

Cave paleozoology in the Judean Desert: assembling records of Holocene wild mammal communities

IGNACIO A. LAZAGABASTER,^{1,2*} NATALIA ÉGÜEZ,^{2,3} MICKA ULLMAN,⁴ ROI PORAT,⁴ IDO WACHTEL,⁴ URI DAVIDOVICH⁴ and NIMROD MAROM²

¹Museum für Naturkunde Berlin, Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany

²School of Archaeology and Maritime Cultures, The Recanati Institute for Maritime Studies, University of Haifa, Israel

³Archaeological Micromorphology and Biomarkers Research Lab, Instituto Universitario de Bio-Organica Antonio González (IUBO), Universidad de la Laguna, Tenerife, Spain

⁴Institute of Archaeology, the Hebrew University of Jerusalem, Israel

Received 10 May 2021; Revised 1 December 2021; Accepted 6 December 2021

ABSTRACT: Long temporal records of Holocene wild mammal communities are essential to examine the role of human impacts and climatic fluctuations in the configuration of modern ecosystems. We show that such records can be assembled through extensive radiocarbon dating of faunal remains obtained from biogenic cave deposits. We dated 110 mammalian remains from 19 different cave sites in the Judean Desert. We use the dates in combination with archaeological survey data and bone collagen/apatite $\delta^{13}\text{C}$ values to study faunal succession in the context of Holocene climate change and human settlement history in the region. Our results suggest a change in the late Holocene, expressed in fewer observations of Arabian leopard (*Panthera pardus nimr*) and gazelle (*Gazella* spp.), and an increase of Syrian striped hyena (*Hyaena hyaena syriaca*), fox (*Vulpes* spp.), Nubian ibex (*Capra nubiana*) and rock hyrax (*Procavia capensis*); suids (*Sus scrofa*) appear for the first time. According to the data distribution, however, the probability of finding a bone diminishes exponentially with time, which implies that the Judean Desert cave paleozoological record is temporally biased. The weight of evidence ultimately favors an explanation of the observed patterns as the consequence of a combined anthropogenic and climatic impact on local food webs.

© 2021 The Authors *Journal of Quaternary Science* Published by John Wiley & Sons, Ltd.

KEYWORDS: Anthropocene; carbon stable isotopes; Dead Sea; Levant; radiocarbon

Introduction

Paleozoological data can inform on species abundance and distribution in the past (Faith and Lyman, 2019), with broad relevance to topics ranging from climate change to extinctions and conservation biology (Boivin et al., 2016; Tyler and Schneider, 2018). Such data, however, are difficult to obtain for the later Holocene, when larger wild mammals almost disappear from the paleozoological record and are replaced by domesticated animals (Diamond, 2002; Tsahar et al., 2009). As a result, tracking the dynamics of later Holocene wild mammal community structure and its relation to anthropogenic and climatic impacts remains a challenge for paleozoologists, especially those working in the earliest centers of human societal complexity, which were also cradles of domestication (Arbuckle, 2018). The problem posed by the deterioration of the 'wildlife signal' in the paleozoological record with the transition to agriculture can be tackled in specific regions where there exists, on the one hand, high-resolution data on human settlement history, and, on the other, natural archives that preserve millennial-scale record of contemporary wildlife (e.g. Byers and Broughton, 2004; Stewart et al., 2021). These regions can be used as windows

to the multiplex interactions between agricultural societies and wildlife communities in the Holocene (Fig. 1).

Such a rare juxtaposition of Holocene human and wildlife records can be found in the southern Judean Desert, west of the Dead Sea (Fig. 2). There, the punctuated settlement history at the major oasis in the region, Ein Gedi, is known from years of survey and excavations and is supplemented by historical sources (Hadas, 2005; Davidovich, 2013; Ussishkin, 2014). This archaeological settlement record is matched by well-preserved biogenic assemblages of faunal remains found in the hundreds of karstic caves dotting the high-relief topography of the region (Horwitz et al., 2002; Frumkin, 2015; Lazagabaster et al., 2021a,b). Together, the archaeological and paleozoological data provide an opportunity to study Holocene wild mammal communities from a binocular perspective, against the background of environmental studies that have been conducted in the Dead Sea (e.g. Neumann et al., 2010; Torfstein et al., 2013).

We use radiocarbon-dated remains of larger wild mammals from the Judean Desert caves in tandem with Holocene settlement dynamics and climatic data to observe diachronic change in the medium to large (>1 kg) mammal community. Ultimately, we investigate whether observed change can be ascribed to biotic interactions (including with humans), environmental change or a mixture of both. To the published paleoenvironmental assessments of the area (e.g. Bar-Matthews et al., 1999; Enzel et al., 2003; Vaks et al., 2003;

*Correspondence Ignacio A. Lazagabaster,
E-mail: ignacio.lazagabaster@mfn.berlin

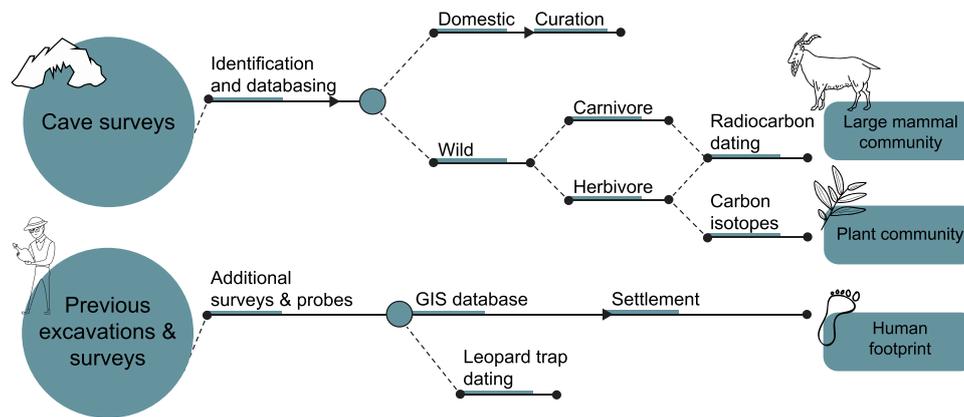


Figure 1. Flow diagram of the research design [Color figure can be viewed at wileyonlinelibrary.com]

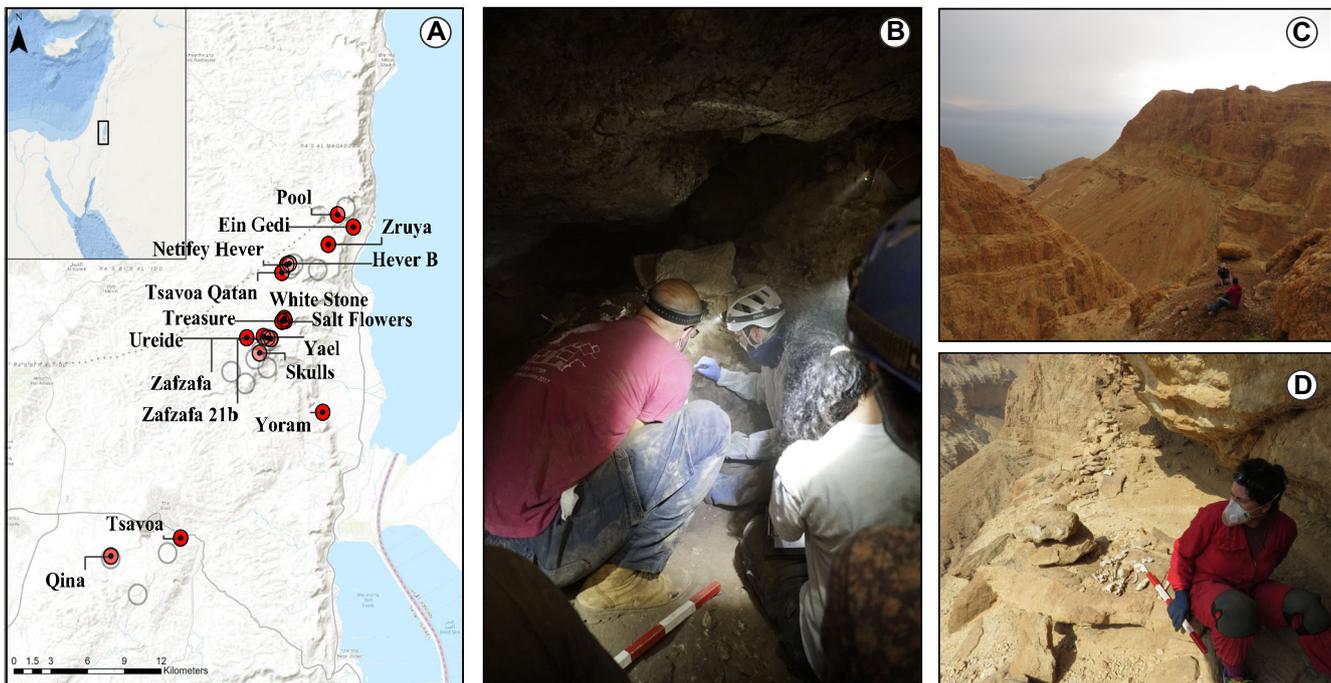


Figure 2. (A) Location map for the surveyed caves. Red circles are caves included in this study. (B) Work in the Cave of Skulls, photographed by M.U. (C) View of the Dead Sea from the Cave of the Pool, photographed by R.P. (D) M.U. with a bone collection at the entrance of Zafzafa East, photographed by R.P. [Color figure can be viewed at wileyonlinelibrary.com]

Litt et al., 2012), we add new bone collagen/apatite $\delta^{13}\text{C}$ results from our paleobiological collection. Disentangling the role of Anthropocene environmental and human influence on a large mammal community is expected to advance our understanding of transformative interactions between humans, other faunas and the environment in the later Holocene, which are difficult to track using other methods.

Paleozoological record

The paleozoological record of the southern Judean Desert caves has been mostly formed by animal feeding and denning activities (Kerbis-Peterhans and Horwitz, 1990; Horwitz et al., 2002; Lazagabaster et al., 2021b). The importance of caves for animals is amplified in this hyper-arid region by the absence of other shelters, such as trees and thickets. In the near-absence of fluvial and eolian sedimentation, cave deposits are typically shallow (<1 m) and almost entirely biogenic, comprising decayed dung, nesting materials and bones from *in situ* mortality and carnivore accumulation (Frumkin, 2015; Frumkin et al., 2017). The dry, loose and shallow sediments have been constantly turbated and

reworked by animals, and, in the last century or so, by cave looters. The result of this deposition history, combined with the pristine condition of dry-preserved organics (Weiner, 2010, p. 10), is that there is no stratigraphic or visual way to estimate the date of faunal remains from the caves without direct radiocarbon chronometry. This archaeologically hopeless situation of sediment mixing implies that the cave paleozoological collection represents a time-random sample of the fauna that has roamed the region mostly during the Holocene and the Late Pleistocene (Lazagabaster et al., 2021a,b).

