Ex Oriente Lux

New Zooarchaeological Insights on Late Pleistocene Subsistence Strategies at Ghar-e Boof (Southern Zagros)

Dissertation

der Mathematisch-Naturwissenschaftlichen Fakultät

der Eberhard Karls Universität Tübingen

zur Erlangung des Grades eines

Doktors der Naturwissenschaften

(Dr. rer. nat.)

vorgerlegt von

Mario Mata-González

aus Atarfe, Spanien

Tübingen

2023

Gedruckt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät der Eberhard Karls Universität Tübingen.

Tag der mündlichen Qualifikation: 26.01.2024

Dekan: Prof. Dr. Thilo Stehle

1. Berichterstatter: Prof. Dr. Nicholas J. Conard

2. Berichterstatter: PD Dr. Britt M. Starkovich

3. Berichterstatter: Prof. Dr. Natalie D. Munro

To my cousin,

David J. Fernández González

In memoriam

Acknowledgments

First and foremost, I am extremely grateful to my supervisors, Nicholas J. Conard and Britt M. Starkovich. I could not have made it without your support and guidance. To Nicholas J. Conard, you not only trusted me with the faunal material from Ghar-e Boof, but you also believed in me and dared me to be brave in the world of science. To Britt M. Starkovich, I do not have the words to express my gratitude for training me in Zooarchaeology, and allowing me to discover my true passion. You were so patient with me and taught me the importance of always being cautious and keeping my feet on the ground. And of course, many thanks to Natalie D. Munro. You welcomed me with an open heart to your Zooarchaeology lab at the University of Connecticut (UConn). You also saw in me what I never thought I could find in myself: the confidence, determination, and courage necessary to pursue a research and teaching career. Your support and kindness over the last year have been invaluable, and I thank you for helping to shape me into the scientist I am today.

Second, I would like to thank all the members of the Tübingen-Iranian Stone Age Research Project (TISARP) team for their hard work during the fieldwork, and for recovering and sorting all the faunal remains that I was able to analyze during my master’s and doctoral studies at the University of Tübingen. Without your great effort, my research project would not have come to fruition. Particularly, I am grateful to Mohsen Zeidi, co-director of the excavations carried out at Ghar-e Boof. You provided me with all the contextual information I needed for my publications, and were always willing to help, even when conducting fieldwork in the middle of nowhere, where the access to internet was very limited. I am especially thankful to my dear friend Saman Hamzavi Zarghani and his family. You not only hosted me during my visits to Iran, but you also treated me like one of your own, and shared your culture with me.

I am also grateful to the faculty members of the Institute for Archaeological Sciences at the University of Tübingen, and the Department of Anthropology at UConn, especially Daniel S. Adler, Gideon Hartman, Christian A. Tryon, and Simone Riehl. I have learned a lot from every single one of you, and your comments, advice, and endless discussions have contributed to improving the quality of my work. You are examples of vocational scientists, who are truly committed to the personal development and success of your students. In addition, I appreciate the support and guidance offered by many members of EVEREST, especially Katharina Foerster. Thanks also to Sam Brown for conducting a preliminary ZooMS analysis of bone specimens from Ghar-e Boof, Elic Weitzel for assisting me with the R scripts and the application of generalized linear models, Flavia Venditti for teaching me how to use the digital microscope Hirox HRX-01, and Svenja Schray, Benjamin Schürch, Firouzeh Ameli, and Mohsen Zeidi for translating the summary of my dissertation to German and Farsi respectively. Moreover, I am thankful to the members of the Equity and Inclusion Committee of the UConn's Department of Anthropology for accepting into the Research Mentoring and Scholarship Training for Emerging Researchers Program. Thanks to this program, I got to meet Hope Romain, a promising young researcher, who was brave enough to become my mentee while I was a visiting scholar at UConn.

My dear friends and constant companions, Ángel Blanco-Lapaz and Elisa Luzi, deserve special thanks. To Ángel, you accompanied me on my first trip to Iran and helped me countless times by sorting, cleaning, and photographing of a large portion of my faunal assemblages. But most importantly, you are one of the most supportive persons I have ever met, and everybody knows if everything works out in our institute it is because of you! To Elisa, you have taken care of me, and given me so much emotional support, especially during the last months. You motivated me to move forward every day with your contagious enthusiasm and love for what you do. And of course, if I have become addicted to caffeine, it is all your fault! Moreover, I feel honored to have had the opportunity to share this journey with many other graduate students at the University of Tübingen and UConn. Among them, I would love to thank Nick A. González for proofreading all the manuscripts I have written since we met. To Nick, I cannot believe you have become such an important part of my life, and invaluable friend. Talking to you (though mostly arguing!) about zooarchaeology is both stimulating and encouraging. I cannot wait to see what the future holds for us.

Last, but definitely not least, I am and I will always be grateful to my family and friends. To Mom, Dad, and brothers, I know it is hard for you to understand my passion for dirt, stones or dead things, but you have supported me regardless. To my friends, I am completely aware of how difficult it is to talk or see each other because of the distance. However, you have always been there for me, when I have needed you the most, or just to celebrate my achievements as if they were also yours. To my aunt María José, I cannot think of anything harder in life for a mother than losing a son. Yet, you are a warrior and a role model. You have taught me to never surrender. Thanks for being the light that guides me toward my dreams. I love you all.

Personal contribution

Appendix 1: Blanco-Lapaz, A., **Mata-González, M.**, Starkovich, B.M., Mohsen, Z., Conard, N.J., 2022. Late Pleistocene environments in the southern Zagros of Iran and their implications for human evolution. Archaeol. Anthropol. Sci. 14, 161. https://doi.org/10.1007/s12520-022-01615-1.

Although I am not the first and corresponding author, my colleague Ángel Blanco-Lapaz and I contributed equally to this publication. Together, we analyzed the small vertebrate assemblage of Ghar-e Boof and wrote the first manuscript. B.M. Starkovich supervised our work, while N.J. Conard, and M. Zeidi led the excavations at the site and provided contextual information. In addition, all the authors contribute to the review and editing of the paper.

Appendix 2: **Mata-González, M.**, Starkovich, B.M., Mohsen, Z., Conard, N.J., 2022. New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran). Quat. Sci. Rev. 279, 107350. https://doi.org/10.1016/j.quascirev.2021.107350.

I am the first and corresponding author. B.M.S. and I designed the research. I analyzed the faunal assemblage under the supervision of B.M.S. Likewise, N.J. Conard, and M. Zeidi conducted excavations at the site and provided contextual information. I wrote the first manuscript, and all the authors participated in the review and editing of the final draft of the paper.

Appendix 3: **Mata-González, M.**, Starkovich, B.M., Mohsen, Z., Conard, N.J., 2023. Evidence for diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros). Sci. Rep. 13, 19006. https://doi.org/10.1038/s41598-023-45974-8.

I am the first and corresponding author. B.M.S., N.J.C., and I designed the research. I analyzed the faunal assemblage under the supervision of B.M.S.; N.J.C. and M.Z. directed and carried out excavations at the site, and provided contextual data. Finally, I wrote the original manuscript, and all the authors contributed to the review and editing of the paper.

Appendix 4: **Mata-González, M.**, Starkovich, B.M., Mohsen, Z., Conard, N.J. Prey choice and changes in site occupation intensity during the Middle and early Upper Paleolithic at Ghar-e Boof (southern Zagros Mountains, Iran). **Manuscript ready for submission to Archaeol. Anthropol. Sci.**

I am the first and corresponding author of this manuscript. B.M.S. and I designed the research. I studied the zooarchaeological material and performed all the analyses included in this paper under the supervision of B.M.S. Excavations at Ghar-e Boof were led by M.Z. and N.J.C., who also contributed contextual information. M.Z. collected and provided the lithic data. Finally, I wrote the first manuscript, while all the authors took part in the review and editing process of the paper.

Zusammenfassung

Das Zagros-Gebirge liegt nicht weit entfernt von der Schnittstelle Afrikas, Südwestasiens und Europas. Die reichen archäologischen und paläontologischen Hinterlassenschaften bezeugen, dass diese Berge und Täler während des späten Pleistozäns Tierkorridor und Migrationsroute für verschiedene Menschegruppen, einschließlich Neanderthalern und anatomisch moderner Menschen, waren. Trotz der strategischen Lage des südlichen Zagros im Iran neben den mesopotamischen Tiefebenen und dem Persischen Golf, blieb die Region in der Forschung im Verhältnis zum zentralen und nördlichen Zagros unterrepräsentiert. Seit 2004 hat das Tübingen-Iranische Steinzeit Forschungsprojekt (TISARP) den Fokus auf die Erforschung und Dokumentation der paläolithischen Besiedlung der Dasht-e Rostam Region in der Fars Provinz im Iran gelegt. Ausgrabungen in Ghar-e Boof haben eine der längsten pleistozänen Sequenzen des Zagros hervorgebracht. Diese datiert zwischen 81 und 35 kya und zeigt das Potential des südlichen Zagros, um neue Einsichten in Besiedlungsdynamiken, techno-kulturelle Anpassungen und den zeitlichen Rahmen des Übergangs vom Mittel- zum Jungpaläolithikum zu erhalten. Bisher war wenig bekannt zur Nahrungsbeschaffung und den Subsistenzstrategien der mittel- und früh jungpaläolithischen Menschen. Hier fasse ich die Ergebnisse der zooarchäologischen und taphonomischen Analysen des spätpleistozänen Fauneninventars von Ghar-e Boof zusammen. Damit können die Paläoumwelt und die menschlichen Subsistenzstrategien rekonstruiert werden und Veränderungen in der Auswahl der Jagdbeute und Intensität der Besiedlung untersucht werden. Darüber hinaus diskutiere ich die archäologischen Implikationen meiner Analysen im Kontext des Übergangs vom Mittel- zum Jungpaläolithikum Eurasiens.

Nach den vorhandenen Taxa von kleinen Vertebraten und deren ökologischen Anforderungen können warme und trockene Umweltbedingungen, eine offene Graslandschaft und felsige Abhänge im Umkreis von Ghar-e Boof rekonstruiert werden. Trotz der Trockenheit war Wasser in der Nähe verfügbar und die Vegetationsdecke bestand vor allem aus Gräsern und Sträuchern. Obwohl die Umweltbedingungen im Zagros aufgrund der komplexen Topographie divers sind, weist die vorhandene Paläoumweltrekonstruktion

darauf hin, dass Menschen im Mittel- und Jungpaläolithikum die selbe mosaikhafte Umwelt des gesamten Zagros-Gebirges bewohnten und nutzten. Veränderungen in der Kleinsäugerfauna von Ghar-e Boof deuten auf einen Umschwung zu kälteren und/oder trockeneren Bedingungen um 48-45 kya hin. Diese scheinen zeitgleich mit dem Heinrich 5 Event aufzutreten und haben möglicherweise demographischen Wandel und kulturelle Anpassung regional beeinflusst. Außerdem habe ich gezeigt, dass die verschiedenen Hominiden, die Ghar-e Boof im späten Pleistozän besiedelten, ihre Nahrungsbeschaffung maximierten indem sie hochrangige Beute, vor allem Ziegen, welche in der näheren Umgebung vorhanden war, bevorzugten. Mittel- und Jungpaläolithische Jäger und Sammler nutzten auch Schildkröten und jagten Gazellen zur Nahrungsbeschaffung, seltener jagten sie Karnivoren, wahrscheinlich wegen der Felle. Obwohl es keine eindeutigen Nachweise für die Ausbeutung von kleinen, sich schnell bewegenden Beutetieren während des Mittelpaläolithikums gibt, haben die jungpaläolithischen Jäger und Sammler des Rostamian Rebhühner gejagt und möglicherweise auch gefischt. In meiner Forschung konnte ich zeigen, dass Menschen, obwohl sie sich hauptsächlich auf Paarhufer verließen, um ihren täglichen Nährstoffbedarf an Fleisch und Knochenmark zu decken, deren Subsistenzverhalten im Zagros stärker diversifiziert war als wir bisher dachten. Die Nutzung von verschiedenen Beutetieren und Ressourcen erlaubte Menschen unterschiedlichen Geschlechts, Alters und unterschiedlicher Fähigkeiten etwas zur Subsistenz der Gruppe beizutragen.

Eine diachrone Betrachtung zeigt, dass die Nutzung von niedrigrangigen Tieren, meist Rebhühnern, im Verhältnis zu langsamen und leicht zu fangenden Schildkröten über die Zeit hinweg zugenommen hat. Diese Veränderungen in der Auswahl der Beutetiere scheint keine Folge der Umweltveränderungen zu sein. Darüber hinaus spielten die Verwendung neuer Technologien und effizienterer Nahrungsbeschaffungsmethoden eine Rolle bei der Reduktion der Kosten des Jagens der Rebhühner. Jedoch lässt sich auch eine Zunahme der Besiedlungsintensität über die Sequenz hinweg verzeichnen. Diese kann entweder auf eine größere Gruppengröße, längere Besiedlungszeiträume, häufigere Besuche der Fundstelle oder einer Kombination einiger dieser, wenn nicht aller der Möglichkeiten, zurück zu führen sein. Veränderungen in der

Besiedlungsintensität und Subsistenzstrategien in Ghar-e Boof gehen einher mit einer intensivierten Ressourcennutzung aufgrund von Bevölkerungswachstum und verstärkter Bejagung während des frühen Jungpaläolithikums. Diese ist vergleichbar mit anderen Ergebnissen aus Eurasien, wie der Levante und dem Balkan. Daher zeigt meine Forschung das komplexe Zusammenspiel von Bevölkerungsdynamiken, Technologie, sozio-ökonomischen Entscheidungen, Mobilität und Besiedlungsmustern, welche den Beginn der frühen jungpaläolithischen kulturellen Tradition und der eindeutigen Ankunft von anatomisch modernen Menschen im Zagros-Gebirge und dem Rest von Eurasien begetter.

چکیده

کوههای زاگرس در فاصله نه چندان دوری از محل تلاقی قاره آفریقا، جنوب غربی آسیا، و قاره اروپا قرار گرفته است. داده‌های غنی باستان‌شناختی و دیرین انسان‌شناختی به دست آمده از منطقه زاگرس در طی اواخر دوران پلیستوسن تایید کننده این است که این منطقه و دره‌های موجود در آن به مثابه کریدور و خط سیر مهاجرتی گروههای مختلف انسانی از جمله نئاندرتال‌ها و همچنین انسان مدرن بوده است. علی‌رغم موقعیت استراتژیکی که منطقه جنوب زاگرس در کنار دشتهای میان‌رودان و همچنین خلیج فارس داراست، در مقایسه با بخشهای مرکزی و شمال زاگرس، به مقدار زیادی دارای فقر مطالعاتی است و به آن توجه چندانی نشده است. از سال ۱۳۸۳ تاکنون، تیم پروژه تحقیقاتی عصر سنگ ایران و توبینگن تمرکز خود را بر مطالعه و مستندنگاری دوران پارینه‌سنگی در استان فارس و به ویژه منطقه دشت رستم قرار داده است. کاوشهای باستان‌شناختی انجام گرفته در غار بوف منجر به شناسایی یکی از توالی‌های استقراری بلندمدت دوران پلیستوسن در منطقه زاگرس شده، که طیفی برابر با ۸۱ هزار تا ۳۵ هزار سال پیش را در برمی‌گیرد. این موضوع بیانگر این است که منطقه زاگرس جنوبی دارای پتانسیل بالایی در زمینه درک هرچه بهتر پویایی‌های استقرار، سازگاریهای فناورانه و فرهنگی، و زمان مراحل انتقالی از دوران پارینه‌سنگی میانه به جدید است. با این وجود، دانش ما از وضعیت و استراتژی معیشتی انسانهای دوران پارینه‌سنگی میانه و مراحل آغازین دوران پارینه‌سنگی جدید که در این منطقه می زیسته‌اند، بسیار اندک است. در اینجا من خلاصه‌ای از نتایج تحلیلهای جانور باستان‌شناختی و تافونومی مجموعه‌های جانوری اواخر دوران پلیستوسن به دست آمده از غار بوف را جهت بازسازی دیرین اقلیم و استراتژی معیشتی انسانهای دوران مذکور ارایه می‌کنم، و تغییرات در انتخاب حیوانات شکار شده و تراکم استقرار در طی زمان را بررسی می کنم. علاوه بر این، به بحث درباره پیامدهای باستان‌شناختی مطالعات خودم در چارچوب دوران انتقالی از پارینه‌سنگی میانه به جدید درسراسر قاره اوراسیا خواهم پرداخت.

بر اساس بقایای گونه‌های مهره‌دار کوچک به دست آمده از کاوش غار بوف و با توجه به نیاز زیست محیطی این گونه‌ها، چشم انداز اطراف محوطه بیشتر با آب و هوای گرم و خشک، مرغزارهای گسترده و صخره‌های بدون درخت و پوشش گیاهی بوده است. علی‌رغم خشکی آب و هوا، منابع آبی در نزدیکی محوطه وجود داشته، و پوشش گیاهی اطراف، بیشتر شامل علف و درختچه بوده است. اگرچه شرایط اقلیمی و زیست محیطی زاگرس به خاطر توپوگرافی متفاوت، بسیار متنوع است، داده‌های دیرین اقلیم موجود از منطقه بیانگر این است که انسانهای دوران پارینه‌سنگی میانه و جدید در چشم‌انداز مشابهی در سراسر منطقه زاگرس می زیسته‌اند و از منابع غذایی مشابهی برخوردار بوده‌اند. تغییراتی که در بقایای پستانداران کوچک به دست آمده از غار بوف وجود دارد، نشان دهنده تغییر در شرایط آب و هوایی مابین ۴۸ تا ۴۵ هزار سال پیش، از گرم و خشک به سرد و خشک است، که همزمان با رخداد هانریش ۵ است، و این امر احتمالا موجب تغییرات جمعیتی و تطابقات فرهنگی به صورت منطقه‌ای شده است.

من همچنین نشان داده‌ام که انسانهایی که در طی اواخر دوران پلیستوسن در غار بوف زندگی می‌کرده‌اند، تلاشهای خود در جهت کسب منابع غذایی را با شکار گونه‌های بُزسان که در پیرامون محوطه موجود بوده‌اند به حداکثر رساندند. شکارگران دوران پارینه‌سنگی میانه و جدید همچنین به جمع‌آوری لاک‌پشت و شکار غزال به عنوان منابع غذایی و در موارد نادری هم به شکار جانوران گوشتخوار، احتمالا برای استفاده از پوست آنها، اقدام کرده‌اند. هرچند مدرک روشنی برای استفاده از حیوانات کوچک و سریع دونده در دوران پارینه‌سنگی میانی وجود ندارد، شکارگران-گردآورندگان غذای دوران آغاز پارینه‌سنگی جدید با فرهنگ رستمی، به شکار کبک، و احتمالا ماهی پرداخته‌اند. من در مطالعات خود نشان داده‌ام که، هرچند که انسانها در دوران پارینه‌سنگی میانه و آغاز پارینه‌سنگی جدید بیشتر از گونه‌های سُم‌دار جهت رفع نیازهای غذایی روزانه خود برای گوشت و مغز استخوان بهره برده اند، شیوه‌های معیشتی آنها با تکیه بر گوشت حیوانات، دارای تنوع بیشتری نسبت به آنچه که تا پیش از این از منطقه زاگرس می‌دانستیم بوده است. استفاده

از گونه‌های مختلف شکار و دیگر منابع، به انسانها از هر جنس، سن، و با مهارتهای متنوع این امکان را داد که به طور جدی‌تری در اقتصاد معیشتی گروه خود مشارکت داشته باشند.

از نظر گاهشناختی، بهره‌برداری و استفاده از حیوانات با ارزش غذایی کم، عمدتا کبک، در مقایسه با حیوانات کوچک، کُندرونده یا لاک‌پشت که به آسانی قابل دسترسی هستند در طول زمان افزایش می یابد. این تغییر در الگوی انتخاب حیوانات برای شکار به نظر نمی‌رسد که نتیجه تغییرات آب و هوایی و زیست محیطی در منطقه باشد. علاوه بر این، اتخاذ یک فناوری جدید و روشهای موثر تهیه غذا احتمالا موجب کاهش هزینه‌های شکار حیواناتی همچون کبک شده بود. با این وجود، تراکم جمعیتی نیز در محوطه در طی زمان افزایش یافته بود، که احتمالا می‌توانسته یا در ارتباط با استقرار گروه بزرگتری از انسانها در محوطه، زمانهای طولانی تر استقرار، استفاده بیشتر از محوطه، و یا ترکیبی از مواردی باشد که در بالا متذکر شدم. تغییرات در تراکم استقرار و استراتژی‌های معیشتی در غار بوف همسان با تراکم منابع غذایی به دلیل افزایش جمعیت و شکار در طی دوران آغازین پارینه‌سنگی جدید است، همانند آنچه که بسیاری از پژوهشگران برای دیگر بخشهای قاره اوراسیا، ازجمله لوانت و بالکان پیشنهاد داده‌اند. بنابراین، مطالعات من نشان دهنده فعل و انفعالات پیچیده تغییرات در جمعیت، فناوری، تصمیماتی که در زمینه اقتصادی و اجتماعی جوامع گرفته شده، حرکت و الگوهای استقراری است، که همگام با آغاز سنتهای فرهنگی دوران پارینه‌سنگی جدید و حضور قطعی انسان مدرن در منطقه زاگرس و مابقی قاره اوراسیا است.

Summary

The Zagros Mountains lie not far away from the junction of Africa, southwestern Asia, and Europe. During the late Pleistocene, the presence of rich archaeological and paleoanthropological records has confirmed that during the Late Pleistocene, these mountains and their valleys constituted biographic corridors and migration routes for different groups of hominins, including Neanderthals and Anatomically Modern Humans (AMHs). Despite the strategic location of the southern Zagros of Iran, alongside the Mesopotamian plains and the Persian Gulf, the region has remained considerably understudied in comparison to the central and northern Zagros. Since 2004, the Tübingen-Iranian Stone Age Research Project (TISARP) team has focused on investigating and documenting the Paleolithic record of the Dasht-e Rostam region, in Fars Province (Iran). Excavations at Ghar-e Boof have revealed one of the longest Pleistocene sequences in the Zagros Mountains, which ranges from ca. 81 to 35 kya, and has demonstrated the potential of the southern Zagros to provide new insights on settlement dynamics, techno-cultural adaptations, and the timing of Middle and Upper Paleolithic transition. Yet, little is known about the foraging conditions and subsistence strategies of the MP and early UP hominins that lived across the region. Here I summarize the results of the zooarchaeological and taphonomic analyses of the Late Pleistocene faunal assemblages from Ghar-e Boof in order to reconstruct the paleoenvironment and hominin subsistence strategies, and examine changes in prey choice and site occupation intensity through time. In addition, I discuss the archaeological implications of my investigation within the context of the Middle-to-Upper Paleolithic transition across Eurasia.

Based on the representation of small vertebrate taxa and their ecological requirements, the landscape surrounding Ghar-e Boof was mainly dominated by warm, dry conditions, open meadows, and rocky slopes. Despite the aridity, there were also some water sources nearby, and the vegetation cover consisted mostly of grass and shrubs. Even though the environmental conditions of the Zagros are very diverse due to their complex topography, the available paleoenvironmental evidence from the region indicates that both MP and UP hominins inhabited and exploited similar mosaic environments across the entire range of the Zagros Mountains. Changes in the small mammal record of Ghar-e Boof point to a shift

towards colder and/or dryer conditions around 48-45 kya, which seems to be coeval with the Heinrich event 5, and may have impacted demographic turnovers and cultural adaptations regionally.

I also demonstrated that the different hominins that occupied Ghar-e Boof during the Late Pleistocene maximized their foraging efforts by targeting the higher-ranked prey available in the nearby landscape, namely caprines. MP and UP foragers also harvested tortoises and hunted gazelles for dietary purposes, and on occasion they exploited carnivores, most likely for their pelts. Although there is no unequivocal evidence for the use of small, fast-moving prey during the MP at Ghar-e Boof, early UP Rostamian hunter-gatherers did hunt partridges, and possibly fish. My research has shown that even if hominins relied mainly on ungulates to meet their daily nutritional demands of meat and marrow during the MP and early UP, their animal subsistence practices were more diversified than previously recognized in the Zagros. The use of different types of prey and resources allowed people of different sexes, ages, and diverse skills to actively contribute to the subsistence economy of the group.

From a diachronic perspective, the exploitation of lower-ranked animals, mostly partridges, relative to small, slow-moving, or easy-to-capture tortoises increased over time. The shift in prey choice does not appear to be the result of environmental changes. Additionally, the adoption of a new technology and more efficient procurement methods might have lowered the capture costs of partridges. However, there is also an increase in site occupation intensity over the sequence, which can be tied to either larger groups of people living at the site, longer periods of occupation, more frequent visits, or a combination of some, if not all, of these possibilities. Changes in occupation intensity and subsistence strategies at Ghar-e Boof are consistent with resource intensification due to population growth and higher hunting pressures during the early UP, similar to what many scholars have suggested for other parts of Eurasia, such as the Levant and the Balkans. Thus, my research evinces the complex interplay of shifts in demography, technology, socioeconomic decisions, mobility, and occupational patterns that accompanied the onset of the early UP cultural traditions and the definitive arrival of AMHs across the Zagros Mountains and the rest of Eurasia.

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Appendix 2: **Mata-González, M.**, Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran). Quat. Sci. Rev. 279, 107350. https://doi.org/10.1016/j.quascirev.2021.107350.

Appendix 3: **Mata-González, M.**, Starkovich, B.M., Zeidi, M., Conard, N.J., 2023. Evidence for diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros). Sci. Rep. 13, 19006. https://doi.org/10.1038/s41598-023-45974-8.

Appendix 4: Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J. Prey choice and changes in site occupation intensity during the Middle and early Upper Paleolithic at Ghar-e Boof (southern Zagros Mountains, Iran). Manuscript ready for submission to Archaeol. Anthropol. Sci.

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1. Introduction

Located not far from the intersection between southwestern Asia, Europe and Africa, the Zagros Mountains spread across a vast territory along the modern-day countries of Turkey, Iraq and Iran. From an archaeological and evolutionary perspective, these mountains and their corresponding valleys likely represented strategic crossroads and migration routes used by groups of hominins during the Late Pleistocene (129–11.7 kya BP). Thus, archaeological research in the region is key to improving our understanding of why, when, and how different hominin populations colonized Eurasia (Field et al., 2007; Vahdati Nasab et al., 2013; Bretzke and Conard, 2017; Shoaee et al., 2021).

