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Unveiling ancient Jerusalem's pastoral dynamics (7th to 2nd centuries BCE) with multi-isotope analysis

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This study explores changes in pastoral practices in the Jerusalem region (Iron Age II - Late Hellenistic) through a multi-isotope approach (strontium, carbon, oxygen, and nitrogen). Based on the analysis of 135 sheep, goat, and cattle teeth and bone samples from Givati Parking Lot we demonstrate the value of this method in reconstructing past animal husbandry, revealing adaptation and resilience of pastoral communities amidst environmental and socio-political changes. Isotopic analysis indicates local sourcing for most animals, with intriguing outliers from distant regions up to 150 km away, suggesting regional exchange networks. Notably, the Persian period (5th century BCE) exhibits a wider isotope range, implying increased flexibility and exploitation of diverse grazing lands, potentially driven by climate shifts and political upheavals. Conversely, Late Hellenistic (2nd century BCE) livestock display restricted movement, while showcasing a rise in desert caprines, indicative of increased import compared to the Persian era. These findings highlight the dynamism and adaptability of past pastoral communities, adjusting their strategies in response to various pressures. This study opens new avenues for understanding human-environment interactions in the Levant and underscores the power of multi-isotope approaches in unraveling intricate socio-economic and ecological dynamics of the past.

Keywords Stable isotopes, Human-animal relations, Southern Levant, Migration, Animal Economy, Urban pastoralism

Delving into the dynamic history of pastoral systems in Jerusalem offers a unique window into the intricate interplay of historical, demographic, environmental, and cultural forces that have shaped the region's socioeconomic and ecological trajectory. During the latter half of the 1st millennium BCE, Jerusalem emerged as a preeminent urban center within the region. Functioning as a central nexus for Judaean cultic practices, the city fostered a diverse and complex array of religious activity. Its dense population and strategic location further facilitated its development as a major trading hub, attracting merchants from a wide geographical expanse. This confluence of economic prosperity and burgeoning cultic significance ultimately cemented Jerusalem's position as the political capital of the Kingdom of Judah and made it a target for conquering forces[1].

Managing livestock, mainly sheep, goats, and cows, has been a cornerstone of human societies throughout history, providing sustenance, labor, and ritualistic offerings[2]. By analyzing the feeding behaviors, ecologies, and mobility of domesticated animals in the latter half of the first millennium BCE through isotopic analysis, we can unveil how Jerusalem's animal economy functioned in an era of prosperity, destruction and revival associated with fluctuating political entities with the destruction of the site at the end of the Iron Age II (586 BCE) and its slow reestablishment throughout the Persian (fifth-fourth century BCE) and Early Hellenistic (third century BCE), and a fully reestablished city in the Late Hellenistic (second century BCE)[3]. We take a multi-isotope approach that integrates carbon, oxygen, nitrogen, and strontium isotopes to overcome the limitations of previous isotopic studies[4–6]. This comprehensive analysis enables us to distinguish between distinct environmental zones, providing a more refined understanding of livestock movements and the associated pastoral practices.

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Jerusalem's history is marked by periods of both prominence and decline. After more than a century of prosperity, Jerusalem experienced a demographic and economic decline due to the siege and destruction of the city in 586/7 BCE by Neo-Babylonian ruler, Nebuchadnezzar II[3]. In the subsequent centuries, the city and its surrounding countryside continued to be inhabited. Zooarchaeology of Givati Parking Lot and the Central Hill region indicate Jerusalem maintained its status as a consumer city with the majority of livestock provided by outside producers and a market economy based on exploiting prime-age livestock for meat consumption, around one to three years of age[7]. By the Late Hellenistic period (end of the second century BCE) Jerusalem fully revived its thriving agricultural and temple economy, with livestock playing a significant role in providing food, wool, labor, and sacrifices[7]. A recorded demographic influx[8] in the Late Hellenistic period likely heightened the demand for livestock products, potentially leading to an intensification of pastoral activities.

Contemporaneous to Jerusalem's Temple, the Eanna Temple of Uruk (active 625 − 520 BCE) relied on a complex system for animal sacrifices[9]. Cuneiform records reveal the temple employed external contractors who raised and managed livestock, potentially near Jerusalem, for ritual needs. The biblical literature note that the Persian ruler, King Darius, supplied animals for the Jerusalem Temple upon its completion in 515 BCE, highlighting the use of dedicated sacrificial herds outside the city walls (Ezra 6:6–14). Previous isotopic studies of cultic centers in the Southern Levant have yielded two contrasting models for pastoral reconstruction. Evidence from Iron Age Tel Dan[4] and Khirbet Summely[5] suggests a localized system, with livestock grazing within a radius of 25 km to maintain pastoral control. In contrast, isotopic analysis of Early Roman Jerusalem[6] indicates a more extensive regional pasturing strategy, supplemented by interregional trade networks that brought livestock from as far as 150 km away, including the region around Lake Galilee to the north and desert settlements to the east and south of Jerusalem. New studies from the southern Levant indicate that urban cities such as, Iron Age I Ashkelon, acquired caprines and cattle from external farmers, who lived further inland in the surrounding countryside[10]. Case studies from Iron Age Zagora[11] and Hellenistic Thessaly[12] in Greece also hint at varying herd management paradigms based on demographic influxes but also mention that herd management followed local grazing rights (*epinomia*).

Building on this foundation, this study investigates the interplay between cult, urban demographic shifts, and herd management practices. Moreover, we question how did animal husbandry practices in Jerusalem evolve and adapt to environmental, political, and socio-economic changes from the late seventh-early sixth century BCE to second century BCE? We aim to understand how fluctuations in urban populations influenced the organization of livestock raising, and how herders adapted their strategies to cope with changing environmental pressures. Zooarchaeological analysis coupled with isotope analysis of faunal remains has established itself as a robust methodology for investigating animal diet, past environments, herd management practices, and animal mobility patterns[13–17]. This comprehensive approach is applied to a curated selection of 36 mandibular molars of sheep (*Ovis aries*) and goat (*Capra hircus*), 17 fragments of cattle (*Bos taurus*) bones, and 82 fragments of caprine (sheep and goat) bones from ancient Jerusalem (Supplementary 1–2). Provenience and sample distribution can be found in Supplementary 2: Table 1.

The assemblage recovered from Area 10 of the Givati Parking Lot excavations spans multiple phases, from the Iron Age IIC (Phase IX) through the Persian (Phase VIII), Early Hellenistic (Phase VII), and Late Hellenistic (Phase VI-III) phase. Area 10 refers to a series of rebuilt public/administrative buildings located just below the summit of the City of David that housed the most important state institutions: the Temple, the palace, and their respective priestly and royal courts. Area 10's location on the western slope became a center of wealth and significance. This phenomenon, which started in the late Iron Age II (seventh century BCE), peaked during the Hellenistic and early Roman periods (fourth century BCE – first century CE)[18]. Photos and stratigraphy for Area 10 can be found in Supplementary 2: Figures 1 and 2[18]. The Givati Parking Lot is currently being excavated by Yuval Gadot and Yiftah Shalev, as collaboration between Tel Aviv University and the Israel Antiquities Authority (license: G71, G10).

Zooarchaeological analysis suggests that Area 10's inhabitants were likely consumers who procured their meat from external sources, such as the marketplace or the temple[7]. This study seeks to test the geographic range of the sourced fauna, using a multi-isotope approach to produce a more refined understanding of livestock movements and the underlying pastoral practices that shaped the region's ecological and socioeconomic landscape.