In contrast to the central importance of the caves to animals in the Judean Desert, these karstic spaces have seen intermittent human use (Davidovich et al., 2015). Archaeological remains in the Judean Desert cliff caves are from three main episodes: late fifth millennium BCE, late 4th millennium BCE and 2nd century CE (Porat et al., 2007; Davidovich, 2013). Human occupation during these episodes was possibly related to temporary refuge and spanned weeks or months and has had little if any input to the faunal accumulation. For instance, we have not found evidence of butchery on any of the studied Holocene wild mammal remains. Visits to certain caves are

documented for other periods as well, yet again connected with ephemeral activities (Davidovich et al., 2015). Human contribution to cave wild mammal assemblage formation on a thousand-year scale is therefore considered negligible.

Settlement record

Many of the faunal remains found in the caves, however, are of domesticated animals (Horwitz et al., 2002). These represent hunted or scavenged household animals from the focal point of human settlement in the region: the Ein Gedi Oasis. This oasis, the major habitable locality along the southern Dead Sea coast (Hirschfeld, 2007; Stern, 2007), has attracted human settlement throughout the late Holocene (see settlement history in the Results). The intensity of distinct settlement episodes in the Ein Gedi oasis is an important variable that can potentially relate to wild animal community structure in the region through time (Lazagabaster et al., 2021a). As the major perennial water source in the region, human settlement and activity at the oasis could limit access to that critical resource. Furthermore, human settlement could have influenced the composition of wild mammal communities by either bottom-up or top-down effects, such as overgrazing, tree-cutting or ungulate hunting, on the one hand, and large predator killing, on the other (Dietl and Flessa, 2017; Thomas, 2020). Scavenging opportunities and protection from predators near settlements would probably join other subtle niche construction by humans that would have affected local biodiversity (Boivin et al., 2016; Zeder, 2016).

Climate

Another independent variable affecting mammal community structure is climate. Numerous paleoenvironmental studies in the region have revealed the complexity of Quaternary climate (e.g. Litt et al., 2012; Torfstein et al., 2015; Kiro et al., 2016; Vaks et al., 2018; Lazagabaster et al., 2021b). From these we learn that during the late Pleistocene the terminal Lake Lisan stand was much higher than that of the Dead Sea, its Holocene successor, probably indicating a lower evaporation rate and potentially higher precipitation in the northern headwaters of the River Jordan that provides most of the water input to the lake. The early Holocene, until the fourth millennium BCE, may have been a wetter period than the late Holocene (Rambeau, 2010). Although the difference is not on par with the Pleistocene/Holocene sharp climatic changes (Torfstein et al., 2015; Lazagabaster et al., 2021b), small climatic fluctuations can be important in marginal regions due to the increase in the flow of spring waters or slight increases in humidity that can determine the survival of resilient flora. Because of a rain shadow effect, however, the Judean Desert would have been ultimately dry under the Mediterranean storm track regime of the Holocene.

Preliminary observations and research questions

Our team has surveyed caves in the southern Judean Desert and has recovered a substantial number of identified large mammal remains. We assumed that the probability of dating a bone is directly related to that taxon's frequency in the life assemblage from the region at a specific period. Using this 'dates as data' (Rick, 1987; Brierley et al., 2018) approach, we tracked the succession of large carnivore remains from the paleozoological cave survey in the Holocene Judean Desert, which suggested a late Holocene decline in the frequency of leopards (*Panthera pardus nimr*) and a concomitant increase in striped hyena (*Hyaena hyaena syriaca*) (Lazagabaster

et al., 2021a). This turnover is temporally correlated with settlement intensification in the region, which suggests that humans could have had an impact on Holocene wild mammal communities. However, the role of aridification leading to a reduction in prey population – and, ultimately, leopard populations – could not be tested based solely on carnivore data.

In this study, we substantially broaden the scope of our previous investigation by adding new radiocarbon dates and stable isotope readings of herbivores to the carnivore dataset. Using these extended data, the Holocene large mammal succession in the study region can be evaluated also from the primary consumer perspective. This is very important, as it can resolve the open question of reduced prey availability as a possible cause of the carnivore turnover from leopards to hyenas and shed light on the carrying capacity of the marginal desert environment throughout the Holocene. More broadly, the new data will be used to discuss large mammal biotic interactions and response to human- and climate-induced landscape change in the region. Specifically, by tracing change in the distribution of radiocarbon dates of primary consumers from the Judean Desert cave sites we would like to see if there is change through time in the composition of the herbivore community in the study region. In case we observe succession, the faunal changes can then be discussed in relation to observed changes in human settlement intensity or the local climatic record.

We state four hypotheses closely related to each other concerning predator–prey dynamics (Hypothesis 1), climate change (Hypothesis 2), intraguild competition (Hypothesis 3) and human impact (Hypothesis 4). Hypothesis 1 suggests that with changes in the carnivore community (e.g. the decrease in leopard population) we will observe changes in the frequency of prey (e.g. an increase in the frequency of leopards' main prey species, the Nubian ibex and the rock hyrax) (Wallach et al., 2017; Winnie and Creel, 2017). An alternative hypothesis (Hypothesis 2) to explain potential changes in large mammal herbivores is climate change: we expect that the increasing trend in heat and aridity in the region towards the late Holocene drier period would adversely affect large herbivore demography (Broughton et al., 2008); this may, in turn, influence predator density. Hypothesis 3 states that with changes in the frequency in one or various carnivore species, other carnivores will show an increase or decrease in numbers (e.g. increase in the frequency of foxes because of the depressed leopard frequencies) (Prugh et al., 2009; Ritchie and Johnson, 2009; Ripple et al., 2013). Alternatively (Hypothesis 4), changes in the density of certain carnivore taxa may be related to human impact (e.g. in the case of striped hyenas, due to new foraging opportunities around human settlements).

Material and methods

Archaeological survey

In the last two decades, R.P. and U.D. have led cave and site surveys and excavations in the region. Their results were integrated with the works of other scholars to a fine-grained synthesis of regional settlement dynamics during the Holocene (see Lazagabaster et al., 2021a: supplementary information for references). In 2019–2020, additional survey and excavation work in the Ein Gedi Oasis was led by R.P. and U.D., aiming to clarify the settlement history during the 5th and the 1st millennia BCE. Their work included polygon surveys, 16 random probes and four small-scale excavations in parts of

the oasis flagged by the new surveys as containing potentially important clues to the spatial and temporal extent of settlement based on pottery techno-typology. The archaeological data collected by the team were integrated with previous published surveys using ArcGIS and used to categorize local human settlement intensity into low (<0.5 ha), medium (0.5–1.0 ha) and high (>1.0 ha) levels based on the area of convex hulls drawn around settlements and find spots (see Lazagabaster et al., 2021a: Table 1).

Paleozoological cave survey

A survey carried out during 2019–2020 recovered 36 faunal assemblages from 43 caves in the southern Judean Desert (Fig. 2). We surveyed caves that could be accessed by experienced persons without rappelling gear, as such caves are approachable by terrestrial mammals and therefore reflect hunting and scavenging in the immediate region. Potentially identifiable bone and tooth fragments of macro-mammals and hyena coprolites were collected from the surface and from crevices and sediment pockets within the surveyed caves by the field teams led by M.U. and R.P. To our survey data we added faunal collections recovered from the Cave of Skulls, excavated by Amir Ganor, Eitan Klein, R.P., M.U. and U.D., on behalf of the Israel Antiquities Authority and the Hebrew University in 2016; and a single carnivore bone (EG-039) collected in an excavation conducted by Gideon Hadas in Ein Gedi.

Archaeozoological analysis

Animal remains from the survey were identified using the comparative collection of the Laboratory of Archaeozoology at the University of Haifa, with reference to the collections at the Steinhardt Museum of Natural History at Tel Aviv University and to the National Collections at the Hebrew University in Jerusalem. The resulting database comprises 2123 identified specimens. A total of 110 bones from 19 sites were sent for radiocarbon dating and stable isotope analysis; 64 belong to primary consumers and are reported here for the first time.

We prioritized dating and isotopic analysis of the large (>21 kg) carnivores *P. pardus nimr* and *H. hyaena*, acknowledging their role as keystone taxa and their relative rarity in the mammal community. Although the carnivore guild of the Judean Desert also contains wolves and jackals, we could not differentiate the small local variants of the Arabian wolf (*Canis lupus arabs*) and the golden jackal (*Canis aureus*) from domestic dogs (*Canis lupus familiaris*), and their remains were not dated. We also dated Blanford's fox (*Vulpes cana*) and

Table 2. Summary of the number of dated bones (number of identified specimens, NISP) and minimum number of individuals (MNI) for each taxon, and the number of sites from which the dated bones were collected.

Taxon	Dated	No. of sites	MNI
<i>Sus scrofa</i>	14	5	11
<i>Capra nubiana</i>	10	6	9
<i>Gazella</i> spp.	15	9	13
<i>Procapra capensis</i>	25	9	21
<i>Hyaena hyaena</i>	20	7	15
<i>Panthera pardus</i>	12	3	6
<i>Vulpes</i> spp.	14	9	14
Total dated	NISP		110
	MNI		89
Total number of sites			19

Vulpes sp. (either Rüppell's fox *V. rueppellii* or red fox *V. vulpes*) specimens. From among the herbivores, we dated only bones that could be identified with certainty as belonging to a wild taxon: gazelles (*Gazella gazella*, *G. dorcas*), rock hyrax (*Procapra capensis*), suids (*Sus scrofa*) and Nubian ibex (*Capra nubiana*). Ibex specimens were selected only when they could be distinguished with confidence from those of domestic goats (*Capra hircus*), as in occipital bones and horn cores. Information on the ecological background (habitat and feeding behaviors) of the local populations of these taxa is summarized in Table 1.

In all cases, effort was made to maximize the number of caves from which the sample of each taxon was obtained (Table 2); this was done both to obtain a spatially balanced sample of the study region, and to reduce potential interdependence between specimens. Specimens from the same taxon but from different caves were considered as belonging to two different individuals; specimens identified to the same taxon but originating in the same cave were considered different individuals if their dates were different by at least two radiocarbon year error intervals.

Radiocarbon dating and $\delta^{13}C$

A total of 110 bones representing at least 89 individuals from 19 sites are included in this study (Appendix S1; Table 2). Primary consumers ($n=64$) include suids ($n=14$), Nubian ibex ($n=10$), gazelle ($n=15$) and rock hyrax ($n=25$). Secondary consumers ($n=46$) include striped hyena ($n=20$), leopard ($n=12$) and fox ($n=14$). While these sample sizes for some taxa are relatively small, they are probably sufficient to

Table 1. Description of the habitat and feeding ecology of the mammal taxa mentioned in this work. Most information is summarized from Mendelsohn and Yom-Tov (1999).