In southwestern Asia, the so-called Middle to Upper Paleolithic (MP-UP) transition is considered a bio-cultural event, marked by the disappearance of local Neanderthal groups and the arrival of anatomically modern humans (AMHs) carrying a new techno-cultural repertoire (Goder-Goldberger and Malinsky-Buller, 2022). Neanderthal remains have been recovered at several MP sites in central and northern Zagros (e.g., Solecki, 1963, 1975; Trinkaus and Biglari, 2006; Pomeroy et al., 2017, 2020; Zanolli et al., 2019; Heydari-Guran et al., 2021). With few exceptions (i.e., Tsanova, 2013), the available archaeological evidence shows a lack of cultural and possibly demographic continuity in the region during the MP-UP transition (Bazgir et al., 2017; Becerra-Valdivia et al., 2017; Bretzke and Conard, 2017; Heydari et al., 2021), though only a few UP sites have yielded AMH remains (Scott and Marean, 2009; Tsanova, 2013; Trinkaus, 2018). Recent studies have provided new radiocarbon and OSL dates that situate the beginning of the Upper Paleolithic (UP) in the Zagros Mountains around 45–40 kya cal. BP (Becerra-Valdivia et al., 2017; Heydari et al., 2021).

In addition, the Zagros Mountains not only extend over 1600 km from northwest to southeast, but they are also characterized by a heterogeneous topography, varying in elevation from approximately 300 to more than 4000 m.a.s.l., and with numerous and diverse microenvironments (Heydari-Guran, 2014). As a result, when different hominin groups first spread across the Zagros, they faced new and very different environments, to which they had to adapt (Boivin et al., 2013). Archaeologists documented evidence for diverse techno-cultural traditions and foraging behaviors during the Late Pleistocene in the region (Hole and Flannery, 1967; Conard and Ghasidian, 2011; Bretzke and Conard, 2017; Ghasidian et al., 2017; Bahraminia et al., 2022; among others), which indicates that past hunter-gatherers displayed a great variety of cultural adaptations and subsistence economies in different landscapes (Ghasidian et al., 2019; Heydari-Guran and Ghasidian, 2020). The complex geographic and ecological systems of the Zagros, along with the archaeological record, highlight the importance of studying hominin subsistence strategies, cultural adaptations, and paleoenvironmental conditions on a regional scale (Bretzke and Conard, 2017).

1.2. Paleolithic and zooarchaeological research in the Zagros Mountains

The history of Paleolithic research in Iran, and particularly in the Zagros Mountains, can be divided into three phases (after Vahdati Nasab; 2011; for an alternative view and updates, see Jayez, 2022): 1) from beginning of the 20th century to 1980, where most excavations and surveys were carried out by Western scholars; 2) an almost absolute absence of Paleolithic research between 1980 to 2000, caused by sociopolitical upheavals, such as the Islamic Revolution, the eight-year war between Iraq and Iran, lack of interest in the Paleolithic period by Iranian authorities, and the impossibility for foreigners to conduct research in the region; and 3) since 2000 onwards, there is a renaissance of Paleolithic studies in the Zagros, with multiple excavations and surveys led by native archaeologists, but also in collaboration with non-native researchers.

Since the beginning of the archaeological investigations in the Zagros, archaeologists demonstrated the potential of the region for improving our understanding of Paleolithic cultural traditions and hominin adaptions (e.g., Garrod, 1930, 1957; Coon, 1951; Solecki, 1958; Braidwood and Howe, 1960, Young and Smith, 1966; Hole and Flannery, 1967; to name a few). Special attention is deserved toward the work done by Dorothy A. E. Garrod at Zarzi Cave (1930, 1957) and Ralph S. Solecki at Shanidar Cave (1958), both located in Iraqi Kurdistan, which allowed them to define the Zarzian (Epipaleolithic) and Baradostian (UP) cultural groups respectively. Subsequently, Hole and Flannery (1967) distinguished between the early and Late Baradostian for the UP, and with the inclusion of the Mousterian for the MP, they established a chrono-cultural framework for the region that has remained almost unchanged until today.

Regarding the zooarchaeological research in the Zagros, Dorothea M. A. Bate was the first to analyze the faunal assemblages recovered by Garrod at Zarzi Cave (Epipaleolithic) and from the MP deposits of Hazard Merd (Garrod, 1930). Unfortunately, she only had access to a small number of bone fragments, and her work consisted only of species lists, alongside some comments and a few linear measurements (Garrod, 1930). In the following decades, almost all the archaeologists that worked in the region reported to some extent faunal data (Coon, 1951; Braidwood and Howe, 1960; Solecki, 1963; Hole and Flannery, 1967). As highlighted by Reitz and Wing (2008) and Gifford-Gonzalez (2018), some of these early excavation projects even included faunal specialists among their personnel (e.g., Braidwood and Howe, 1960). They acknowledged the importance of bone remains to reconstruct the paleoenvironments in which hunter-gatherers lived, as well as the fact that the accumulation of faunas in Paleolithic sites most likely results from the "cultural filter" (Reed and Braiwood, 1960). With the emergence of the "New Archaeology" during the late '60s and '70s and a more anthropological approach to archaeology, the focus of research shifted to the study of human behavior, leading to an increasing interest in the role of animals in human societies (Albarella, 2017). Thus, the analysis of zooarchaeological assemblages from the Zagros that were shipped to Western institutions soon became the central topic of several publications (Turnbull and Reed, 1974; Turnbull, 1975; Evins, 1982; Hesse, 1989).

The Islamic Revolution of 1979 and the eight-year war between Iran and Iraq (1980-1989) stopped all the Paleolithic fieldwork conducted by foreign scholars in the Zagros Mountains (Vahdati Nasab, 2011; Jayez, 2022). Besides the political stability in the region, Vahdati Nasab (2011) also pointed to a lack of enthusiasm in the Paleolithic period by Iranian archaeologists. During the next 20 years, Western scholars had to concentrate on analyzing and/or revisiting archaeological material from previous excavations stored mostly in American museums or universities (Vahdati Nasab, 2011; Jayez, 2022); for instance, Smith (1986) published the first synthesis of the Paleolithic of Iran, while Dibble and colleagues studied MP and UP lithic artifacts from the Zagros to develop and test the “scraper reduction” model (i.e., Dibble, 1984, 1995; Dibble and Holdaway, 1993).

In general, especially since the late ’70s onward, zooarchaeologists mostly focused on taphonomy, “economic anatomy”, mortality profiles, and the discussion of methodological approaches, to elucidate the interpretative potential and behavioral implications of faunal assemblages, and contribute to major debates in the study of human evolution (e.g., Binford, 1981; Klein and Cruz-Uribe 1984; Marean and Spencer, 1991; Lyman, 1994; Stiner, 1994, Fisher, 1995; among many others). In this context, Marean and colleagues analyzed numerous zooarchaeological assemblages recovered from MP and UP caves in the Zagros during the ‘50s and ‘60s, including Kobeh, Kunji, Bisotun, and Tamtama (Marean and Frey, 1997; Lam et al., 1998; Marean, 1998; Marean and Kim, 1998; Marean and Assefa, 1999; Marean and Cleghorn, 2003; Marean et al., 2004). They assessed the integrity of these faunal collections and also provided valuable information regarding the hunting, transport, and butchery strategies of MP and UP foragers in the region (Marean, 1998; Marean and Kim, 1998; Marean and Cleghorn, 2003; Marean et al., 2004). They were more concerned with methodological questions and analytical problems, such as the impact of density-mediate attrition on faunal remains (Lam et al., 1998), and how to reconstruct and evaluate skeletal element representation, which was denominated as the “shaft critique” (Marean and Frey, 1997; Marean, 1998; Marean and Kim, 1998; Marean et al., 2004). Nevertheless, these studies on zooarchaeological assemblages from the Zagros allowed Marean and colleagues to propose that MP hominins and AMHs procured primarily animal resources by hunting, rather than from scavenging, as it was commonly claimed at the time (Marean, 1998; Marean and Kim, 1998; Marean and Assefa, 1999; for criticisms, see Stiner, 1998).

Paleolithic research in the Zagros Mountains of Iran started to flourish during the ‘90s, and particularly since the beginning of the 21st century, thanks to the individual efforts of a group of Iranian archaeologists (Jayez, 2022), who started revisiting sites previously excavated by foreign scholars, but also conducted systematic surveys to document new sites (e.g., Biglari and Heydari, 2001; Roustaei et al., 2002, 2004; Shidrang, 2006). These surveys and subsequent excavations were facilitated by the foundation of a research center for Paleolithic studies by the Iranian Cultural Heritage and Tourism Organization (ICHTO) in 1999 (Vahdati Nasab, 2011). During the late 2000s, the inclusion of Paleolithic studies at the main universities of the country allowed the formation of a new generation of Iranian archaeologists who did not have to pursue an education in European or American universities (Jayez, 2022). As a result, the number of research projects focused on Paleolithic surveys and excavations in the Zagros and led by Iranians has increased significantly during the last years (i.e., Heydari-Guran and Ghasidian, 2017; Zeynivand et al., 2018; Biglari and Shidrang, 2019; Jayez et al., 2019; Bahraminia et al., 2022; Bonilauri et al., 2022).

Another major change that took place in Iran during the beginning of the new century was the reopening of the country to non-Iranian archaeologists, mostly in the form of conjoint scientific missions (Vahdati Nasab, 2011; Jayez, 2022). Several European organizations have conducted Paleolithic fieldwork in the Zagros, including the University of Liége, in collaboration with the University of Bordeaux and the French National Center for Scientific Research at the National History Museum of Paris (CNR; Otte et al., 2007, 2011; Mashkour et al., 2009), the Catalan Institute of Human Paleoecology and Social Evolution (IPHES; Bazgir et al., 2014, 2017; Allúe et al., 2017; Rey-Rodríguez et al., 2021), and of course, the University of Tübingen and the Tübingen-Iranian Stone Age Research Project (TISARP) team (e.g., Conard et al., 2006, 2007; Zeidi et al., 2006; Conard and Ghasidian, 2011; Ghasidian, 2014; Heydari-Guran, 2014; Conard and Zeidi, 2019). Likewise, archaeologists from the University of Cambridge, and the University of Liverpool, among others, are also leading collaborative excavation projects at some of the most emblematic Paleolithic and Epipaleolithic sites in the Zagros Mountains of Iraqi

Kurdistan, such as Shanidar Cave (Reynolds et al., 2016, 2018; Pomeroy et al., 2017, 2020), and Palegawra Cave (Asouti et al., 2020). Hence, all these projects carried out during the last two decades by both native and foreign archaeologists have demonstrated the relevance of the Zagros Mountains to contribute to existing debates on the Paleolithic of Eurasia and the MP-UP transition, thanks to new chronometric data (Otte et al., 2011; Becerra-Valdivia et al., 2017; Heydari et al., 2021), Neanderthal remains (Zanolli et al., 2019; Pomeroy et al., 2017; Heydari-Guran et al., 2021), and a better understanding of the spatio-temporal patterning, complexity, and diversity of the techno-cultural record of the region (Conard and Ghasidian, 2011; Ghasidian, 2014; Ghasidian et al., 2017, 2019; Reynolds et al., 2018).

Likewise, recent excavations have not only yielded large amounts of faunal remains, but archaeologists have also water-screened systematically the excavated sediments and used ≤ 2 mm meshes (e.g., Conard and Zeidi, 2019; Rey-Rodríguez et al., 2020; Tilby et al., 2022), recovering even the smallest bone fragments and teeth. Although the restudy of faunal collections from the ‘50s to ‘70s is ongoing and can still offer important information (Hodgkins and Marean, 2017; Campana and Crabtree, 2019), the newly excavated zooarchaeological assemblages constitute unique research opportunities for zooarchaeologists like me to further investigate local paleoenvironmental conditions, hominin subsistence strategies and socioeconomic adaptations across the MP to early UP in the Zagros Mountains.

2. Objectives, research questions, and working hypotheses

The main goal of my doctoral research project was to investigate hominin-animal-environment interactions in the southern Zagros Mountains during the MP and early UP. To do so, I focused on the zooarchaeological and taphonomic analysis of the faunal remains recovered by the TISARP team at Ghar-e Boof (southern Zagros, Fars Province, Iran). All the specific objectives, research questions, and working hypotheses can be summarized in four main points:

1. **Paleoenvironmental reconstruction.** Alongside my colleague Ángel Blanco-Lapaz, I studied the small vertebrate assemblages of Ghar-e Boof to provide taxonomic identifications and paleoenvironmental reconstructions based on habitat requirements and ecological tolerances of modern-day taxa. Our paleoenvironmental study addressed two research questions: 1) how did the landscape surrounding the Ghar-e Boof look like during the Late Pleistocene? 2) Did the local climate and environmental conditions fluctuate throughout the sequence? By correlating the techno-cultural record of Ghar-e Boof with the small vertebrate assemblages, we sought to test the following hypothesis: paleoenvironmental changes influenced demographic turnovers and cultural developments locally and/or regionally.
2. **Site formation processes.** The taphonomic analysis of the macrofaunal remains aimed to identify the agent(s) responsible for the accumulation or modifications of bones at the site. Additionally, it also allowed me to examine whether or not the faunal assemblages have been affected by density-mediated attrition or other post-depositional processes, and determine their interpretative potential for reconstructing hominin behaviors.
3. **Prey choice and subsistence strategies.** I also analyzed species representation and relative abundances, anatomical and mortality profiles, and anthropogenic modifications to address several questions: which species were exploited by MP and early UP foragers? Which ones represented the bulk of the animal fraction of their diets? How did hominins hunt, transport, butcher, and process carcasses? Did the occupants of the site exploit animals for purposes other than food?
4. **Long-term diachronic trends.** Last, I used zooarchaeological data and models derived from optimal foraging theory to evaluate changes in prey choice and animal use through time. I also included the analysis of find densities, accumulation rates, and frequencies of retouched lithic artifacts as proxy measures of site occupation intensity. Are there any temporal

trends in prey choice at Ghar-e Boof? If so, did prey choice and the occupation intensity of the cave co-vary? Following Stiner and Munro (2011), I hypothesized that changes in prey choice and subsistence strategies at Ghar-e Boof were driven by intensification efforts in response to increased demographic and hunting pressures, rather than representing local or regional temporary adjustments to shifting paleoenvironmental conditions.

3. Paleoclimatic and paleoenvironmental context

Nowadays, the climate of the Zagros Mountains is mainly governed by the northern hemisphere westerly jet (Fig. 1, Alijani, 2008). Seasonal changes in the position of the Inter-Tropical Convergence Zone also impact the precipitation in the region (Jafari and Lashkari, 2020). In contrast, these mountains represent a barrier to easterly monsoon airflow (Giannakopoulou and Toumi, 2012). During the Late Pleistocene, shifts in the location and intensity of these systems as a result of fluctuations in solar insolation and/or orbital oscillations most probably caused climate and environmental changes (Kehl, 2009; Mehterian et al., 2017), which might have affected the evolutionary history of hominin groups, and their subsistence strategies and cultural adaptations in the Zagros Mountains.

According to deep ice cores from Greenland, deep sea cores from the eastern Mediterranean Sea, and speleothem records from Anatolia and the Levant, during the Late Pleistocene, the northern hemisphere witnessed numerous gradual but also abrupt paleoclimate changes, such as the Dansgaard-Oeschger events or the Heinrich events (Fig. 2, Grootes and Stuiver, 1997; Rossignol-Strick and Paterne, 1999; Bar-Matthews al., 2003; North Greenland Ice Core Project members, 2004; Svensson et al., 2008; Ünal-İmer et al., 2015). These paleoclimate records offer a global chronological framework in which I can track and test for the occurrence of paleoenvironmental and paleoclimatic variations, such as increase/decrease in temperature/precipitation, at predictable time ranges on a more regional or local scale. Therefore, does the paleoclimate record of the Zagros follow or match major global climatic events documented for the northern hemisphere?

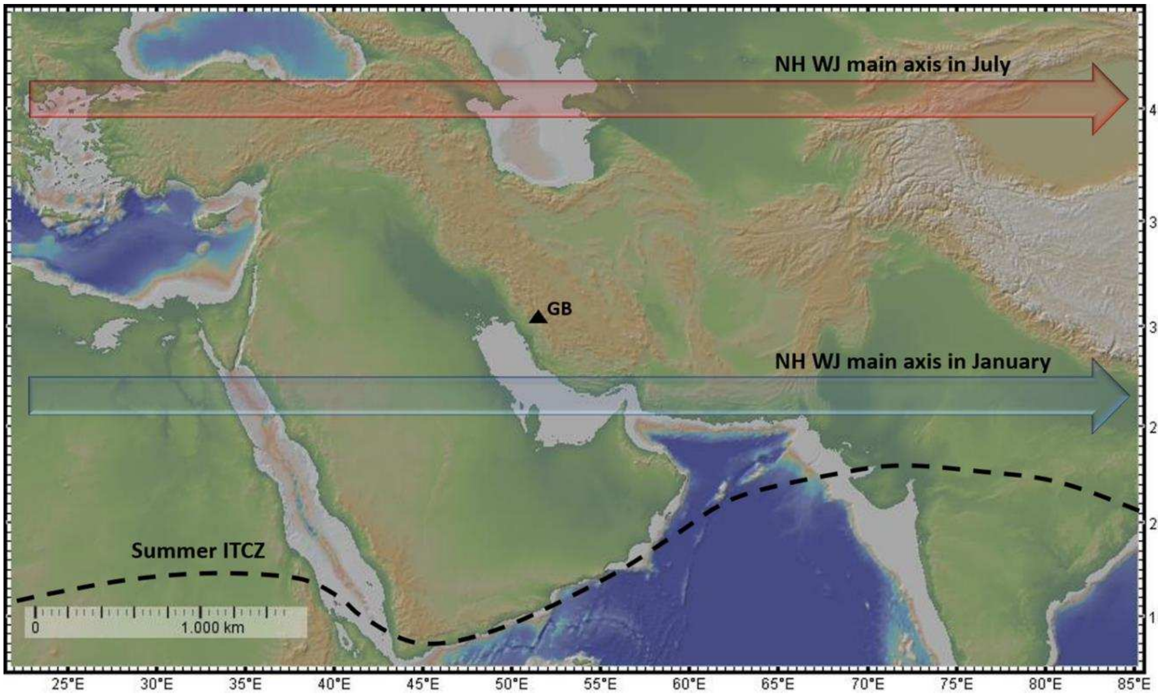

Fig. 1. Location of Ghar-e Boof in the Zagros Mountains, along with the current position of the main axis of the Northern Hemisphere Westerly Jet (NH WJ) during winter (January, blue arrow) and summer (July, red arrow). The map also includes the Summer Inter-Tropical Convergence Zone (ITCZ, dashed black line). Fig. by Mata-González (adapted from Schiemann et al., 2009; and Mehterian et al., 2017). Source: ©GeoMapApp.

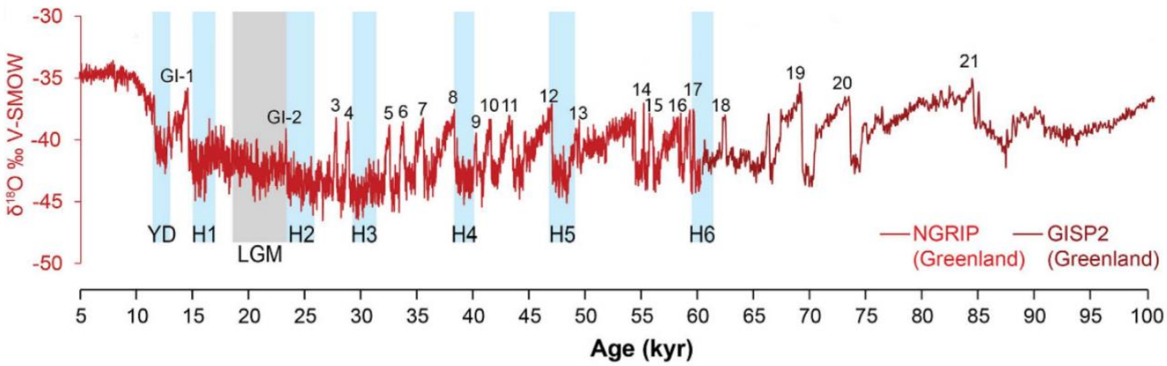

Fig. 2. δ^{18}O ice-core time series from Greenland NGRIP and GISP2 (figure adapted from Ünal-İmer et al., 2015; original data from Grootes and Stuiver, 1997; and Svensson et al., 2008). Numbers indicate Greenland Interstadials (Dansgaard-Oeschger; e.g. GI-1), while the duration of

Younger Dryas (YD), Heinrich (H) events, and LGM are highlighted by light blue and grey areas, respectively.

In order to reconstruct the paleoclimate and the paleoenvironmental conditions of the Zagros Mountains during the Late Pleistocene, scholars have applied diverse proxies, such as the analysis of pollen from cave deposits and coprolites (Djamali et al., 2011; Fiacconi and Hunt, 2015), oxygen isotopes from speleothems (Mehterian et al., 2017), paleosols and loess sediments (Kehl et al., 2005), lake sediment cores (van Zeist and Bottema, 1977; Snyder et al., 2001; Wasylikowa, 2005; Djamali et al., 2008a, 2008b), small mammals (Rey-Rodríguez et al., 2020; Tilby et al., 2022) and charcoal remains (Allué et al., 2018). Despite the relatively large number of paleoclimatic and paleoenvironmental records available for the Zagros, numerous issues hamper the reconstruction of paleoclimate in relation to long-term hominin settlement adaptations or major demographic and cultural shifts in the region: some records are either disturbed or reworked (Kehl et al., 2005; Djamali et al., 2011), represent short-term sequences (Mehterian et al., 2017), or lack of absolute age determinations before ~30 kya cal. BP (Djamali et al., 2008a). Despite that, up to now lake sediment cores constitute the best and longest paleoenvironmental and paleoclimate archives in the region for the Late Pleistocene. Situated in the northern Zagros, Lake Urmia yielded a pollen record that spans ca. 200 kya (Djamali et al., 2008a, 2008b) that was correlated to other records from the Indian Ocean, Arabian Sea, and Mediterranean Basin. Lake Zeribar, in the central Zagros, also offers seed, pollen, and diatom records ranging to over 43 kya (van Zeist and Bottema, 1977; Snyder et al., 2001; Wasylikowa, 2005).

The study of sediment cores from both Lake Urmia and Lake Zeribar shows that the landscape of the Zagros was mainly dominated by shrub/grass steppe vegetation throughout the Late Pleistocene, which includes Chenopodiaceae, Umbelliferae, Poaceae, and *Artemisia* sp. taxa, among others (van Zeist and Bottema 1977; Djamali et al. 2008a). Alongside grasses, palynologists have revealed the presence of some scattered trees, namely junipers, deciduous oak, maple, and pistachio (van Zeist and Bottema 1977; Djamali et al. 2008a). Both sequences reflect arid environments, and colder than present temperatures (van

Zeist and Bottema 1977; Wasylikowa 2005; Djamali et al. 2008a). Overall, the proportion of arboreal pollen relative to non-arboreal pollen evinces paleoclimatic and paleoenvironmental fluctuations in the region during the Late Pleistocene (van Zeist and Bottema 1977; Wasylikowa 2005; Djamali et al. 2008a). For example, pollen data from Lake Urmia suggest that during the last interglacial period (Eemian, between ca. 130–105 kya), the Zagros was characterized by slightly warmer and moister conditions than today (Djamali et al., 2008a). During the Last Glacial Maximum (ca. 20 kya) botanists observed at Lake Zeribar lower temperatures and drier conditions than current values, almost devoid of vegetation cover (van Zeist and Bottema 1977; Wasylikowa 2005). However, these major climatic events fall outside of the temporal range determined for Ghar-e Boof (ca. 81 to 35 kya, after Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017; Heydari et al., 2021). Within the chronological range of the site, variations in the arboreal/non-arboreal pollen ratio documented at Lake Urmia are more moderate (Djamali et al., 2008a). Yet, high percentages of Cyperaceae and *Sparganium*/*Typha* sp. (freshwater plants, which cannot tolerate high salinities) towards the middle part of the last glacial period (MIS 3, ca. 39 kya BP) indicate high lake level stands, probably related to lower evaporation rates as a result of decreased summer temperatures (Djamali et al., 2008b).

Nonetheless, due to the complex topography and variations in elevation across the Zagros region and the Iranian plateau, local gradients in rainfall and temperature can be very pronounced (Kehl, 2009). For instance, the Zagros Mountains are aligned in a northwest-southeast direction (Alijani, 2008). Consequently, the western slopes of the mountains receive more moisture from the Mediterranean Sea and/or the Persian Gulf, which causes more condensation and greater precipitation in the western slopes than in the eastern slopes (Zaitchik et al., 2007; Alijani, 2008). The southern Zagros Mountains are also more exposed to moist air masses coming from the sea (Alijani, 2008). Although the penetration of sea breezes from the Persian Gulf over the northern coast is quite limited, the thermal effect of the Zagros Mountains strengthens the depth and penetration, both landward and seaward, of land–sea breeze circulation over the eastern coast (Zhu and

Atkinson, 2004). Therefore, even if lakes Urmia and Zeribar sediment cores most likely reflect major paleoenvironmental changes, we are still left with the objective difficulty of correlating regional paleoclimate proxies with a given archaeological sequence and inferring local paleoenvironmental conditions.

4. Ghar-e Boof: stratigraphic, chronological and cultural sequence

Since the TISARP team visited Ghar-e Boof for the first time in 2005 (Conard et al., 2006), and after four seasons of excavations (Conard et al., 2007; Conard and Zeidi, 2019; Zeidi and Conard, 2019), researchers have conducted many detailed geological and chronological analyses, along with techno-typological studies of lithic artifacts (Conard and Ghasidian, 2011; Baines et al., 2014; Ghasidian, 2014; Becerra-Valdivia et al., 2017; Bretzke and Conard, 2019; Heydari et al., 2021). These investigations have established Ghar-e Boof as one of the most exceptional Pleistocene sites in the Zagros due to its long, well-dated, and high-resolution stratigraphic sequence of MP and early UP hominin occupations. Each line of investigation has provided its own independent datasets, but as part of my doctoral research, I also developed and provided general syntheses of the stratigraphic, chronological, and cultural sequence for the site (for more details, see Appendices 1 to 4, and Table 1). Except for a small number of animal specimens (NSP = 62; NISP = 56) from AH III described by Heydari-Guran (2014:130), my zooarchaeological study is the first to analyze all the identifiable faunal remains recovered from the MP and early UP deposits of Ghar-e Boof, representing the latest scientific contribution in the history of the TISARP. Thus, I offer a refined view of the cultural, socioeconomic, paleoenvironmental, and demographic changes that took place in the Dasht-e Rostam region of the southern Zagros Mountains across the MP to early UP.