Isotope and environmental background

Nestled within the Central Highlands of the southern Levant, Jerusalem's Xeric Mediterranean environment blends with the arid landscapes of the Steppe and Desert, creating a unique ecological mosaic (Fig. 1)[6,15,19]. The Steppe vegetation includes transitional Mediterranean, Irano-Turanian, and Saharo-Arabian plant species, with C_3 and C_4 vegetation available[6,15,19]. Palynological studies have provided valuable insights into the vegetation history of the Jerusalem region[24,25]. The diversity of plant types suggests that livestock could have grazed on a variety of resources, depending on the season and the availability of fodder. It is expected, based on past carbon and nitrogen isotopic studies from Early Roman Jerusalem, that livestock were mobile between Jerusalem, its hinterland, and as far as Desert environs, e.g., Judean Desert[6]. This study's interpretation of isotopic data draws from previous research on carbon, nitrogen, oxygen, and strontium isotopes.

Livestock isotope composition is causally linked to the plants and water they consume. Stable nitrogen isotope values, $\delta^{15}N$, are typically influenced by soil nitrogen isotope values[20,21]. These soil values are determined by various factors, including mean annual rainfall and temperature[19,20]. Plant nitrogen isotope composition is also influenced by internal factors, such as the nitrogen source, physiological processes within the plant, and environmental conditions[22]. The second half of the 1st millennium BCE witnessed a period of fluctuating precipitation patterns across the Levant, as evidenced by paleoenvironmental data[48]. These variations likely impacted regional plant communities; however, the extent to which they affected faunal populations and nitrogen

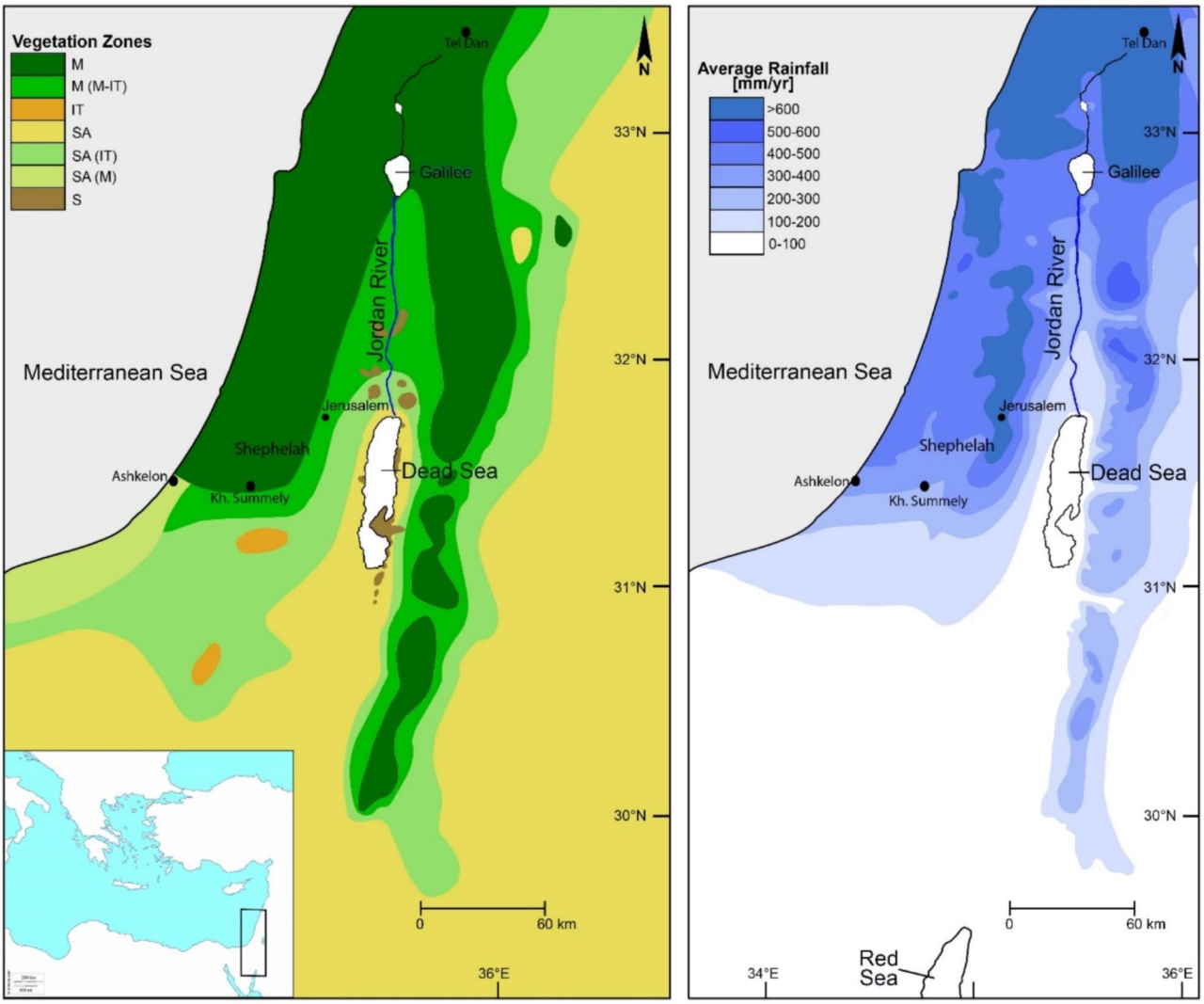

Fig. 1. Phytogeographic zones and average rainfall after Zohary (1962). Base maps courtesy of Mark Cavanaugh.

isotope values remains an open question. For diachronic participation patterns see Langgut and Lipschits 2017: Pl.VIII[48].

Stable carbon isotope ($\delta^{13}C$) variability is primarily driven by differences in the carbon isotopic compositions of C_3, C_4, and CAM (Crassulacean acid metabolism) plants linked to differences during photosynthesis. The proportions of these plants in a given habitat is shaped by their relative tolerances to environmental conditions, such as temperature, aridity, and altitude[23]. The Southern Levant region is primarily dominated by C_3 vegetation, thriving in areas with annual rainfall between 350 and 1000 + mm/year[24]. Caprines herded in the Central Highlands are expected to exhibit $\delta^{13}C$ values matching a 100% C_3 consumer (<-10‰ for tooth enamel bioapatite), with minor variability due to seasonality[25–27]. The region also contains C_4 plants, primarily dicotyledon species of the chenopod family, which are more prevalent in areas with annual rainfall below 350 mm/year[24]. The nearest regions with available C_4 vegetation for livestock are the arid zones, with the Judean Desert, roughly 20 km from Jerusalem, being the closest[6,23]. Other arid zones include the Negev, the Arabah, the Transjordan regions, and the Nile Delta, all of which are between 80 and 400 km from Jerusalem. Furthermore, the inclusion of crops for animal fodder, such as local grasses, legumes, and cereals, adds another layer of complexity when interpreting isotopic values.

Isotopic studies of bioapatite are common in diet analysis, but limitations exist. This study addresses them by incorporating bone collagen analysis, providing a more comprehensive picture. $\delta^{13}C$ values can be influenced by both vegetation input and climate. To account for this, we additionally analyzed $\delta^{15}N$, a climate proxy, for a more robust interpretation.