Taxon	Habitat	Feeding
<i>Gazella</i> cf. <i>Gazella dorcas</i>	Desert, <150 mm per annum	Leaves, flowers and pods of <i>Acacia</i> trees, twigs and leaves of other bushes; grazing on annuals in season
<i>Capra nubiana</i>	Cliffs in desert regions	Grasses and herbs during winter, browsing in the summer
<i>Procapra capensis</i>	Rocky terrain in different environments. In desert regions they are more numerous near water sources	Herbs and grass in the winter and spring, leaves in the summer. Can subsist of plants with high concentration of secondary metabolites
<i>Panthera pardus nimr</i>	Desert oases, wadis and cliffs	Mainly hyrax and ibex
<i>Sus scrofa</i>	Dense thickets, forests, riverine habitats	Omnivorous: small vertebrates, insects, carrion, nuts, acorns, berries, rhizomes, seeds
<i>Hyaena hyaena</i>	Generalist	Carrion, bone, hunting rare
<i>Vulpes cana</i>	Rocky slopes, canyons and cliffs in arid and hot regions	Insectivores, frugivores

compare central tendencies in the dates between taxa. The selected bones were dated in the Oxford Radiocarbon Accelerator Unit (ORAU; $n=57$) and at the Center for Applied Isotope Studies (CAIS), University of Georgia ($n=55$). When possible, organic carbon from collagen was used for radiocarbon dating; otherwise, carbon from bioapatite was dated. Although bioapatite is susceptible to contamination by soil carbonates, in arid environments with dry sediments this method is considered reliable (Zazzo and Saliège, 2011). Nevertheless, we dated two specimens using both collagen and bioapatite to check for the possible effect of contamination on bioapatite carbon results. The dates obtained were comparable, suggesting no significant contamination of soil carbonates (see Lazagabaster et al., 2021a).

The $^{13}\text{C}/^{12}\text{C}$ ($\delta^{13}\text{C}$) ratios were measured separately using a stable isotope ratio mass spectrometer and expressed as $\delta^{13}\text{C}$ with respect to PDB, with an error of $<0.1\%$. The $\delta^{13}\text{C}$ values are used to discuss possible shifts in animal diet and environment through time in terrestrial ecosystems. Due to differences between isotope spacing in different tissue and mineral fractions (collagen and bone apatite), an average $\Delta^{13}\text{C}_{\text{carb-coll}}$ spacing of 5% correction fraction was applied to the bioapatite samples ($n=10$) (Lee-Thorp et al., 1989; France and Owsley, 2015; Codron et al., 2018). Nitrogen isotopes were not used because of contamination, to which we were alerted when specimens with high nitrogen content were found not to have preserved collagen. The source of contamination is probably animal urine.

In the presentation of the results and in the analyses, the samples are temporally grouped following the formal subdivision of the Holocene epoch into Early, Middle and Late according to Walker et al. (2019): the Early–Middle Holocene Boundary is situated at 8200 a BP and the Middle–Late Holocene Boundary at 4200 a BP.

The laboratory protocols of the radiocarbon dating facilities are available online (CAIS: <https://cais.uga.edu/facilities/radiocarbon-ams-facility/>; ORAU: <https://c14.arch.ox.ac.uk/methods.html>).

Data analysis

The radiocarbon ages were calibrated using the Intcal20 curve. Our primary means for interpreting changes in large mammal

communities is bootstrap ($n=1000$) confidence intervals (95%) calculated for the median cal a BP dates of each taxon, presented along with the jitter of calibrated dates and probability density plots. This gives a simple and robust measure for the peak frequency of a taxon in the sample, with minimal assumptions. A comparison between median dates employed a Kruskal–Wallis test and a post-hoc Dunn test with Bonferroni correction. Finally, to account for potential preservation biases on the overall sample, we fit various probability distributions to the data and choose the best fit based on Akaike's information criterion (AIC) values. Fitting distributions to data is a very common task in statistics and consists in choosing a probability distribution modeling the random variable, as well as finding parameter estimates for that distribution (Motulsky and Christopoulos, 2004). Data analysis was facilitated by libraries 'rcarbon', 'tidyverse', 'FSA' and 'fitdistrplus' in R, using R Studio.

Results

Historical human settlement intensity in Ein Gedi

Three distinct phases of human settlement can be observed at the oasis of Ein Gedi (Fig. 3). The first was during an early stage of the Late Chalcolithic period, probably around the third quarter of the 5th millennium BCE and is best known by the isolated building complex above the main spring known as the Ein Gedi Shrine (Ussishkin, 1980). Several nodes of activity from the same period observed along the Ein Gedi spring slope indicate the existence of a sparsely populated hamlet (Shai et al., 2007). The second phase of settlement in the Ein Gedi oasis occurred from the 7th century BCE to the 6th century CE, with short (decadal scale) occupation gaps. During this span, from the later Iron Age to the Byzantine period, Ein Gedi was a thriving community owing to the substantial profits related to the local growing of cash-crops, mainly date palms and perfumes (Hirschfeld, 2007; Stern, 2007). Settlement remains from these periods are abundant, and agricultural terraces and water systems turned the oasis into an intensively managed landscape severely impacted by human activities, which peaked in the Roman–Byzantine era (Hadas, 2012). The area occupied by

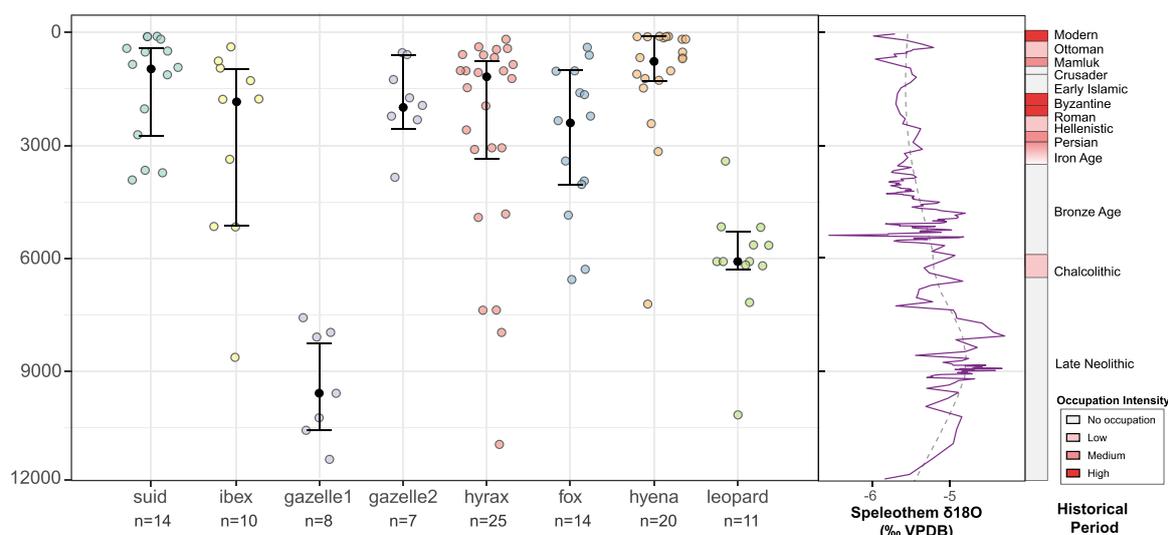


Figure 3. The distribution of median calibrated dates BP in the cave sample, presented for each taxon as a jitter plot with medians and 95% confidence intervals through time (left panel) and $\delta^{18}\text{O}$ curve from Soreq cave speleothems (right panel) (Bar-Matthews et al., 2003). The occupation intensity in each historical period is derived from the area occupied by historical settlements, with gray colors indicating no occupation and red colors indicating higher occupation intensity; data from Lazagabaster et al. (2021a: table 2 and supplementary information S1) [Color figure can be viewed at wileyonlinelibrary.com]

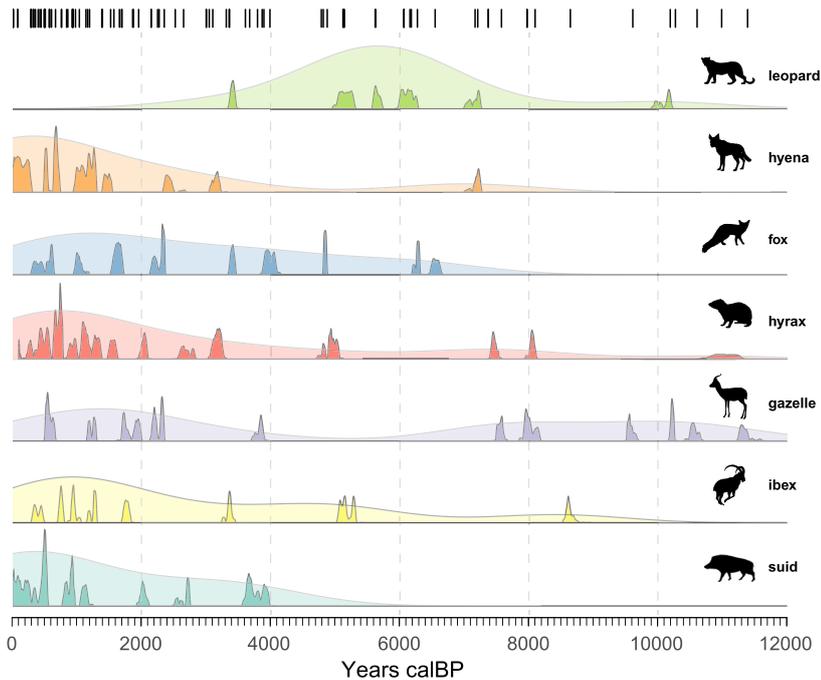


Figure 4. The distribution of median calibrated dates BP in the cave sample, presented for each taxon as a density distribution through time. Each black vertical bar represents a date [Color figure can be viewed at wileyonlinelibrary.com]

Table 3. The results of statistical comparisons of median cal a BP dates between taxa using non-parametric Kruskal–Wallis and multiple pairwise Kolmogorov–Smirnov tests with False Discovery Rate correction. Significant statistical differences are highlighted in bold.