Table 1. Ghar-e Boof. Summary of stratigraphic and chrono-cultural information: radiocarbon dates (from Conard and Ghasidian, 2011; Baines et al., 2014; calibrated dates from Ghasidian, 2014), OSL dates (from Heydari et al., 2021), sedimentology (from Conard and Ghasidian, 2011; Ghasidian, 2014; Conard and Zeidi, 2019; Zeidi and Conard, 2019; Heydari et al., 2021; and Appendix 1), and cultural attributions and technological characteristics of the lithic industries (from Conard and Ghasidian, 2011; Ghasidian, 2014; Ghasidian et al., 2017; Bretzke and Conard, 2017; Conard and Zeidi, 2019; Zeidi and Conard, 2019; but for AHs IVc and IVd, see also Heydari et al., 2021).

AH	^{14}C dates (cal. BP)	OSL dates (general range – Kya)	Sedimentology	Cultural attribution	Lithic technology
I	-	-	Mixed, gray, ashy silts of the surface and subsurface	Mixed	Chipped flint Epipaleolithic/UP artifacts, along with historic pottery sherds, a small number of metal and glass objects
II	-	-	In-situ laminated ashy silt layers of black, red, orange, yellow, gray, white and various brown hues		
IIa	-	-	Dark brown/gray ashy silts	Primarily Zarzian (Epipaleolithic), but slightly mixed	Microlithic industry (i.e., thumbnail scrapers, small backed triangles), but a few pottery sherds are still present
IIb	1,080 ± 45 1,243 ± 17	-	Medium brown ashy silts to a light, gray/brown silts. Massive geogenic layer (IIb.1) of limestone cobles located at the bottom of this layer		
III	35,152 ± 368	-	Homogenous light gray to yellow-brown ashy silts, similar to loess. Ample lateral variation	Rostamian (Early UP)	Laminar technology orientated towards the production of unidirectional bladelets and blades from small, single platform cores.
IIIa	-	37 – 39	Medium brown ashy silts		
IIIb	38,994 ± 1419 39,949 ± 921	38 – 39	Light brown ashy silts with alternating gray-black, white-brown, and light brown silts		
IIIc	NA	39 – 40	Light brown silts, starting with an irregular cemented crust		
IV	37,529 ± 682 41,355 ± 326	40 – 41	Light brown silts with small angular fragments of limestone		Small assemblages representing incomplete reduction sequence, but attributed to the Rostamian techno-cultural tradition based on the presence of characteristic UP artifacts, such as Arjeneh (a.k.a. Font-Yves or el-Wad) points and perforated shells
IVa	-	40 – 42	Brown silts with small angular fragments of limestone		
IVb	-	-	Light brown silts, but less rocky than AHs IV and IVa		
IVc	-	-	Fine rocky brown silts	MP – UP (?)	Due to low find densities, the cultural attribution of these layers remains unclear, though typical UP artifacts are missing
IVd	-	45 – 48	Fine rocky light brown silts		

Table 1. Continued.

AH	^{14}C dates (cal. BP)	OSL dates (general range – Kya)	Sedimentology	Cultural attribution	Lithic technology
V	-	46 – 49	Light brown but less rocky silts, underlaid by a thin dark brown band and then by a medium brown silty sediment	MP	Assemblages characterized by isolated artifacts, which, nonetheless, point to a lithic technology mainly focused on flake production
Va	-	51 – 55 55 – 58	Mostly light brown silty matrix with many small sharp-edged pieces of limestone, though thin bands of brown silts were observed		
Vb	-	56 – 60	Still mostly rocky light brown silty matrix, along with red brown silts		
Vc	-	58 – 63	Light brown silts		
Vd	-	63 – 70	Light brown to yellow brown silts		
VI	-	72 – 78 75 – 81	Homogeneous brown to gray-light/yellow brown silts, with small limestone clasts, laying over the bedrock		

5. Material and methods

In total, I analyzed a sample of 4,022 macrofaunal remains, including ungulates, birds, tortoises, fish, and small and large carnivores. Within this sample, I considered specimens identified up to species, genus, or family level, and those with less diagnostic features that I assigned to body size categories (see “Material and methods” sections, in Appendices 2 to 4). Additionally, the small vertebrate assemblage of Ghar-e Boof consists of 744 NISP and comprises small mammals (rodents, insectivores, and pikas), squamate reptiles (snakes, and agamid and lacertid lizards), amphibians, and small birds or Passeriformes (Appendix 1)[1].

For the sake of brevity, here I only list the analyses that I carried out in the different papers that encompass my dissertation. For a detailed description of the methods concerning each analysis, the reader is referred to following appendices:

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[1] Note that the total sample sizes for macro- and microfauna presented here are somehow different from those reported in Appendices 1 and 2, since some taxonomic groups, such as Passeriformes, insectivores (Erinaceidae) or fish, were reported in both studies. However, when I examined diachronic trends across the MP and early UP at Ghar-e Boof, I used only remains that were exclusively or potentially accumulated by hominins (Appendix 4), including fish, while I excluded taxa that were deposited by either birds of prey or died naturally (e.g., Passeriformes and insectivores).

- **Appendix 1 (small vertebrate assemblages):** a) taxonomic and taphonomic analysis; and b) habitat weighting method.
- **Appendix 2 (early UP Rostamian faunal assemblages):** a) density-mediated attrition and bone surface modifications; b) species representation and relative abundances; c) prey mortality profiles; d) skeletal element representation; and e) butchery and carcass processing.
- **Appendix 3 (MP faunal assemblages):** a) species representation; b) skeletal element representation and density-mediated attrition; and c) bone surface modifications.
- **Appendix 4 (diachronic trends in prey choice and site occupation intensity across the MP and early UP):** a) bone fragmentation; b) relative species abundances; c) site occupation intensity, as determined from find densities, accumulation rates, and frequency of retouched lithic artifacts.

5.1. Zooarchaeology, site occupation intensity and principal component analysis: a synthesis

Here, I use principal component analysis (PCA) following Reynard (2022) to synthesize how changes in prey choice correlates with the intensity of occupation at Ghar-e Boof across time. In the PCA, I integrate all the zooarchaeological data and proxy measures of occupational intensity by layer included in Appendix 4: Small Game Index (proportion of small game relative to large game), Fast-Moving Game Index (proportion of small, fast-moving game relative to small, slow-moving game), find densities and accumulation rates for total NISP, burned NISP, and counts of lithic artifacts; and frequency of retouched lithic artifacts relative to the total amount of lithic debris. I also incorporate sedimentation rates in the PCA, whose values were estimated by dividing the average thickness of each archaeological layer (in cm) by the duration (in years) over which the sediment accumulated (Stein et al., 2003; Reynard, 2022). I reported the thickness of all archaeological layers in Appendix 1 (see Table 1, and references therein) and duration estimates in Appendix 4 (Table

2). The PCA was performed in PAST statistics software (Hammer et al., 2001), and I normalized all the variables with the following expression: (x-mean)/stdev.

Some zooarchaeologists have used the reciprocal of Simpson's Index (or 1/D) to examine trends in species diversity and diet breadth (i.e., Stiner, 2001, 2009; Stiner and Munro, 2011; Starkovich, 2012a). The index is calculated as $1/\Sigma(p_i)^2$, and measures the proportionality (p) of species (i) in a given sample (*sensu* Lyman, 2008). In anthropogenic assemblages, low 1/D values reflect a narrow diet, while high values signify a broad diet (e.g., Stiner, 2009). According to the diet breadth model, foragers are expected to have a narrow diet when high-ranked prey are encountered frequently and the opportunity and search costs of preferred animals are lower than ignoring low-return food items (Stephens and Krebs, 1986; Kelly, 1995). Instead, if the availability of high-ranked prey decreases, foragers can raise the carrying capacity of their environment by broadening their diets to include lower-ranked resources (Flannery, 1969; Stiner, 2001, 2009), particularly because it reduces searching costs for available prey and increase overall foraging returns (Pianka, 1974). Thus, I applied the 1/D index to the faunal assemblages of Ghar-e Boof to further supplement my analysis of diet breadth. For calculating 1/D values, I only took into account specimens identified to species and genus, which reduces drastically the available sample size for each archaeological layer (Table S1). Although the index is designed to control the impact of sample size through the use of a square-root function, I only considered 1/D values for layers that have more than 29 NISP (after Stiner and Munro, 2011). Following Weitzel (2023), I fitted a log-normal family generalized linear model to the 1/D values as a function of time (for more details, see "Statistics" in the "Material and methods" section of Appendix 4, and references therein). There is a positive and statistically significant relationship between 1/D values and time (Fig. S1, $X^2 = 12.917$, df = 1, $p = < 0.001$; $D^2 = 0.725$). However, I also found a positive and statistically significant relationship between 1/D and sample size (Fig. S2a, $X^2 = 4.176$, df = 1, $p = 0.0410$; $D^2 = 0.341$), and richness (Fig. S2b, $X^2 = 9.961$, df = 1, $p = 0.002$; $D^2 = 0.631$) respectively. Thus, I did not report the results in Appendix 4 or integrate 1/D values into my PCA, since both sample size and richness appear to affect evenness (Faith and Du, 2018).

5.2. Bone retouchers

In Appendices 2 and 3, I documented the presence of a small number of osseous tools or potential osseous tools at Ghar-e Boof, namely retouchers, but no further details were reported. To better understand how MP and UP hominins selected, used, and discarded bone retouchers, and to link animal exploitation with the manufacture of lithic tools, here I complement the analysis of bone retouchers and reconstruct their life histories after Mallye et al. (2012) and Abrams et al. (2014). For the close-up photographs of the retouching marks, I used a digital microscope Hirox HRX-01.

Furthermore, Dr. Samantha Brown carried out a preliminary ZooMS analysis following previously reported protocols (Welker et al., 2015; Buckley et al., 2019; Brown et al., 2021). To avoid sampling and unnecessarily damaging the bone retouchers until we were sure that it was possible to identify collagen peptides from the faunal remains recovered at Ghar-e Boof, the ZooMs analysis focused on six long bone shaft fragments with similar characteristics to those of the retouchers in terms of length, cortical thickness and taphonomic alterations (Table S2). Unfortunately, taxonomic identifications were not possible as no collagen peptides were identified in the samples, and consequently, she did not sample any of the bone retouchers.

6. Results

6.1. Principal component analysis

In Table 2, I present all the calculations included in the PCA. Fig. 3a shows the first and second components, which explain 55.0% and 13.3% of the total variance respectively. All the loading scores for PCA 1 are positive, except for frequencies of retouched lithic artifacts relative to the total amount of lithic debris (Fig. S3a). PCA 1 groups all the MP layers (AHs VI to V) and those that may represent the transitional period between the MP and UP (AHs IVd and IVc) in the negative axis of PCA 1. In contrast, early UP layers (AHs IVb to III) are clustered in

Table 2. Ghar-e Boof. Calculations of the different variables used as proxy measures of site occupation intensity. Data from Appendix 4, except for sedimentation rates, which are reported here for the first time.

Layer	Culture	Small game	Fast-moving game	NISP/liters	NISP accumulation rates	Burned NISP/liters	Burned NISP accumulation rates	Lithic artifacts (N)/liters	Lithic accumulation rates	Frequencies of retouched lithic artifacts	Sedimentation rates (cm/100 yrs.)
III	UP	0.32	0.73	0.183	0.061	0.023	0.008	6.492	2.164	0.010	1.3
IIIa	UP	0.40	0.65	0.256	0.512	0.046	0.092	3.572	7.144	0.004	4.0
IIIb	UP	0.33	0.90	0.363	0.363	0.024	0.024	2.861	2.861	0.015	6.0
IIIc	UP	0.32	0.70	0.370	0.370	0.030	0.030	3.446	3.446	0.015	2.0
IV	UP	0.42	0.27	0.228	0.456	0.016	0.032	0.598	1.196	0.050	5.0
IVa	UP	0.15	0.32	0.329	0.165	0.032	0.016	0.467	0.234	0.025	0.8
IVb	UP	0.30	0.65	0.202	0.202	0.020	0.020	0.551	0.551	0.007	1.5
IVc	MP-UP (?)	0.31	0.68	0.190	0.127	0.007	0.005	0.408	0.272	0.036	0.7
IVd	MP-UP (?)	0.19	0.33	0.122	0.122	0.007	0.007	0.151	0.151	0.050	1.5
V	MP	0.28	0.15	0.204	0.028	0.024	0.003	0.267	0.037	0.099	0.6
Va	MP	0.30	0.20	0.255	0.080	0.005	0.002	0.453	0.142	0.059	1.9
Vb	MP	0.32	0.26	0.225	0.090	0.020	0.008	0.273	0.109	0.067	1.0
Vc	MP	0.28	0.18	0.264	0.044	0.005	0.001	0.425	0.071	0.045	0.3
Vd	MP	0.32	0.23	0.080	0.008	0.006	0.001	0.227	0.023	0.054	0.3
VI	MP	0.03	1.00	0.130	0.014	0.011	0.001	0.125	0.014	0.116	0.9

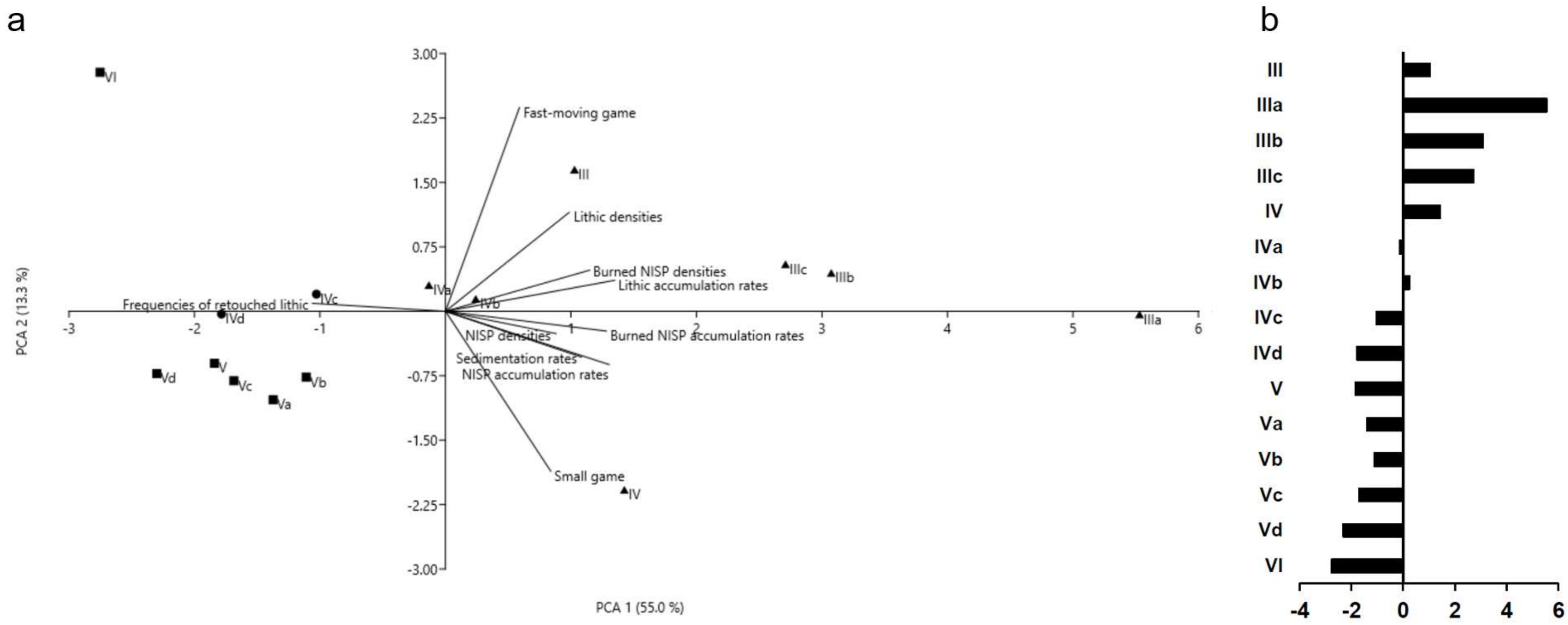

Fig. 3. Ghar-e Boof. a) PCA of variables used as proxy measures of site occupation intensity, along with biplots for each variable; symbols: squares (MP), dots (MP-UP?), and triangles (UP). b) plot of PCA 1 scores by layer, arranged from youngest (UP, top) to oldest (MP, bottom). For the PCA, I used normalized values from Table S3.

the positive axis, with the only exception of AH IVa, for which the PCA 1 score is close to 0 and does not overlap with any of the MP layers. Therefore, PCA 1 reflects differences between the MP and early UP layers in terms of occupational intensity. Yet, PCA 1 scores for AHs IVa and IVb (Fig. 3b) also signal that site occupation intensity remains moderately low during the beginning of the early UP, starting to increase significantly only from AH IV onwards.

PCA 2 is mainly modulated by the Small Game Index (negative axis) and Fast-moving Game Index (positive axis, Fig. S3b). Likewise, most MP layers show negative values along axis 2, whereas the majority of the early UP layers display positive values. Nonetheless, there are two clear outliners within both groups: 1) in AH VI (MP), I did not record any tortoise remains, and the small game fraction consists exclusively of medium birds (Fast-Moving game = 1.00; but still it is based on NISP = 6; MNI = 1); 2) AH IV (early UP) has a considerably high proportion of small, slow-moving game relatively to small, fast-moving game (see Appendix 4, Tables 4 and S2). Despite this, PCA 2 mostly tracks changes in prey choice. During the MP, the occupants of Ghar-e Boof hunted mostly large game prey, and to a lesser extent, they also harvested tortoises. Instead, even if early UP foragers relied primarily on large game, the proportion of large game relative to small game seems to decrease slightly over the early UP, in parallel with a significant increase in the proportion of small, fast-moving game relative to small, slow-moving tortoises. Overall, the combination of components 1 and 2 reveals a discernable concordance between the zooarchaeological record and the occupational intensity of Ghar-e Boof.

6.2. Bone retouchers

Among the 4,022 NISP that comprise the macrofaunal MP and early UP assemblages of Ghar-e Boof, I documented at least seven bone fragments that were used as retouchers, alongside another potential one. Their contextual, descriptive, and morphometric data are shown in Table 3. I identified five bone retouchers in the MP deposits and only two in the early UP layers. All of them are long bone shaft fragments of medium-bodied ungulates. The mean length of the bone blanks is 7.25

Table 3. Bones retouchers from Ghar-e Boof. Contextual, descriptive, and morphometric data. In bold, potential retoucher.

Bone ID	AH	Quadrant	Taxon	Element	Portion	Length (cm)	Width (cm)	Thickness (cm)	Cortical thickness (cm)	Weight (g)
276	III	7/9	Medium ungulate	Long bone	Shaft fragment	9.75*	1.15	0.48	0.42	5.5
1099	IIIb	6/7	Medium ungulate	Metapodial	Anterior groove	6.15*	1.32	0.77	0.32	5.1
596	IVc	6/8	Medium ungulate	Long bone	Shaft fragment	6.91*	1.09	0.47	0.44	3.8
619	Va	6/8	Medium ungulate	Tibia	Shaft fragment	7.30	1.37	0.80	0.35	4.3
663	Va	6/8	Medium ungulate	Tibia	Shaft fragment	4.87	2.12	1.04	0.44	6.6
719	Vb	6/8	Medium ungulate	Long bone	Shaft fragment	9.39	1.79	0.84	0.42	9.8
730	Vb	6/8	Medium ungulate	Humerus	Shaft fragment with foramen	6.88	1.87	1.15	0.36	7.0
878	VI	6/8	Medium ungulate	Femur	Shaft fragment	6.82	2.61	1.46	0.37	11.5

Asterisks (*) indicate specimens with recent fractures, so the length is incomplete.

cm, though three of them have recent breaks and were slightly larger. On average, their width is 1,67 cm, overall thickness is 0.88 cm, and the cortical thickness is 0.39 cm. Regarding the non-anthropogenic bone surface modifications, four retouchers exhibit chemical weathering, and only one is partly covered by sediment concretion (Table 4). In addition, four specimens are cut-marked, and two have cone fractures or scraping marks. All the bone blanks were unmodified with green (split/spiral) fractures. The only exception is a potential bone retoucher (highlighted in bold in the tables, Fig. S4), which seems to have been knapped entirely across one of its edges. Anthropogenic modifications are superimposed in a single specimen, and in this case, cut and scraping marks preceded the retouching marks, which partially obliterate some of them (Fig. 4.a). In Table 5, I show the technological and traceological data. At Ghar-e Boof, almost all the bone retouchers have solely a use area. Most of them are convex, but I also found retouchers with flat or plano-convex use areas. The retouching marks are either located laterally or centered. In addition, these traces are characterized by pits, which present depressions with somehow ovoid or triangular shapes, or scores/deep rectilinear incisions (Fig. 4), and they can be found either dispersed, concentrated, or isolated. Finally, the bone retouchers were mainly low to slightly used, and the overall use areas were relatively small.

7. Discussion and conclusions

7.1. Paleoenvironmental conditions in the southern Zagros Mountains during the Late Pleistocene, potential changes, and archaeological implications

In Appendix 1, my colleague Ángel Blanco-Lapaz and I analyzed the small vertebrate assemblage of Ghar-e Boof. Based on the ecological preferences and habitat requirements of the identified taxa, we reconstructed the paleoenvironment around the site during the Late Pleistocene. Overall, our data show that the MP and early UP occupants of Ghar-e Boof inhabited a landscape mostly characterized by warm, dry conditions, open meadows, and rocky terrains. The scarce vegetation cover consisted of grass and shrubs, and there were permanent water sources

Table 4. Bone retouchers from Ghar-e Boof. Synthesis of type of green fractures, anthropogenic and non-anthropogenic modifications. Plus sign (+) indicates that a given modification is present. In bold, potential retoucher.

Bone ID	AH	Fractures	Anthropogenic modifications					Non-anthropogenic modifications		Sequence of modifications*
			Percussion damage	Cut marks	Scraping marks	Worked	Retouching marks	Chemical weathering	Sediment concretion	
276	III	Split/spiral					+		+	RT > CO
1099	IIIb	Split/spiral					+	+		RT > CW
596	IVc	Split/spiral					+	+		RT > CW
619	Va	Split/spiral					+	+		RT > CW
663	Va	Split/spiral	+	+			+			
719	Vb	Split/spiral		+		Knapped	?	+		KN > CW
730	Vb	Split/spiral		+	+		+			CM/SM > CW
878	VI	Split/spiral	+	+	+		+			CM/SM > RT

*When there was no overlap between the different types of modifications, I did not establish the sequence of modifications. Abbreviations: RT (retouching marks); CO (partially covered by sediment concretion); CW (chemical weathering); KN (knapped); CM (cut marks); and SM (scraping marks).

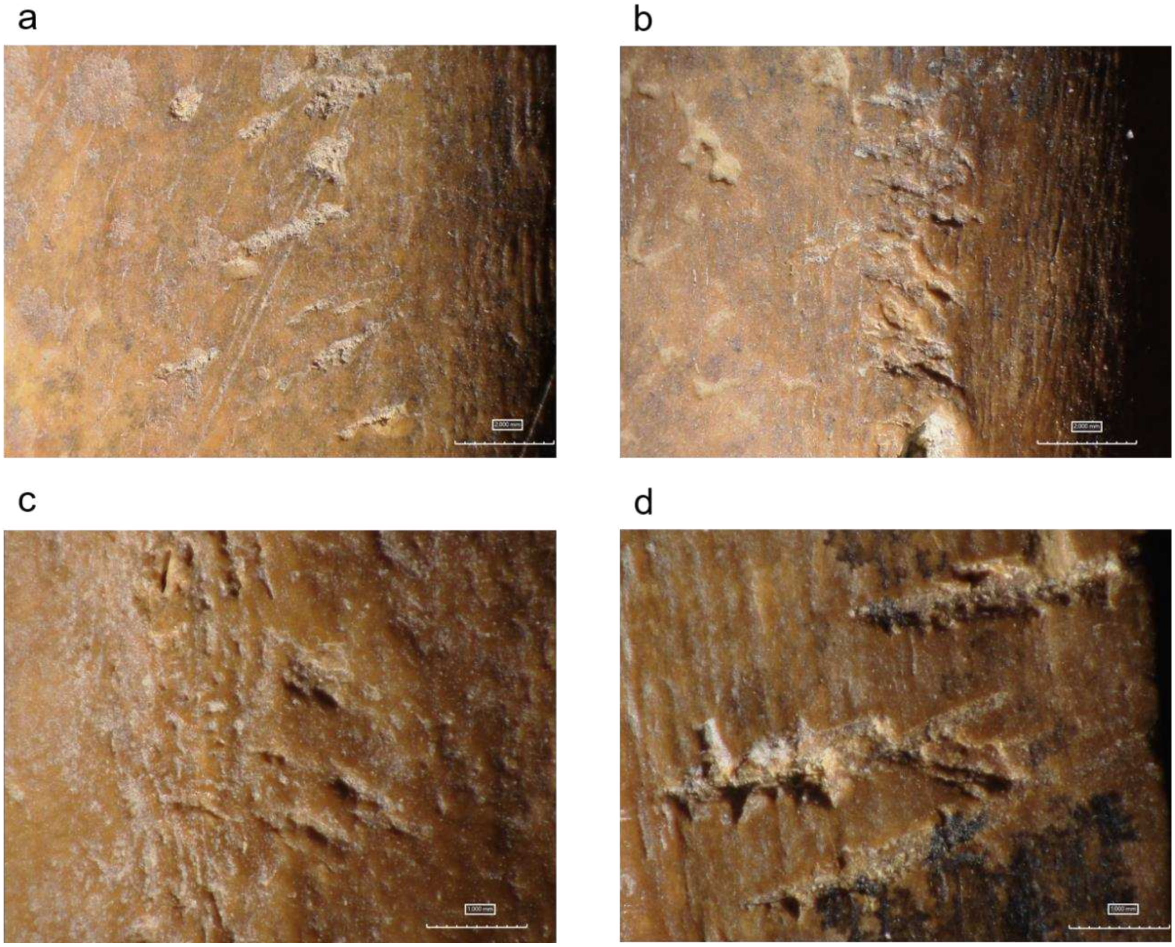

Fig. 4. Ghar-e Boof. Close-up views of retouching marks. Photographed specimens: a) 878 - AH VI (scale = 2 mm); b) 730 - AH Vb (scale = 2 mm); c) 663 - AH Va (scale = 1 mm); and d) 619 - AH Va (scale = 1 mm).

nearby. Our study suggests relatively favorable paleoenvironmental conditions that facilitated repeated hominin occupations of the cave during the MP and early UP, from where hunter-gatherers could have access to water, and plants (Baines et al., 2014; Conard et al., 2023), and exploited different types of terrestrial and aquatic animal resources (Appendices 2 and 3). Despite the environmental heterogeneity of the Zagros Mountains (Heydari-Guran, 2014), we also proposed that both MP and early UP hominins had similar habitat preferences across the entire range of the Zagros, inhabiting mostly mosaic environments dominated by arid to semi-arid conditions, with grasslands/steppes, shrublands, and rocky slopes, and to a lesser extent, some open forests (for a more in-depth discussion and comparison with other

Table 5. Bones retouchers from Ghar-e Boof. Traceological data. In bold, potential retoucher.