The interpretation of $\delta^{15}N$ and $\delta^{13}C$ values derived from animal bone collagen in this study is anchored by a comprehensive review of past isotope baseline data from the Levant[4–6,10,23]. We identify three distinct environmental zones, each characterized by distinct mean isotope values: the Mesic Mediterranean (mean $\delta^{15}N$: 5.72‰ ± 1.2, mean $\delta^{13}C$: -20.7‰ ± 0.7), the Steppe/Xeric (mean $\delta^{15}N$: 5.91‰ ± 1.1, mean $\delta^{13}C$: -20.7‰ ± 1.3),

and the Desert (mean δ^{15}N: 8.45‰ ± 2.6, mean δ^{13}C: -19.7‰ ± 1.5)[6]. While the isotope values for the Mesic Mediterranean and Steppe/Xeric zones overlap to some extent, the Desert zone exhibits more distinct signatures. δ^{15}N values for the Desert range from 5.9 to 11.0‰, with a clear threshold of 7‰ denoting exposure to desert environments[6]. Similarly, δ^{13}C values for the Desert overlap with the Mesic, Steppe, and Xeric zones, but those exceeding −19.5‰ can be confidently assigned to desert environments, indicating a diet primarily composed of C_4 and CAM plants[6].

Stable oxygen isotope (δ^{18}O) analyses can be used to further clarify the past herding spheres around Jerusalem. Oxygen isotope signatures are influenced by environmental variables such as temperature, humidity, latitude, and altitude[28,29]. Therefore, δ^{18}O values from an animal's tissues can be used as a proxy for geographic residence during the period of tissue formation[26,30,31]. Jerusalem's $\delta^{18}O_w$ values for precipitation are relatively low in the past as well as today, averaging $-6.4 \pm 2.2\%$[32,33]. The presence of local springs, such as the perennial Gihon, as well as anthropogenic pools and wells, would have provided accessible water sources for the livestock[34]. Additionally, groundwater would also influence the $\delta^{18}O_w$ values of consumed local vegetation and fodder.

Strontium isotope ratios analyzed from animal tooth enamel bioapatite have emerged as a valuable tool for identifying the geographical origins and movements of livestock during the sampled tissue's period of formation[13,35–37] The radiogenic isotope ^{87}Sr, a product of radioactive decay from rubidium-87 (^{87}Rb), varies in its natural abundance[38,39]. The resulting ^{87}Sr/^{86}Sr ratios are largely determined by the types and ages of minerals present in a given geologic setting, as well as the relative abundance of rubidium to strontium in these rocks[36]. Strontium isotope ratios serve as valuable geochemical indicators because, as livestock consume strontium-bearing plants, it replaces calcium in their enamel apatite with minimal metabolic fractionation[30–32]. However, while geological strontium provides a baseline, factors like plant type, water chemistry, and soil pH significantly influence the amount and type of strontium that is 'bioavailable' to an organism and that is ultimately absorbed into the enamel[30,31,37].

Rock and soil samples from across present day Southern Levant have shown bioavailable strontium isotope ratios to be between approximately 0.7078 and 0.7095[40]. The region around the Golan and Galilee exhibits slightly lower values, ranging from 0.7047 to 0.7069[37–39,41,42]. This variation is attributed to the presence of young basalts, which have a lower 87Sr/86Sr ratio. Bedrock samples from the Central Highlands have indicated strontium isotope ratios between 0.7082 and 0.7087, while a more recent study suggests a broader range, between 0.7078 and 7085, by Wang et al. (2023)[40].

Results

Full bioapatite and collagen isotope results, along with full descriptive statistics for the caprine and cattle individuals, are provided in Supplementary 1 and Supplementary 2: Tables 2, 3, 4 and 5 Additionally, examples of sequentially sampled teeth are provided in Supplementary 2: Fig. 4.

Stable carbon and nitrogen isotope analysis of bone collagen

The 64 caprine and 10 cattle collagen results are detailed in Supplementary 1, Supplementary 2: Table 2, and 3, and plotted in Figs. 2 and 3. The majority (91%) of samples show excellent collagen preservation, yielding atomic C/N ratios between 2.9 and 3.6% and collagen yields of 0.2–0.7% mg. Samples that did not meet these thresholds were eliminated from the dataset but can be found in Supplementary 1[43,44]. For the purposes of this study, the interpretation of δ^{15}N and δ^{13}C values is supported by a review of past collagen isotope baseline data from the Levant[4–6].

Regarding δ^{13}C values of analyzed collagen, caprines throughout all periods exhibit δ^{13}C values ranging from −23.2‰ to -17.0‰. Non-parametric tests show that there was no statistical significance in differences in δ^{13}C values between temporal periods (Kruskall-Wallis: $X^2 = 3.26$, df = 2, $p = 0.19$). The δ^{13}C range for each period was minimal (< 5‰) with the largest range documented in the Iron Age II (-23.2‰ to -18.3‰), likely due to a singular outlier at -23.2‰. Removing that singular outlier, the relative range of δ^{13}C is even smaller (3‰), with the largest range being the Late Hellenistic period (-20.2‰ to -17.3‰).

Cattle exhibit δ^{13}C values from −20.2‰ to -16.5‰. Cattle δ^{13}C values display a ~ 3‰ range in the Persian (-20.1‰ to -18.3‰) and Early Hellenistic (-19.8‰ to -16.5‰) periods and the smallest range in the Late Hellenistic (-19.2‰ to -18.4‰). Caprines and cattle both reflect a primary consumption of C_3 plants. Cattle δ^{13}C median values were slightly higher, suggesting they may have fed on a diet that included a greater proportion of C_4 vegetation than caprines. However, caprine and cattle δ^{13}C values were found to be statistically indistinguishable from each other (Kruskall-Wallis: $X^2 = 2.94$, df = 2, $p = 0.22$).

Caprine δ^{15}N values ranged from 4.2‰ to 11.2‰, while cattle δ^{15}N values ranged from 3.9‰ to 9.8‰. Cattle had slightly higher δ^{15}N median values, with a median difference of 2.5‰ compared to 1.1‰ difference for caprines. However, regardless of the period, δ^{15}N values between species, i.e., caprines and cattle, were not significantly different ($p = 0.1$). Furthermore, there was no significant difference in δ^{15}N values between periods for either caprines or cattle (Kruskal-Wallis test: caprines: $X^2 = 3.82$, df = 2, $p = 0.14$; cattle: $X^2 = 0.78$, df = 2, $p = 0.67$). This suggests that caprines and cattle were likely pastured in similar habitats and that their feeding behaviors were similar, at least as far as is detectable isotopically.

Caprine δ^{15}N values demonstrated limited variability in the Iron Age II (4.7 to 9.2‰), Early Hellenistic (5.5 to 10‰), Late Hellenistic periods (3.9 to 9.3‰), with a greater variability during the Persian period (4.1 to 11.2‰). Drawing upon the established δ^{15}N threshold of 7‰ for the Desert zone[6], we can cautiously estimate that at least 40% of caprines and 36% of cattle were pastured in desert environments. Over time, the volume of desert caprines fluctuates, with 46% in the Iron Age II, 29% in the Persian, 55% in the Early Hellenistic, and 47% in the Late Hellenistic. This conservative approach acknowledges that some animals may have been herded in various environments, with the isotopic value representing a mixture of feeding in different environments. Nevertheless, even with this conservative assessment, our findings underscore the significant role played by

