and assemblages for this period. Our Early Holocene sequence begins at c. 10,500 cal BP (PPNB) when moister conditions are witnessed in the Azraq Basin with springs re-established suggesting locally wetter, warmer and better vegetation conditions (Jones and Richter, 2011; Jones et al., 2022). Gazelle metrical data show initially relatively large-bodied animals in the Early Holocene (PPNB) after the Final Pleistocene diminution, likely reflecting lusher forage conditions, although they do not reach the sizes of the largest Late Pleistocene animals. Between 9000–7500 cal BP (Late Neolithic), however, we see a steep size decline, interpreted above as reflecting the addition of a smaller gazelle population/species.

The impact of the short cold conditions of the 8.2 kya event is increasingly viewed as having a significant impact on the southern Levant. Widescale drying across north Africa and the Middle East is observed between 8500–8000 cal BP, accompanied by the reduced northern migration of the ITCZ (Berger and Guilaine, 2009; Rohling and Pälike, 2005; Weninger et al., 2006). Bar-Yosef (2011, 2019) argues that the abandonment of many PPNB sites, Late Neolithic settlement shifts, and the intensification of Neolithic mobile pastoralism, all result from changing environmental conditions at this time, in the form of aridity. Others propose that local droughts would have triggered population migrations (see also Gebel, 2009; Rollefson, 2009). Current geoarchaeological investigations in the Azraq Basin attempt to pinpoint when increased aridity or ‘desertification’ began (Jones et al., 2022) but with no firm evidence yet. It is tempting to interpret the evidence of a smaller species of gazelle entering the Azraq Basin from c. 9000–8500 cal BP, as linked to increasing aridity leading to reduced and patchier vegetation (from c.8.2 kya but can't be exactly pin-pointed with methods used here, see 4.2.2). Hare also show a similar trend, with a steep size decrease at c. 8500 cal BP, although whether this reflects intra- or inter-specific shifts is complex as discussed below.

In sum, variations in the body size of the three taxa we have examined are evidenced across the 24,000–7500 cal BP. timeframe. Visible body size disruptions (diminutions) are clear in the Final Pleistocene/Epipalaeolithic (14,000–11,500 cal BP) and again in the Late Neolithic at 9000–7500 cal BP. Viewing these size shifts alongside regional and local climate and palaeoenvironmental evidence suggests the drivers for body size change correlate better with conditions of nutrient availability (underlaid by both temperature and precipitation) rather than any single climatic factor. In particular, body size trends do not confirm Bergmann's rule, which would predict mammalian body size to be larger in cooler conditions, and smaller in warmer climates. Our data for gazelle and hare show the opposite trends: they are smaller in the cooler Late Pleistocene Younger Dryas conditions, and larger in Early Holocene warmer lusher environments. We can therefore reject thermoregulation alone as a driver of body size in our case study, as many others do (section 6.1 above).

We now briefly review the ecologies of our three study taxa (gazelle - a mobile grazing/browsing ruminant herbivore; hare - a small more localized generalist herbivore; and fox - an opportunistic omnivore) to better understand the drivers of body size variation.

6.4. Taxa ecology and adaptations

6.4.1. Gazelle, hare and fox ecology

The ecological, taxonomic and behavioural information reviewed in

this section inevitably derives from modern animal studies, but nevertheless highlights how these mammal populations respond to ecological shifts.

6.4.1.1. Gazelles. All Levantine gazelles – *G. gazella*, *G. dorcas* and *G. subgutturosa* (described in 5.2.2) are resilient ruminant herbivores, independent of standing water, and can switch seasonally between graze and browse to meet nutritional requirements. They have overlapping distributions and are also highly adaptive to environmental conditions in terms of population sizes and seasonal mobility (Martin, 2000). *G. subgutturosa* – the proposed main inhabitant of eastern Jordan - is seasonally territorial displaying a range of mobility behaviours from long-distance seasonal migrations (in central Asia; Zhevnerov, 1984) to local seasonal aggregation and dispersals in Arabia (Cunningham and Wronski, 2011). In the Azraq Basin, archaeo-isotope analyses found gazelles to be year-round residents in the Early/Middle Epipalaeolithic, with no need to migrate (Henton et al., 2018), but likely saw seasonal herd displacements (migrations?) in the Early Holocene, whether stimulated by grassland expansions c. 9000 cal BP, or retreats towards 8000 cal BP (Dinies et al., 2015) is as yet unclear.