Bone ID	AH	N-Use areas	Convexity	Location	Type of traces	Distribution	Use intensity	Length (cm) of the use area	Width (cm) of the use area
276	III	1	Flat	Apical[a]	Scores	Concentrated	Slightly used	0.78[a]	0.50[a]
1099	IIIb	1	Convex	Lateral (right)	Scores	Isolated	Low used	0.61	0.38
596	IVc	1	Plano-convex	Lateral(right)	Scores	Dispersed	Low used	1.26	0.39
619	Va	2	Plano-convex	Lateral (right)	Scores	Dispersed	Slightly to moderate used	0.69 & 0.75	0.54 & 0.54
663	Va	1	Convex	Lateral (left)	Pits and scores	Concentrated	Low used	1.02	0.75
719	Vb	1	Convex	Centered	Scores	Isolated	Low used	NA[b]	NA[b]
730	Vb	1	Convex	Centered	Pit and scores	Concentrated and superimposed	Slightly used	0.64	0.40
878	VI	1	Convex	Centered	Pit and scores	Concentrated	Low used	0.87	0.53

[a] However, it presents a recent break near the use area.

[b] NA (Not available). I was unable to clearly distinguish and measure the use area.

available paleoenvironmental records from the Zagros, see Appendix 1, subsection “Ghar-e Boof microvertebrate record in the context of the Zagros Mountains”, and references therein).

Moreover, we not only aimed to test the hypothesis that the paleoenvironment fluctuated between ca. 81–35 kya in the Dasht-e Rostam region of the southern Zagros, but we also examined whether or not there is a correlation between local environmental change and the techno-cultural discontinuity documented at the site across the MP to early UP. Or, in other words, did paleoenvironmental shifts influence demographic turnovers and cultural adaptations locally and/or regionally in the Zagros mountains? At Ghar-e Boof, AHs IVd and IVc seem to represent the transitional period between the MP and early UP, and an OSL age situated AH IVd in the range of 48–45 kya. Despite the small sample size, it is striking that rodents are particularly uncommon in these layers compared to others, and we only identified Afghan pika (*Ochotona* cf. *rufescens*) in AH IVc. The presence of Afghan pika in the assemblage most likely indicates a decrease in temperatures and/or drier conditions (Appendix 1, and references therein). Chronologically, the observed changes in species representation within the small mammal assemblage of Ghar-e Boof seem to concur with the Heinrich event 5, and in agreement with deep ice cores from Greenland and speleothems records from the eastern Mediterranean region (Fig. 2; e.g., North Greenland Ice Core Project members, 2004; Ünal-İmer et al., 2015).

Besides Ghar-e Boof, Kaldar Cave represents the only site in which archaeologists have evaluated the possible impact of paleoenvironmental shifts on the cultural changes that took place between the MP and UP (Rey-Rodríguez et al., 2020), though they did not find any major environmental or climatic changes. Rey-Rodríguez et al. (2020) analyzed all the small mammal remains of layer 4 (UP) combined. However, this layer has a very wide chronometric range: 1) it yielded thermoluminescence dates of 23.1 ± 3.3 to 29.4 ± 2.3 kyr BP at its top; 2) available AMS radiocarbon dates for the bottom of the same layer range between 38.65–36.75, 44.2–42.35, and 54.4–46.05 kyr cal. BP (Bazgir et al., 2017; Becerra-Valdivia et al., 2017). I consider that the available chronometric data for Kaldar Cave do not allow the precise assessment of the timing of MP-UP transition (Bazgir et al., 2017), and the site lacks enough chronostratigraphic resolution to detect any presumed environmental shifts that might have occurred between 48–39 kya BP. In fact, Rey-Rodríguez et al. (2021) acknowledged that, even though some species are present in the same layers, it does not mean that they were accumulated at the same time, and some taxa could have been replaced by others over time. Even if the paleoenvironmental and paleoclimatic inferences drawn from the small vertebrate record of Ghar-e Boof must be taken with caution due to the small sample size, thus far, we cannot reject the hypothesis that paleoenvironmental fluctuations were one of the major driving forces behind local and/or regional population replacements and the appearance of cultural innovations across the MP to early UP transition in the Zagros Mountains.

7.2. Ghar-e Boof: subsistence strategies and site occupation intensity

In Appendices 2 and 3, I reported the main results and conclusions of my zooarchaeological and taphonomic analyses of the faunal assemblages recovered from Ghar-e Boof, which I divided between the early UP and MP respectively in order to further explore the regional significance of my research for different chronological periods.

In summary, hominins accumulated the majority of the animal remains at the site throughout the entire Late Pleistocene sequence based on the high proportions of specimens exhibiting anthropogenic modifications. Instead, bone specimens with carnivore tooth marks and rodent gnawing are rare, as well as the presence of carnivore remains, indicating that the cave was not frequently visited by carnivores or used as a den. Furthermore, density-meditated attrition does not appear to have influenced significantly the faunal assemblages from Ghar-e Boof. Thus, patterns in species representation, relative abundances, mortality and anatomical profiles, and anthropogenic modifications reflect primarily hominin socioeconomic decisions and subsistence practices.

The MP occupants of Ghar-e Boof exploited a diverse range of animals, from small- to very larger-bodied ungulates, such as caprines, gazelles, equids, red deer, wild pig, and wild cattle, alongside tortoises and the very occasional use of large carnivores. I was not able to rule out the potential exploitation of partridges by hominins at the site during the MP. Nevertheless, MP foragers relied mostly on caprines for dietary purposes, followed by gazelles and tortoises. Regarding transport decisions of ungulate carcasses, the analysis of skeletal element representation and food utility indices shows that during the MP the site's occupants preferentially selected and transported skeletal body parts or elements with high content of marrow and unsaturated fatty acids to the cave. Unfortunately, I did not provide mortality data because of the small sample sizes for dental wear and bone fusion for the MP assemblages.

MP and early UP Rostamian foragers also had similar hunting behaviors and diverse diets. Yet, there are some important differences in their animal economies. First, I found evidence for the use of partridges and medium birds during the early UP at the site, which represents the second most important type of prey by body size group or predator scape characteristics after caprines, and also followed by gazelles and tortoises. Rather than large carnivores, early UP humans exploited sporadically small carnivores, as inferred from a fox specimen with cut marks. I did not observe any anthropogenic damage on fish remains, but I considered that their presence at the cave could have resulted from fishing activities since none of the bones were digested. Although the sample size is small, the mortality data seem to reflect a main focus on hunting prime-aged adult caprines. During the early UP, skeletal profiles for medium ungulates indicate that humans transported complete carcasses to the cave, and they most likely hunted nearby. At Ghar-e Boof, early UP foragers were less selective than their MP counterparts in terms of transport decisions and bone processing behaviors, mostly because they even carried to the site and processed elements with low utility or small marrow cavies, such as phalanges.

Finally, I also examined whether or not there are any temporal trends in prey choice and site occupation intensity at Ghar-e Boof during the early UP in Appendix 2, and across the MP to early UP in Appendix 4, but also in my dissertation with the application of PCA. First, I documented a decrease in large game over the early UP (from AHs IVb to III), but I also emphasized that X^2_{trend} values for the Cochran's test of linear trend were low, which means this change in prey abundances was relatively subtle (Appendix 2). Second, when I analyzed shifts in prey choice through the entire archaeological sequence, the same pattern is discernable in the negative axis of PCA 2. Yet, PCA 2 only represents

13.3% of the total variance. Third, even though there was a positive relationship between time and the proportion of small game relative to large game, the trend was neither strong nor statistically significant (Appendix 4). Therefore, I concluded that both MP and early UP foragers maximized their foraging efforts by hunting large game taxa, mostly caprines, or in other words, the highest-ranked prey available in the Dasht-e Rostam region, with just subtle variations over time.

Instead, the use and economic importance of lower-ranked animals, such as partridges, relative to small, slow-moving, and easy-to-catch tortoises increased significantly throughout the stratigraphic sequence of Ghar-e Boof (Appendices 2 and 4). As I already discussed in Appendix 4, most likely this diachronic trend did not result from changes in the local paleoenvironmental conditions. Alternatively, the introduction of a new technology or harvesting methods might have allowed the early UP Rostamian foragers to lower the procurement costs of small, fast-moving taxa. However, I consider that my data better support the hypothesis that the increased exploitation of partridges observed at Ghar-e Boof signifies resource intensification due to higher hunting pressures and population growth in the southern Zagros.

The occupation intensity of Ghar-e Boof, as determined from find densities, accumulation rates, and frequencies of retouched lithic artifacts relative to the total amount of lithic debris, also increased over time (Appendix 4). Overall, my data reflect transient hominin occupation episodes at the cave during the MP, while early UP foragers used the site more intensively. Moreover, the TISARP team has demonstrated that MP sites in the Dasht-e Rostam region are very uncommon (Conard and Ghasidian, 2011). Consequently, my colleagues and I have proposed that the region was either inhabited by small groups of hominins or it was just characterized by low population densities during the MP. In contrast, the ubiquity of early UP sites most likely reflects population growth or higher population densities across the southern Zagros.

Nonetheless, my analyses do not evince a mere dichotomy between the MP and early UP occupations of Ghar-e Boof. As shown by the scores of PCA 1 in my dissertation (see also Appendices 2 and 4, “Discussion and conclusions”), the site occupation intensity remained low during the beginning of the early UP sequence, only increasing significantly from AH IV (~40 kya) onwards. Thus, based on the available chronometric data (Becerra-Valdivia et al., 2017; Heydari et al., 2021), shifts in prey choice and occupation intensity are only apparent at Ghar-e Boof approximately three millennia after the onset of the early UP in the Zagros Mountains.

7.3. Use of bone retouchers in the Zagros Mountains

In my study, I also demonstrated that the MP and early UP occupants of Ghar-e Boof not only exploited ungulates for nutritional purposes but also used their bones as tools. The presence of percussive osseous implements, such as bone retouchers, even if it is uncommon, allows me to establish a direct connection between carcass butchery and processing, waste disposal activities, and the manufacture of lithic artifacts.

As for the selection of bone blanks, foragers only utilized diaphyseal portions of medium ungulate long bones as retouchers, which are unmodified and exhibit green fractures. Nevertheless, I found a potential retoucher that has modified edges. Independently if retouchers were intentionally modified or not, Abrams et al. (2014) and Kolobova et al. (2020), among others, have suggested that hominins searched intentionally for a predetermined shape of bone blanks based on their ergonomic or handling characteristics. Besides green fractures, some retouchers are cut-marked or have cone fractures related to filleting, defleshing, and marrow processing, indicating that the retouchers most probably constituted bone fragments selected from food waste. In addition, two specimens show scraping marks, which at least in one case occurred prior to the retouching damage. Abrams et al. (2014) proposed that the bone fragments were scraped in order to clean and remove the remaining flesh that was still attached to them. Alternatively, Mallye et al. (2012) stated that scraping the surfaces of bone retouchers may have improved their functioning. Most of the retouchers have only a single-use area, and the retouching traces are isolated, dispersed, or concentrated, in relatively small areas. Finally, the use intensity was low or light, which reveals that these bone retouchers were expedient tools that had a short use-life before they were definitely discarded.

Due to the small number of retouchers, any interpretations regarding their importance within the techno-cultural repertoire of the hominins that occupied Ghar-e Boof during the MP and early UP must be taken with caution. Although the analysis of the MP lithic artifacts recovered from the site is still ongoing, Bretzke and Conard (2017) demonstrated that there is no techno-cultural continuity between the MP and early UP lithic traditions. Whereas the MP lithic artifacts represent a flake technology (Bretzke and Conard, 2017), the early UP Rostamian industries are dominated by diminutive blades and bladelet artifacts (Conard and Ghasidian, 2011; Ghasidian, 2014; Ghasidian et al., 2017). In general, archaeologists have excavated the early UP layers more intensively and exposed larger horizontal areas compared to the MP deposits. Yet, I identified more bone retouchers among the faunal remains recovered from the MP sequence. It is unlikely that the scarcity of bone retouchers recovered from the early UP deposits reflects identification bias caused by the effects of chemical weathering or the presence of sediment concretions, since these surface modifications are equally abundant in the MP faunal assemblage and their frequencies remain more or less stable throughout the sequence. Instead, the use of bone retouchers to manufacture or resharpen lithic artifacts may have been a more habitual practice for MP hominins, while early UP Rostamian hunter-gatherers very rarely utilized bones as retouchers, though further archaeological research would still be necessary to support such a claim.

Bone retouchers have been recovered from Lower to UP sites, located across all over Eurasia, from the Iberian Peninsula to Siberia and China (Jéquier et al., 2012; Tartar, 2012; Blasco et al., 2013a; van Kolfschoten et al., 2015; Doyon et al., 2018; Tourloukis et al., 2018; Yeshurun et al., 2018; Kolobova et al., 2020, to just name a few). With such a broad chronological and geographical range, are the bone retouchers recovered from Ghar-e Boof of any significance? These tools constitute the first record of bone retouchers in the Zagros. Yeshurun et al. (2018) suggested that in the Levant bone retouchers are most likely underrepresented since the use of percussive bone tools by hominins has not been the primary objective of most zooarchaeological research projects in the region. I could make the same argument for the Paleolithic faunal record of the Zagros Mountains. For instance, as I mentioned above, Marean and colleagues have extensively revisited MP and UP faunal collections from old excavations conducted in the Zagros and currently stored in American institutions (Marean and Frey, 1997; Lam et al., 1998; Marean, 1998; Marean and Kim, 1998; Marean and Cleghorn, 2003, among others). However, they mostly focused on methodological questions regarding the correct reconstruction, assessment, and interpretation of ungulate skeletal profiles. In my zooarchaeological study of the faunal remains recovered at Ghar-e Boof, I aimed to reconstruct the complete range of the subsistence strategies of the site’s occupants related to the use of animal resources. Besides evidence for the exploitation of ungulates, carnivores, birds, and tortoises reported in Appendices 2 to 4, the recovery of bone tools at Ghar-e Boof also highlights the diversity of subsistence strategies and techno-cultural adaptations of the hunter-gatherers who inhabited the Zagros Mountains during the MP and early UP.

7.3. The Middle-Upper Paleolithic transition in Eurasia and the significance of the zooarchaeological record of Ghar-e Boof and the Zagros Mountains

Neanderthals were spread across a vast territory, from the Atlantic coasts of Europe to the Altai Mountains in east-Central Asia (Krause et al., 2007; Romagnoli et al., 2022), and they existed between ca. 400–35 kya (Rosas et al., 2022; and references therein). However, Neanderthals were not the only hominin species that lived in Eurasia during the MP. For instance, genetic data from the Altai Mountains have allowed the discovery of Denisovans, which constitute a sister group of Neanderthals (Krause et al., 2010; Reich et al., 2010; Brown et al., 2016) and appear to have been widespread in Asia (Viola, 2022). Archaeologists and paleoanthropologists have also documented fossil remains that demonstrated the early, but seemingly sporadic, presence of *Homo sapiens* in southwestern Asia (Grün et al., 2005; Hershkowitz et al., 2018), east Asia (Liu et al., 2015; Freidline et al., 2023), and even Europe (Harvati et al., 2019; Slimak et al., 2022) since ~210 kya onwards. Besides different hominin species, there is evidence for inter-breeding and gene flow between Neanderthals and AMH populations (Prüfer et al., 2013; Kuhlwilm et al., 2016; Harvati and Ackermann, 2022). Hence, it is currently almost impossible not only to draw a comprehensive view of the MP from a geographic, taxonomic, and evolutionary standpoint but also regarding subsistence strategies and socioeconomic adaptations.

As I mentioned briefly above and in Appendix 3, the MP paleoanthropological record of the Zagros is so far exclusively represented by Neanderthal or Neanderthal-like remains discovered in the following sites: Shanidar Cave (Solecki, 1963, 1975; Pomeroy et al., 2017, 2020, among others), Bisotun Cave (Trinkaus and Biglari, 2006), Wezmeh Cave (Zanolli et al., 2019), and Bawa Yawan Rockshelter (Heydari-Guran et al., 2021). Yet, the southern Zagros Mountains lie outside of the current known geographic range of the Neanderthal populations, and Heydari et al. (2021) have suggested that the MP occupants of Ghar-e Boof could have been either Neanderthals or AMHs. Likewise, in my dissertation, I have used the more neutral term "MP hominins" without adding any particular taxonomic designation.

Despite the complexity and patchy nature of the Late Pleistocene paleoanthropological record across Eurasia, how do the zooarchaeological data from Ghar-e Boof and the Zagros Mountains fit within the current body of knowledge about hominin subsistence strategies and paleodemography during the MP to early UP?

Across the entire range of the Zagros Mountains, MP hominins were large game hunters, with a narrow focus on caprines, alongside gazelles, equids, and other ungulates (Appendix 3, Fig. 1; Solecki, 1963; Turnbull, 1975; Evins, 1982; Hesse, 1989; Marean and Frey, 1997; Marean, 1998; Marean and Kim, 1998; Bazgir et al., 2017; Hodgkins and Marean, 2017; Biglari and Shidrang, 2019; Campana and Crabtree, 2019). The MP zooarchaeological record from the Zagros is not exceptional by any means. Instead, hunting large game is one of the main defining aspects of the subsistence economies, foraging behavior, and ecology of MP hominins all over Eurasia (Stiner, 2013; and references therein). According to Bar-Yosef (2004) and Stiner (2013), geographic variations are mostly restricted to the ungulate species available to MP hunters in each different region, such as horse and reindeer in central Europe (Conard et al., 2012), fallow deer in the Peloponnese (Starkovich, 2012b), Caucasian tur and steppe bison in the Caucasus (Adler et al., 2006); gazelle and Mesopotamian fallow deer in the Levant (Ravinovich and Hovers, 2004; Stiner, 2009), and wild goat in the Zagros (Hodkings and Marean, 2017; Appendix 3), among many others.

In Appendix 3, I also demonstrated that MP hominins in the southern Zagros also exploited carnivores and small game taxa. However, except for tortoises, which are easy-to-collect resources and therefore have very low capture-costs (Stiner et al., 1999, 2000; Stiner and Munro, 2002), the occupants of Ghar-e Boof only hunted carnivores and possibly quick-moving partridges very occasionally. Evins (1982) has also proposed the use of tortoises by MP foragers at Shanidar Cave. Despite the scarce data regarding small game exploitation during the MP in the Zagros Mountains, the zooarchaeological record of the region is consistent with what it is known for southwestern Asia, particularly the Levant, which, by comparison, has been more intensively studied (e.g., Speth and Tchernov, 2002; Stiner, 2005, 2009; Biton et al., 20017; Crater Gershtein et al., 2022). From the eastern coasts of the Mediterranean Sea to the Zagros, the MP foragers relied on large game ungulates to cover their daily demands of animal proteins and fats, supplemented by low-cost and easy-to-collect, small, slow-moving or sessile taxa (Stiner, 2013; Appendix 3). Based on the prey choice model of optimal foraging theory and its premises related to hunting pressures (i.e., Stiner et al., 1999, 2000; Stiner and Munro, 2002; Stiner, 2013), such dependence on high-ranked prey may imply low population densities or that hominins generally lived in small population groups across southwestern Asia and beyond during the MP.

Recently, Blasco et al. (2022) have compiled a large number of archaeological sites that support the use of small game taxa by Neanderthals in Eurasia. Although it is accepted that Neanderthals were ecologically flexible and had the necessary skills to exploit small, fast-moving taxa, such as rabbits, hares, and birds, the majority of evidence comes from sites located in western Europe (see Blasco et al., 2022; and reference therein). Despite the effort of Blasco et al. (2022) to establish the systematic utilization of small, fast-moving game as a general aspect of the Neanderthal's foraging spectrum, this practice appears to have been more restricted to some localities with unique characteristics (Stiner, 2013), such as site function, seasonality, and duration of the occupation, but also determined by local environmental conditions and the availability of prey (e.g., Cochard et al., 2012; Blasco et al., 2013b; Pelletier et al., 2019). Thus, diet breadth tended to be narrow and hunting behaviors were rather specialized almost everywhere during the MP (Stiner, 2013).

Returning to the demographic implications of my research, I also emphasized that the MP archaeological deposits of Ghar-e indicate short-term, sporadic hominin occupations, in concordance with the demographic inferences drawn from the diet breadth observed at the site. After numerous archaeological surveys, Conard and Ghasidian (2011) only documented a small number of MP sites in the Dasht-e Rostam region, and the density of diagnostic MP lithic artifacts was low as well, which once again points to small and thinly scattered groups of hominins living in the southern Zagros during the MP. Even if the taxonomic status of the MP hominins that occupied Ghar-e Boof is still unknown, Neanderthals were present in the neighboring central and northern Zagros regions during the same period. In fact, there is an emerging consensus in the scientific community that Neanderthals went extinct most likely due to demographic factors, such as small population size and limited interconnectedness (Vaesen et al., 2021, and references therein), which is also supported by genetic data, from the Iberian Peninsula to the Altai Mountains (i.e., Lalueza-Fox et al., 2010; Prüfer et al., 2017; Skov et al., 2022).

Based on the study of small vertebrate remains from Ghar-e Boof, my colleague, Ángel Blanco-Lapaz, and I have suggested that the paleoenvironmental conditions did not remain stable throughout the MP to early UP in the southern Zagros Mountains. Particularly, the small mammal assemblages appear to indicate that there was an increase in aridity and/or colder conditions in the region starting around 48–45 kya, which is synchronous with a change in the techno-cultural record of Ghar-e Boof. It is possible that harsher climatic and environmental conditions influenced the presence of hominins in the Dasht-e Rostam region at that time. However, we have also been very cautious regarding the available sample size, and our results should be considered tentatively. Fortunately, the analysis of botanical remains recovered from AHs IVd to IV is currently ongoing, which would allow us to further assess whether or not, or to which extent, the paleoenvironmental conditions fluctuated during the MP to early UP at Ghar-e Boof. Needless to say, most paleoanthropologists do not consider that environmental factors played a pivotal role in the demise of

Neanderthals (Vaesen et al., 2021; but see Sánchez-Goñi, 2022). Yet, there are paleoenvironmental and paleoclimatic records across Eurasia that suggest temperature and vegetation changes, including alternating cool-wet and arid events, which may have driven Neanderthals to extinction (e.g., Finlayson and Carrión, 2007), or at least locally and/or regionally (Shea, 2008; Golovanova et al., 2010; Álvarez-Vena et al., 2021; Fagoaga et al., 2021, among others; for criticisms and an alternative view from the Levant, see also Belmaker and Hovers, 2011).

The beginning of the UP in the Zagros Mountains has consistently been dated ca. 45–40 kya cal. BP (Becerra-Valdivia et al., 2017; Heydari et al., 2021), and generally archaeologists agree on the association of early UP techno-cultural assemblages solely with AMHs (Otte et al., 2011; Bazgir et al., 2017; Bretzke and Conard, 2017; Ghasidian et al., 2017; Heydari et al. 2021; Goder-Goldberger and Malinsky-Buller, 2023). However, only the following early UP sites have yielded AMH fossil remains: Eshkaft-e Gavi (southern Zagros; Scott and Marean, 2009), Warwasi rockshelter (Tsanova, 2013), and Gar Arjeneh (Trinkaus, 2018), both of them located in the central Zagros. It is still unclear if these human groups came from the west or the east (Ghasidian et al., 2017). But, despite the relatively adverse conditions that might have prevailed in the region till the end of the Heinrich event 4 or ~39 kya cal. BP (Appendix 1), AMHs were able to successfully adapt and colonize the entire region. Bretzke and Conard (2017) hypothesized that new hunting technologies, as reflected in the laminar components of the early UP lithic industries, may have been key in this process.

So, what did early UP humans eat and hunt across the Zagros Mountains? Like their MP predecessors, they also relied on large game animals, mainly caprines, but also equids, gazelles, red deer, wild pigs and wild cattle (Perkins, 1964; Turnbull, 1975; Evins, 1982; Hesse, 1989; Otte et al., 2007; Mashkour et al., 2009; Hodgkins and Marean, 2017). Or, as Bar-Yosef (2004) put it simply, AMHs just ate and hunted what was largely available in the territories they inhabited. Evidence for the use of small game and carnivores during the early UP in the Zagros is very scant. Yet, my study (Appendix 2) has demonstrated that early UP Rostamian foragers also harvested tortoises, and exploited partridges, which constituted the second most important prey group during the early UP.

Additionally, Conard and colleagues (Conard and Ghasidian, 2011; Conard and Zeidi, 2019) have found perforated shells that were most probably used as personal ornaments during the early UP.

When assessing diachronic trends in prey abundances throughout the MP and early UP at Ghar-e Boof (Appendix 4), the most robust trend is represented by a significant increase in the use of small, fast-moving game or lower-ranked taxa relative to the higher-ranked and easier-to-capture tortoises. Following the prey choice model (*sensu* Stiner et al., 1999, 2000; Stiner and Munro, 2002), I have interpreted the observed temporal shifts as resource intensification caused by increased hunting pressures and population growth, which is also supported by the fact that occupation intensity of Ghar-e Boof increased with time. Since Ghar-e Boof is currently the only site in the Zagros Mountains in which changes in prey choice and occupation intensity during the MP to early UP have been documented, do these shifts reflect local or regional sociodemographic trends? Or, instead, do they track supraregional processes?

For instance, archaeologists have observed similar increased economic reliance on small, fast-moving game across the MP to early UP or during the early/initial UP in the Levant (Stiner et al., 1999; Stiner, 2009; Yeshurun et al., 2021) and the Peloponnese (Starkovich, 2012a, 2014, 2017), that most likely signal resource intensification or higher demographic pressures. Moreover, there are many sites located in different regions across Europe and southwestern Asia that became more intensively occupied by humans during the same period (Grayson and Delpech, 2003; Münzel and Conard, 2004; Kuhn et al., 2009; Conard et al., 2012; Starkovich, 2017; Smith et al., 2021; Yeshurun et al., 2021; Real and Villaverde, 2022; to just name a few), which may have resulted from a combination of factors, including population growth, larger social group sizes, more frequent visits, longer stays on site, and less mobility. Even though some of the methods and assumptions applied to the study of Paleolithic demography are problematic or controversial (e.g., Dogandžić and McPherron, 2013; French, 2015), and there are also many deviations from the above-mentioned patterns (see Appendix 4, “Introduction” section, and references therein), early UP humans in Eurasia exhibited greater demographic potential than their MP predecessors (Stiner and Kuhn, 2006; Stiner, 2013).