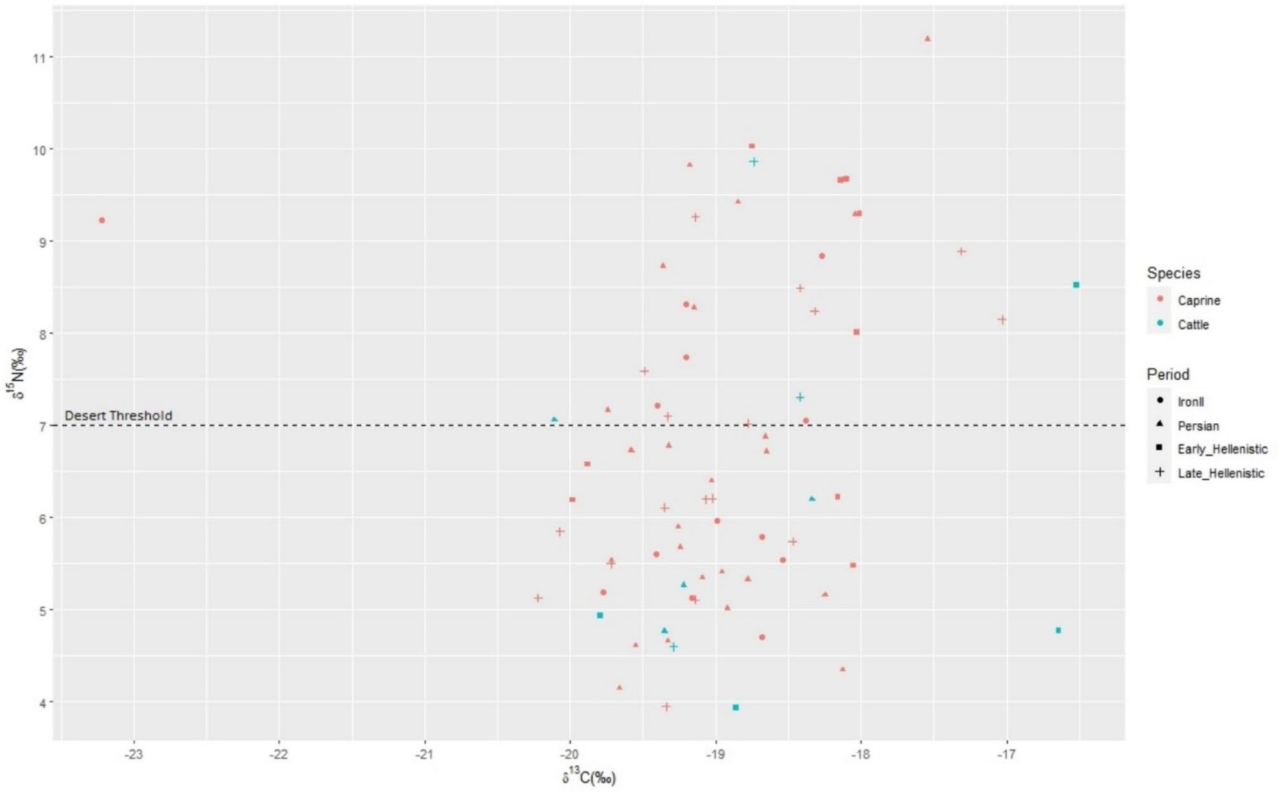

Fig. 2. Carbon and nitrogen bone collagen scatterplot.

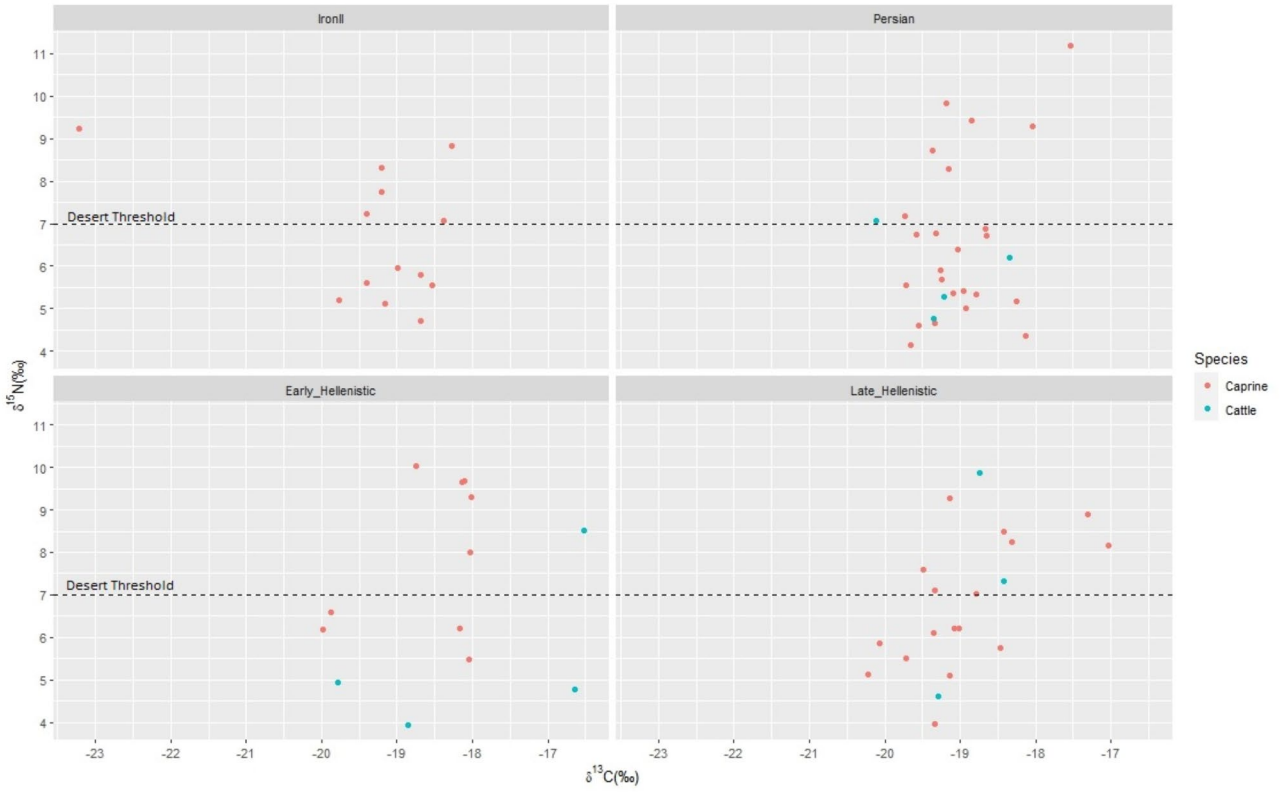

Fig. 3. Carbon and nitrogen bone collagen scatterplot by period.

desert environments in the livestock economy of Jerusalem during the Iron Age II, Persian, Early Hellenistic, and Late Hellenistic periods.

Stable carbon and oxygen isotope values of bioapatite

Sequential $\delta^{13}C$ and $\delta^{18}O$ results of 21 sheep and 15 goat mandibular molars are shown in Supplementary Tables 4 and plotted in Figs. 4 and 5.

Sequential $\delta^{13}C$ values for sheep ranged from −11.9‰ to -4.6‰, with an average of -8.6‰ ± 1.5‰. Goat $\delta^{13}C$ values ranged from −12.1‰ to -3.9‰, with an average of -9.1‰ ± 1.9‰. Goats exhibited a wider intra-tooth variability in $\delta^{13}C$ values than sheep, and the difference in median $\delta^{13}C$ values between the two species appears to be statistically significant (Mann-Whitney U, $p = 0.04$). The Persian period exhibits the largest $\delta^{13}C$ inter-tooth variability (-11‰ to -3.9‰), whereas the Early Hellenistic period demonstrates the smallest (-10.0‰ to -6.6‰). This difference in the range of $\delta^{13}C$ of all sequential values between temporal periods appears to be significant (Kruskall-Wallis: $X^2 = 22.08$, df = 3, $p < 0.01$).

The bioapatite data further supports that sheep and goats were primarily C_3 consumers in the Late Hellenistic period (#4003, #4588, #6049, #7688, #7689). The Persian period (samples #9740 and #12938) saw some higher $\delta^{13}C$ values suggesting a greater proportion of their diet included C_4 and CAM vegetation. While the Persian sheep and goats were not exclusive C_4 or CAM consumers, their diet during the first and second years of life contained a significant proportion of C_4 and CAM plants. Notably, the two deciduous dp4 samples from the Late Hellenistic period reveal distinct patterns of vegetation consumption for sheep and goats during their early life stages. Sheep #2034 exhibits a median $\delta^{13}C$ value of -11.2‰, indicating a primary reliance on C_3 plants, while Goat #3234 displays a median $\delta^{13}C$ value of -9.4‰, suggesting a diet based on an 80:20 ratio of C_3 and C_4 plants[26,45,46].