Gazelle body size is clearly correlated not only with phylogeny (species/sub-species) but also nutrient availability (Martin, 2000, Table 5, p19); for example, *G. dorcas* in desert environments with patchy forage have smaller body size than those in lusher steppe grasslands. Nutrient availability, in addition to species assignation, is therefore a key consideration for determining gazelle body size.

6.4.1.2. Hare. The southern Levant is assumed to be home to two hare species, *Lepus capensis* (the Cape Hare) and *Lepus europaeus* (European hare), and often seen as a ‘contact zone’ between them, with the latter having a more northerly distribution (Angermann, 1983; Hacklander and Schai-Braun, 2019). Hare evolution, however, is complex and the phylogenetics of *Lepus* are not well understood (Hoffman and Smith, 2005), with genetic evidence showing high conspecificity in modern animals. For example, Ben Slimen et al. (2006) found some north African hares (*L. capensis*) genetically very similar to European hares (*L. europaeus*); their study also found support for a hypothesis that *L. europaeus* might be included within the *L. capensis* species. Similarly, in a modern southern Levantine study, hares in desert zones (assumed to be *L. capensis*) were not genetically distinct from those in Mediterranean zones (assumed to be *L. europaeus*) (Ben Slimen et al., 2008). This suggests that the two hare taxa are currently highly polymorphic, with much geneflow between them resulting from interbreeding. The two hare taxa have also been noted to be conspecific in southern Africa in recent times (Suchentrunk et al., 2009).

For the Late Pleistocene/Early Holocene, most zooarchaeologists assume hares in the southern Levant to be *Lepus capensis* (Bar-El and Tchernov, 2000; Bar-Oz et al., 2004; Gourichon and Helmer, 2008; Munro, 2003, 2009; Tchernov 1992, 1997) without morphometric or palaeogenetic justification, while others call some specimens *L. europaeus* (Campana and Crabtree, 1990), highlighting the confusion. Given the inability to distinguish modern species genetically, it seems unwise to attempt species attribution to archaeological specimens of *Lepus* from the Levant.

Nevertheless, Yom-Tov and Geffen (2006) find a north-south size cline in recent hare size in the Southern Levant, suggesting some adaption in body size. Hares are specialised herbivores feeding on shrubs, grasses, seeds and agricultural crops (Flux and Angermann, 1990); their wide variations in body size can be viewed as adaptations to specific local habitats, including food availability, resulting from temperature and rainfall regimes (Mohamed and Basuony, 2016; following Yom-Tov and Nix, 1986).

In sum, for our Azraq Basin case study we cannot assume that size shifts represent species shifts in hare, for reasons discussed above (and until there are aDNA studies), but should rather consider intra-specific

size shifts as resulting from selective pressures of forage, environment and climate drivers.

6.4.1.3. Fox. Four fox species currently inhabit the southern Levant. In decreasing size they are: *Vulpes vulpes* (the Red Fox), *V. ruppellii* (Rupell's Sand Fox), *V. cana* (Blandford's Fox), and *V. zerda* (the Fennec fox) (Dayan et al., 1992; Harrison and Bates, 1991). *V. vulpes* has the widest distribution, adapting to all habitats across Europe, the Middle East, Arabia and beyond, while *V. ruppellii* prefers steppe-desert habitats and is common in north Africa and Arabia, although it fringes the southernmost part of the Levant. *V. cana* is currently found only in isolated deserts, but enters the southern Levantine part of the rift valley, while the Fennec fox is now distributed in the Sinai peninsula, being more at home in north Africa and parts of the Arabian gulf (Harrison and Bates, 1991). These small solitary carnivores - or rather opportunistic omnivores - tend to forage on rodents, birds, insects and reptiles alongside fruit and vegetal material, although the larger red fox is also known to eat prey as large as hares (Basuony et al., 2005; Dayan et al., 1992).