Kruskal–Wallis $\chi^2 = 36.769$, d.f. = 6, $p < 0.0001$

Taxon comparisons		D-stat	<i>p</i> -value
Gazelle1	Fox	0.38	0.5091
Gazelle2	Fox	1.00	<0.0001
Hyena	Fox	0.56	0.0115
Hyrax	Fox	0.27	0.6482
Ibex	Fox	0.17	0.9779
Leopard	Fox	0.77	0.0022
Suid	Fox	0.43	0.2410
Gazelle2	Gazelle1	1.00	0.0011
Hyena	Gazelle1	0.50	0.1431
Hyrax	Gazelle1	0.28	0.8390
Ibex	Gazelle1	0.30	0.8390
Leopard	Gazelle1	0.92	0.0020
Suid	Gazelle1	0.43	0.3593
Hyena	Gazelle2	1.00	<0.0001
Hyrax	Gazelle2	0.92	0.0008
Ibex	Gazelle2	0.90	0.0022
Leopard	Gazelle2	0.92	0.0028
suid	Gazelle2	1.00	0.0001
Hyrax	Hyena	0.40	0.1066
Ibex	Hyena	0.50	0.1090
Leopard	Hyena	0.95	<0.0001
Suid	Hyena	0.21	0.9124
Ibex	Hyrax	0.22	0.9124
Leopard	Hyrax	0.76	0.0008
Suid	Hyrax	0.27	0.6534
Leopard	Ibex	0.73	0.0115
Suid	Ibex	0.37	0.4283
Suid	Leopard	0.92	0.0002

Roman period remains could have been as large as 27.7 ha, reduced to 5.9 ha during the Byzantine period (Lazagabaster et al., 2021a). Following a long abandonment, the oasis was briefly resettled during the Mamluk period in the 14th–15th

centuries CE, when a small hamlet was built above the Byzantine ruins (Hirschfeld, 2007).

Distribution of radiocarbon dates and taxonomic succession

The earliest concentration of dates corresponds to early Holocene gazelles, with a range of 10 560–7829 cal a BP [95% confidence interval (CI); median = 9578 cal a BP]. The leopard dates also peak early, between 6082 and 5174 cal a BP (95% CI; median 6082 cal a BP). A similarly early 10 560–7829 cal a BP (95% CI) range brackets the peak frequency of early Holocene gazelles (median 9578 cal a BP). The dates of the other taxa, however, appear to have climaxed significantly later: the ibex (5164–949 cal a BP 95% CI; median 1773 cal a BP), the hyrax (3064–854 cal a BP 95% CI; median 1226 cal a BP) and the group of Late Holocene gazelles (2320–591 cal a BP 95% CI; median = 1838 cal a BP). Foxes (4036–1031 cal a BP 95% CI; median 2283 cal a BP), suids (2717–425 cal a BP 95% CI; median 890 cal a BP) and hyenas (11 109 – 145 cal a BP 95% CI; median 668 cal a BP) share even later peak frequencies (Figs. 3 and 4). These observations on the dissimilar distribution of dates between taxa are supported by a Kruskal–Wallis test ($\chi^2 = 47.66$, d.f. = 6, $p < 0.0001$; see Table 3 for Kolmogorov–Smirnov multiple-comparison tests).

We also consider the possibility that the temporal patterns emerging from the radiocarbon dates are due to inherent preservation biases of the paleozoological record. We fit three common probability distributions to the data, including normal, logarithmic and exponential (Fig. 5). The data are better explained by an exponential distribution with an exponential parameter of 0.329 (Table 4). This means that the probability of finding a bone decreases exponentially with time. If this is true, then we cannot simply assume that more dates of a particular taxon in the paleozoological record reflect more overall abundance in the environment. Rather, the discussion of dates needs weighting each sample relative to its age. This matter is discussed in the following sections.

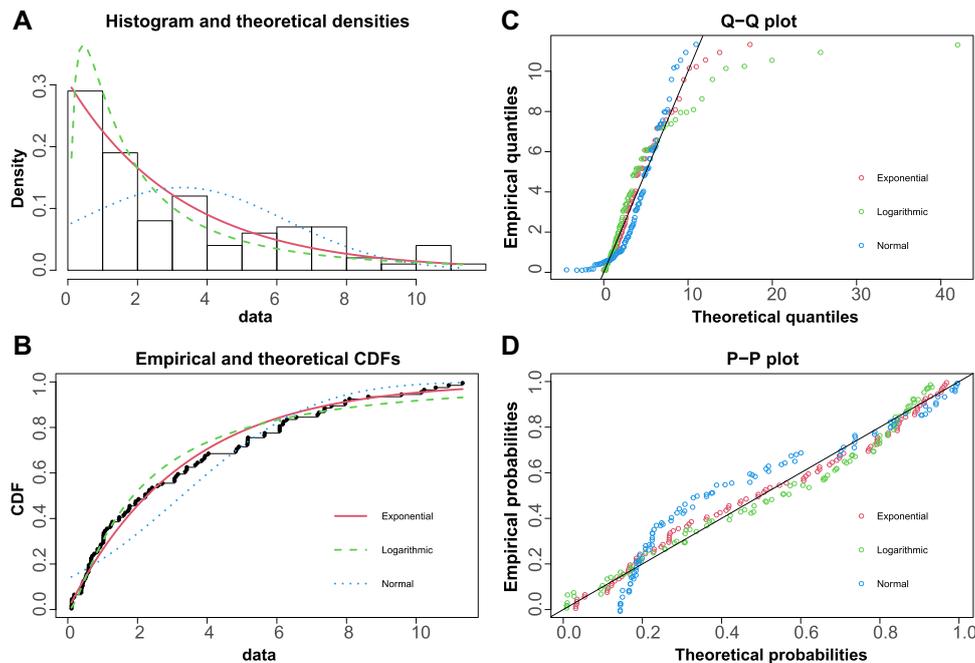


Figure 5. Different probability distributions fitted to the radiocarbon data. Note that the exponential distribution (in red) better explains the data than logarithmic (green) and normal (blue) distributions [Color figure can be viewed at wileyonlinelibrary.com]

Table 4. Parameters of various probability distribution models fitted to the data. AIC, Akaike's information criterion.

	Estimate	SE	Log-likelihood	AIC
Exponential	0.329	0.031	-231.979	468.659
Logarithmic	0.482	0.122	-235.999	475.999
Normal	3.031	0.281	-275.034	554.069

Carbon stable isotopes

The $\delta^{13}\text{C}$ results are presented in Table 5 and Fig. 6, and in Appendix S1 for the three major primary consumer taxa that existed in the Judean Desert throughout the Holocene: gazelle, ibex and hyrax.

Carbon isotope ratios of bone collagen are predominantly routed from dietary protein and represent the weighted average of foods consumed over a period of several years (Froehle et al., 2010). Herbivore tissue $\delta^{13}\text{C}$ therefore reflects the carbon composition of the plants that they consumed (Jim et al., 2004; Richards, 2020). Three photosynthetic pathways influence the $\delta^{13}\text{C}$ values of plants: C_3 , C_4 and Crassulacean Acid Metabolism (CAM). Most plants that use the C_3 photosynthetic pathway (trees, most forbs and shrubs) have $\delta^{13}\text{C}$ values that range between -35 and -20‰ with a mean of ca. -27‰ ; C_4 plants include dry adapted grasses, and some forbs and shrubs, and exhibit higher values than C_3 , ranging between -15 and -7‰ with a mean of ca. -12‰ ; CAM plants (cacti, succulents and epiphytes) have $\delta^{13}\text{C}$ values that range between -22 and -10‰ (Kohn, 2010; Sage et al., 2012; Munroe et al., 2021). Previous research in modern local C_3 vegetation of Tell es-Safi/Gath (west coast of Israel) shows $\delta^{13}\text{C}$ values ranging from -29 to -25‰ (Arnold et al., 2016).

Our samples show mean $\delta^{13}\text{C}$ values in herbivores of -17.6‰ in the Early Holocene, -17‰ in the Middle Holocene and -18.2‰ in the Late Holocene. These results suggest herbivores such as gazelles were eating vegetation from a mixed C_3/C_4 environment, which is consistent with grazing typical of this antelope in the Levant (see Hartman, 2012)

during the early period, with more strong presence of C_4 vegetation for two of the hyrax samples, as reflected by their carbon isotope values, which range from -14.3 to -18.5‰ . Instead, towards the recent Holocene, a slight increment on C_3 diet appears to occur for hyraxes as $\delta^{13}\text{C}$ values are more depleted (ranging from -18 to -20.6‰). Ibex samples from the last two periods show a larger component of C_3 in their diet, consistent with caprine mixed feeding behavior (Hartman, 2012). Unfortunately, with only one sample of ibex from the earlier Holocene, we cannot monitor major changes in their diet.

Discussion

Dates equal data? Understanding the distribution of radiocarbon dates in the paleozoological record

The cave biogenic assemblages of the Judean Desert are natural archives of the wildlife living in the region throughout history. The formation of the different cave deposits and skeletal assemblages reported in this study can vary greatly depending on the size and spatial arrangement of the caves, the different inhabitants of the caves (including humans), the predators that accumulated bones, the impact of anthropogenic activities (including modern alteration by looters, hikers, archaeologists, local Bedouins) and abiotic processes (e.g. water, temperature, soil pH, mineral diagenesis). The study of these caves is challenging as the bone assemblages often present hardly any stratigraphy, with anachronous remains mixed and dispersed throughout (Lazagabaster et al., 2021a,b). Thus, the potential to overcome these biases and understand how the deposits were formed is limited. Radiocarbon dating gets us as close as we could to a true paleozoological record. Our underlying assumption is simple, yet useful: among other factors the possibility of finding a bone of a certain taxon in the paleozoological record is related to the abundance of that taxon in the surroundings. Other factors might include ecological guild, life history and innate behaviors. Thus, when

Table 5. Summary statistics of carbon stable isotope data of primary consumers. EH, Early Holocene; LH, Late Holocene; max, maximum, MH; mid-Holocene; min, minimum; SD, standard deviation.