Sequential $\delta^{18}O$ values for sheep ranged from −5.1 to 5.1‰ (mean = -1.2 ± 2.3‰). Goat $\delta^{18}O$ values ranged from −8.7 to 2.5‰ (mean = -1.5 ± 2.5‰). Overall, the $\delta^{18}O$ values suggest that both species were exposed to seasonal variations in precipitation. There was no significant difference in $\delta^{18}O$ values between sheep and goats (Mann-Whitney U, $p = 0.1$). The $\delta^{18}O$ values for the Iron Age II period range from −4.5‰ to 3.0‰, with mean values for sheep and goats of -1.4‰ and −0.7‰, respectively. However, due to the limited sample size, firm conclusions about seasonality cannot be drawn for this period. The sequential $\delta^{18}O$ values from the Persian through Late Hellenistic periods exhibit pronounced intra-tooth variability, with $\delta^{18}O$ ranges exceeding 6‰.

The patterns unveiled by sequential $\delta^{18}O$ and $\delta^{13}C$ values for individual specimens (Supplementary 2: Fig. 3) offer a compelling glimpse into the subtle patterns of pastoral management. These sinusoidal curves depict a pattern of slight oscillations in opposition to each other. These observational trends indicate subtle fluctuations in $\delta^{18}O$ and $\delta^{13}C$ values, likely reflecting changes in isotopic values due to climatic shifts during seasonal change.

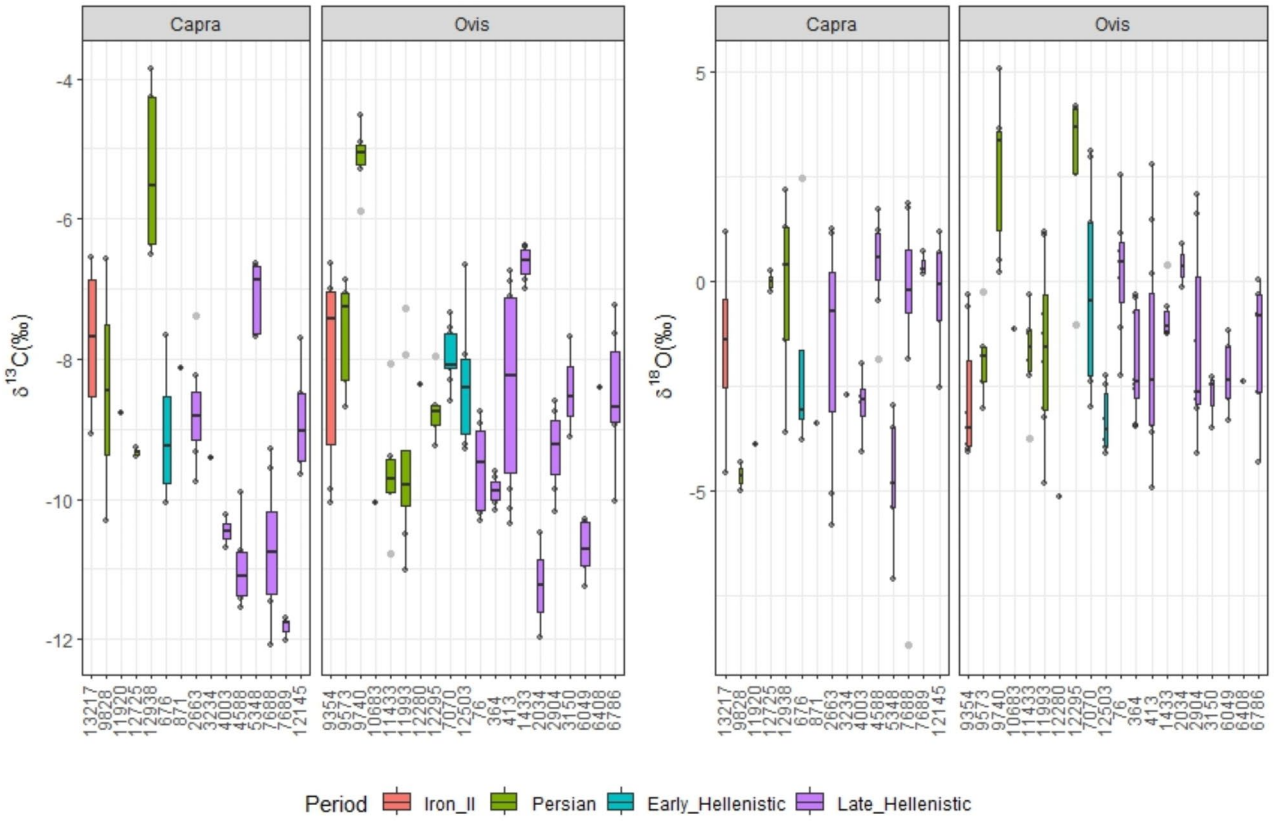

Fig. 4. Carbon and oxygen bioapatite box plots by species.