Socioeconomic differences between the MP and early UP as inferred from the archaeological record of Eurasia regarding prey choice and site occupation intensity not only may attest to population growth and hunting pressure during the later period but also more social and economic roles that needed to be filled by different members of a hunter-gatherer group (Kuhn and Stiner, 2006). During the MP and early UP, the use of diverse types of prey and resources, such as ungulates, tortoises, and plants, alongside the production of lithic artifacts most certainly meant that people of different sexes, ages, and skills actively contributed to the subsistence economy of the group (i.e., Kuhn and Stiner, 2006; Starkovich, 2017). However, due to the comparatively narrower diet and lower range of activities performed by MP hominins in the Zagros Mountains and across Eurasia, Kuhn and Stiner (2006) and Stiner (2013) have hypothesized that men, women, and children might have participated routinely in the same tasks, even in large game hunting. Instead, even if UP foragers were also large game hunters, their daily socioeconomic activities were significantly more diverse. For example, the use of shell beads and personal ornaments became widespread during the UP (Stiner and Kuhn, 2006), while exploiting fast-moving animals most probably involved the manufacture and maintenance of trapping technologies, such as traps, snares and nets (Madsen and Schmitt, 1998; Starkovich, 2017; Morin et al., 2020, among others). Thus, once again, the main discernable differences between the MP and early UP in Eurasia could be a matter of the number of people and social group sizes (Stiner, 2013).

Since the TISARP team was founded almost 20 years ago, my colleagues have demonstrated the exceptional MP and UP records of the southern Zagros Mountains, and particularly the relevance of the Dasht-e Rostam region to offer new insights on hominin settlement dynamics and techno-cultural adaptations during the Late Pleistocene. Building on their extraordinary work, alongside the contributions of many other Iranian and foreign scholars, my doctoral research of the zooarchaeological assemblages from Ghar-e Boof has allowed me to present a refined picture of the paleoenvironmental, socioeconomic, and demographic shifts that occurred in the southern Zagros across the MP to early UP. Of course, needless to say, further research is needed to clarify whether the patterns I have documented at Ghar-e Boof are exceptional to the site and its location, or, if instead, they reflect regional or supraregional population processes. Yet, except for the type of animals in the landscape, MP and early UP hominins had similar dietary habits, subsistence strategies, and demographic characteristics across many regions of Eurasia.

References

Abrams, G., Bello, S.M., Di Modica, K., Pirson, S., Bonjean, D., 2014. When Neanderthals used cave bear (*Ursus spelaeus*) remains: bone retouchers from unit 5 of Scladina Cave (Belgium). Quat. Int. 326-327, 274–287.

Adler, D.S., Bar-Oz, G., Belfer-Cohen, A., Bar-Yosef, O., 2006. Ahead of the game. Middle and Upper Palaeolithic hunting behaviors in the southern Caucasus. Curr. Anthropol. 47(1), 89–118.

Albarella, U., 2017. Zooarchaeology in the twenty-first century: where we come from, where we are now, and where we are going. In: Albarella, U., Rizzetto, M., Russ, H., Vickers, K., Viner-Daniels, S. (Eds.), The Oxford Handbook of Zooarchaeology. Oxford University Press, Oxford, pp. 3–22.

Alijani, B., 2008. Effect of the Zagros Mountains on the spatial distribution of precipitation. J. Mt. Sci. 5, 218–231.

Allúe, E., Expósito, I., Tumung, L., Ollé, A., Bazgir, B., 2018. Early evidence of *Prunus* and *Prunus* cf. *amygdalus* from Palaeolithic sites in the Khorramabad valley, western Iran. C. R. Palevol. 17, 335–345.

Álvarez-Vena, A., Álvarez-Lao, D.J., Laplana, C., Quesada, J.M., Rojo, J., García-Sánchez, E., Menéndez, M., 2021. Environmental context for the Late Pleistocene (MIS 3) transition from Neanderthals to early Modern Humans: analysis of small mammals from La Güelga Cave, Asturias, northern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 562, 110096.

Asouti, E., Baird, D., Kabukcu, C., Swinson, K., Martin, L., García-Suárez, A., Jenkins, E., Rasheed, K., 2020. The Zagros Epipalaeolithic revisited: new excavations and ^{14}C dates from Palegawra cave in Iraqi Kurdistan. PLoS One 15 (9), e0239564.

Baines, J.A., Riehl, S., Conard, N.J., Zeidi, M., 2014. Upper Palaeolithic archaeobotany of Ghar-e Boof cave, Iran: a case study in site disturbance and methodology. Archaeol. Anthropol. Sci. 7, 245–256.

Bahraminia, M., Niknami, K.A., Khosrowzadeh, A., Nymark, A., 2022. High altitude Middle Palaeolithic open-air locales of the Miankouh, Thrust Zagros Mountains, Iran. J. Archaeol. Sci. Rep. 44, 103537.

Bar-Matthews, M., Ayalon, A., Gilmour, M., Matthews, A., Hawkesworth, C.J., 2003. Sea–land oxygen isotopic relationships from planktonic foraminifera and speleothems in the Eastern Mediterranean region and their implication for paleorainfall during interglacial intervals. Geochim. Cosmochim. Acta 67(17), 3181–3199.

Bar-Yosef, O., 2004. Eat what is there: hunting and gathering in the world of Neanderthals and their neighbours. Int. J. Osteoarchaeol 14, 333–342.

Bazgir, B., Otte, M., Tumung, L., Ollé, A., Deo, S.G., Joglekar, P., López-García, J.M., Picin, A., Davoudi, D., van der Made, J., 2014. Test excavations and initial results at the Middle and Upper Paleolithic sites of Gilvaran, Kaldar, Ghamari caves and Gar Arjene rockshelter, Khorramabad Valley, western Iran. C. R. Palevol 13, 511–525.

Bazgir, B., Ollé, A., Tumung, L., Becerra-Valdivia, L., Douka, K., Higham, T., van der Made, J., Picin, A., Saladié, P., López-García, J.M., Blain, H.A., Allué, E., Fernández-García, M., Rey-Rodríguez, I., Arceredillo, D., Bahrololoumi, F., Azimi, M., Otte, M., Carbonell, E., 2017. Understanding the emergence of modern humans and the disappearance of Neanderthals: insights from Kaldar Cave (Khorramabad Valley, western Iran). Sci. Rep. 7, 43460.

Becerra-Valdivia, L., Douka, K., Comeskey, D., Bazgir, B., Conard, N.J., Marean, C.W., Ollé, A., Otte, M., Tumung, L., Zeidi, M., Higham, T.F.G., 2017. Chronometric investigations of the Middle to Upper Paleolithic transition in the Zagros Mountains using AMS radiocarbon dating and Bayesian age modelling. J. Hum. Evol. 109, 57–69.

Belmaker, M., Hovers, E., 2011. Ecological change and the extinction of the Levantine Neanderthals: implications from a diachronic study of micromammals from Amud Cave, Israel. Quat. Sci. Rev. 30, 3196–3209.

Biglari, F., Heydari, S., 2001. Do-Ashkaft: a recently discovered Mousterian cave site in the Kermanshah Plain, Iran. Antiquity, 75(289), 487–488.

Biglari, F., Shidrang, S., 2019. Rescuing the Paleolithic Heritage of Hawraman, Kurdistan, Iranian Zagros. Near East. Archaeol. 82(4), 226–225.

Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.

Biton, R., Sharon, G., Oron, M., Steiner, T., Rabinovich, R., 2017. Freshwater turtle or tortoise? The exploitation of testudines at the Mousterian site of Nahal Mahanayeem Outlet, Hula Valley, Israel. J. Archaeol. Sci. Rep. 14, 409–419.

Blasco, R., Rosell, J., Cuartero, F., Fernández-Peris, J., Gopher, A., Barkai, R., 2013a. Using bones to shape stones: MIS 9 bone retouchers at both edges of the Mediterranean Sea. PLoS ONE 8(10), e76780.

Blasco, R., Rosell, J., Fernández-Peris, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013b. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). Quat. Sci. Rev. 70, 124–144.

Blasco, R., Cochard, D., Colonese, A.C., Laroulandie, V., Meier, J., Morin, E., Rufà, A., Tassoni, L., Thompson, J.C., 2022. Small animal use by Neanderthals. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals: Understanding Behavioral Complexity in the Late Middle Palaeolithic. Elsevier Academic Press, London, pp. 123-143.

Boivin, N., Fuller, D.Q., Dennell, R., Allaby, R., Petraglia, M.D., 2013. Human dispersal across diverse environments of Asia during the Upper Pleistocene. Quat. Int. 300, 32–47.

Bonilauri, S., Giraud, J., Alahmadi, M.J., Lemée, M., Mesfin, I., Boëda, E., Muram, M., Ahmed Saber, S. Raeuf Aziz, K., Biglari, F., Rasheed Raheem, K., 2022. The Paleolithic of northwestern Zagros. 2012–2019 MAFGS Survey: Data and preliminary results. Anthropologie 126(3), 103053.

Bretzke, K., Conard, N.J., 2017. Not just a crossroad: population dynamics and changing material culture in southwestern Asia during the Late Pleistocene. Curr. Anthropol. 58(S17), S449–S462.

Braidwood, R.J., Howe, B., 1960. Prehistoric Investigations in Iraqi Kurdistan. University of Chicago Press, Chicago.

Brown, S., Higham, T., Slon, V., Pääbo, S., Meyer, M., Douka, K., Brock, F., Comeskey, D., Procopio, N., Shunkov, M., Derevianko, A., Buckley, M., 2016. Identification of a new hominin bone from Denisova cave, Siberia using collagen fingerprinting and mitochondrial DNA analysis. Sci. Rep. 6, 23559.

Brown, S., Hebestreit, S., Wang, N., Boivin, N., Douka, K., Richter, K., 2020. Zooarchaeology by Mass Spectrometry (ZooMS) for bone material - Acid insoluble protocol. https://doi.org/10.17504/protocols.io.bf43jqyn

Buckley, M., Collins, M., Thomas-Oates, J., Wilson, J.C., 2009. Species identification by analysis of bone collagen using matrix-assisted laser desorption/ionisation time-of-flight mass spectrometry. Rapid Commun. Mass Spectrom. 23, 3843–3854.

Campana, D.V., Crabtree, P., 2019. Evidence for skinning and craft activities from the Middle Paleolithic of Shanidar Cave, Iraq. J. Archaeol. Sci. Rep. 25, 7–14.

Cochard, D., Brugal, J.P., Morin, E., Meignen, L., 2012. Evidence of small fast game exploitation in the Middle Paleolithic of Les Canalettes Aveyron, France. Quat. Int. 264, 32–51.

Conard, N.J., Ghasidian, E., 2011. The Rostamian cultural group and the taxonomy of the Iranian Upper Palaeolithic. In: Conard, N.J., Drechsler, P., Morales, A. (Eds.), Between Sand and Sea: the Archaeology and Human Ecology of South-Western Asia. Kerns Verlag, Tübingen, pp. 33–52.

Conard, N.J., Zeidi, M., 2019. New research on the Paleolithic occupation of Ghar-e Boof, Fars Province. J. Iranian Center Archaeol. Res. 2, 7–16.

Conard, N.J., Ghasidian, E., Heydari, S., Zeidi, M., 2006. Report on the 2005 survey of the Tübingen Iranian Stone Age Research Project in the Provinces of Esfahan, Fars and Kohgiluyeh-Boyerahmad. In: Azarnoush, M. (Ed.), Archaeological Reports 5. ICAR, Tehran, pp. 9–34.

Conard, N.J., Ghasidian, E., Heydari, S., Naderi, R., Zeidi, M., 2007. The 2006 season of the Tübingen-Iranian Stone Age Research Project in the Provinces of Fars and Markazi. In: Fazeli, H. (Ed.), 9th Annual Report of Archaeological Organisation. ICAR, Tehran, pp. 43–67.

Conard, N.J., Bolus, M., Münzel, S.C., 2012. Middle Paleolithic land use, spatial organization and settlement intensity in the Swabian Jura, southwestern Germany. Quat. Int. 247, 236–245.

Conard, N.J., Miller, C.E., Riehl, S., Zeidi, M., 2023. Testing the Palaeolithic harvesting hypothesis at Ghar-e Boof with improved botanical recovery. In: Richter, T., Darabi, H. (Eds.), The Epipalaeolithic and Neolithic in the Eastern Fertile Crescent. Revisiting the Hilly Flanks. Routledge, London, pp. 350–370.

Coon, C.S., 1951. Cave Explorations in Iran, 1949. University Museum, University of Pennsylvania, Philadelphia.

Crater Gershtein, K.M., Zaidner, Y., Yeshurun, R., 2022. A campsite on the open plain: Zooarchaeology of Unit III at the Middle Paleolithic site of Nesher Ramla, Israel. Quat. Int. 624, 49–66.

Dibble, H.L., 1984. The Mousterian industries from Bisitun Cave (Iran). Paléorient 10(2), 23–34.

Dibble, H.L., 1995. Middle Paleolithic scraper reduction: background, clarification, and review of the evidence to date. J. Archaeol. Method Theory 2, 299–368.

Dibble, H.L., Holdaway, S. 1993. The Middle Paleolithic of Warwasi Rockshelter. In: Olszewski, D., Dibble, H.L. (Eds.), The Paleolithic Prehistory of the Zagros-Taurus. University Museum Press, University of Pennsylvania, Philadelphia, pp. 75–99.

Djamali, M., de Beaulieu, J.L., Shah-Hosseini, M., Andrieu-Ponel, V., Ponel, P., Amini, A., Akhani, H., Leroy, S.A.G., Stevens, L., Lahijani, H., Brewer, S., 2008a. A Late Pleistocene long pollen record from Lake Urmia, NW Iran. Quat. Res. 69, 413–420.

Djamali, M., Kürschner, H., Akhani, H., de Beaulieu, J.L., Amini, A., Andrieu-Ponel, V., Ponel, P., Stevens, L., 2008b. Palaeoecological significance of the spores of the liverwort *Riella* (Riellaceae) in a late Pleistocene long pollen record from the hypersaline Lake Urmia, NW Iran. Rev. Palaeobot. Palynol. 152, 66–73.

Djamali, M., Biglari, F., Kamyar Abdi, K., Andrieu-Ponel, V., de Beaulieu, J.L., Mashkour, M., Ponel, P., 2011. Pollen analysis of coprolites from a late Pleistocene–Holocene cave deposit (Wezmeh Cave, west Iran): insights into the late Pleistocene and late Holocene vegetation and flora of the central Zagros Mountains. J. Archaeol. Sci. 38, 3394–3401.

Dogandžić, T., McPherron, S.P., 2013. Demography and the demise of Neandertals: a comment on ‘Tenfold population increase in Western Europe at the Neandertal-to-modern human transition’. J. Hum. Evol. 64, 311–313.

Doyon, L., Li, Z., Li, H., d'Errico, F., 2018. Discovery of *circa* 115,000-year-old bone retouchers at Lingjing, Henan, China. PLoS ONE 13(3), e0194318.

Evins, M.A., 1982. The fauna from Shanidar Cave: Mousterian wild goat exploitation in northeastern Iraq. Paléorient 8, 37–58.

Fagoaga, A., Laplana, C., Marquina-Blasco, R., Machado, J., Marin-Monfort, M.D., Crespo, V.D., Hernández, C.M., Mallol, C., Galván, B., Ruiz-Sánchez, F.J., 2021. Palaeoecological context for the extinction of the Neanderthals: a small mammal study of Stratigraphic Unit V of the El Salt site, Alcoi, eastern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 567, 110221.

Faith, J.T., Du, A., 2018. The measurement of taxonomic evenness in zooarchaeology. Archaeol. Anthropol. Sci. 10, 1419–1428.

Fiacconi, M., Hunt, C.O., 2015. Pollen taphonomy at Shanidar Cave (Kurdish Iraq): An initial evaluation. Rev. Palaeobot. Palynol. 223, 87–93.

Field, J.S., Petraglia, M.D., Mirazón-Lahr, M., 2007. The southern dispersal hypothesis and the South Asian archaeological record: examination of dispersal routes through GIS analysis. J. Anthropol. Archaeol. 26, 88–108.

Finlayson, C., Carrión, J., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. Trends Ecol. Evol. 4, 213–22.

Fisher, J.W.J., 1995. Bone surface modifications in zooarchaeology. J. Archaeol. Method Theory 2, 7–68.

Flannery, K.V., 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko, P.J., Dimbleby, G.W. (Eds.), The Domestication and Exploitation of Plants and Animals. Duckworth, London, pp. 73–100.

Freidline, S.E., Westaway, K.E., Joannes-Boyau, R., Duringer, P., Ponche, J.-L., Morley, M.W., Hernandez, V.C., McAllister-Hayward, M.S., McColl, H., Zanolli, C., Gunz, P., Bergmann, I., Sichanthongtip, P., Sihanam, D., Boualaphane, S., Luangkhoth, T., Souksavatdy, V., Dosseto, A., Boesch, Q., Patole-Edoumba, E., Aubaile, F., Crozier, F., Suzzoni, E., Frangeul, S., Bourgon, N., Zachwieja, A., Dunn, T.E., Bacon, A.-M., Hublin, J.-J., Shackelford, L., Demeter, F., 2023. Early presence of *Homo sapiens* in Southeast Asia by 86–68 kyr at Tam Pà Ling, Northern Laos. Nat. Commun. 14, 3193.

French, J.C., 2015. Demography and the Palaeolithic archaeological record. J. Archaeol. Method Theory 23, 150–199.

Garrod, D.A.E., 1930. The Paleolithic of southern Kurdistan: excavations in the caves of Zarzi and Hazar Merd. Bull. Am. Sch. Prehist. Res. 6, 9–43.

Garrod, D.A.E., 1957. Notes sur le Paléolithique Supérieur du Moyen Orient. Bull. Soc. Prehist. Fr. 54, 439–445.

Ghasidian, E., 2014. Early Upper Palaeolithic Occupation at Ghar-E Boof Cave: a Reconstruction of Cultural Traditions in Southern Zagros Mountains of Iran. Kerns Verlag, Tübingen.

Ghasidian, E., Bretzke, K., Conard, N.J., 2017. Excavations at Ghar-e Boof in the Fars Province and its bearing on models for the evolution of the Upper Paleolithic in the Zagros. J. Anthropol. Archaeol. 47, 33–49.

Ghasidian, E., Heydari-Guran, S., Mirazón-Lahr, M., 2019. Upper Paleolithic cultural diversity in the Iranian Zagros Mountains and the expansion of modern humans into Eurasia. J. Hum. Evol. 132, 101e118.

Giannakopoulou, E.M., Toumi, R., 2012. The Persian Gulf summertime low-level jet over sloping terrain. Q. J. R. Meteorol. Soc. 138, 145–157.

Goder-Goldberger, M., Malinsky-Buller, A., 2022. The Initial Upper Paleolithic and its place within the Middle-to-Upper Paleolithic transition of Southwest Asia: what hides behind the curtain of taxonomies? J. Paleolit. Archaeol. 5, 2.

Golovanova, L.V., Doronichev, V.B., Cleghorn, N.E., Koulkova, M.A., Sapelko, T.V., Shackley, M.S., 2010. Significance of ecological factors in the Middle to Upper-Paleolithic transition. Curr. Anthropol. 51, 655–691.

Grayson, D.K., Delpech, F., 2003. Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France). J. Archaeol. Sci. 30, 1633–1648.

Grootes, P.M., Stuiver, M., 1997. Oxygen 18/16 variability in Greenland snow and ice with 10^{-3}- to 10^{5}-year time resolution. J. Geophys. Res. 102, 26455–26470.

Grün, R., Stringer, C., McDermott, F., Nathan, R., Porat, N., Robertson, S., Taylor, L., Mortimer, G., Eggins, S., McCulloch, M., 2005. U-series and ESR analyses of bones and teeth relating to the human burials from Skhul. J. Hum. Evol. 49, 316–334.

Hammer, Ø., Harper, D.A., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1–9.

Harvati, K., Ackermann, R.R., 2022. Merging morphological and genetic evidence to assess hybridization in Western Eurasian late Pleistocene hominins. Nat. Ecol. Evol. 6, 1573–1585.

Harvati, K., Röding, C., Bosman, A.M., Karakostis, F.A., Grün, R., Stringer, C., Karkanas, P., Thompson, N.C., Koutoulidis, V., Moulopoulos, L.A., Gorgoulis, V.G., Kouloukoussa, M.,

2019. Apidima Cave fossils provide earliest evidence of Homo sapiens in Eurasia. Nature 571, 500–504.

Hershkovitz, I., Weber, G.W., Quam, R., Duval, M., Grün, R., Kinsley, L., Ayalon, A., Bar-Matthews, M., Valladas, H., Mercier, N., Arsuaga, J.L., Martinón-Torres, M., Bermúdez de Castro, J.M., Fornai, C., Martín-Francés, L., Sarig, R., May, H., Krenn, V.A., Slon, V., Rodríguez, L., García, R., Lorenzo, C., Carretero, J.M., Frumkin, A., Shahack-Gross, R., Bar-Yosef Mayer, D.E., Cui, Y., Wu, X., Peled, N., Groman-Yaroslavski, I., Weissbrod, L., Yeshurun, R., Tsatskin, A., Zaidner, Y., Weinstein-Evron, M., 2018. The earliest modern humans outside Africa. Science 359(6374), 456–459.

Hesse, B., 1989. Paleolithic faunal remains from Ghar-i Khar, western Iran. In: Crabtree, P.J., Campana, D., Ryan, K. (Eds.), Early Animal Domestication and its Cultural Context. MASCA, the University Museum of Archaeology and Anthropology. University of Pennsylvania, Philadelphia, pp. 37–45.

Heydari, M., Guérin, G., Zeidi, M., Conard, N.J., 2021. Bayesian luminescence dating at Ghar-e Boof, Iran, provides new chronology for Middle and Upper Paleolithic in the southern Zagros. J. Hum. Evol. 151, 102926.

Heydari-Guran, S., 2014. Paleolithic Landscapes of Iran. BAR international series, Oxford.

Heydari-Guran, S., Ghasidian, E., 2017. The MUP Zagros Project: tracking the Middle-Upper Palaeolithic transition in the Kermanshah region, West-Central Zagros, Iran. Antiquity, 91(355), E2.

Heydari-Guran, S., Ghasidian, E., 2020. Late Pleistocene hominin settlement patterns and population dynamics in the Zagros Mountains: Kermanshah region. Archaeological Res. Asia 21, 100161.

Heydari-Guran, S., Benazzi, S., Talamo, S., Ghasidian, E., Hariri, N., Oxilia, G., Asiabani, S., Azizi, F., Naderi, R., Safaierad, R., Hublin, J.J., Foley, R.A., Mirazón-Lahr, M., 2021. The discovery of an *in situ* Neanderthal remain in the Bawa Yawan Rockshelter, West-Central Zagros Mountains, Kermanshah. PLoS ONE 16(8), e0253708.

Hodgkins, J.M., Marean, C.W., 2017. New information from old excavations: a comparative analysis of Paleolithic zooarchaeological assemblages from the Zagros Mountains. In: Biglari, F., Mashkour, M., Shidrang, S. (Eds.), The Pleistocene Archaeology of Iran and Neighboring Regions. National Museum of Iran Paleolithic Studies Series, No. 1. National Museum of Iran, Tehran.

Hole, F., Flannery, K.V., 1967. The Prehistory of southwestern Iran: a preliminary report. Proc. Prehist. Soc. 33, 147–206.

Jafari, M., Lashkari, H., 2020. Study of the relationship between the intertropical convergence zone expansion and the precipitation in the southern half of Iran. J. Atmos. Sol. Terr. Phys. 210, 105439.

Jayez, M., 2022. What has been done and what has to be done? Statistical Assessment of Iranian Paleolithic Research 1906-2021. Iran. Antiq. 57, 173–258.

Jayez, M., Molla Mirzai, K., Aldin Niknami, K., 2019. Introduction of Late Pleistocene cultural material of an intermediate region: Paleolithic sites of Pion and Izeh plain between Central and Southern Zagros, Southwest Iran. Quat. Int. 512, 52–66.

Jéquier, C.A., Romandini, M., Peresani, M., 2012. Les retouchoirs en matières dures animales : une comparaison entre Moustérien final et Uluzzien. C. R. Palevol 11, 283–292.

Kehl, M., 2009. Quaternary climate change in Iran—the state of knowledge. Erdkunde 63 (1), 1–17.

Kehl, M., Frechen, M., Skowronek, A., 2005. Paleosols derived from loess and loess-like sediments in the Basin of Persepolis, Southern Iran. Quat. Int. 140–141, 135–149.

Kelly, R.L., 1995. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. Smithsonian Institution Press, Washington.

Klein, R.G., Cruz-Uribe, K., 1984. The analysis of animal bones from archaeological sites. University of Chicago Press, Chicago.

Kolobova, K., Rendu, W., Shalagina, A., Chistyakov, P., Kovalev, V., Baumann, M., Koliasnikova, A., Krivoshapkin, A., 2020. The application of geometric-morphometric shape analysis to Middle Paleolithic bone retouchers from the Altai Mountains, Russia. Quat. Int. 559, 89–96.

Krause, J., Orlando, L., Serre, D., Viola, B., Prüfer, K., Richards, M.P., Hublin, J.J., Hänni, C., Derevianko, A.P., Pääbo, S., 2007. Neanderthals in central Asia and Siberia. Nature 449, 902–904.

Krause, J., Fu, Q., Good, J.M., Viola, B., Shunkov, M.V., Derevianko, A.P., Pääbo, S., 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature 464, 894–897.

Kuhlwilm, M., Gronau, I., Hubisz, M.J., de Filippo, C., Prado-Martinez, J., Kircher, M., Fu, Q., Burbano, H.A., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Rudan, P., Brajkovic, D., Kucan, Ž., Gušic, I., Marques-Bonet, T., Andrés, A.M., Viola, B., Pääbo, S., Meyer, M., Siepel, A., Castellano, S., 2016. Ancient gene flow from early modern humans into Eastern Neanderthals. Nature 530, 429–433.

Kuhn, S.L., Stiner, M.C., 2006. What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. Curr. Anthropol. 47, 953–980.

Kuhn, S.L., Stiner, M.C., Güleç, E., Özer, I., Yılmaz, H., Baykara, I., Açıkkol, A., Goldberg, P., Martínez Molina, K., Ünay, E., Suata-Alpaslan, F., 2009. The early Upper Paleolithic occupations at Üçağızlı Cave (Hatay, Turkey). J. Hum. Evol. 56, 87–113.