Debates over fox species and sizes in the southern Levant centre around observations of a size decrease through the Late Pleistocene and Early Holocene which Davis (1977) attributed to temperature increase impacting a single species (believed to be *V. vulpes*). Dayan and colleagues (1989) however, suggested a more complex scenario whereby *V. vulpes* and *V. ruppellii* were sympatric, and size variation may represent niche partitioning depending on ecological variables such as temperature and rainfall.

Genetic studies of modern north African foxes shed light on evolutionary relationships of regional fox species: Leite et al. (2015) found that while *V. vulpes* and *V. ruppellii* are clearly separate entities, *V. ruppellii* are more closely related to north African than Eurasian *V. vulpes* sub-clades; they suggest introgression between the two species in north Africa, and further that *V. ruppellii* represents an arid ecotype of *V. vulpes* which became isolated (in a southern refuge) during a period of climate transition. Other phylogenetic studies in southern Levantine-/North African regions (Saleh et al., 2018) demonstrate how fox species have shifted distributions through the Pleistocene, dispersing particularly in periods of climatic change. The picture of Late Pleistocene-Early Holocene species distributions and displacements emerges as unsurprisingly complex.

6.4.2. Species distribution shifts

Previous authors investigating southern Levantine mammalian body size change through the Late Pleistocene and Early Holocene find either: i) dwarfing, interpreted as intra-specific responses to temperature increase (ie. Bergmann's rule); ii) diminutions in gazelle size, interpreted as intra-specific change resulting from anthropogenic factors such as overhunting, landscape fragmentation, and indirectly demographic pressure; these interpretations see minimal impact from climatic shifts; iii) no mammal size changes through the time periods (see section 2.1.1).

Results from our Azraq Basin case-study see consistent patterns supporting a different interpretation. We find the long-term size shifts in the three taxa examined – gazelle, hare and fox – broadly mirroring each other, although with some temporal variation. In section 6.2 above, we argue to reject anthropogenic factors as being a prime cause of the size shifts, since there is no evidence that hunting pressures or landscape fragmentation were severe enough, or broadly concurrent with the size diminutions documented. That the three different taxa witness similar size shifts also lends support to ecological explanations.

We can also dismiss temperature change alone as a driver of body size shifts, ie. Bergmann's rule of thermoregulation. Our metrical trends show gazelle to increase in size during Middle/Late Epipalaeolithic warming, and decrease in size during the colder Younger Dryas, which is opposite to Bergmannian predictions. Hare and fox too see overall diminution in the Late Pleistocene, parallel to gazelle, suggesting

broader ecological factors are at play. Further diminutions of gazelle and hare are seen into the Early Holocene and around/following the cold and abrupt 8.2 kya event, again suggesting complex ecological drivers of body size shifts. Following Henry and colleagues (2023) we propose a resource availability hypothesis as a more convincing driver of the body size trends seen, than temperature alone. Under this scenario the overall productivity of forage resources underpinned by the changing combination of precipitation and temperature evidenced through the Late Pleistocene and Early Holocene provides a better fit with the mammal body size shifts seen.

The Azraq Basin body size patterns are also indicative of species turnover for gazelle at least, otherwise known as *inter-specific*, or between-species, shifts. For gazelle, we have argued above that smaller-bodied animals appear alongside (and overlap with) larger ones between 9000–7000 cal BP when our data-set ends. This coincides with Early Holocene warm conditions, interrupted by the 8.2 kya event when climate records suggest increasing aridification and regional drying (e.g. Berger and Guilaine, 2009). We propose that a smaller Arabian gazelle species shifted northwards into the Azraq Basin in this period as habitats experienced increased aridity which would have affected rains and forage vegetation (Weninger et al., 2006). Whether the range shift was permanent or seasonal (in the form of spring/early summer migrations north for graze) we cannot yet determine. *Gazella marica* (the Arabian sand gazelle) was until recently believed to be an Arabian sub-species of *G. subgutturosa* – then labelled *G. subgutturosa marica* – since it shares morphological similarities while being smaller (e.g. Harrison and Bates, 1991, 203). Since 2010 *G. marica* has been identified through genetic analyses as a separate species (Wacher et al., 2011), closely related to north African gazelles (Hassanin et al., 2012). Indeed, most Levantine arid-zone steppic gazelles are currently viewed as either *G. marica*, or most commonly an ongoing introgression between *G. subgutturosa* and *G. marica* (Murtashvvaladze et al., 2012), showing natural gene-flow between these two nominal species, as far north as Anatolia. Geneticists do not speculate as to when introgression began, but genetic analyses highlight that species distributions, contact zones and hybridization of sub-species shift and evolve over time.