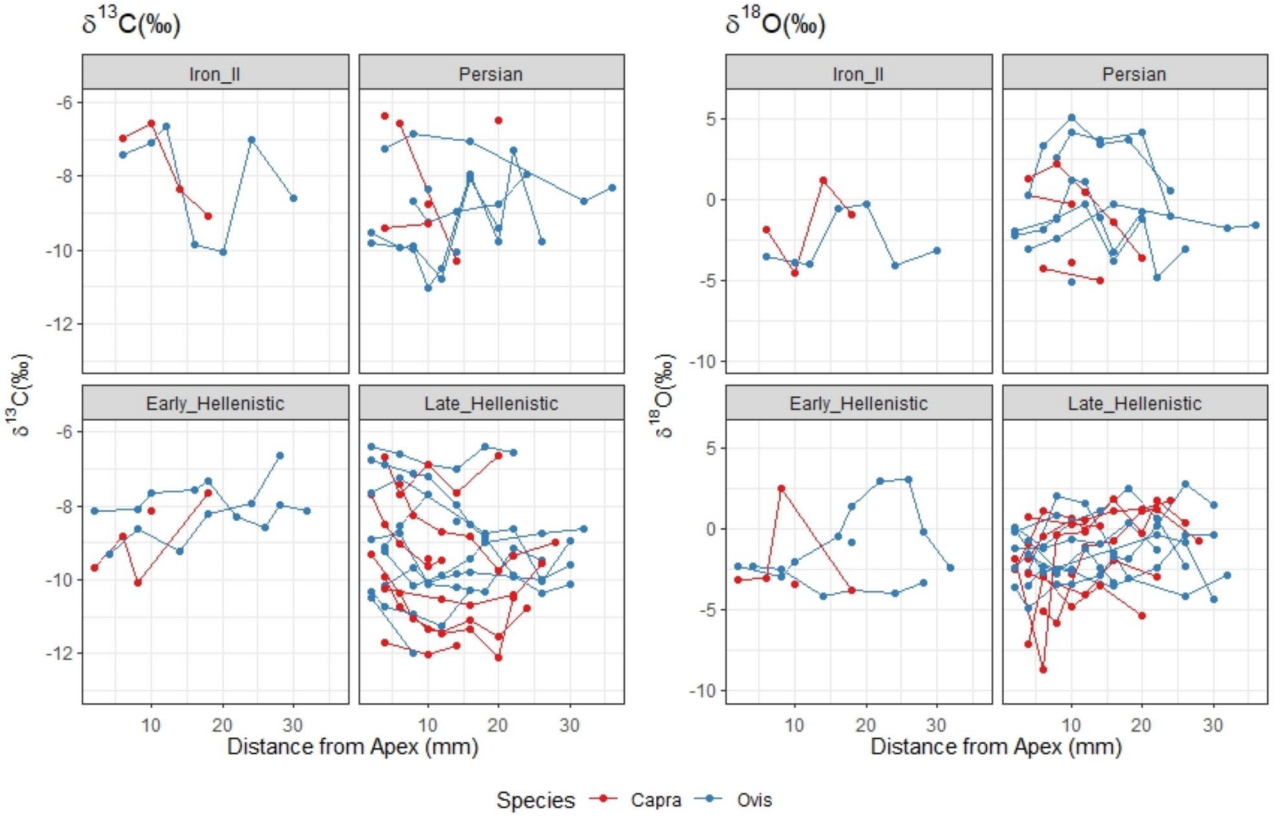

Fig. 5. Carbon and oxygen bioapatite sequential scatterplot for sheep and goat by period.

The absence of pronounced shifts in the isotopic curves suggests that either movements were relatively short-distance and likely involved opportunistic foraging within a familiar landscape or that they were provided with fodder from a relatively niche area.

Strontium isotope analysis of bioapatite

Sequential strontium isotope results are presented chronologically in Fig. 6, with the local range marked to identify outliers. The local range is determined from previously reported bioavailable $^{87}Sr/^{86}Sr$ values for the region, as summarized in Wang et al. (2023)[40].

The sheep assemblage comprises eleven mandibular M3s and three mandibular M2s that were sequentially sampled. Sheep strontium isotope ratios (0.70780 to 0.70869) primarily fall within the local range. However, outliers did exist, with one sheep from the Iron Age II (#9354, 0.70780) and two from the Persian period (#9740, 0.70780; #12294, 0.70869) displaying values outside this range. These outliers were observed at the distal tips of the molars, closer to the enamel-root junction (ERJ), indicating their formation during early tooth development[47]. While dentine inclusion remains a theoretical possibility for the outlier values, our rigorous sampling methods significantly reduce its likelihood. The assemblage of ten goats consisted of sequential samples from one mandibular dP4 and nine mandibular M3s. Goats exhibited a narrower range of strontium isotope variability (0.70795 to 0.70829). All goat strontium isotope ratios, including the singular dp4 (#9828, 0.7081), remained within the local range of the Central Highlands as established by Wang et al. 2023 (Fig. 6)[40].

Discussion

This study sheds light on the evolution of animal husbandry practices in Jerusalem from the late Iron Age II through the Late Hellenistic period (late seventh-early sixth century BCE to second century BCE). By analyzing animal remains from an affluent public/administrative building, we reveal how the sites inhabitants adapted their livestock management strategies in response to a confluence of environmental and political changes. Jerusalem transitioned from Neo-Assyrian to Neo-Babylonian, Persian, Greek, Hasmonean, and ultimately Roman control during this diachronic sequence. Our multi-isotopic approach offers a unique perspective on these transformations, enabling us to reconstruct past dietary patterns of caprines and cattle and infer pastoral management practices over time.

Isotopic analysis of sheep and goat remains revealed a consistent reliance on C_3 plants throughout all periods. However, a subtle $\delta^{13}C$ increase during the Persian period potentially suggests a minor incorporation of C_4 or CAM plants into their diets. This shift aligns with the paleoenvironmental record of C_4 plant expansion due the region's drier climate in the Persian period[48]. Interestingly, the Persian period exhibits a somewhat broader range

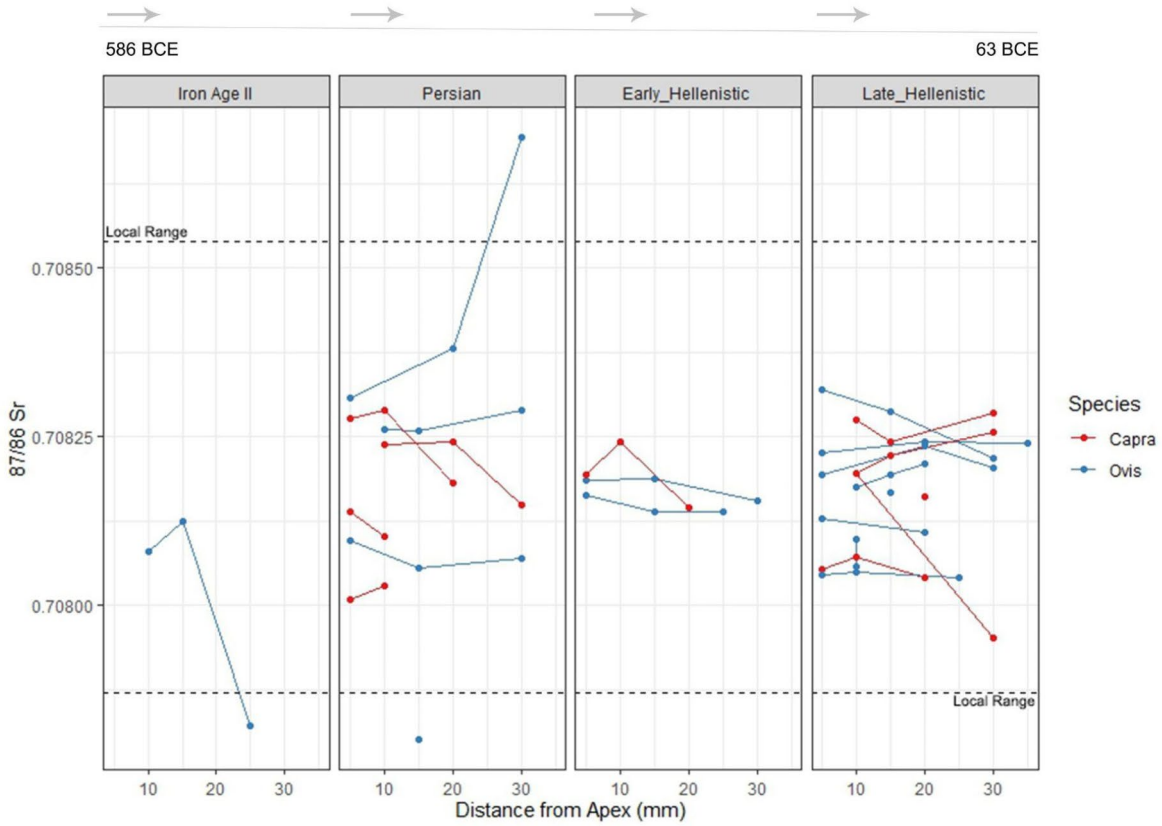

Fig. 6. Strontium bioapatite sequential scatterplot of sheep and goat by period.

of isotope values compared to both the preceding Iron Age and following Hellenistic periods. However, it is important to note that these values remain within the established boundaries for this region (~ 50 km) based on existing baseline data[6]. This variation suggests that pastoralist groups during this period were utilizing a broader array of known environmental zones and available fodder sources.

The increased consumption of C_4 or CAM plants and elevated nitrogen values identified in sheep and goat diets during the Persian period potentially suggests a more varied pastoral system. The destruction of Jerusalem in 586 BCE triggered a series of socio-political changes, including political deportations, a series of abandoned settlements, and the diminished influence of temple-based economies. This, in turn, could have led to a decline in centralized management of agricultural lands (with neglected water irrigation systems, fields abandoned due to a lack of labor, and so on). This created an environment where pastoralist groups had greater autonomy to explore and exploit a wider range of lands for available fodder. Furthermore, paleoclimatic reconstructions of periods of aridity during the Persian era suggest climate change may have prompted pastoralists to expand their foraging range in search of water and fodder[48]. This flexibility highlights the resilience of pastoral communities, demonstrating their ability to navigate a complex interplay of environmental, economic, and socio-political shifts.