Lalueza-Fox, C., Rosas, A., Estalrrich, A., Gigli, E., Campos, P.F., García-Tabernero, A., García-Vargas, S., Sánchez-Quinto, F., Ramírez, O., Civit, S., Bastir, M., Huguet, R., Santamaría, D., M. Gilbert, T.P., Willerslev, E., de la Rasilla, M., 2010. Genetic evidence for patrilocal mating behavior among Neandertal groups. Proc. Natl. Acad. Sci. USA 108, 250-253.

Lam, Y.M., Chen, X., Marean, C.M., Frey, C.J., 1998. Bone density and long bone representation in archaeological faunas: comparing results from CT and photon densitometry. J. Archaeol. Sci. 25, 559–570.

Liu, W., Martinón-Torres, M., Cai, Y.-J., Xing, S., Tong, H.-W., Pei, S.-W., Sier, M.J., Wu, X.-H., Edwards, R.L., Cheng, H., Li, Y.-Y., Yang, X.-X., Bermúdez de Castro, J.M., Wu, X.J., 2015. The earliest unequivocally modern humans in southern China. Nature 526, 696–699.

Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge.

Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge Manuals in Archaeology. Cambridge University Press, New York.

Madsen, D.B., Schmitt, D.N., 1998. Mass collecting and the diet breadth model: a Great Basin Example. J. Archaeol. Sci. 25, 445–455.

Mallye, J.-B., Thiébaut, C., Mourre, V., Costamagno, S., Claud, É., Weisbecker, P., 2012. The Mousterian bone retouchers of Noisetier Cave: experimentation and identification of marks. J. Archaeol. Sci. 39, 1131–1142.

Marean, C.W., 1998. A critique of the evidence for scavenging by Neandertals and early modern humans: new data from Kobeh Cave (Zagros Mountains, Iran) and Die Kelders Cave 1 Layer 10 (South Africa). J. Hum. Evol. 35, 111–136.

Marean, C.W., Spencer, L.M., 1991. Impact of carnivore ravaging on zooarchaeological measures of element abundance. Am. Antiq. 56, 645–658.

Marean, C.W., Frey, C.J., 1997. Animal bones from caves to cities: reverse utility curves as methodological artefacts. Am. Antiq. 62, 698–711.

Marean, C.W., Kim, S.Y., 1998. Mousterian large-mammal remains from Kobeh Cave. Behavioral implications for Neanderthals and early modern humans. Curr. Anthropol. 9(S1), S79–S113.

Marean, C.W., Assefa, Z., 1999. Zooarchaeological evidence for the faunal exploitation behavior of Neandertals and early modern humans. Evol. Anthropol. 8, 22–37.

Marean, C.W., Cleghorn, N., 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. J. Taphon. 1, 15–42.

Marean, C.W., Domínguez-Rodrigo, M., Pickering, T.R., 2004. Skeletal element equifinality in zooarchaeology begins with methods: the evolution and status of the "shaft critique". J. Taphon. 2, 69–98.

Mashkour, M., Radu, V., Mohaseb, A., Hashemi, N., Otte, M., Shidrang, S., 2009. The Upper Paleolithic faunal remains from Yafteh cave (central Zagros) 2005 campaign. A preliminary study. In: Otte, M., Biglari, F., Jaubert, J. (Eds.), Le Paleolithique D'Iran. Archaeopress, Oxford, pp. 73–85.

Mehterian, S., Pourmand, A., Sharifi, A., Lahijani, H.A.K., Naderi, M., Swart, P.K., 2017. Speleothem records of glacial/interglacial climate from Iran forewarn of future water availability in the interior of the Middle East. Quat. Sci. Rev. 164, 187–198.

Morin, E., Bliege Bird, R., Bird, D., 2020. Mass procurement and prey rankings: insights from the European rabbit. Archaeol. Anthropol. Sci. 12, 262.

Münzel, S.C., Conard, N.J., 2004. Change and continuity in subsistence during the Middle and Upper Palaeolithic in the Ach Valley of Swabia (South-west Germany). Int. J. Ostearchaeol. 4(3–4), 225–243.

North Greenland Ice Core Project members, 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. Nature 431, 147–151.

Otte, M., Biglari, F., Flas, D., Shidrang, S., Zwyns, H., Mashkour, M., Naderi, R., Mohased, A., Hashemi, N., Darvish, J., Radu, V., 2007. The Aurignacian in the Zagros region: new research at Yafteh cave, Lorestan, Iran. Antiquity 81, 82–96.

Otte, M., Shidrang, S., Zwyns, N., Flas, D., 2011. New radiocarbon dates for the Zagros Aurignacian from Yafteh cave, Iran. J. Hum. Evol. 61, 340–346.

Pelletier, M., Desclaux, E., Brugal, J.P., Texier, P.J., 2019. The exploitation of rabbits for food and pelts by last interglacial Neandertals. Quat. Sci. Rev. 224, 105972.

Perkins, D.J., 1964. Prehistoric fauna from Shanidar, Iraq. Science 144, 1565–1566.

Pianka, E.R., 1974. Evolutionary Ecology. Harper and Row, New York.

Pomeroy., E., Mirazón-Lahr, M., Crivellaro, F., Farr, L., Reynolds, T., Hunt, C.O., Barker, G., 2017. Newly discovered Neanderthal remains from Shanidar Cave, Iraqi Kurdistan, and their attribution to Shanidar 5. J. Hum. Evol. 111, 102–118.

Pomeroy, E., Bennett, P., Hunt, C.O., Reynolds, T., Farr, L., Frouin, M., Holman, J., Lane, R., French, C., Barker, G., 2020. New Neanderthal remains associated with the ‘flower burial’ at Shanidar Cave. Antiquity 94(373), 11–26.

Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., Siebauer, M., Theunert, C., Tandon, A., Moorjani, P., Pickrell, J., Mullikin, J.C., Vohr, S.H., Green, R.E., Hellmann, I., Johnson, P.L.F., Blanche, H., Cann, H., Kitzman, J.O., Shendure, J., Eichler, E.E., Lein, E.S., Bakken, T.E., Golovanova, L.V., Doronichev, V.B., Shunkov, M.V., Derevianko, A.P., Viola, B., Slatkin, M., Reich, D., Kelso, J., Pääbo, S., 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505, 43–49.

Prüfer, K., de Filippo, C., Grote, S., Mafessoni, F., Korlević, P., Hajdinjak, M., Vernot, B., Skov, L., Hsieh, P., Peyrégne, S., Reher, D., Hopfe, C., Nagel, S., Maricic, T., Fu, Q., Theunert, C., Rogers, R., Skoglund, P., Chintalapati, M., Dannemann, M., Nelson, B.J., Key, F.M., Rudan, P., Kućan, Ž., Gušić, I., Golovanova, L.V., Doronichev, V.B., Patterson, N., Reich, D., Eichler, E.E., Slatkin, M., Schierup, M.H., Andrés, A.M., Kelso, J., Meyer, M., Pääbo, S., 2017. A high-coverage Neandertal genome from Vindija Cave in Croatia. Science 358, 655–658.

Rabinovich, R., Hovers, E., 2004. Faunal analysis from Amud Cave: preliminary results and interpretations. Int. J. Osteoarchaeol. 14, 287–306.

Real, C., Villaverde, V., 2022. Subsistence activities and settlement dynamics of the first anatomically modern humans in the central–eastern Mediterranean Iberia: new insights from Cova de les Cendres (Alicante, Spain). Quat. Sci. Rev. 285, 107533.

Reed, C.A., Braidwood, R.J., 1960. Toward the reconstruction of the environmental sequence of northeastern Iraq. In: Braidwood, R.J., Howe, B., 1960. Prehistoric Investigations in Iraqi Kurdistan. University of Chicago Press, Chicago, pp. 163–173.

Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B., Briggs, A.W., Stenzel, U., Johnson, P.L.F., Maricic, T., Good, J.M., Marques-Bonet, T., Alkan, C., Fu, Q., Mallick, S., Li, H., Meyer, M., Eichler, E.E., Stoneking, M., Richards, M., Talamo, S., Shunkov, M.V., Derevianko, A.P., Hublin, J.-J.J., Kelso, J., Slatkin, M., Pääbo, S., 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468, 1053–1060.

Reitz, E.J., Wing, E.S., 2008. In: Zooarchaeology, 2nd ed. Cambridge University Press, Cambridge.

Rey-Rodríguez, I., López-García, J.M., Blain, H.A., Stoetzel, E., Denys, C., Fernández- García, Tumung, L., Ollé, A., Bazgir, B., 2020. Exploring the landscape and climatic conditions of Neanderthals and anatomically modern humans in the Middle East: the rodent assemblage from the late Pleistocene of Kaldar Cave (Khorramabad Valley, Iran). Quat. Sci. Rev. 236, 106278.

Rey-Rodríguez, I., Arnaud, J., López-García, J.M., Stoetzel, E., Denys, C., Cornette, R., Bazgir, B., 2021. Distinguish between three modern *Ellobius* species (Rodentia, Mammalia) and identification of fossil *Ellobius* from Kaldar Cave (Iran) using geometric morphometric analyses of the first lower molar. Palaentol. Electron. 24(1), a01.

Reynard, J.P., 2022. Tracking occupational intensity using archaeo-faunal data: case studies from the Late Pleistocene in the southern Cape of South Africa. J. Archaeol. Method Theory 29, 214–250.

Reynolds, T., Boismier, W., Farr, L., Hunt, C., Abdulmutalb, D., Barker, G., 2016. New investigations at Shanidar Cave, Iraqi Kurdistan. In: Kopanias, K., MacGinnis, J. (Eds.), The Archaeology of the Kurdistan Region of Iraq and Adjacent Regions. Archaeopress, Oxford, pp. 29–48.

Reynolds, T., Farr, L., Hill, E., Hunt, C., Jones, S., Gratuze, B., Nymark, A., Abdulmutalb, D., Barker, G., 2018. Shanidar Cave and the Baradostian, a Zagros Aurignacian industry. Anthropologie 122, 737–748.

Romagnoli, F., Chabai, V., Gravina, B., Hérisson, D., Hovers, E., Moncel, M.-H., Peresani, M., Uthmeier, T., Bourguignon, L., Chacón, M.G., Di Modica, K., Faivre, J.-P., Kolobova, K., Malinsky-Buller, A., Neruda, P., Rios-Garaizar, J., Weiss, M., Wisniewski, A., Wragg-Sykes, R., 2022. Neanderthal technological variability: a wide-ranging geographical perspective on the final Middle Palaeolithic. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals: Understanding Behavioral Complexity in the Late Middle Palaeolithic. Elsevier Academic Press, London, pp. 163–205.

Rosas, A., Bastir, M., García-Tabernero, A., 2022. Neanderthals: anatomy, genes, and evolution. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals: Understanding Behavioral Complexity in the Late Middle Palaeolithic. Elsevier Academic Press, London, pp. 71–87.

Rossignol-Strick, M., Paterne, M., 1999. A synthetic pollen record of the eastern Mediterranean sapropels of the last 1 Ma: implications for the time-scale and formation of sapropels. Mar. Geol. 153, 221–237

Roustaei, K., Biglari, F., Heydari, S., Vahdati Nasab, H., 2002. New research on the Palaeolithic of Lurestan, West Central Iran. Antiquity, 76(291), 19–20.

Roustaei, K., Vahdati Nasab, H., Biglari, F., Heydari, S., Clark, G.A., Lindly, J.M., 2004. Recent Paleolithic Surveys in Luristan. Curr. Anthropol. 45(5), 692–707.

Sánchez-Goñi, 2022. The climatic and environmental context of the Late Pleistocene. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals: Understanding

Behavioral Complexity in the Late Middle Palaeolithic. Elsevier Academic Press, London, pp. 17–38.

Schiemann, R., Lüthi, D., Schär, C., 2009. Seasonality and interannual variability of the westerly jet in the Tibetan plateau region. J. Clim. 22, 2940–2957.

Scott, J.E., Marean, C.W., 2009. Paleolithic hominin remains from Eshkaft-e Gavi (southern Zagros Mountains, Iran): description, affinities, and evidence for butchery. J. Hum. Evol. 57, 248–259.

Shea, J.J., 2008. Transitions or turnovers? Climatically-forced extinctions of *Homo sapiens* and Neanderthals in the east Mediterranean Levant. Quat. Sci. Rev. 27, 2253–2270.

Shidrang, S. 2006. Warkaini: a new Palaeolithic site near Kermanshah in West-central Zagros, Iran. Antiquity Project Gallery 80(310).

Shoaee, M.J., Vahdati Nasab, H., Petraglia, M.D., 2021. The Paleolithic of the Iranian Plateau: Hominin occupation history and implications for human dispersals across southern Asia. J. Anthropol. 1205 Archaeol. 62, 101292.

Skov, L., Peyrégne, S., Popli, D., Iasi, L.N.M., Devièse, T., Slon, V., Zavala, E.I., Hajdinjak, M., Sümer, A.P., Grote, S., Bossoms Mesa, A., López Herráez, D., Nickel, B., Nagel, S., Julia Richter, Essel, E., Gansauge, M., Schmidt, A., Korlević, P., Comeskey, D., Derevianko, A.P., Kharevich, A., Markin, S.V., Talamo, S., Douka, K., Krajcarz, M.T., Roberts, R.G., Higham, T., Viola, B., Krivoshapkin, A.I., Kolobova, K.A., Kelso, J., Meyer, M., Pääbo, S., Peter, B.M., 2022. Genetic insights into the social organization of Neanderthals. Nature 610, 519–525.

Slimak, L., Zanolli, C., Higham, T., Frouin, M., Schwenninger, J.-L., Arnold, L.J., Demuro, M., Douka, K., Mercier, N., Guérin, G., Valladas, H., Yvorra, P., Giraud, Y., Seguin-Orlando, A., Orlando, L., Lewis, J.E., Muth, X., Camus, H., Vandevelde, S., Buckley, M., Mallol, C., Stringer, C., Metz, L., 2022. Modern human incursion into Neanderthal territories 54,000 years ago at Mandrin, France. Sci. Adv. 8, eabj9496.

Smith, P.E.L., 1986. Paleolithic Archaeology in Iran. University Museum Press, University of Pennsylvania, Philadelphia.

Smith, G.M., Spasov, R., Martisius, N.L., Sinet-Mathiot, V., Aldeias, V., Rezek, Z., Ruebens, K., Pederzani, S., McPherron, S.P., Sirakova, S., Sirakov, N., Tsanova, T., Hublin, J.-J., 2021. Subsistence behavior during the Initial Upper Paleolithic in Europe: site use, dietary practice, and carnivore exploitation at Bacho Kiro Cave (Bulgaria). J. Hum. Evol. 161, 103074.

Snyder, J.A., Wasylik, K., Fritz, S.C., Wright, H.E., 2001. Diatom-based conductivity reconstruction and palaeoclimatic interpretation of a 40-ka record from Lake Zeribar, Iran. Holocene, 11(6), 737–745.

Solecki, R.S., 1958. The Baradostian Industry and the Upper Palaeolithic in the Near East. Unpublished Ph.D. dissertation. Colombia University, USA.

Solecki, R.S., 1963. Prehistory in Shanidar Valley northern Iraq. Science 139, 179–193.

Solecki, R.S., 1975. Shanidar IV, a Neanderthal flower burial in Northern Iraq. Science 190(4217), 880–881.

Speth, J.D., Tchernov, E., 2002. Middle Paleolithic tortoise use at Kebara Cave (Israel). J. Archaeol. Sci. 29, 471–483.

Starkovich, B.M., 2012a. Intensification of small game resources at Klissoura Cave 1 (Peloponnese, Greece) from Middle Paleolithic to Mesolithic. Quat. Int. 264, 17–31.

Starkovich, B.M., 2012b. Fallow deer (*Dama dama*) hunting during the late Pleistocene at Klissoura cave 1 (Peloponnese, Greece). Mittl. Ges. für Urgesch. 21, 11–36.

Starkovich, B.M., 2014. Optimal foraging, dietary change, and site use during the Paleolithic at Klissoura Cave 1 (southern Greece). J. Archaeol. Sci. 52, 39–55.

Starkovich, B.M., 2017. Paleolithic subsistence strategies and changes in site use at Klissoura Cave 1 (Peloponnese, Greece). J. Hum. Evol. 111, 63–84.

Stein, J.K., Deo, J.N., Phillips, L.S., 2003. Big sites–short time: accumulation rates in archaeological sites. J. Archaeol. Sci. 30, 297–316.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Monographs in Behavior and Ecology. Princeton University Press, Princeton.

Stiner, M.C., 1994. Honor Among Thieves: a Zooarchaeological Study of Neandertal Ecology. Princeton University Press, Princeton.

Stiner, M.C., 1998. Comments on ‘Mousterian large-mammal remains from Kobeh Cave. Behavioral implications for Neanderthals and early modern humans’. Curr. Anthropol. 9(S1), S98–S103.

Stiner, M.C., 2001. Thirty years on the “Broad Spectrum Revolution” and Paleolithic demography. Proc. Natl. Acad. Sci. U.S.A. 98, 6993–6996.

Stiner, M.C., 2005. The Faunas of Hayonim Cave, Israel: a 200,000 Year Record of Paleolithic Diet, Demography, and Society. In: Peabody Museum of Archaeology and Ethnology, vol. 48. American School of Prehistoric Research Bulletin, Cambridge, Massachusetts. Harvard University.

Stiner, M.C., 2009. Prey choice, site occupation intensity & economic diversity in the Middle e early Upper Palaeolithic at the Üçağızlı Caves, Turkey. Before Farming 3, 1–20.

Stiner, M.C., 2013. An unshakable Middle Paleolithic? Trends versus conservatism in the predatory niche and their social ramifications. Curr. Anthropol. 54, S288–S304.

Stiner, M.C., Kuhn, S.L., 2006. Changes in the ‘Connectedness’ and Resilience of Paleolithic Societies in Mediterranean Ecosystems. Hum. Ecol. 34, 693–712.

Stiner, M.C., Munro, N.D., 2002. Approaches to prehistoric diet breadth, demography, and prey ranking systems in time and space. J. Archaeol. Method Theory 9, 181–214.

Stiner, M.C., Munro, N.D., 2011. On the evolution of diet and landscape during the Upper Paleolithic through Mesolithic at Franchti Cave (Peloponnese, Greece). J. Hum. Evol. 60, 618–636.

Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E., Bar-Yosef, O., 1999. Paleolithic population growth pulses evidenced by small animal exploitation. Science 283, 190–194.

Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small-game use, the Broad-Spectrum Revolution, and Paleolithic demography. Curr. Anthropol. 41, 39–73.

Svensson, A., Andersen K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Davies, S.M., Johnsen, S.J., Muscheler, R., Parrenin, F., Rasmussen, S.O., Röthlisberger, R., Seierstad, I., Steffensen, J.P., Vinther, B.M., 2008. A 60,000 year Greenland stratigraphic ice core chronology. Clim. Past. 4, 47–57.

Tartar, E., 2012. The recognition of a new type of bone tools in Early Aurignacian assemblages: implications for understanding the appearance of osseous technology in Europe. J. Archaeol. Sci. 39, 2348–2360.

Tilby, E., Miracle, P., Barker, G., 2022. The microvertebrates of Shanidar Cave: preliminary taphonomic findings. Quaternary 5(1), 4.

Tourloukis, V., Thompson, N., Panagopoulou, E., Giusti, D., Konidaris, G.E., Karkanas, P., Harvati, K., 2018. Lithic artifacts and bone tools from the Lower Palaeolithic site Marathousa 1, Megalopolis, Greece: Preliminary results. Quat. Int. 497, 47–64.

Trinkaus, E., 2018. Pleistocene human remains from Iran. In: Biglari, F., Shidrang, S., Mashkour, M. (Eds.), The Pleistocene Archaeology of the Iranian Plateau, Iraq and the Caucasus. National Museum of Iran, Tehran, pp. 53–63.

Trinkaus, E., Biglari, F. 2006. Middle Paleolithic Human Remains from Bisitun Cave, Iran. Paléorient 32, 105–111.

Tsanova, T., 2013. The beginning of the Upper Paleolithic in the Iranian Zagros. A taphonomic approach and techno-economic comparison of early Baradostian assemblages from Warwasi and Yafteh (Iran). J. Hum. Evol. 65, 39–64.

Turnbull, P.F., 1975. The mammalian fauna of Warwasi Rock Shelter, West-Central Iran. Fieldiana Geol. 33, 141–155.

Turnbull, P.F., Reed, C.A., 1974. The fauna from the terminal Pleistocene of Palegawra Cave, a Zarzian occupation site in northeastern Iraq. Fieldiana Anthropol. 63(3), 81–146

Ünal-İmer, E., Shulmeister, J., Zhao, J.X., Uysal, I.T., Feng, Y.X., Nguyen, A.D., Yüce, G., 2015. An 80 kyr-long continuous speleothem record from Dim Cave, SW Turkey with paleoclimatic implications for the Eastern Mediterranean. Sci. Rep. 5, 13560.

Vaesen, K., Dusseldorp, G.L., Brandt, M.J., 2021. An emerging consensus in palaeoanthropology: demography was the main factor responsible for the disappearance of Neanderthals. Sci. Rep. 11, 4925.

Vahdati Nasab, H., 2011. Paleolithic Archaeology in Iran. Int. J. Humanit. 18(2), 63–87.

Vahdati Nasab, H., Clark, G.A., Torkamandi, S., 2013. Late Pleistocene dispersal corridors across the Iranian Plateau: a case study from Mirak, a Middle Paleolithic site on the northern edge of the Iranian Central desert (Dasht-e kavir). Quat. Int. 300, 267–281.

van Kolfschoten, T., Parfitt, S.A., Serangeli, J., Bello, S.M., 2015. Lower Paleolithic bone tools from the ‘Spear Horizon’ at Schöningen (Germany). J. Hum. Evol. 89, 226–263.

van Zeist, W., Bottema, S., 1977. Palynological investigations in western Iran. Palaeohistoria 19, 19–85.

Viola, B., 2022. Different species on the horizon: the Denisova hominins. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals: Understanding Behavioral Complexity in the Late Middle Palaeolithic. Elsevier Academic Press, London, pp. 55–69.

Wasylikowa, K., 2005. Palaeocology of Lake Zeribar, Iran, in the Pleniglacial, Lateglacial and Holocene, reconstructed from plant macrofossils. Holocene 15(5), 720–735.

Weitzel, E.M., 2023. Resilience of white-tailed deer (*Odocoileus virginianus*) to human hunting in precolonial New England: the faunal remains from the Morgan Site (6HT120), Rocky Hill, Connecticut. J. Archaeol. Sci. Rep. 48, 103913.

Welker, F., Soressi, M., Rendu, W., Hublin, J.-J., Collins, M., 2015. Using ZooMS to identify fragmentary bone from the Late Middle/Early Upper Palaeolithic sequence of Les Cottés, France. J. Archaeol. Sci. 54, 279–286.

Yeshurun, R., Tejero, J.-M., Barzilai, O., Hershkovitz, I., Marder, O., 2018. Upper Palaeolithic bone retouchers from Manot Cave (Israel): a preliminary analysis of an (as yet) rare phenomenon in the Levant. In: Hutson, J.H., García-Moreno, A., Noack, E.S., Turner, E., Villaluenga, A., Gaudzinski-Windheuser, S. (eds), The Origins of Bone Technologies. Verlag des Römisch-Germanischen Zentralmuseums, Mainz, pp. 287–296.

Yeshurun, R., Schneller-Pels, N., Barzilai, O., Marder, O., 2021. Early Upper Paleolithic subsistence in the Levant: zooarchaeology of the Ahmarian-Aurignacian sequence at Manot Cave, Israel. J. Hum. Evol. 160, 102619.

Young, T.C., Smith, P.E.L., 1966. Research in the Prehistory of Central Western Iran. Science 153, 386–391.

Zaitchik, B.F., Evans, J.P., Smith, R.B., 2007. Regional impact of an elevated heat Source: the Zagros Plateau of Iran. J. Clim. 20(16), 4133–4146.

Zanolli, C., Biglari, F., Mashkour, M., Abdi, K., Monchot, H., Debue, K., Mazurier, A., Bayle, P., Le-Luyer, M., Rougier, H., Trinkaus, E., Macchiarelli, R., 2019, A Neanderthal from the Central Western Zagros, Iran. Structural reassessment of the Wezmeh 1 maxillary premolar. J. Hum. Evol. 135, 102643.

Zeidi, M., Conard, N.J., 2019. The fourth season of excavation at Ghar-e Boof, Rostam County, Fars Province. In: Shirazi, R.A. (Ed.), 16th Annual Symposium of the Iranian Archaeology. Iranian Center for Archaeological Research, Tehran, pp. 234–238 (in Farsi).

Zeidi, M., McCall, B., Khosrowzadeh, A., 2006. Survey of Dasht-e Rostam-e Yek and Dasht-e Rostam-e Do. In: Potts, D.T., Roustaei, K. (Eds.), The Mamasani Archaeological Project Stage One: a Report on the First Two Seasons of the ICAR–University of Sydney Expedition to the Mamasani District, Fars Province, Iran. Iranian Center for Archaeological research, Tehran, pp. 147–168.

Zeynivand, M., Bahramiyan, S., Mazaheri, K., 2018. The Palaeolithic of Seimarreh Valley in the Central Zagros, Iran. Antiquity, 92(362), E1.

Zhu, M., Atkinson, B.W., 2004. Observed and modelled climatology of the land-sea breeze circulation over the Persian Gulf. Int. J. Climatol. 24, 883–905.

Supplementary material

Table S1. Ghar-e Boof. Richness (N-Taxa) and reciprocal of Simpson's index (1/D) values by layer and for all taxa, ungulates and small game species.

AH	Total NISP	All Taxa N-taxa	All 1/D	Ungulate NISP	Ungulate Taxa	Ungulate 1/D	Small game NISP	Small game N-taxa	Small game 1/D
III	367	11	4.17	153	6	2.22	208	3	1.99
IIIa	92	5	3.31	35	3	1.98	57	2	1.68
IIIb	137	9	4.32	81	5	2.27	53	2	1.94
IIIc	53	8	3.06	16*	5	3.66	36	2	1.53
IV	71	5	1.79	17*	3	2.65	54	2	1.08
IVa	51	8	3.65	25*	6	3.57	26*	2	1.26
IVb	24*	6	3.16	10*	4	1.92	14*	2	1.51
IVc	26*	5	3.48	13*	3	1.61	13*	2	1.90
IVd	4*	3	2.67	0*	0	0.00	2*	2	1.80
V	33	5	1.93	5*	2	1.47	24*	2	1.09
Va	64	6	1.26	5*	3	2.78	58	2	1.04
Vb	44	6	1.64	7*	4	2.58	37	2	1.18
Vc	34	2	1.49	7*	1	1.00	27*	1	1.00
Vd	16*	2	1.88	6*	1	1.00	10*	1	1.00
VI	19*	5	2.93	18*	4	2.66	1*	1	1.00

*Asterisks indicate small sample size. The minimum threshold here is 30 NISP (after Stiner and Munro, 2011).