Taxon Period	Gazelle			Hyrax			Ibex			Suid LH
	LH	MH	EH	LH	MH	EH	LH	MH	EH	
min	-18.5	-18.1	-18.0	-20.9	-18.8	-18.5	-18.3	-17.4	-17.1	-20.7
max	-15.3	-16.1	-15.4	-14.5	-14.3	-18.5	-15.9	-17.0	-17.1	-16.5
mean	-16.8	-17.0	-17.4	-18.6	-17.0	-18.5	-17.7	-17.2	-17.1	-18.8
SD	1.1	1.0	1.3	1.4	1.9	NA	0.8	0.3	NA	1.2

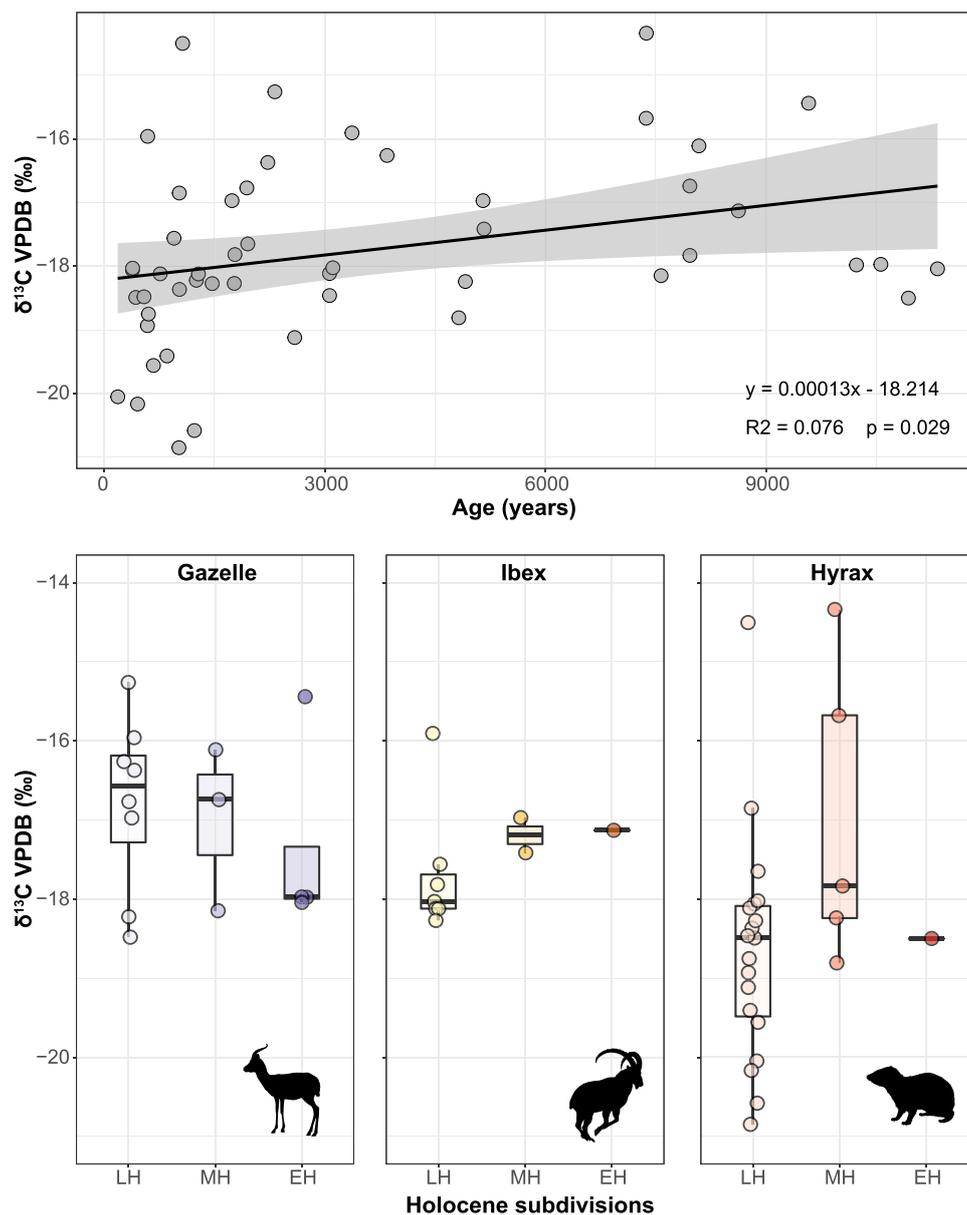


Figure 6. Changes through time in bone collagen/bioapatite $\delta^{13}\text{C}$ of primary consumers in the Holocene Judean Desert suggest stability in plant composition, and hyrax population growth in the oasis [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

there are apparent gaps in the record, it does not necessarily imply that a given taxon disappears from the region, but rather that its population was probably lower than in other times. The paleontological motto ‘absence of evidence is not evidence of absence’ readily applies in this context. This is exemplified by the absence of leopard remains younger than 3500 cal a BP in the record (Lazagabaster et al., 2021a). We know from historical sources, molecular analyses and modern sightings

that leopards had been present historically in the Judean Desert until the last one was killed in a road accident 15 years ago (Perez et al., 2006). Therefore, the absence of leopards in the paleozoological record probably reflects a reduction in their population instead of its complete disappearance from the region.

When examining the distribution of dates using the logic behind ‘radiocarbon dates as data points’, distinguishable

patterns emerge for the different taxa analyzed. The data suggest significant change in the fauna of the Holocene Judean Desert. The early and mid-Holocene saw the peak in frequency of both leopards and gazelles. The late Holocene marks a drastic change. Gazelle and leopard numbers drop; ibex and hyrax become the dominant herbivores; smaller foxes, and then synanthropic hyena, step to the frontline of the carnivore guild. The late Holocene also marks the first appearance of suids in the regional record; these may be the ancestors of the small isolated wild boar population of Mount Sodom on the coast of the Dead Sea. Preliminary morphological work (Marom et al., 2019) suggests that the extant Dead Sea boar population is morphologically indistinguishable from wild suids in the Mediterranean regions of the country. Thus, we suggest that the Dead Sea boars could have been introduced during the Late Holocene and subsequently became feral; this hypothesis is awaiting further investigation.

When all the data are pooled together, however, it is evident that the distribution of radiocarbon dates is skewed, with dates concentrated towards recent times. We have fit various common probability distributions and we show that the data approach an exponential distribution. This means that the probability of finding a bone in the Judean Desert Holocene record diminishes exponentially with time. This effect may be due to preservation or taphonomic factors. As time passes, natural degradation of the bone matrix can result in bone destruction (Keenan and Engel, 2017; Kendall et al., 2018); the low sedimentation in the caves would explain why there is almost no fossil diagenesis and why pre-Holocene remains are usually not preserved. This explanation, however, has a caveat: the state of bones in the caves remains physically pristine, even with specimens beyond the limit of radiocarbon dating maintaining full structural integrity. Moreover, the abundance and preservation of skeletal remains in caves is greatly influenced by spatial variation in preservation conditions and the mineralogical composition. Karkanas et al. (2000) proposed stepwise mineral diagenetic processes rather than uniform gradual transformations to explain why some materials could be affected differently. An alternative explanation could be the increase in the presence of hyenas in the Late Holocene. Many of the most fructiferous caves are active or inactive hyena dens and hyenas are known to be efficient bone accumulators (Kerbis-Peterhans and Horwitz, 1990; Orbach and Yeshurun, 2021). These are not the only bone accumulators in the desert though; certainly porcupines, foxes and other small carnivores are cave dwellers and can contribute to the assemblages with their remains and that of their prey (Horwitz et al., 2002; Lazagabaster et al., 2021a). Hyraxes also seek refuge in caves and crevices and contribute to the *in situ* mortality (Yom-Tov, 1993). Finally, large ibex and gazelle remains are brought to the caves by large carnivores, including leopards, wolves and hyenas. The importance of caves as feeding and resting places to bone accumulators is expected to have increased as trees disappeared from the region due to late Holocene dryness and human exploitation.

Nevertheless, the exponential decrease in the likelihood of finding a bone with time demands that we interpret the data with caution. If more 'weight' is given to bones found in older time periods than those found in recent time periods, then the Late Holocene peak in abundance flattens, except for hyenas and suids. The populations of ibex, gazelle, hyrax, fox and leopard would have been higher during the early and mid-Holocene, with numbers reduced in the Late Holocene. If we assume that the high abundance of prey (ibex, gazelle, hyrax, suid) in the Late Holocene is a taphonomic artifact – either due to negative diagenetic processes or to increased hyena activity – then the absence of leopard remains in the paleozoological

record is even more telling and would tend to reinforce our previous suggestion that leopard abundance in the Judean Desert drastically declined after ~3500 cal a BP (Lazagabaster et al., 2021a). The Late Holocene would have consequently seen a generalized downgrading of the ecosystem probably due to the combined effect of top-down cascading effects, aridification and human impacts.

Faunal carbon stable isotope ecology in relation to Holocene environmental fluctuations

Although the magnitude of regional Holocene climatic oscillations was smaller in comparison with those that occurred during the Pleistocene (Bar-Matthews et al., 1999; Lisker et al., 2010; Torfstein et al., 2013, 2015; Frumkin and Comay, 2021), the Judean Desert has seen environmental fluctuations throughout the Holocene that could have affected the composition of mammal communities. Today, the Judean Desert shows arid conditions with high temperatures and mean annual rainfall below 150 mm. The region's environment is determined by Mediterranean seasonal climate regimes, characterized by wet, cool winters and dry, hot summers (Soto-Berelov et al., 2015). Rainfall patterns are influenced by synoptic-scale circulation patterns forced by an upper-level Mediterranean trough (Armon et al., 2019). Active subtropical jets and active Red Sea troughs, in addition to heavy precipitation in the highlands, can also contribute to sporadic rainstorms that produce intense floods in the wadis that discharge into the Dead Sea. The Dead Sea water level, however, is mainly controlled by Mediterranean cyclones and the amount of water discharged into the Dead Sea, especially from the Lower Jordan River (Armon et al., 2019). The vegetation of the Judean Desert consists mostly of Saharo-Arabian flora, with some Irano-Turanian and Sudanian components, the latter especially in the areas surrounding the Dead Sea (Miebach et al., 2019). Arid-adapted grasses using the C₄ photosynthetic pathway represent 17% of the vegetation in the Judean uplands, but this number increases to 50% in the Dead Sea valley, including around the area of Ein Gedi. The C₄ plants are mostly associated with rocky terrain, crevices and wadi slopes, while C₃ vegetation dominates in open plains and loess soils (Vogel et al., 1986). There are few trees and bushes, and these are mostly concentrated near water springs, such as in Ein Gedi.

Regional paleoclimatic records derived from the analysis of cave speleothems (e.g. Soreq Cave) show that the modern seasonal regime of wet winters and dry summers in the southern Levant has been in place since the beginning of the Holocene (Orland et al., 2012). However, the reduction in precipitation in the western hills during periods of Mediterranean drought could have influenced the local availability of water and the amount of vegetation cover. For example, it has been suggested that a drop in annual rainfall of about ~200 mm on average occurred between 4600 and 4000 cal a BP (Bar-Matthews and Ayalon, 2004). Pollen remains recovered from a sediment core drilled near Ein Gedi suggest that three major Holocene climatic time intervals characterize the region (Litt et al., 2012): a relatively dry and warm period in the Pre-Pottery Neolithic and Pottery Neolithic (~10–6.5 ka cal a BP); though this interpretation seems contradictory with the high Dead Sea lake stand, see Migowski et al., 2006); a relatively wet and cool interval between the Chalcolithic and the Late Bronze Age (~6.3–3.3 ka cal a BP); and a rapid change to drier and warmer conditions at ~3200 cal a BP. The Late Holocene drying trend coincides with a relatively sharp drop in the Dead Sea level at ~3500 cal a BP (Frumkin et al., 2001; Enzel et al., 2003; Bookman et al., 2004;

Migowski et al., 2006; Stein et al., 2010; Kagan et al., 2015); these drier conditions were maintained for the rest of the Holocene, with fewer and relatively smaller oscillations (Frumkin et al., 2001; Bar-Matthews and Ayalon, 2004; Morin et al., 2019). The absence of travertine deposition during at least 2000 years in Moringa Cave, situated near the Ein Gedi spring, confirms that precipitation during the Late Holocene was not enough to support speleothem deposition (Lisker et al., 2007). Plant remains found in the 'Caves of the Spear' from around the time of the Bar-Kokhba revolt (~135 CE) indicate the presence of relict vegetation that was more abundant and diverse in the area than it is today (Simchoni and Kislav, 2009). Thus, it is evident that the aridification trend has persisted until today and is likely to continue in the future.