Our hypothesis is that the warmer and subsequently drier Early Holocene Azraq Basin environments may have witnessed smaller gazelle populations (*G. marica?*) expanding distribution northwards from Arabian habitats. The relatively large gazelles we have demonstrated to be present in the Azraq Basin Late Pleistocene assemblages may represent *G. subgutturosa subgutturosa* (the Persian goitered gazelle) which is currently distributed further north and east (into Central Asia) (see Fig. 10). This larger animal may have lost habitat to a better adapted and smaller arid-zone gazelle, or may have hybridized leading to the genetic signatures found today.

Our Azraq Basin hare osteometric evidence show larger sizes in the Late Pleistocene and smaller bodied animals in the Early Holocene. Discussion in 6.4.1 above (Hare section) warns against simple interpretations of larger hare representing *Lepus europaeus* and smaller sizes representing *L. capensis*, since hare taxonomy is complex. There is not only much observed sympatry in modern-day hares in the region, but some authors view them as the same species. So while the IUCN gives distinct distributions to the more northerly *L. europaeus* and more southerly *L. capensis* (see Fig. 10) with the Levant as an area of overlap/sympatry, genetic studies caution against these species distinctions (Ben Sliman et al. 2006, 2008), making discussion of inter-specific Pleistocene-Holocene turnover in hares unwise. Instead, we might consider the Azraq Basin shifts in hare body size as intra-specific (within species shifts), with small Late Pleistocene sizes driven by cool Younger Dryas limits to vegetation growth, with larger hare sizes at c. 9000 cal BP reflecting warmer lusher Early Holocene conditions, and the post 8500 cal BP size decline perhaps linked to the drying 8.2 kya event, again reflecting more limited vegetation ability.

It is tempting to see the shift in fox size as inter-specific turnover, as with gazelle, with Late Pleistocene/Early Holocene specimens