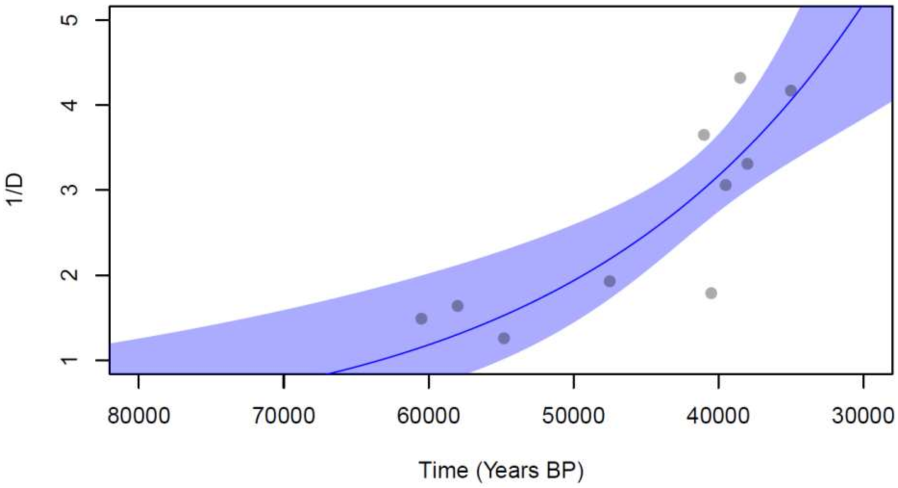

Fig. S1. Ghar-e Boof. 1/D values as a function of time. Data from Table S1 (all taxa).

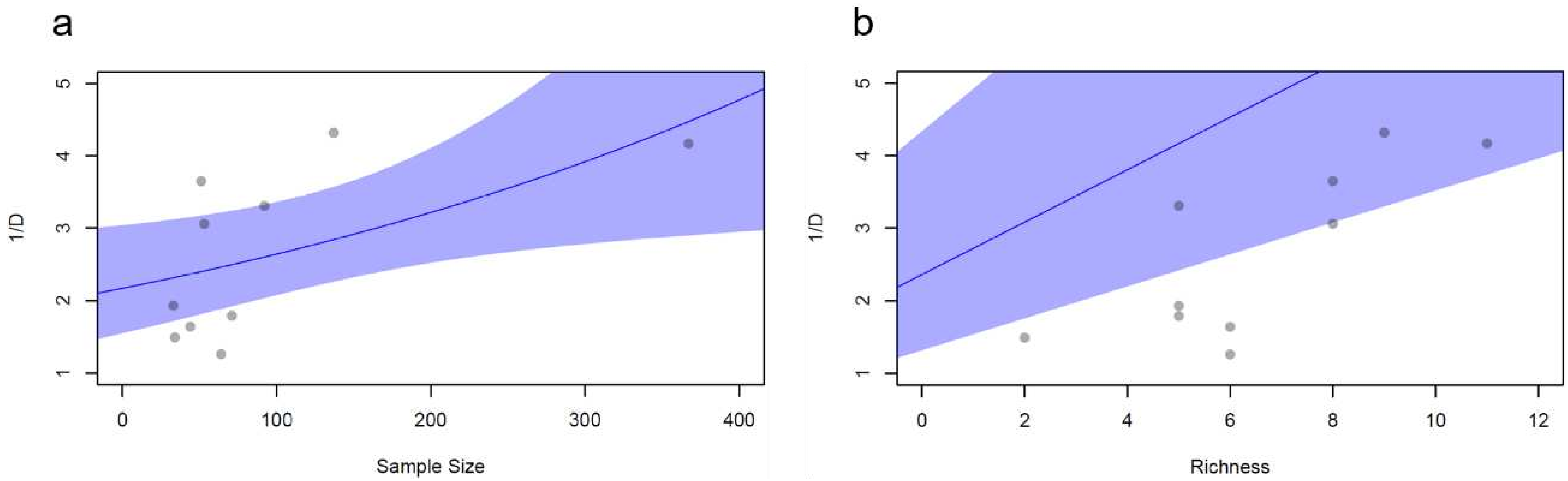

Fig. S2. Ghar-e Boof: 1/D values as a function of sample size (a), and as a function of richness (b). Data from Table S1 (all taxa).

Table S2. Ghar-e Boof. Bone specimens sampled for ZooMS analysis.

ZooMS ID	Bone ID	AH	Quadrant	Taxon	Element	Portion	Length (cm)	Weight (g)	Type of fracture	Anthropogenic damage	Natural surface alterations
GEB0336	673	Va	6/8	M. ungulate	Metatarsal	Anterior groove	7.5	5.2	Split/spiral	Cone fracture	Chemical weathering and oxide staining
GEB0358	685	Va	6/8	M. ungulate	Long bone	Shaft fragment	3.5	4.1	Split/spiral	-	Chemical weathering and oxide staining
GEB0328	716	Vb	6/8	M. ungulate	Tibia	Shaft fragment	7.0	6.5	Split/spiral	-	Chemical weathering, root etching and oxide staining
GEB0329	748	Vb	6/8	M. ungulate	Radius	Shaft fragment	8.0	8.5	Transverse	-	Chemical weathering and oxide staining
GEB0393	795	Vc	6/8	M. ungulate	Tibia	Shaft fragment	8.7	8.0	Split/spiral	-	Chemical weathering and oxide staining
GEB0360	984	VI	6/8	M. ungulate	Long bone	Shaft fragment	3.8	2.2	-	-	Chemical weathering and oxide staining

Table S3. Ghar-e Boof. Normalized values used in the PCA (untransformed data are reported in Table 2).

Layer	Culture	Small game	Fast-moving game	NISP/liters	NISP accumulation rates	Burned NISP/liters	Burned NISP accumulation rates	Lithic artifacts (N)/liters	Lithic accumulation rates	Frequencies of retouched lithic artifacts	Sedimentation rates (cm/100 yrs.)
III	UP	0.3642	0.8660	-0.5205	-0.6866	0.3845	-0.3702	2.7429	0.4720	-1.0103	-0,3166
IIIa	UP	1.1888	0.5852	0.3483	2.0030	2.3071	3.2182	1.1840	2.9823	-1.1914	1.2284
IIIb	UP	0.4673	1.4629	1.6217	1.1144	0.4681	0.3133	0.8044	0.8233	-0.8593	2.3728
IIIc	UP	0.3642	0.7607	1.7050	1.1562	0.9697	0.5696	1.1167	1.1182	-0.8593	0.0839
IV	UP	1.3949	-0.7490	0.0151	1.6690	-0.2006	0.6550	-0.4038	-0.0160	0.1972	1.8006
IVa	UP	-1.3881	-0.5735	1.2171	-0.0664	1.1368	-0.0285	-0.4738	-0.5009	-0.5575	-0.6027
IVb	UP	0.1581	0.5852	-0.2944	0.1543	0.1338	0.1424	-0.4289	-0.3411	-1.1008	-0.2022
IVc	MP-UP (?)	0.2611	0.6905	-0.4372	-0.2930	-0.9529	-0.4984	-0.5053	-0.4817	-0.2254	-0.6600
IVd	MP-UP (?)	-0.9758	-0.5384	-1.2464	-0.3228	-0.9529	-0.4130	-0.6425	-0.5427	0.1972	-0.2022
V	MP	-0.0481	-1.1703	-0.2706	-0.8834	0.4681	-0.5838	-0.5806	-0,6002	1.6764	-0.7172
Va	MP	0.1581	-0.9948	0.3364	-0.5733	-1.1201	-0.6266	-0.4813	-0.5473	0.4689	0.0267
Vb	MP	0.3642	-0.7841	-0.0206	-0.5137	0.1338	-0.3702	-0.5774	-0.5639	0.7104	-0.4883
Vc	MP	-0.0481	-1.0650	0.4435	-0.7880	-1.1201	-0.6693	-0.4962	-0.5831	0.0463	-0.8888
Vd	MP	0.3642	-0.8894	-1.7463	-1.0027	-1.0365	-0.6693	-0.6019	-0.6073	0.3180	-0.8888
VI	MP	-2.6250	1.8140	-1.1512	-0.9670	-0.6186	-0.6693	-0.6564	-0.6118	2.1895	-0.5455

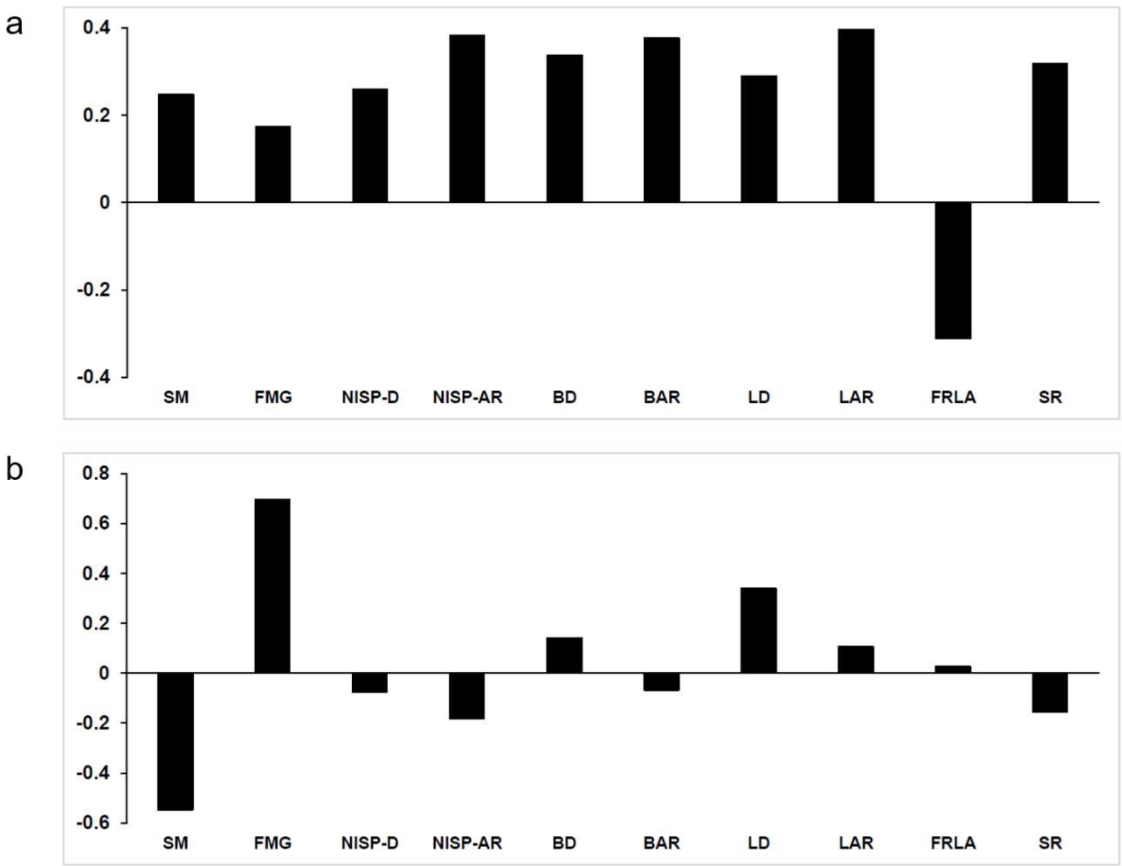

Fig. S3. Ghar-e Boof. Loading scores for each variable and for PCA 1 (a) and PCA 2 (b): SG (Small Game Index); SFMG (Fast-Moving Game Index); NISP-D (NISP densities), NISP-AR (NISP accumulation rates); BD (burned NISP densities); BAR (burned NISP accumulation rates); LD (lithic artifact densities); LAR (lithic artifact accumulation rates); FRLA (frequency of retouched lithic artifacts); and SR (sedimentation rates).

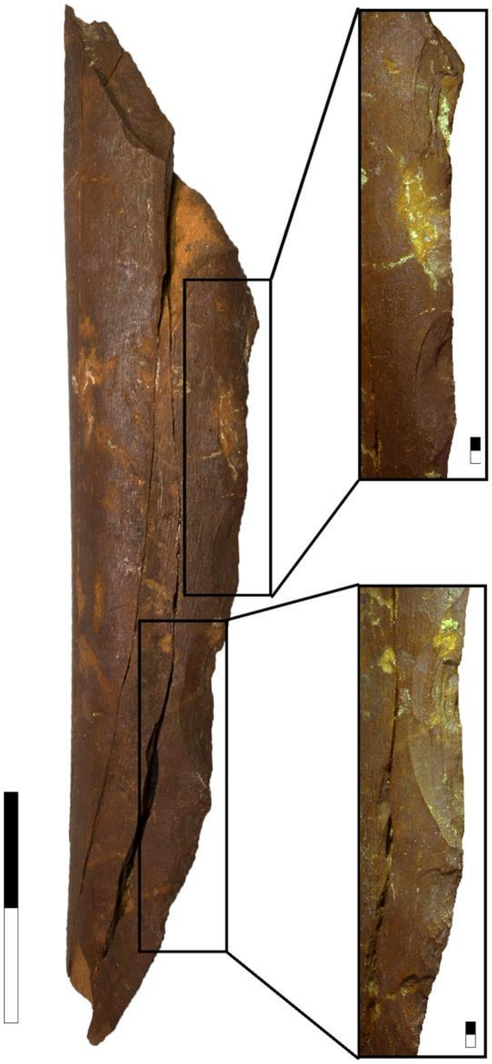

Fig. S4. Ghar-e Boof. Potential bone retoucher, which has a modified/knapped edge (fig. by Ángel Blanco-Lapaz). Scale: general view = 20 mm; closer-up view = 2 mm.

APPENDIX 1

Blanco-Lapaz, A., **Mata-González, M.**, Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. Late Pleistocene environments in the southern Zagros of Iran and their implications for human evolution. Archaeol. Anthropol. Sci. 14, 161. https://doi.org/10.1007/s12520-022-01615-1.

Submitted to the journal: 1 February 2022.

Accepted: 29 June 2022.

Archaeological and Anthropological Sciences (2022) 14:161
https://doi.org/10.1007/s12520-022-01615-1

ORIGINAL PAPER

Late Pleistocene environments in the southern Zagros of Iran and their implications for human evolution

Angel Blanco-Lapaz[1,2] · **Mario Mata-González**[2] · **Britt M. Starkovich**[1,2] · **Mohsen Zeidi**[1,3] · **Nicholas J. Conard**[1,2,3]

Received: 1 February 2022 / Accepted: 29 June 2022

Abstract

The Zagros Mountains represent a strategic geographic region near the junction of Africa, Europe, and Asia, and valleys within the mountain range likely correspond to migration corridors used by archaic and modern humans. Ghar-e Boof, a key archeological site in the southern Zagros, is located at an altitude of 905 m.a.s.l. in the Dasht-e Rostam region of the Fars Province, Iran. On the basis of lithic artifacts and radiocarbon and luminescence dating, the Late Pleistocene archeological record of the site spans from the Middle Paleolithic (MP) to the Late Epipaleolithic. Ghar-e Boof includes find horizons of the early Upper Paleolithic (UP) Rostamian dating to 42–35 ka cal. BP. These Rostamian-UP assemblages are typically attributed to modern humans. The high-resolution stratigraphy and microvertebrate record offer a unique opportunity for reconstructing the paleoenvironment of the southern part of the Zagros Mountains during the Late Pleistocene and contribute to a better understanding of long-term hominin settlement dynamics and cultural adaptations in this area. The current paper presents the first analysis of the microvertebrate remains recovered by the Tübingen-Iranian Stone Age Research Project (TISARP) team. All groups of small vertebrates, including fish, amphibians, squamate reptiles, birds, and micromammals, are present in the assemblage from Ghar-e Boof (NISP = 755). The key micromammal taxa used to reconstruct the paleoenvironment during the MP and UP include Libyan jird (*Meriones* cf. *libycus*), Vinogradov's jird (*Meriones vinogradovi*), Indian gerbil (*Tatera indica*), Brandt's hedgehog (*Paraechinus* cf. *hypomelas*), house mouse (*Mus musculus*), and mole vole (*Ellobius* sp.). Other taxa, such as amphibians (toad, *Bufo*/*Bufotes* sp.), fish (nase, *Chondrostoma* sp.), and squamate reptiles (agamids, lizards, Eastern Montpelier snake—*Malpolon insignitus*—and viper), also support the presence of an environment mainly characterized by warm, arid conditions with open, dry meadows, rocky terrain, and water sources close to the site throughout most of the sequence. During the shift from MP to UP, we record Afghan pika (*Ochotona* cf. *rufescens*), while all rodents, except very few remains of the Persian vole (*Microtus* cf. *irani*) and the Libyan jird (*M.* cf. *lybicus*) and some non-hibernating vertebrate species, are absent and reappear in later UP horizons. The presence of pikas could reflect a period of slightly colder and/or drier conditions. While the record from Ghar-e Boof is the only dataset from the southern Zagros, previous studies on microvertebrates from the central and northern Zagros show no clear change during the shift from the MP to the UP. Data from sediment cores and pollen analyses document numerous environmental and climatic fluctuations during the Late Pleistocene of the Zagros. The microvertebrate record from Ghar-e Boof improves our understanding of paleoenvironments during the Late Pleistocene and opens new opportunities to reconstruct the ecological conditions that helped to shape hominin settlement dynamics in the region.

Keywords Zagros Mountains · Rostamian · Small vertebrates · Paleoenvironment · Human occupations

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This article is part of the Topical Collection on *Microvertebrate Studies in Archaeological Contexts: Middle Paleolithic to early Holocene past environments*.

✉ Angel Blanco-Lapaz
angel.blanco-lapaz@uni-tuebingen.de

[1] Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstrasse, 12 72074 Tübingen, Germany

[2] Institute for Archaeological Sciences, University of Tübingen, Hölderlinstrasse, 12 72074 Tübingen, Germany

[3] Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Burgsteige, 11 72070 Tübinge, Germany

Introduction

The strategic location of the Zagros Mountains, near the intersection between Africa, Europe, and southwestern Asia, most probably represented a major biographical corridor used by archaic and anatomically modern humans (AMHs) during the Late Pleistocene (Field et al. 2006; Oppenheimer 2009; Boivin et al. 2013; Vahdati-Nasab et al. 2013; Shoaee et al. 2021). The anthropological and archeological potential of this geographic area for the understanding of human dispersals and cultural adaptations across Eurasia has been demonstrated with the discovery of Neanderthal and AMH remains associated with lithic industries at several localities in the Zagros (i.e., Solecki 1958; Solecki 1963; Trinkaus 1983, 2018; Trinkaus and Biglari 2006; Cowgill et al. 2007; Trinkaus et al. 2008; Churchill et al. 2009; Scott and Marean 2009; Tsanova 2013; Pomeroy et al. 2017, 2020; Trinkaus and Villotte 2017; Zanolli et al. 2019; Heydari-Guran et al. 2021a). Regardless of the precise timing and nature of the shift from Neanderthals to AMH, when different human groups first spread across Asia, they had to adapt to new and diverse environmental conditions (Boivin et al. 2013).

Local environmental reconstructions are especially relevant to understand the human response to landscape changes and, in particular, the Zagros Mountains contain numerous microenvironments and heterogeneous topography, so both MP and UP hunter-gatherers adopted various cultural adaptations and subsistence strategies in different landscapes and environments (Bretzke and Conard, 2017; Ghasidian et al. 2019; Heydari-Guran and Ghasidian 2020). Consequently, paleoenvironmental reconstructions of the Zagros during the MP and UP provide valuable new information for a better understanding of long-term hominin settlement dynamics and cultural adaptations.

Many environmental reconstructions available for the Zagros Mountains during the Late Pleistocene come from the analyses of sediment cores. Lake Urmia, located in the northern Zagros, has produced a long pollen record spanning 200 kya (Djamali et al. 2008a, 2008b). Moreover, botanists have also analyzed the pollen and seeds from Lake Zeribar, in the Western-Central Iran, with a record that covers the last 42 kya (van Zeist and Bottema 1977; Wasylikowa 2005). These studies have shown that during most of the Late Pleistocene, the environment of the Zagros Mountains was mainly characterized by the presence of shrub/grass steppe vegetation (i.e., Chenopodiaceae, Umbelliferae, Poaceae, and *Artemisia* sp.) with some scattered trees, such as junipers, deciduous oak, maple, and pistachio (van Zeist and Bottema 1977; Djamali et al. 2008a). Although this vegetation indicates a very arid landscape with colder temperatures than today, the environment fluctuated significantly

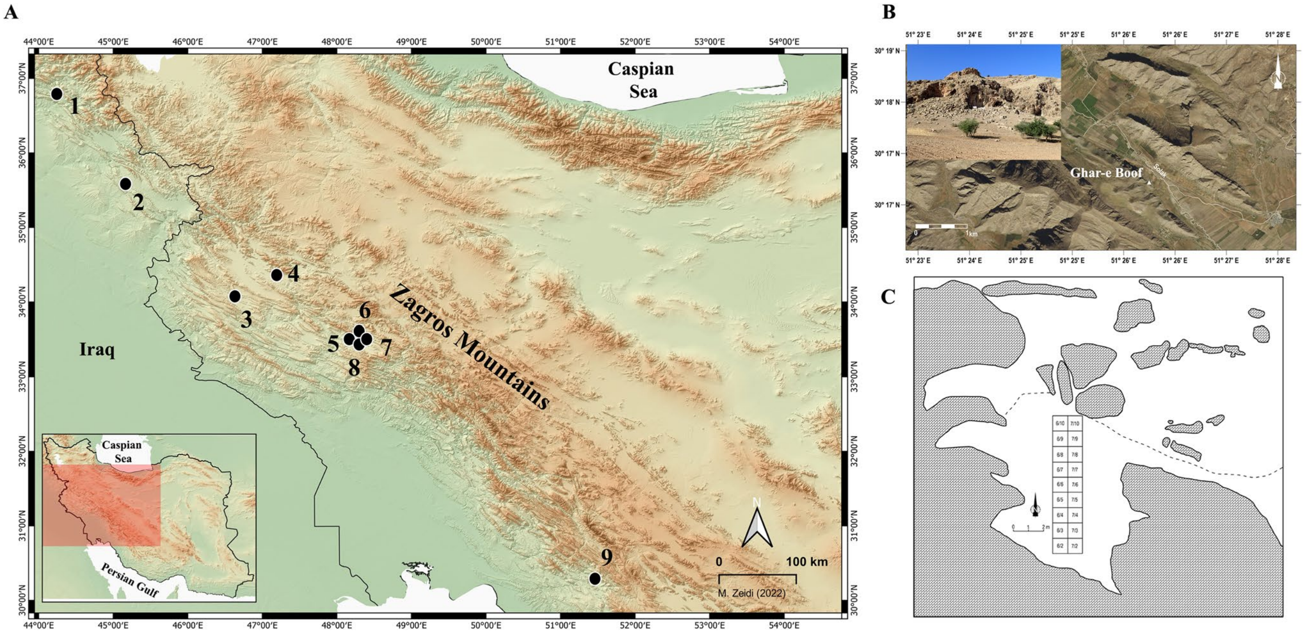

Fig. 1 **A** Location of archeological sites mentioned in the text: 1. Shanidar Cave; 2. Palegawra Cave; 3. Wezmeh Cave; 4. Warwasi Cave; 5. Gar Ajeneh; 6. Kaldar Cave, Pa-Sangar, Yafteh Cave; 7. Kunji Cave; 8. Ghamari Cave; 9. Ghar-e Boof. Map created by M. Zeidi. Source: Natural Earth 2. **B** Location of Ghar-e Boof Cave and its overview during the 2017 campaign (**B**. Figure created by M. Zeidi. Source: Bing Maps. Ghar-e Boof photo: M. Zeidi). **C** Ghar-e Boof excavation area divided into quadrants, with the cave entrance to the north (map created by M. Zeidi (modified after Conard and Ghasidian 2011)

during the Late Pleistocene between cold, warm, dry, and wet conditions (van Zeist and Bottema 1977; Wasylikowa 2005; Djamali et al. 2008a). Due to the complex topography of the Zagros and their altitudinal variations, the mountains offer a large variety of ecosystems with marked contrasts (Heydari and Mahdavi 2009; Noroozi et al. 2020; Mostafavi et al. 2021). Although the sediment cores probably reflect major environmental changes, they cannot be used for inferring a particular site environment.

It is well-known that small vertebrates represent good paleoenvironmental indicators and are very frequently found well-preserved and in relatively large quantities in archeological and paleontological sites, especially in rock shelters and caves (Andrews 1990; Avery 2007; Fernández-Jalvo et al. 2016). Small vertebrates are often used for inferring and reconstructing environmental conditions because, among other characteristics, they have limited geographic ranges, rapid turn-over rates, and unique habitat requirements, such as specific humidity conditions or levels of vegetation cover (Andrews and O'Brien 2000; Avery 2007; Blain et al. 2009; Belmaker and Hovers 2011).

Since the second half of the twentieth century, researchers have studied numerous Late Pleistocene small vertebrate assemblages associated with MP and UP artifacts and human remains in the Zagros Mountains (Fig. 1A), including Shanidar Cave (Perkins 1964; Tilby et al. 2022); Gar Arjeneh, Kunji Cave and Pa-Sangar (Hole and Flannery 1967); Ghamari Cave (Hole and Flannery 1967; Bazgir et al. 2014); Yafteh Cave (Hole and Flannery 1967; Hashemi et al. 2006; Otte et al. 2007; Mashkour et al. 2009a); Palegawra Cave (Turnbull and Reed 1974; Asouti et al. 2020); Warwasi Cave (Turnbull 1975); Wezmeh Cave (Mashkour et al. 2009b); and Kaldar Cave (Bazgir et al. 2014, 2017; Rey-Rodríguez et al. 2020, 2021). However, with the exception of Rey-Rodríguez et al. (2020), who provided a thorough paleoenvironmental and paleoclimatic reconstruction for the MP and UP deposits of Kaldar Cave, these studies mainly consist of preliminary taxonomic lists and the majority of studied taxa correspond only to micromammals. Squamata reptiles, amphibians, birds, and fish have also been recovered at some sites (Turnbull and Reed 1974; Otte et al. 2007; Mashkour et al. 2009b; Bazgir et al. 2017; Asouti et al. 2020). Despite the limited data, small vertebrate assemblages are still the primary source of information for reconstructing the environment in which Neanderthals and AMHs lived during the MP and UP in the Zagros Mountains.