The vegetation cover of the rocky slopes of the Judean Desert produces pasture for local herbivores, mainly for the Nubian ibex and the rock hyrax (Vogel et al., 1986; Alaba, 2016). The carbon stable isotope data on the bones of these herbivorous mammals do not show significant changes in diet throughout the Holocene. However, there is a trend towards more negative $\delta^{13}\text{C}$ values with time (Fig. 6). This trend may indicate a slight reduction in C_4 grasslands and a change to feeding more often in dense vegetation spots with more abundant C_3 plants near water springs. The change towards diets with a higher C_3 plant component is evident in the hyrax during the Late Holocene. Thus, it is possible that these values reflect a general reduction in the Judean Desert's vegetation outside of the local aquifers and springs that irrigate the different oases. Furthermore, the diminishment of leopards (the main predator) could have produced a change in the ecology of hyraxes, which would have ventured more safely next to the water springs. In general, the $\delta^{13}\text{C}$ values of C_3 plants are more negative in those growing in wetter conditions. By contrast, water availability does not appear to influence C_4 plant $\delta^{13}\text{C}$ values, as they are generally less sensitive to environmental variation (Zhao et al., 2010). However, some desert plants obtain most of their water from secondary sources, namely water channeled by local topographic features rather than direct rainfall, as in the case of oasis vegetation, resulting in more negative $\delta^{13}\text{C}$ values than plants from exposed ridge desert microhabitats (Hartman and Danin, 2010).

According to the Israeli Nature and Parks Authority, the Ein Gedi Natural Reserve has a diverse flora, including some of the densest concentrations of tropical plants growing in Israel and the northernmost point at which some of these tropical species can be found. Although some of these plants are less abundant today due to the use of part of the reserve's water, the Ein Gedi Oasis is still a biodiversity hotspot of fauna and flora in the desert. Thus, it is likely that with the increase in aridity towards the Late Holocene and the diminishment of vegetation, the whole faunal community of the Judean Desert turned to these humid and vegetated refugia for food and water.

Trophic cascades and ecological collapse: towards an integrative ecological view of Holocene human–environment interactions

The Dead Sea area has been the subject of extensive paleoclimatic and paleoenvironmental studies, including regarding Dead Sea level fluctuations (Enzel et al., 2003; Bookman et al., 2004; Migowski et al., 2006; Kagan et al., 2015), cave speleothems (Bar-Matthews et al., 1999; Vaks et al., 2006; Lisker et al., 2007; Vaks et al., 2018), dating of cave wood detritus (Frumkin et al., 1991), pollen archives (Leroy, 2010; Neumann et al., 2010; Litt et al., 2012; Langgut et al., 2014; Miebach et al., 2017; Chen and Litt, 2018) and sedimentology (Dayan and Morin, 2006; Kiro et al., 2016). However, no record of Holocene faunal changes in the Judean Desert had previously been published. The paleozoological survey and radiocarbon dates of cave skeletal assemblages is the first attempt to reconstruct changes in wild faunal communities in the Judean Desert (Lazagabaster et al., 2021a,b). This is a step forward in the integration of multiple avenues of data with the overarching goal of providing an holistic view of the evolution of the ecosystem in the area through time and examining historical human–environment interactions. Furthermore, paleoenvironmental reconstructions of the Judean Desert derived from Dead Sea pollen records and cave speleothems should be taken with caution, because they reflect regional, rather than local, environmental conditions (see discussion in Lazagabaster et al., 2021a,b). The cave paleozoological assemblages, by contrast, are local archives of the fauna that lived near the caves.

We suggest that the later part of the Holocene, and especially the first millennium BCE and the early first millennium CE, has seen changes in the environment, human settlement intensity and large mammal community structure (Table 6). With regard to human settlement intensity, our fieldwork has confirmed and quantified previous observations on the extent of human use of the major oasis of Ein Gedi throughout the Holocene, as a proxy for the general impact of humans on the southern Judean Desert (Lazagabaster et al., 2021a). Surveys and excavation in the oasis have not discovered a substantial mid-Holocene settlement but have enlarged the known size of the first millennium BCE and CE settlements.

Circling back to the hypotheses of our study, is it possible to ascribe a cause for the observed changes to predator–prey dynamics, climatic factors, intraguild competition or anthropogenic impacts? The answer is, as usual, not clear-cut. Interpreting the results at face value, the increase in hyrax and ibex numbers, which goes against the tide of adverse climate and more intensive human settlement, is suggested to have been caused by relief of predation stress following a reduction of the leopard population, confirming Hypothesis 1. Hypothesis 2, which stated that the number of larger ungulates would decrease in the late Holocene drier period due to the increasing trend in heat and aridity, can be rejected, as

Table 6. Description of the animal, human and environmental changes in the Holocene of the Judean Desert described in this study.

Parameter		Early and mid-Holocene	Late Holocene	Summary
Human settlement		Hamlet, ritual, ephemeral	Large village, intensive agriculture	Intensification
Environment		Oasis, grassland	Oasis, no grassland	Aridification
Mammal community structure	<i>Herbivores</i>	More gazelle, more C_4 grazing	More ibex and hyrax, introduction of pigs, larger numbers	Increase + introduction & feralization
	<i>Carnivores</i>	Leopards	Fox and hyena	Mesopredators & scavengers

both ibex, hyrax, and suids seem to proliferate. Despite the possible loss of earlier Holocene habitats and the decline in the population of gazelles, the overall primary consumer community has not been impoverished. Foxes would also have benefitted from the disappearance of the top predator in the local ecosystem (Prugh et al., 2009), so there is reason to believe that, to some extent, carnivoran intraguild competition has also played an important factor in shaping the Holocene large mammal communities of the Judean Desert (Hypothesis 3).

However, we also show the possibility that the paleozoological record of the Judean Desert is temporally biased (Fig. 5), which implies that the apparent abundance of ibex and hyrax populations in the Late Holocene could be an artifact of the record. Regardless of the different interpretations of the data, what is noticeable from the radiocarbon dates is that the diminishment of leopard populations occurs before the peak in dated remains of its major prey, ibex, gazelle and hyrax. The herbivore succession should have supported the leopard population throughout the Late Holocene and thus our previous hypothesis that the decrease in leopards and the increase in hyenas was caused by human activities (e.g. hunting and waste) is strongly supported (Hypothesis 4; Lazagabaster et al., 2021a). These conclusions are, of necessity, still preliminary, and await the results of an ongoing genetic study on the Holocene demographic trends of these key carnivore and herbivore taxa. The new research presented here, however, takes another step in the effort to unravel the intricate interactions between animals, humans and the environment in the difficult depositional conditions of the post-domestication Holocene of the Judean Desert.

Acknowledgements. We thank Ardem Hulme-Beaman and an anonymous reviewer for suggestions and help with statistical analyses. I.A.L. acknowledges a Postdoctoral Fellowship from the Israeli Council for Higher Education and a Humboldt Foundation Postdoctoral grant. We thank Dudi Greenbaum, Jamil al Atrash and Muhammad Ali Ibrahim Bdur from the National Parks Authority for their assistance in our fieldwork; Avi Mashlach for his help with the geospatial and archaeological data; and the volunteers who helped us in excavation and survey. We thank Alex Cherkinsky, from the Center of Applied Isotope Studies in Georgia, and Tom Higham, Peter Ditchfield and Thibaut Deviese, from the Oxford Radiocarbon Unit, for their help with radiocarbon analyses. We thank Aya Marck for the illustration work. Special thanks to Liora Horwitz, Guy Bar-Oz, Reuven Yeshurun and Shai Meiri. This research was funded by an ERC-stg grant (No. 802752 to N.M.) for the DEADSEA_ECO Project (<https://sites.google.com/view/deadsea-eco/home>). Open Access funding enabled and organized by Projekt DEAL.

Conflict of Interest—The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are openly available in Open Science Framework at <https://osf.io/x6w24/>.

Supporting information

Additional supporting information can be found in the online version of this article.

Appendix S1. Specimen list and radiocarbon and carbon isotope data.

References

Albaba I. 2016. The terrestrial mammals of Palestine: A preliminary checklist. *International Journal of Fauna and Biological Studies* **3**: 28–35.