The distinctiveness of the Persian period is further corroborated by the isotope values of Early and Late Hellenistic livestock, which suggest limited animal movement. The narrower range of isotope values observed, particularly in the Late Hellenistic period, suggests a potential increase in control over herds or the selective use of specific herds or environments. This aligns with the establishment of the Hasmonean Monarchy's political dominance and the establishment of prebendal systems observed in earlier Babylonian cults[9,49]. Concurrently, the Early and Late Hellenistic period also witnessed a noticeable increase in the proportion of caprines from desert environments, demonstrating a rise in imported livestock compared to the Persian period.

Our stable nitrogen isotope analysis ($\delta^{15}N$) of caprines reveals that a significant portion (29–55%) had $\delta^{15}N$ values of 7‰ or higher meaning they originated from, or grazed in, desert environments. While desert livestock isotope ratios reflect dietary choices influenced by climate, it is important to consider the potential circularity of defining deserts solely on climate-linked factors like $\delta^{15}N$ values. Interestingly, the driest period, the Persian era, coincides with the lowest percentage of caprines exhibiting desert $\delta^{15}N$ values. This, along with palynological evidence[48] suggesting increased aridity during this time period, supports the notion that caprines foraged or gathered fodder away from desert environments. Conversely, the Early Hellenistic period, marked by increased

precipitation based on palynological data[48], shows the highest percentage of caprines with desert $\delta^{15}N$ values, suggesting with the cooler climate a shift in grazing and foddering practices.

The Judean Desert, despite its low annual rainfall (less than 150 mm), remains classified as a desert due to a combination of factors beyond just precipitation. These include low overall plant productivity, specific vegetation types adapted to aridity, and high rates of evaporation. Located approximately 20 km east of Jerusalem, the driest areas of the Judean Desert are beyond the daily grazing range of herders from Jerusalem or its neighboring hinterland due to an elevation difference of over 1,000 m[6,50]. Similarly, in the later Early Roman period, approximately 37% of caprines originated from the desert[6]. This trend has been attributed to the rise of inter-provincial trade a hypothesis supported by post-destruction Talmudic sources that mention Edomite merchants importing thousands of caprines from desert regions[51].

Previously, it was assumed that the incorporation of desert livestock was driven by the growing demands of Roman Jerusalem, including supporting its larger population and the heightened intensity of cultic activities[6]. A more diachronic perspective reveals that Jerusalem has exhibited a continuous presence of desert caprines, at least since the late Iron Age II. Even during periods of population decline, when pastoralists ventured further afield during the dry spell of the Persian period, they still utilized desert caprines, albeit in a lower frequency. This indicates that pastoralists in the Jerusalem region were actively utilizing desert pasturelands to supplement their livestock's diet. The incorporation of desert caprines had several implications for pastoral practices and the overall economy of the Jerusalem region. Firstly, it allowed pastoralists to expand their livestock holdings and enhance their productivity. Secondly, it provided a valuable source of food and resources during periods of drought or other political and climatic challenges. Thirdly, it contributed to the regional economy by generating trade opportunities and connecting the Jerusalem region to peripheral markets.

The analysis of strontium isotopes revealed outlier sheep only in the Iron Age II and the Persian period. The Iron Age II outlier (#9354), potentially originating from the Galilee or Golan Heights region approximately 150 km north of Jerusalem, suggested by its strontium isotope ratio ($^{87}Sr/^{86}Sr$) of 0.7078, which falls within the range for this geological area (0.7047–0.7069), spent the rest of its life grazing within Jerusalem's local range. This finding suggests the transportation and integration of animals from the Galilee into Jerusalem's pastoral systems, indicating the establishment of trade networks or exchange mechanisms between these regions, but on a smaller scale than observed during the Early Roman period. In the Early Roman period, the incorporation of mesic Mediterranean caprines was causally linked to the import of livestock for sacrifices by pilgrims. While definitive conclusions cannot be drawn from a single sample, the presence of this Iron Age II sheep from the Galilee suggests that movement of people and livestock did occur during the period when Jerusalem's cult was at its zenith.

Continuing the trend observed in the Iron Age, the Persian period included two outlier sheep – one potentially from the Galilee and Golan Heights and another from the Shephelah, a lowland region between the Jerusalem highlands and the coastal plain. The presence of these outliers' hints at ongoing interactions that took place between Jerusalem's pastoral communities and its surrounding regions, even during a period of relatively low population density. Most animals were raised locally, especially in the Hellenistic periods where strontium isotope analysis did not detect any outliers. However, strontium isotope analysis of sheep and goats from the Jerusalem region further corroborates the observations made in the Early Roman period, demonstrating a slight inclusion of caprines from areas outside Jerusalem's immediate vicinity. The presence of outliers from the Galilee and Shephelah regions indicates the incorporation of animals from distinct environmental zones, suggesting a well-established network of trade and pastoral practices was maintained before and after periods of major geopolitical conflict.

The movement of livestock and pastoral knowledge documented in Jerusalem reflects broader patterns observed in regions like Mesopotamia and Egypt. For instance, the integration of animals from geographically distinct areas observed in Jerusalem aligns with cuneiform texts documenting exchange networks for livestock across the Achaemenid Empire during the Persian period[49]. Similarly, the rise of inter-provincial trade in the Early Roman period, evidenced by the increased presence of desert caprines in Jerusalem, mirrors similar trends observed in other Roman provinces[6,50].

This study contributes to a growing body of research exploring the interconnectedness of animal husbandry practices across the Levant and the broader Mediterranean world. By situating Jerusalem's practices within this wider context, we gain a deeper appreciation for the complex interplay of local environmental conditions, political structures, and long-distance trade that shaped livestock management strategies in antiquity. Future comparative analyses of animal isotope data from Jerusalem with contemporaneous Levantine and Mediterranean sites would offer a more nuanced understanding of the scale and organization of these exchange networks. Additionally, investigations into the social and economic factors that influenced pastoral mobility across the region could provide valuable insights into the dynamics of interaction between different communities.

Conclusions

This study applied a comprehensive multi-isotopic approach, encompassing stable carbon and nitrogen isotope analysis of bone collagen and strontium isotope, stable oxygen isotope, and stable carbon isotope analysis of tooth enamel bioapatite. Our findings suggest that the livestock that arrived in Jerusalem originated from diverse environmental zones, including Steppe, Xeric, and Desert landscapes. This pattern indicates the continuity of pastoral practices and the utilization of foddering systems. Moreover, the multi-isotopic approach revealed that while most livestock were pastured within a radius of fifty kilometers of the site there were exceptions, with a few sheep coming from much farther afield. These findings underscore the importance of isotopic analysis in unraveling the complex interactions between human populations and their environment, particularly in regions with a rich history of animal husbandry and trade.

Materials and methods

Sample selection

A well-curated selection of 17 fragments of cattle (*Bos taurus*) bones and 82 fragments of caprine (sheep and goat) bones were chosen for carbon and nitrogen isotope analysis of bone collagen (Supplementary 2: Table 1). Additionally, 36 mandibular molars of sheep and goat were selected for carbon and oxygen isotopic analysis of bioapatite, with 25 of those also sampled for strontium isotope analysis (Supplementary 2: Table 1, and 2). These samples, encompassing loose and in situ mandibular dP4, M2s, and M3s, were meticulously sourced from Iron Age IIC through Late Hellenistic occupational layers in Givati Parking Lot (Area 10, Str. IX-III).