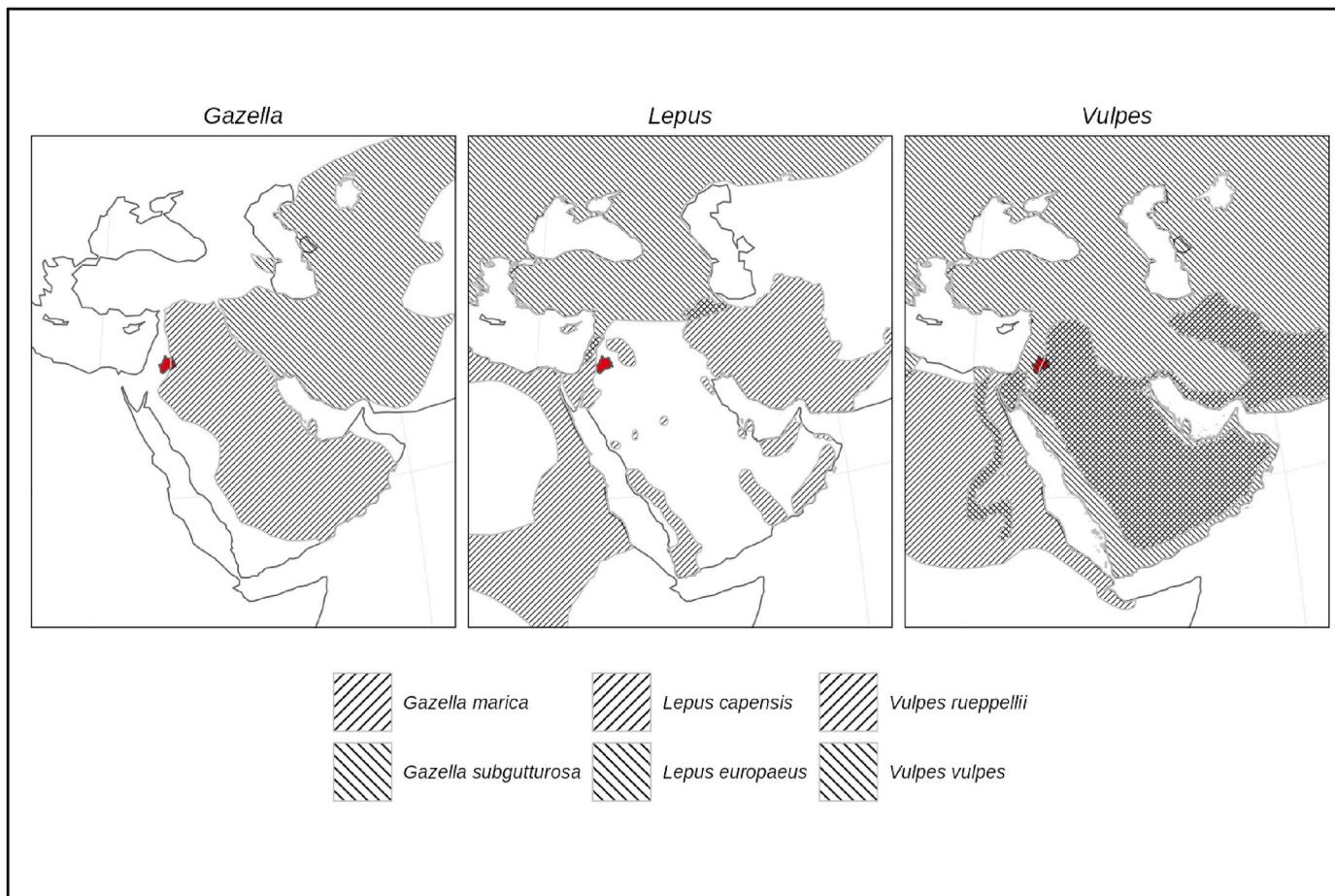


Fig. 10. Schematic maps showing the modern distributions of different species of *Gazella* (left), *Lepus* (centre), and *Vulpes* (right), and their areas of overlap, following IUCN data (2022). The Azraq Basin is indicated in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

representing a smaller Arabian species, likely *Vulpes rupelli* (Rupell's sand fox) distinct from the much larger *V. vulpes* (red fox). The two species currently have broadly overlapping distributions in Arabia and eastern Jordan (Fig. 10). We propose, based on albeit limited osteometric datasets, that the Azraq Basin witnessed distribution shifts north of the smaller *Vulpes rupelli* in the Late/Terminal Pleistocene, which locally displaced the larger *V. vulpes*. Dayan and colleagues' (1989) study of modern/recent Levantine foxes report a similar character displacement of *V. vulpes* by *Vulpes rupelli* in southern-most Levantine areas which have Saharo-Arabian environments and vegetation, lending support to our hypothesis. The scenario also fits Saleh and colleagues (2018) genetic studies demonstrating north African fox dispersals into the Levant during the Pleistocene at times of climatic fluctuation.

7. Conclusion

The proposal detailed in this paper is that Jordan's Azraq Basin witnessed mammalian species distribution shifts during the Late Pleistocene and Early Holocene for gazelle and probably fox, alongside climate and resource-driven shifts for hare. The hypothesis of species shifts augments, and provides further detail to, earlier research by Tchernov (1992, 1997) into long-term faunal turnover in the western area of the Levant. Tchernov noted the disappearance of some Palearctic species in the early Holocene, especially small mammals, and the immigration into the Mediterranean zone of species originating in Arabia and the Saharan belt. He also argued that the Early Holocene saw the distribution shift of Saharo-Arabian species such as oryx and *Gazella dorcas* north into the southern Levantine Negev and Sinai deserts (1997,

215; Tchernov et al., 1986), attributed to climatic shifts.