- Arbuckle BS. 2018. Early history of animal domestication in southwest Asia. *Oxford Research Encyclopedia of Environmental Science*. <https://doi.org/10.1093/acrefore/9780199389414.013.548>
- Armon M, Morin E, Enzel Y. 2019. Overview of modern atmospheric patterns controlling rainfall and floods into the Dead Sea: implications for the lake's sedimentology and paleohydrology. *Quaternary Science Reviews* **216**: 58–73. [<https://doi.org/10.1016/j.quascirev.2019.06.005>]
- Arnold ER, Hartman G, Greenfield HJ et al. 2016. Isotopic evidence for early trade in animals between old kingdom Egypt and Canaan. *PLoS ONE* **11**: e0157650. [<https://doi.org/10.1371/journal.pone.0157650>] [PubMed: 27322197]
- Bar-Matthews M, Ayalon A. 2004. Speleothems as palaeoclimate indicators, a case study from Soreq Cave located in the eastern Mediterranean Region, Israel. In *Past Climate Variability Through Europe and Africa*, Battarbee RW, Gasse F, Stickley CE (eds). Springer Netherlands: Dordrecht; 363–391.
- Bar-Matthews M, Ayalon A, Gilmour M et al. 2003. Sea-land oxygen isotopic relationships from planktonic foraminifera and speleothems in the Eastern Mediterranean region and their implication for paleorainfall during interglacial intervals. *Geochimica et cosmochimica acta* **67**: 3181–3199. [https://doi.org/10.1016/S0016-7037\(02\)01031-1](https://doi.org/10.1016/S0016-7037(02)01031-1) [
- Bar-Matthews M, Ayalon A, Kaufman A et al. 1999. The eastern Mediterranean paleoclimate as a reflection of regional events: Soreq cave, Israel. *Earth and Planetary Science Letters* **166**: 85–95. [[https://doi.org/10.1016/S0012-821X\(98\)00275-1](https://doi.org/10.1016/S0012-821X(98)00275-1)]
- Boivin NL, Zeder MA, Fuller DQ et al. 2016. Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences of the United States of America* **113**: 6388–6396. [<https://doi.org/10.1073/pnas.1525200113>] [PubMed: 27274046]
- Bookman R, Enzel Y, Agnon A et al. 2004. Late Holocene lake levels of the Dead Sea. *Geological Society of America Bulletin* **116**: 555–571.
- Brierley C, Manning K, Maslin M. 2018. Pastoralism may have delayed the end of the green Sahara. *Nature Communications* **9**: 4018. [<https://doi.org/10.1038/s41467-018-06321-y>] [PubMed: 30275473]
- Broughton JM, Byers DA, Bryson RA et al. 2008. Did climatic seasonality control late Quaternary artiodactyl densities in western North America? *Quaternary Science Reviews* **27**: 1916–1937. [<https://doi.org/10.1016/j.quascirev.2008.07.005>]
- Byers DA, Broughton JM. 2004. Holocene environmental change, artiodactyl abundances, and human hunting strategies in the Great Basin. *American Antiquity* **69**: 235–255. [<https://doi.org/10.2307/4128418>]
- Chen C, Litt T. 2018. Dead Sea pollen provides new insights into the paleoenvironment of the southern Levant during MIS 6–5. *Quaternary Science Reviews* **188**: 15–27. [<https://doi.org/10.1016/j.quascirev.2018.03.029>]
- Codron D, Clauss M, Codron J et al. 2018. Within trophic level shifts in collagen-carbonate stable carbon isotope spacing are propagated by diet and digestive physiology in large mammal herbivores. *Ecology and Evolution* **8**: 3983–3995. [<https://doi.org/10.1002/ece3.3786>] [PubMed: 29721273]
- Davidovich U. 2013. The chalcolithic – early Bronze Age transition: A view from the Judean Desert caves, southern Levant. *Paléorient* **39**: 125–138. <https://doi.org/10.3406/paleo.2013.5491> [
- Davidovich U, Porat R, Ullman M. 2015. Judean Desert caves: archaeology and history. In *Atlas of the Holy Land-Judean Desert Caves*, Frumkin A (ed.). Magnes Press: Jerusalem; 23–37.
- Dayan U, Morin E. 2006. Flash flood-producing rainstorms over the Dead Sea: a review. *Special Paper of the Geological Society of America* **401**: 53–62.
- Diamond J. 2002. Evolution, consequences and future of plant and animal domestication. *Nature* **418**: 700–707. [<https://doi.org/10.1038/nature01019>] [PubMed: 12167878]
- Dietl GP, Flessa KW. 2017. *Conservation Paleobiology: Science and Practice*. University of Chicago Press: Chicago.
- Enzel Y, Bookman (Ken Tor) R, Sharon D et al. 2003. Late Holocene climates of the Near East deduced from Dead Sea level variations and modern regional winter rainfall. *Quaternary Research* **60**: 263–273.

- Faith TJ, Lyman RL. 2019. *Paleozoology and Paleoenvironments: Fundamentals, Assumptions, Techniques*. Cambridge University Press: Cambridge.
- France CAM, Owsley DW. 2015. Stable carbon and oxygen isotope spacing between bone and tooth collagen and hydroxyapatite in human archaeological remains. *International Journal of Osteoarchaeology* **25**: 299–312. [https://doi.org/10.1002/oa.2300]
- Froehle AW, Kellner CM, Schoeninger MJ. 2010. FOCUS: effect of diet and protein source on carbon stable isotope ratios in collagen: follow up to. *Journal of Archaeological Science* **37**: 2662–2670. [https://doi.org/10.1016/j.jas.2010.06.003]
- Frumkin A. 2015. *Atlas of the Holey Land-Judean Desert Caves*. Magnes Press: Jerusalem.
- Frumkin A, Comay O. 2021. The last glacial cycle of the southern Levant: paleoenvironment and chronology of modern humans. *Journal of Human Evolution* **160**: 102609. [https://doi.org/10.1016/j.jhevol.2019.04.007.] [PubMed: 31142433]
- Frumkin A, Kadan G, Enzel Y *et al.* 2001. Radiocarbon chronology of the Holocene Dead Sea: attempting a regional correlation. *Radiocarbon* **43**: 1179–1189. [https://doi.org/10.1017/S0033822200038479]
- Frumkin A, Langford B, Porat R. 2017. The Judean Desert – the major hypogean cave region of the southern Levant. In *Hypogean Karst Regions and Caves of the World*, Klimchouk A, Palmer AN, De Waele J, Auler AS, Philippe A (eds). Springer International Publishing: Cham; 463–477.
- Frumkin A, Magaritz M, Carmi I *et al.* 1991. The Holocene climatic record of the salt caves of Mount Sedom Israel. *Holocene* **1**: 191–200. [https://doi.org/10.1177/095968369100100301]
- Hadas G. 2005. The ancient village of Ein Gedi in the light of recent excavations. *Bulletin of the Anglo-Israel Archaeological Society* **23**: 193–193.
- Hadas G. 2012. Ancient agricultural irrigation systems in the oasis of Ein Gedi, Dead Sea, Israel. *Journal of Arid Environments* **86**: 75–81. [https://doi.org/10.1016/j.jaridenv.2011.08.015]
- Hartman G. 2012. Impacts of environmental deterioration on the carbon isotope values of modern vegetation and gazelles in the southern Levant: predicting the severity of the Younger Dryas. *Palaeogeography, Palaeoclimatology, Palaeoecology* **321–322**: 55–64. [https://doi.org/10.1016/j.palaeo.2012.01.015]
- Hartman G, Danin A. 2010. Isotopic values of plants in relation to water availability in the eastern Mediterranean region. *Oecologia* **162**: 837–852. [https://doi.org/10.1007/s00442-009-1514-7.] [PubMed: 19956974]
- Hirschfeld Y. 2007. *En-Gedi Excavations II: Final Report (1996–2002)*. Israel Exploration Society, Institute of Archaeology, Hebrew University of Jerusalem
- Horwitz LK, Tchernov E, Lerna O. 2002. The fauna from caves in the northern Judean Desert. *Atiqot* **41**: 257–280.
- Jim S, Ambrose SH, Evershed RP. 2004. Stable carbon isotopic evidence for differences in the dietary origin of bone cholesterol, collagen and apatite: implications for their use in palaeodietary reconstruction. *Geochimica et Cosmochimica Acta* **68**: 61–72. [https://doi.org/10.1016/S0016-7037(03)00216-3]
- Kagan EJ, Langgut D, Boaretto E *et al.* 2015. Dead Sea levels during the Bronze and Iron ages. *Radiocarbon* **57**: 237–252. [https://doi.org/10.2458/azu_rc.57.18560]
- Karkanas P, Bar-Yosef O, Goldberg P *et al.* 2000. Diagenesis in prehistoric caves: the use of minerals that form in situ to assess the completeness of the archaeological record. *Journal of Archaeological Science* **27**: 915–929. [https://doi.org/10.1006/jasc.1999.0506]
- Keenan SW, Engel AS. 2017. Early diagenesis and recrystallization of bone. *Geochimica et Cosmochimica Acta* **196**: 209–223. [https://doi.org/10.1016/j.gca.2016.09.033]
- Kendall C, Eriksen AMH, Kontopoulos I *et al.* 2018. Diagenesis of archaeological bone and tooth. *Palaeogeography, Palaeoclimatology, Palaeoecology* **491**: 21–37. [https://doi.org/10.1016/j.palaeo.2017.11.041]
- Kerbis-Peterhans JC, Horwitz LK. 1990. A bone assemblage from a striped hyaena (*Hyaena hyaena*) den in the Negev Desert, Israel. *Israel Journal of Ecology and Evolution* **37**: 225–245.
- Kiro Y, Goldstein SL, Lazar B *et al.* 2016. Environmental implications of salt facies in the Dead Sea. *Geological Society of America Bulletin* **128**: 824–841. [https://doi.org/10.1130/B31357.1]
- Kohn MJ. 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and (paleo) climate. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 19691–19695. [https://doi.org/10.1073/pnas.1004933107.] [PubMed: 21041671]
- Langgut D, Neumann FH, Stein M *et al.* 2014. Dead Sea pollen record and history of human activity in the Judean Highlands (Israel) from the Intermediate Bronze into the Iron Ages (~2500–500 BCE). *Palynology* **38**: 280–302. [https://doi.org/10.1080/01916122.2014.906001]
- Lazagabaster IA, Rovelli V, Fabre PH *et al.* 2021b. Rare crested rat subfossils unveil Afro–Eurasian ecological corridors synchronous with early human dispersals. *Proceedings of the National Academy of Sciences of the United States of America* **118**: e2105719118. [https://doi.org/10.1073/pnas.2105719118.] [PubMed: 34312232]
- Lazagabaster IA, Ullman M, Porat R *et al.* 2021a. Changes in the large carnivore community structure of the Judean Desert in connection to Holocene human settlement dynamics. *Scientific Reports* **11**: 3548. [https://doi.org/10.1038/s41598-021-82996-6.] [PubMed: 33574447]
- Lee-Thorp JA, Sealy JC, van der Merwe NJ. 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *Journal of Archaeological Science* **16**: 585–599. [https://doi.org/10.1016/0305-4403(89)90024-1]
- Leroy SAG. 2010. Pollen analysis of core DS7-1SC (Dead Sea) showing intertwined effects of climatic change and human activities in the Late Holocene. *Journal of Archaeological Science* **37**: 306–316. [https://doi.org/10.1016/j.jas.2009.09.042]
- Lisker S, Porat R, Davidovich U *et al.* 2007. Late Quaternary environmental and human events at En Gedi, reflected by the geology and archaeology of the Moringa Cave (Dead Sea area, Israel). *Quaternary Research* **68**: 203–212. [https://doi.org/10.1016/j.yqres.2007.03.010]
- Litt T, Ohlwein C, Neumann FH *et al.* 2012. Holocene climate variability in the Levant from the Dead Sea pollen record. *Quaternary Science Reviews* **49**: 95–105. [https://doi.org/10.1016/j.quascirev.2012.06.012]
- Marom N, Meiri M, Tepper Y *et al.* 2019. Zooarchaeology of the social and economic upheavals in the Late Antique–Early Islamic sequence of the Negev Desert. *Scientific Reports* **9**: 6702. [https://doi.org/10.1038/s41598-019-43169-8.] [PubMed: 31040351]
- Mendelssohn H, Yom-Tov Y. 1999. *Fauna Palestina: Mammalia of Israel*. Jerusalem: Israel Academy of Sciences and Humanities
- Miebach A, Chen C, Schwab MJ *et al.* 2017. Vegetation and climate during the Last Glacial high stand (ca. 28–22 ka BP) of the Sea of Galilee, northern Israel. *Quaternary Science Reviews* **156**: 47–56. [https://doi.org/10.1016/j.quascirev.2016.11.013]
- Miebach A, Stolzenberger S, Wacker L *et al.* 2019. A new Dead Sea pollen record reveals the last glacial paleoenvironment of the southern Levant. *Quaternary Science Reviews* **214**: 98–116. [https://doi.org/10.1016/j.quascirev.2019.04.033]
- Migowski C, Stein M, Prasad S *et al.* 2006. Holocene climate variability and cultural evolution in the Near East from the Dead Sea sedimentary record. *Quaternary Research* **66**: 421–431. [https://doi.org/10.1016/j.yqres.2006.06.010]
- Morin E, Ryb T, Gavrieli I *et al.* 2019. Mean, variance, and trends of Levant precipitation over the past 4500 years from reconstructed Dead Sea levels and stochastic modeling. *Quaternary Research* **91**: 751–767. [https://doi.org/10.1017/qua.2018.98]
- Motulsky H, Christopoulos A. 2004. *Fitting Models to Biological Data Using Linear and Nonlinear Regression: a Practical Guide to Curve Fitting*. Oxford University Press: Oxford.
- Munroe SEM, McLnerney FA, Andrae J *et al.* 2021. The photosynthetic pathways of plant species surveyed in Australia's national terrestrial monitoring network. *Scientific Data* **8**: 97. [https://doi.org/10.1038/s41597-021-00877-z.] [PubMed: 33795698]
- Neumann FH, Kagan EJ, Leroy SAG *et al.* 2010. Vegetation history and climate fluctuations on a transect along the Dead Sea west shore and their impact on past societies over the last 3500 years. *Journal of Arid Environments* **74**: 756–764. [https://doi.org/10.1016/j.jaridenv.2009.04.015]