The precise growth and development chronology preserved in mandibular molars enables the detection and reconstruction of potential herd management changes throughout the caprine's life, as supported by previous studies[22,25,42,52,53]. Sequential sampling across the molars enables the reconstruction of the caprine's lifespan, providing valuable insights into dietary intake and pastoral practices. Most of the sampled teeth belonged to adult caprines, owing to the enamel's non-porous structure and hard crystalline composition, minimizing diagenesis-related alterations. For caprines, the formation of the mandibular M3 commences around one year of age, taking twelve months to complete, with approximately six months for enamel mineralization[22,54–56]. Mandibular M2s were only used for strontium analysis and, when sampled, they were obtained from in situ mandibles with corresponding M3s that were sampled for carbon and oxygen analysis. The few deciduous premolar samples were intended to account for the reconstruction of herd management prior to the first year of life.

Caprine teeth were identified as either *Capra hircus* (goat) or *Ovis aries* (sheep) based on morphometric differences in molar structure[57] and cross-checked with the faunal comparative collection at Steinhardt Museum of Natural History. Of the sampled teeth, 17 were identified as goats and 19 were identified as sheep. Additionally, long bones and ribs of caprines and cattle were included in the analyses to compare small stock and large stock management patterns and provide more information for periods with limited amounts of mandibular molars (Supplementary Table 1).

Sampling strategy for mandibular molars

To prepare the enamel for analysis, the outer surface of each tooth was mechanically abraded using a Dremel tool to remove all dentine and cementum. A diamond-tipped bit was employed to drill a series of 1.0-mm wide bands horizontally across the mesial surface of each tooth, commencing at the crown and progressing towards the root enamel junction. The number of bands varied per tooth based on overall tooth size, ranging from two to eleven. The diamond drill tip was thoroughly rinsed with acetone between each sampled band to prevent contamination. The collected enamel powder was weighed on weighing paper and transferred into a 1.5-mL Eppendorf tube for further preparation. Examples of sequentially sampled teeth can be found in Supplementary 2: Fig. 4.

Carbon and oxygen enamel isotopic analysis

Stable carbon and oxygen isotopic analyses of teeth enamel were carried out at the Max Planck Institute for Geoanthropology in Jena, Germany. Multiple samples were taken from each sampled tooth for sequential analysis, ranging from 1 to 11 samples per tooth, with 5–7 mg of enamel powder collected for each sequential sample. Initially, 0.1 M acetic acid was added to the samples and soaked for 10 min, followed by thorough rinsing with purified H2O three times. The samples were then placed in a freezer for 24 h before being freeze-dried to remove any residual moisture. After treating the enamel samples with 100% phosphoric acid, gasses evolved from the samples were analyzed for stable carbon and oxygen isotopic composition using a Thermo Gas Bench II connected to a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS), for machine precision and standard values see Supplementary 2: Table 6.

Carbon and nitrogen collagen isotopic analysis

Carbon and nitrogen isotopic analyses of bone collagen were carried out at the Max Planck Institute for Geoanthropology in Jena, Germany. Bone samples were labeled 12-ml glass test tubes and filled with 10 mL of 0.5 M HCl solution and aggregated. The samples were then covered with aluminum foil and chilled in a refrigerator for 48 h to facilitate demineralization. Once the demineralization process was complete, the samples were rinsed three times with purified water (MilliQ) to remove any remaining acid or impurities. Each sample was then treated with 10 mL of pH3 HCl solution to further break down the collagenous proteins. The samples were then placed in a freezer for 24 h before being freeze-dried to remove any residual moisture. The collagen was then weighed to approx. 0.5 mg and placed in tin capsules for analysis on a Thermo Conflo IV Elemental Analyzer (EA) connected to a Delta V Advantage IRMS, for machine precision and standard values see Supplementary 2: Table 6. Each sample was run in duplicate to determine accuracy of the data.

Strontium bioapatite analysis

Tooth samples were prepared at the Stable Isotope Laboratory, Max Planck Institute of Geoanthropology, Jena, Germany before being analyzed at the clean laboratory in the Department of Geological Sciences at the University of Cape Town. For sequential analysis, two to three powdered samples of 20 mg were obtained from each specimen in Jena using a Dremel drill and sent to Cape Town for further analysis. The samples were dissolved in 2 mL of 65% nitric acid (HNO_3) in a closed Savillex PFA beaker and heated at 140 °C for one hour on a hotplate. After cooling, the samples were dried down and re-dissolved in 1.5 mL of 2 M HNO_3. Strontium separation was performed using established methods[58]. Following separation, the solutions for each sample were dried, dissolved in 2 mL of 0.2% HNO_3, and diluted to 200 ppb Sr concentrations for strontium isotope analysis.

The radiogenic $^{87}Sr/^{86}Sr$ ratios were measured using a Nu Instruments Nu Plasma HR MC-ICP-MS in the Department of Geological Sciences at the University of Cape Town. Sample values were corrected for

instrumental mass fractionation using the exponential law and an $^{86}Sr/^{88}Sr$ ratio of 0.1194, and for isobaric ^{87}Rb interference using the measured ^{85}Rb signal and the natural Rb isotope ratio. Isobaric Kr interferences were corrected by subtracting an on-peak background measured in the running acid. All data presented here are referenced to bracketing analyses of NIST SRM987 ($^{87}Sr/^{86}Sr$ reference value of 0.710255)[59]. Repeat analyses of an in-house carbonate reference material (NM95) processed and measured with the batches of unknown samples in this study gave an average $^{87}Sr/^{86}Sr$ ratio of 0.708905 ($2\sigma = 0.000019$; $n = 7$) and agree with long-term results for this in-house reference material (average $^{87}Sr/^{86}Sr$ ratio of 0.708911; $2\sigma = 0.000040$; $n = 414$). Total procedural elemental Sr blanks agreed with typical values of < 250 pg in this facility, and therefore negligible.

Standard deviations for bioapatite strontium isotope ratios and for carbon and oxygen isotope values are reported as two standard deviations from the mean (2σ).

Statistical analysis

Statistical analyses were performed using R Studio version 2023.09.0 + 463 for Windows.

Data availability

Data AvailabilityAll data used and/or analysed during the current study are reported in this published article see Supplementary I. For further details or access to raw data, please contact the corresponding author, Abra Spiciarich.

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Author contributions

A.S.: Conceptualization, Methodology, Investigation of All Isotopes, Formal Analysis, Writing - Original Draft, Review & Editing, Prepared Figs. 1, 2, 3, 4, 5 and 6. Supplementary Figs. 2-4, Funding acquisition. Y.G.: Resourc-

es, Writing - Review & Editing. Y.S.: Resources, Writing - Review & Editing , Prepared Supplementary Fig. 1. L.S.H.: Writing - Review & Editing, E.S.: Investigation of Carbon, Nitrogen, Oxygen Isotopes, Writing - Review & Editing. P.le R.: Investigation of Strontium Isotopes. P.R.: Conceptualization, Supervision, Investigation of Carbon, Nitrogen, Oxygen Isotopes, Writing - Review & Editing. P.W.S.: Conceptualization, Supervision, Writing - Review & Editing, Project administration, Funding acquisition.

Declarations

Competing interests
The authors declare no competing interests.

Ethical approval
This study did not involve experiments on live vertebrates and therefore did not require approval from an institutional animal care and use committee (IACUC) or a similar licensing body. As such, the ARRIVE guidelines (Animal Research: Reporting In Vivo Experiments) were not applicable. However, all procedures were conducted in accordance with relevant institutional and national guidelines and regulations.

Additional information
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