Our Azraq Basin case-study draws on a long sequence of osteometric data across three taxa allowing proposals for intra- and inter-specific shifts. The well-dated sequence shows hare size shifts to occur in the Early Holocene period, with fox body size shifts likely from the Late Pleistocene/Natufian period. Smaller mammals like hare and fox are well understood to be sensitive to localized habitat and resource availability changes (e.g. Henry et al., 2023; Vigne and Valladas, 1996), adhering to more restricted ranges than larger mammals. Smaller hare appear in the Holocene, argued to represent intra-specific diminution from what is known of contemporary hare size variation. Smaller fox species appear to displace larger species by the Late Pleistocene/Late Epipalaeolithic and into the Holocene, proposed here as a likely inter-specific shift and character displacement, again drawing on observations from modern Levantine zoological studies. The larger bodied gazelle appear to undergo intra-specific size changes in response to Late Pleistocene climate and vegetational shifts, but we only see convincing inter-specific shifts (i.e. metrical range shifts) in the Early Holocene (from c. 9000 cal BP). We argue for the appearance of the smaller bodied Arabian *G. marica* in the Azraq Basin at this time, and previous archaeo-isotope work hints that they possibly migrated seasonally on a route from Arabia northwards into the Jordanian desert area from the Neolithic onwards (Henton et al., 2018).

In terms of drivers and mechanisms of these faunal changes, the body size evidence presented in this study does not fit with the expectations of Bergmann's rule, with body size scaling to temperature shifts alone. Instead, a 'resource availability hypothesis' (Henry et al., 2023) taking into account potentials for vegetational growth, productivity and

limitations, provides a better fit with the evidence for local Azraq Basin temperature and moisture shifts through the time-frame (outlined in Section 6.3).

Our hypotheses of character displacement in the Late Pleistocene and Early Holocene for fox and gazelle species, can only be confirmed with future palaeogenetic studies. So far, poor collagen preservation in archaeological faunal specimens from the Azraq Basin has precluded obtaining genetic sequences (Yeomans et al., 2019) but future avenues will be pursued (Jensen et al., 2023). If correct, questions remain as to why fox might experience character displacement earlier than gazelle, which perhaps relates to their more local habitat, smaller body size, and/or higher trophic level of feeding, which may make them more sensitive to resource fluctuations.

The implication of mammalian species shifts for the Azraq Basin suggests some Saharo-Arabian faunas (and maybe vegetation) gradually outcompete European/Palearctic taxa, which may adhere to wetter Irano-Turanian vegetation zones. Aridification of parts of the north-east Jordanian steppe/deserts has long been noted as a Holocene phenomenon, but pinpointing the beginnings of the process has proved challenging (Jones et al., 2019). Mammalian species shifts help identify climatic changes which appear to favour some smaller (Arabian?) taxa from c. 9000 cal BP. This also coincides with shifts in human use of the Azraq Basin, when mobile livestock pastoralism expanded across the steppe and deserts (Rollefson et al., 2014) and hunting traps, or ‘kites’, are constructed in large numbers (Abu-Azizeh et al., 2021; Crassard et al., 2022; Betts and Burke, 2015), most likely to trap gazelle seasonally migrating north from Arabia. Examples of Saharo-Arabian faunas also begin to appear on rock art in the Azraq Basin, which, although hard to date, are often associated with PPNB or Later Neolithic (9000–7000 cal BP) sites (Rollefson et al., 2008). Oryx, ibex, addax and even kudu are suggested in rock art, which are all Arabian or Saharan-belt species and not evidenced in the large faunal assemblages throughout the Late Pleistocene. This hints at larger-scale faunal shifts north from Arabia into the eastern Levant from the Neolithic onwards, finding niche habitats there as aridification increased.

This paper demonstrates that zooarchaeological studies of mammalian body size change should, where possible, focus on multiple species, and should consider inter-species shifts and character displacement, as well as intra-species adaptations. The clear ecologically-driven size shifts seen during the Late Pleistocene and Early Holocene in the Azraq Basin (on taxa which were never domesticated) also caution against simple interpretations of animal size changes as evidence for domestication. Size change in the wider Middle East in these same time-periods is often taken as evidence of animal domestication. Greater acknowledgement is needed of the considerable evidence of ecological change and climate-drivers on faunal populations, and mammalian size (following Zeder, 2001) alongside anthropogenic impacts.

CRediT authorship contribution statement

Louise Martin: Conceptualization, Data collection, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Joe Roe:** Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Lisa Yeomans:** Data collection, Methodology, Writing – review & editing.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2024.109147>.

Data availability

All data used in this article is available as csv files in Appendix A.

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