- Orbach M, Yeshurun R. 2021. The hunters or the hunted: human and hyena prey choice divergence in the Late Pleistocene Levant. *Journal of Human Evolution* **160**: 102572. [https://doi.org/10.1016/j.jhevol.2019.01.005.] [PubMed: 30850235]
- Orland JJ, Bar-Matthews M, Ayalon A *et al.* 2012. Seasonal resolution of eastern Mediterranean climate change since 34ka from a Soreq Cave speleothem. *Geochimica et Cosmochimica Acta* **89**: 240–255. [https://doi.org/10.1016/j.gca.2012.04.035]
- Perez I, Geffen E, Mokady O. 2006. Critically endangered Arabian leopards *Panthera pardus nimr* in Israel: estimating population parameters using molecular scatology. *Oryx* **40**: 295–301. [https://doi.org/10.1017/S0030605306000846]
- Porat R, Eshel H, Frumkin A. 2007. Finds from the Bar Kokhba Revolt from two caves at En Gedi. *Palestine Exploration Quarterly* **139**: 35–53. [https://doi.org/10.1179/003103207x163004]
- Prugh LR, Stoner CJ, Epps CW *et al.* 2009. The rise of the mesopredator. *BioScience* **59**: 779–791. [https://doi.org/10.1525/bio.2009.59.9.9]
- Rambeau CMC. 2010. Palaeoenvironmental reconstruction in the Southern Levant: synthesis, challenges, recent developments and perspectives. *Philosophical Transactions. Series A, Mathematical, Physical, and Engineering Sciences* **368**(1931): 5225–5248. [https://doi.org/10.1098/rsta.2010.0190.] [PubMed: 20956369]
- Richards MP. 2020. Isotope analysis for diet studies. In *Archaeological Science: an Introduction*, Richards MP, Britton K (eds). Cambridge University Press: Cambridge; 125–144.
- Rick JW. 1987. Dates as data: an examination of the Peruvian Pre-ceramic radiocarbon record. *American Antiquity* **52**: 55–73. [https://doi.org/10.2307/281060]
- Ripple WJ, Wirsing AJ, Wilmer CC *et al.* 2013. Widespread mesopredator effects after wolf extirpation. *Biological Conservation* **160**: 70–79. [https://doi.org/10.1016/j.biocon.2012.12.033]
- Ritchie EG, Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**: 982–998. [https://doi.org/10.1111/j.1461-0248.2009.01347.x.] [PubMed: 19614756]
- Sage RF, Sage TL, Kocacinar F. 2012. Photorespiration and the evolution of C4 photosynthesis. *Annual Review of Plant Biology* **63**: 19–47. [https://doi.org/10.1146/annurev-arplant-042811-105511.] [PubMed: 22404472]
- Shai Y, Porat R, Eshel H *et al.* 2007. Moringa Cave, En Gedi, Excavations I, Final Report (1961–1965), Conducted by B. Mazar and I. Dunayevsky. Israel Exploration Society: Jerusalem; 391–403.
- Simchoni O, Kislev ME. 2009. Relict plant remains in the 'Caves of the Spear'. *Israel Exploration Journal* **59**, 47–62.
- Lisker S, Vaks A, Bar-Matthews M *et al.* 2010. Late Pleistocene palaeoclimatic and palaeoenvironmental reconstruction of the Dead Sea area (Israel), based on speleothems and cave stromatolites. *Quaternary Science Reviews* **29**: 1201–1211. [https://doi.org/10.1016/j.quascirev.2010.01.018]
- Soto-Berelov M, Fall PL, Falconer SE *et al.* 2015. Modeling vegetation dynamics in the Southern Levant through the Bronze Age. *Journal of Archaeological Science* **53**: 94–109. [https://doi.org/10.1016/j.jas.2014.09.015]
- Stein M, Torfstein A, Gavrieli I *et al.* 2010. Abrupt aridities and salt deposition in the post-glacial Dead Sea and their North Atlantic connection. *Quaternary Science Reviews* **29**: 567–575. [https://doi.org/10.1016/j.quascirev.2009.10.015]
- Stern E. 2007. *En Gedi Excavations I, Conducted by B. Mazar and I. Dunayevsky, Final Report (1961–1965)*. Israel Exploration Society, Institute of Archaeology, Hebrew University of Jerusalem
- Stewart M, Andrieux E, Clark-Wilson R *et al.* 2021. Taphonomy of an excavated striped hyena (*Hyaena hyaena*) den in Arabia: implications for paleoecology and prehistory. *Archaeological and Anthropological Sciences* **13**: 1–25. [https://doi.org/10.1007/s12520-021-01365-6]
- Thomas CD. 2020. The development of Anthropocene biotas. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **375**: 20190113. [https://doi.org/10.1098/rstb.2019.0113.] [PubMed: 31983342]
- Torfstein A, Goldstein SL, Kushnir Y *et al.* 2015. Dead Sea drawdown and monsoonal impacts in the Levant during the last interglacial. *Earth and Planetary Science Letters* **412**: 235–244. [https://doi.org/10.1016/j.epsl.2014.12.013]
- Torfstein A, Goldstein SL, Stein M *et al.* 2013. Impacts of abrupt climate changes in the Levant from Last Glacial Dead Sea levels. *Quaternary Science Reviews* **69**: 1–7. [https://doi.org/10.1016/j.quascirev.2013.02.015]
- Tsahar E, Izhaki I, Lev-Yadun S *et al.* 2009. Distribution and extinction of ungulates during the Holocene of the southern Levant. *PLoS ONE* **4**: e5316. [https://doi.org/10.1371/journal.pone.0005316.] [PubMed: 19401760]
- Tyler CL, Schneider CL. 2018. An overview of conservation paleobiology. In *Marine Conservation Paleobiology*, Tyler CL, Schneider CL (eds). Springer International Publishing: Cham; 1–10.
- Ussishkin D. 1980. The Ghassulian Shrine at En-gedi. *Tel Aviver Jahrbuch für deutsche Geschichte/herausgegeben vom Institut für Deutsche Geschichte* **7**: 1–44.
- Ussishkin D. 2014. The Chalcolithic temple in Ein Gedi: fifty years after its discovery. *Near Eastern Archaeology* **77**: 15–26. [https://doi.org/10.5615/neareastarch.77.1.0015]
- Vaks A, Bar-Matthews M, Ayalon A *et al.* 2003. Paleoclimate reconstruction based on the timing of speleothem growth and oxygen and carbon isotope composition in a cave located in the rain shadow in Israel. *Quaternary Research* **59**: 182–193. [https://doi.org/10.1016/S0033-5894(03)00013-9]
- Vaks A, Bar-Matthews M, Ayalon A *et al.* 2006. Paleoclimate and location of the border between Mediterranean climate region and the Sahara–Arabian Desert as revealed by speleothems from the northern Negev Desert, Israel. *Earth and Planetary Science Letters* **249**: 384–399. [https://doi.org/10.1016/j.epsl.2006.07.009]
- Vaks A, Bar-Matthews M, Ayalon A *et al.* 2018. Pliocene–Pleistocene palaeoclimate reconstruction from Ashalim Cave speleothems, Negev Desert, Israel. *Geological Society, London, Special Publications* **466**: 201–216. [https://doi.org/10.1144/SP466.10]
- Vogel JC, Fuls A, Danin A. 1986. Geographical and environmental distribution of C3 and C4 grasses in the Sinai, Negev, and Judean deserts. *Oecologia* **70**: 258–265. [https://doi.org/10.1007/BF00379249.] [PubMed: 28311667]
- Walker M, Gibbard P, Head MJ *et al.* 2019. Formal Subdivision of the Holocene Series/Epoch: a summary. *Journal of the Geological Society of India* **93**: 135–141. [https://doi.org/10.1007/s12594-019-1141-9]
- Wallach AD, Dekker AH, Lurgi M. 2017. Trophic cascades in 3D: network analysis reveals how apex predators structure ecosystems. *Methods in Ecology and Evolution* **8**: 135–142. [https://doi.org/10.1111/2041-210X.12663]
- Weiner S. 2010. *Microarchaeology: Beyond the Visible Archaeological Record*. Cambridge University Press: Cambridge.
- Winnie J, Creel S. 2017. The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs* **12**: 88–94. [https://doi.org/10.1016/j.fooweb.2016.09.002]
- Yom-Tov Y. 1993. Does the rock hyrax, *Procavia capensis*, conform with Bergmann's rule? *Zoological Journal of the Linnean Society* **108**: 171–177. [https://doi.org/10.1111/j.1096-3642.1993.tb00293.x]
- Zazzo A, Saliège J-F. 2011. Radiocarbon dating of biological apatites: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* **310**: 52–61. [https://doi.org/10.1016/j.palaeo.2010.12.004]
- Zeder MA. 2016. Domestication as a model system for niche construction theory. *Evolutionary Ecology* **30**: 325–348. [https://doi.org/10.1007/s10682-015-9801-8]
- Zhao L, Xiao H, Cheng G *et al.* 2010. Correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in C4 and C3 plants of natural and artificial sand-binding microhabitats in the Tengger Desert of China. *Ecological Informatics* **5**: 177–186. [https://doi.org/10.1016/j.ecoinf.2009.08.004]