Archeological sites with available environmental data obtained from the analysis of small vertebrates are mainly located in western/central and the northern Zagros, while little is known about the Late Pleistocene environmental conditions of the southernmost part of the mountain range. Although the southern Zagros is less studied, archeologists have long recognized the importance of this area for human and cultural evolution, with the documentation, for example, of MP and UP sites such as Eshkaft-e Ghadi Barmishur and Eshkaft-e Gavi (Piperno 1972, 1974; Ikeda 1979; Rosenberg 1979, 1985, 1988; Scott and Marean 2009).

Since 2004, the Tübingen-Iranian Stone Age research project (TISARP) team has conducted numerous surveys and excavations in the Fars Province (Iran) in the southern Zagros and documented more than 120 archeological sites (Conard et al. 2006, 2007, Zeidi et al. 2006; Conard and Ghasidian 2011; Heydari-Guran 2014). Among these sites, the most promising one was Ghar-e Boof, with a Late Pleistocene stratigraphic sequence spanning from the MP until the Late Epipaleolithic (Conard and Ghasidian 2011; Baines et al. 2014; Becerra-Valdivia et al. 2017; Conard and Zeidi 2019; Zeidi and Conard 2019; Heydari et al. 2021).

Based on the analysis of different lithic assemblages recovered at Ghar-e Boof, archeologists observed that there is no technological continuity between the MP and the UP, suggesting a population replacement or settlement discontinuity (Bretzke and Conard 2017). Furthermore, Ghar-e Boof is the type locality for the early UP Rostamian cultural group, which is characterized by unidirectional bladelet production and small platform cores (Conard and Ghasidian 2011; Ghasidian 2014). The definition of this cultural tradition has revealed a high degree of cultural diversity within the Zagros Mountains during the early UP, with archeologists observing different population and developmental trajectories (Conard and Ghasidian 2011; Ghasidian 2014; Ghasidian et al. 2017, 2019).

In this context, Ghar-e Boof also offers a unique opportunity for improving our understanding of the paleoenvironmental conditions in the southern Zagros and assessing possible correlations between cultural and demographic shifts and local environmental fluctuations. Thus, here we present a detailed taxonomic analysis of the small vertebrate assemblages from the MP and early UP sequence of Ghar-e Boof. Our main goals are the following: (1) the identification and description of the different small vertebrate taxa and (2) to infer the habitat requirements of the small vertebrates in order to reconstruct the paleoenvironment in which humans lived during the Late Pleistocene at Ghar-e Boof.

Ghar-e Boof

Ghar-e Boof (N 30.2839°, E 51.4352°) is a cave located in the Dasht-e Rostam region, on the northwestern edge of the Fars Province (Fig. 1A, B). The site lies at an altitude of 905 m.a.s.l., ca. 40 m above the valley bottom, and it is situated in the Yagheh Sangar, a narrow corridor in the topography that divides the Dasht-e Rostam region in half (Conard et al. 2006; Conard and Ghasidian 2011). From this location, the Solak seasonal stream is just 200 m away towards the northeast. The inside area of Ghar-e Boof is about 60 m^2, and the entrance of the cave faces north (Fig. 1C, Conard and Ghasidian 2011).

Originally documented as Eshkaft-e Yagheh Sangar, Ghar-e Boof was visited for the first time by the TISARP team in 2005 (Conard et al. 2006; Zeidi et al. 2006). Since then, the team has carried out four campaigns of excavation at the site in 2006, 2007, 2015, and 2017 (Conard et al. 2006, 2007; Conard and Ghasidian 2011; Conard and Zeidi 2019; Zeidi and Conard 2019). The excavation area is 2 × 9 m, and it extends along the north–south axis of the cave, from near the dripline at the entrance toward the back of the cave (Fig. 2, Conard and Ghasidian 2011), and is approximately 6 m deep (Heydari et al. 2021). Archeologists divided each square meter into 50-cm sub-squares and excavated artificial spits of 2 to 3 cm deep following the slope of the geological deposits (Conard and Zeidi 2019). Overall, the stratigraphic sequence of Ghar-e Boof consists of six main archeological horizons (AHs) and 13 sub-horizons (Fig. 2). For the sake of clarity, we summarize the sedimentological characteristics, thickness, absolute dates, and cultural affiliations by AH in Table 1.

At the top of the sequence, AHs I and II comprise Holocene silts and ash deposits. Towards the center and bottom levels of AH II (sublayers IIa and IIb), there were many diagnostic Zarzian lithic artifacts (Zeidi and Conard 2019). However, the presence of a few pottery sherds and a grain of barley from AH IIb dated by ^{14}C to ca. 1250 cal. BP still indicates some degree of disturbance with the uppermost Holocene sediments (Baines et al. 2014; Ghasidian 2014). The bottom of AH IIb also includes a layer of limestone cobbles with sizes from 5 to 25 cm in the central part of the excavation area, which seems to mark the distinction with the underlying undisturbed Paleolithic deposits (Conard and Ghasidian 2011).

The early UP sequence starts with AH III and spans downward until IVb. Here, OSL and radiocarbon dating analyses provided dates within the range of 42–35 kya cal. BP (Conard and Ghasidian 2011; Baines et al. 2014; Becerra-Valdivia et al. 2017; Heydari et al. 2021). These layers have yielded high concentrations of lithic artifacts representing the assemblage type used for defining the Rostamian technocomplex (Conard and Ghasidian 2011; Ghasidian 2014), which is characterized by a predominance of small bladelets, retouched bladelet tools, and abundant platform cores

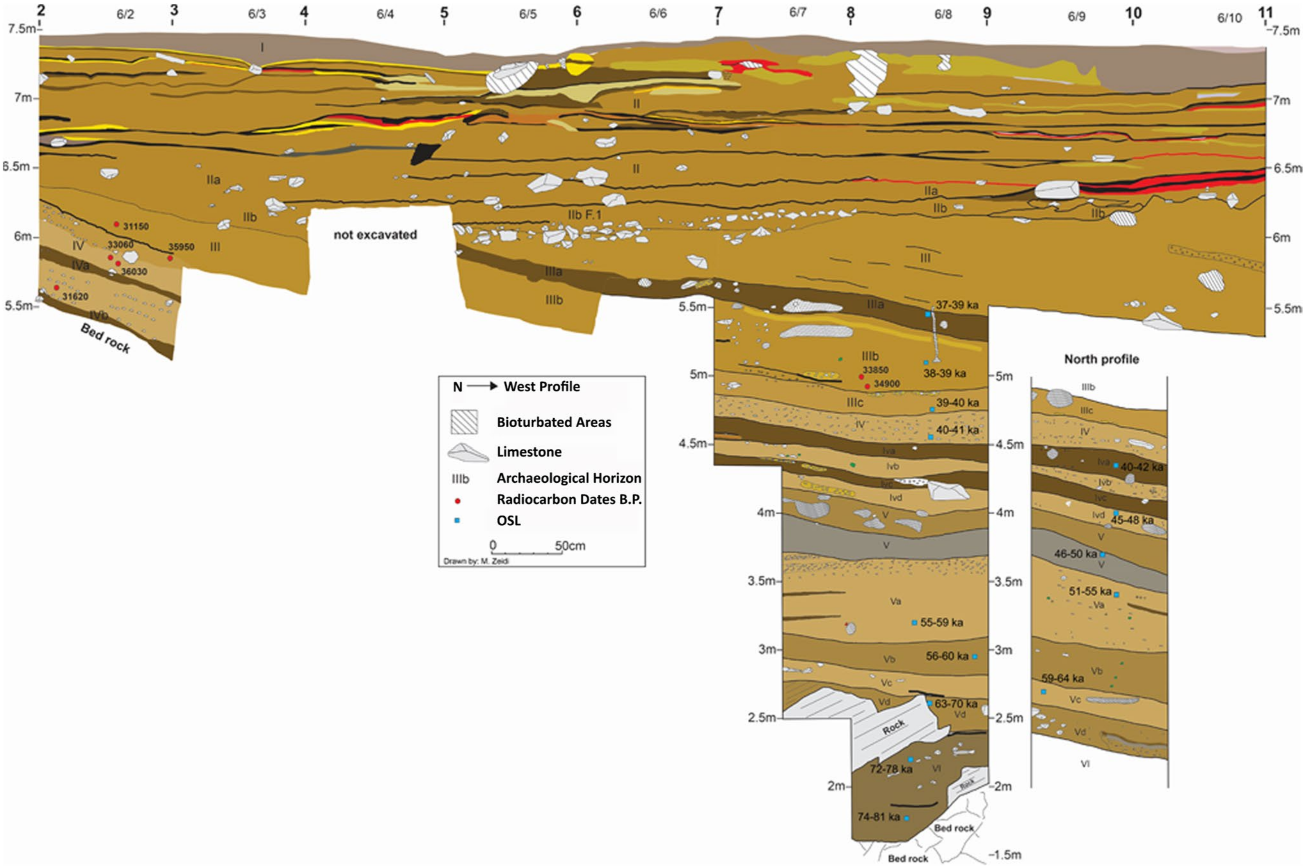

Fig. 2 Ghar-e Boof statigraphic sequence: west profile and part of the north. Radiocarbon dates are calibrated. Modified from Heydari et al. (2021)

Table 1 Stratigraphic information for Ghar-e Boof

AH	Sedimentological characteristics[1]	Thickness[1]	Dates (yr. BP)[2]	Cultural affiliations[3]
I	Mixed, gray, ashy silts of the surface and subsurface	5 to 20 cm	-	Historical periods (Late Sassanid and Early Islamic)
II	In situ laminated ashy silt layers of black, red, orange, yellow, gray, white, and various brown hues	100 cm		
IIa	Dark brown/gray ashy silts	15 cm		Mainly Zarzian (Epipaleolithic), but pottery sherds still present
IIb	Medium brown ashy silt to a light,gray/brown silt. Massive geogenic layer (IIb.1) of limestone cobles located at the bottom of this AH	10 cm	1225–1260 cal	
III	Homogenous light gray to yellow brown ashy silts, similar to loess. Ample lateral variation	10 to 70 cm	35,152 ± 368 cal	Rostamian (Early UP)
IIIa	Medium brown ashy silts	20 cm	-	
IIIb	Light brown ashy silts with alternating gray-black, white-brown, and light brown silts	60 cm	38,994 ± 1419 cal 39,949 ± 921 cal	
IIIc	Light brown silts, starting with an irregular cemented crust	20 cm	-	
IV	Light brown silts with small angular fragments of limestone	25 cm	41,355 ± 326 cal	
IVa	Brown silts with small angular fragments of limestone	15 cm	42–40 ka	
IVb	Light brown silts, but less rocky than IV and IVa	15 cm	-	
IVc	Fine rocky brown silts	10 cm	-	MP-UP transition (?)
IVd	Fine rocky light brown silts	15 cm	48–45 ka	
V	Light brown but less rocky silts, underlaid by a thin dark brown band and then by a medium brown silty sediment	40 cm	50–46 ka	MP
Va	Mostly light brown silty matrix with many small sharp-edged pieces of limestone, though thin bands of brown silts were observed	60 cm	55–51 ka 59–55 ka	
Vb	Still mostly rocky light brown silty matrix, along with red brown silts	25 cm	60–56 ka	
Vc	Light brown silts	15 cm	64–59 ka	
Vd	Light brown to yellow brown silts	25 cm	70–63 ka	
VI	Homogeneous brown to gray-light yellow brown silts, with small limestone clasts, laying over the bedrock	80 cm	78–72 ka 81–74 ka	

[1] Conard and Ghasidian 2011; Ghasidian 2014; Conard and Zeidi 2019; Zeidi and Conard 2019; Heydari et al. 2021; present study. The total thickness (cm) for each AH is approximate. [2] Radiometric dates from Conard and Ghasidian 2011, Baines et al. 2014, and Becerra-Valdivia et al. 2017; calibrated dates from Ghasidian 2014 and Ghasidian et al. 2019; OSL dates from Heydari et al. 2021. [3] Conard and Ghasidian 2011; Ghasidian, 2014; Ghasidian et al. 2017; Bretzke and Conard 2017; Conard and Zeidi 2019; Zeidi and Conard 2019

(Ghasidian 2014). Along with the lithic artifacts, excavators documented combustion features and uncovered personal ornaments, such as perforated shell beads and large amounts of well-preserved faunal and botanical remains (Conard and Zeidi 2019). During the Rostamian, Ghar-e Boof was used as a camp site, and hunter-gatherers primarily exploited caprines for meat and marrow, though gazelles, partridges, and tortoises might have been recurrent dietary supplements (Mata-González et al. 2022). Botanical studies also suggest that the accumulation of some large pulses might have resulted from dietary plant use by humans (Baines et al. 2014).

Currently, AHs IVc and IVd cannot be attributed with confidence to either the MP or UP due to the low find densities of lithic artifacts (Heydari et al. 2021). However, the layers lack Arjeneh points and perforated shells, which have been recorded in AHs IV to IVb and are considered characteristic components of the UP techno-cultural complexes in the Zagros. Consequently, based on an OSL date of 48–45 kya for AH IVd, Heydari et al. (2021) have proposed that AHs IVc and IVd may represent the transition period between the MP and UP at Ghar-e Boof. Moving deeper, AHs V to VI yielded MP industries, though find densities are still very low, reflecting ephemeral occupations at the site in the Dasht-e Rostam region (Bretzke and Conard 2017; Conard and Zeidi 2019; Zeidi and Conard 2019). The OSL chronology for AHs V to VI resulted in the range of 81–45 kya, at a 68% confidence interval (Heydari et al. 2021).

Zooarchaeological, archaeobotanical, and lithic analyses for these layers are ongoing. Nevertheless, the preliminary assessment of animal bones has already revealed that the humans at Ghar-e Boof were the main agent of bone accumulation in the cave, and that while they consumed mostly caprines, other small- to very large-bodied ungulates and small-game animals were also part of the diet.

Material and methods

The Ghar-e Boof small vertebrate assemblage used for this study includes a total of 755 identified specimens from the early UP and MP sequence (AHs III to VI). The material was recovered during the four excavation campaigns conducted at the site between 2006–2007 and 2015–2017 (Conard and Ghasidian 2011; Conard and Zeidi 2019). In order to collect small vertebrates, archeologists water-screened all sediments through superimposed 5- and 2-mm mesh (Ghasidian 2014; Conard and Zeidi 2019), processing in total more than 18,000 L of sediment. A few small vertebrates were also documented and recovered as single finds.

Taxonomy

In this work, we describe all recovered taxa of microvertebrates, though micromammals, amphibians, and squamate reptiles represent better proxies for paleoenvironmental reconstructions than fish or small birds, especially because their unique habitat and ecologic requirements limit their geographic range (Andrews and O'Brien 2000; Avery 2007; Blain et al. 2008; Blain 2009; Belmaker and Hovers 2011).

We identified the small vertebrate remains recovered at Ghar-e Boof mainly by using the modern reference collection at the University of Tübingen. When necessary, we also consulted several taxonomic atlases and published papers for the study of micromammals (Yusefi 2002; Pavlinov 2008; Kryštufek and Vohralík 2005, 2009; López-García 2011; Tesakov 2016; Rey-Rodríguez et al. 2020), amphibians and squamate reptiles (Delfino 2004; Blain 2009; De Lapparent et al. 2020; Biton et al. 2021), fish (Escala and Miranda 2002; Keivany et al. 2016), and small birds (Baumel et al. 1993; Wójcik 2002; Kessler 2015; Kaboli et al. 2016). We analyzed this assemblage using a ZEISS Stemi 305 stereo microscope and photographed the material using a Zeiss Stereo Discovery V8 and a Keyence VHX-500F. Moreover, the quantification of the Ghar-e Boof microvertebrate remains is solely based on the number of identified specimens (NISP), which refers to the total number of skeletal elements and/or fragments that have been identified to their taxonomic order, family, genus, or species, without involving any further derived calculation (Grayson 1984; Lyman 2008).

Taphonomy

In the present paper, we preliminarily analyzed a total of 514 micromammal remains including incisors, molars, and mandibles according to the criteria described in Andrews (1990) and Fernández-Jalvo et al. (2016), observing the degree of digestion marks. We also observed the possible compression and uniaxial mechanical deformation for the fish remains (Blanco-Lapaz et al. 2021; Frontini et al. 2021) and the possible digestion in 63 humeri and ilia belonging to *Bufo/Bufotes* sp. In this study, we also analyzed possible bite marks. The presence of bite marks, crushed bones, and digestive marks can give us insight into predatory activities carried out by terrestrial carnivores and birds of prey (Andrews 1990; Nicholson 1993). The preliminary observations could indicate if the predation activity by birds of prey or carnivores was the origin of at least part of the accumulation. We also analyzed the evidence of burning on microvertebrate remains, using the method of five stages of thermal-induced discoloration following Cáceres et al. (2002), which are based on heat-induced color alterations described by Shipman et al. (1984) and Stiner et al. (1995) for large mammal bones (see also Lloveras et al. 2009b; Medina et al. 2012; Walker et al. 2015, Fernández-Jalvo and Avery 2015 and Rhodes et al. 2016 for applications to microvertebrates). The stages correspond to 0 (no discoloration), 1 (yellowish with reddish-brown spots; < 100 to 300 °C), 2 (dark brown to black coloration; < 400 to 550 °C), 3 (charred bone, dark black or blue coloration over 50–100% of the surface; 500 to < 700 °C), 4 (gray-white coloration, partial calcination; 650 to < 950 °C), and 5 (calcined bone, white coloration over 50–100% of the surface; > 700 °C) (Shipman et al. 1984; Cáceres et al. 2002).

Paleoenvironmental reconstruction

Here, we use the habitat weighting method, also known as the taxonomic habitat index (Evans et al. 1981; Andrews 2006) in order to reconstruct the paleoenvironment and landscape of Ghar-e Boof. The method is based on the present distribution of each taxon in a given type of habitat where it is presently found (Evans et al. 1981; Andrews 2006; modified by Blain et al. 2008; López-García 2011; Rey-Rodríguez et al. 2020). The analysis of zooarchaeological remains recovered at Late Pleistocene sites in the Zagros Mountains has yielded taxa that are still extant in Iran (e.g., Otte et al. 2007; Mashkour et al. 2009a; Bazgir et al. 2014, 2017; Rey-Rodríguez et al. 2020). Therefore, due to the fact that there are no extinct species at Ghar-e Boof, we assume that the small vertebrate species identified in this assemblage had equivalent ecological and habitat requirements to their modern relatives.

For this study, we applied the habitat weighting method to small mammal taxa, which was adapted from Blain et al.

Table 2 Scores attributed to each key micromammal species found at Ghar-e Boof according to its ecological requirements, used for the habitat weighting method: forest (Fo), shrubland (Sh), grassland (Gr), desert (De), wetland (We), and rocky (Ro)

Taxon	Species	Fo	Sh	Gr	De	We	Ro
Eulipotyphla	*Paraechinus* cf. *hypomelas*		0.33	0.33	0.33		
Lagomorpha	*Ochotona* cf. *rufescens*	0.33	0.33		0.33		
Rodentia	*Ellobius* sp.		0.33	0.33	0.33		
	Tatera indica	0.25	0.25	0.25	0.25		
	Meriones libycus		0.33		0.33	0.33	
	Meriones vinogradovi		0.5				0.5
	Mus musculus		0.33	0.33		0.33	

(2008), López-García (2011), and Rey-Rodríguez et al. (2020). Here, we distinguish the following types of habitats: forest (Fo), shrubland (Sh), grassland (Gr), desert (De), wetland (We), and rocky (Ro). Each taxon has a score of 1.00, which is divided between the habitats where the species are found today (Table 2; Rey-Rodríguez et al. 2020).

The score and the habitat preference of each species were obtained from the IUCN Red List of Threatened Species (https://www.iucnredlist.org/resources/spatial-data-download). Due to the small sample size available for each particular layer, we combined all UP layers (III to IVb) and all MP layers (V to VI), excluding the presumable MP-UP shift period layers (IVc to VI AHs) since the number and type of recovered remains are not enough for applying the habitat weighting method. Nevertheless, we also examine and discuss species' presence/absence and changes in relative species abundances by layer in order to identify possible environmental fluctuations over time at Ghar-e Boof.

Results

Taxonomic identifications, ecology, and current distribution

In the MP-UP Rostamian sequence of Ghar-e Boof, we identified a total of 498 micromammal remains to genus or species level, 16 micromammal remains to order/family level, 77 specimens identified as squamate reptiles, 75 remains of amphibians, 73 small bird remains, and 11 fish remains (Fig. 3, Table 3).

Micromammals

Order Lagomorpha Brandt, 1855.
Family Ochotonidae Thomas, 1897.
Genus *Ochotona* Link, 1795.
Ochotona cf. *rufescens* Gray, 1842.

Material NISP = 3. All of these specimens were recovered from AH IVc and correspond to a left maxillary fragment. Only the P4 and the M1 are present, though the alveolus of the M2 is also visible.

Description and discussion Generally, the key element to classify lagomorphs to species level is the p3, which is missing in our material. Our specimen shows the M1 and the P4 with the typical morphological characteristic to differentiate ochotonids from leporids: the absence of dentine bridges connecting anterior and posterior lobes (Laplana et al. 2015). Due the absence of the p3, we could not classify our specimen to the species level but in comparison with modern collections, the sample could be attribute to the Afghan pika (*Ochotona* cf. *rufescens*), the only representative of the Ochotonidae family in Iran (Firouz 2005; Čermák et al. 2006; Karami et al. 2016).

The record of Afghan pika at Ghar-e Boof would represent the southernmost appearance of this taxon in the Zagros. Besides Ghar-e Boof, archeologists tentatively documented Afghan pika in the MP-UP deposits of Warwasi Cave (Turnbull 1975), in the UP sequence of Yafteh Cave (Mashkour et al. 2009a), and during the Epipaleolithic of Palegawra Cave (Turnbull and Reed 1974). Hole and Flannery (1967) also reported the taxon in several other MP up to Epipaleolithic sites from the Khorramabad region, including Pa-Sangar, Ghar Arjaneh, Yafteh, Kunji, and Ghamari caves, but they did not specify from which sites Afghan pika were recovered.

Habitat and distribution In Iran, the Afghan pika mostly lives in cold shrublands and grasslands of mountainous areas with a very wide altitudinal range, including parts of the Alborz and Zagros mountains higher than 3000 m.a.s.l. (Firouz 2005; Karami et al. 2016). Moreover, the species occurs in rocky terrain and steppes, where it either burrows or uses crevices as shelter (Firouz 2005). Although the Afghan pika inhabits areas with very low temperatures, it does not hibernate (Gromov and Erbajeva 1995; Karami et al. 2016).

Order Rodentia Bowdich, 1821.
Family Cricetidae Fisher, 1817.
Subfamily Arvicolinae Gray, 1821.

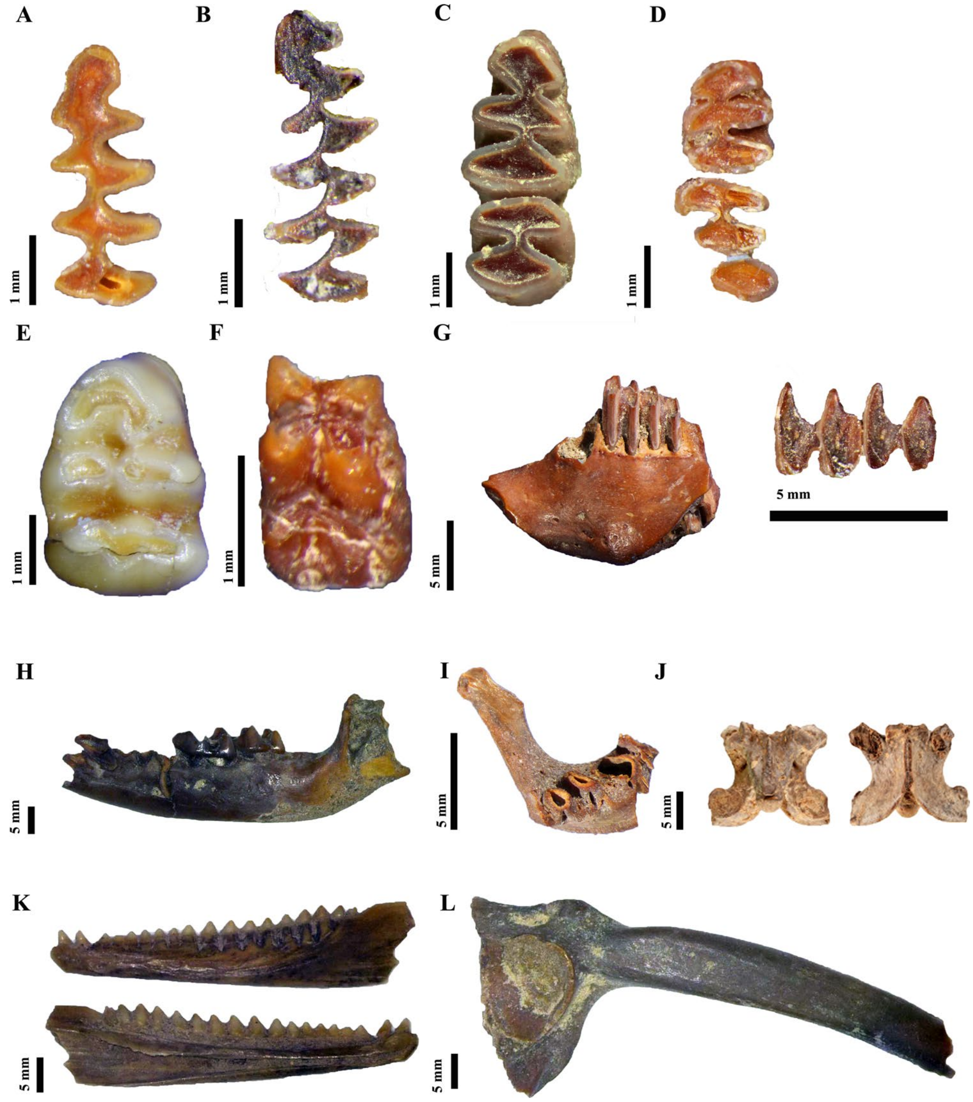

Fig. 3 Some microvertebrate remains identified at Ghar-e Boof. **A** *Elliobus* sp. left m1 (Qu: 6/8 Nr: 939 AH: VI); **B** *Microtus* cf. *irani* left m1 (Qu: 6/7 Nr: 1213 AH: IVc); **C** *Meriones vinogradovi* right m1-m2 (Qu: 6/7 Nr: 625 AH: III); **D** *Meriones lybicus* (Qu: 6/7 Nr: 1223 AH: IVc); **E** *Tatera indica* right m1 (Qu: 6/9 Nr: 488 AH: III); **F** *Mus musculus* right m1 (Qu: 7/8 Nr: 136, AH: III); **G** *Ochotona* cf. *rufescens* fragment of left maxillary (P4-M1) and occlusal view (P4-M1) (Qu: 6/7 Nr: 151AH: IVc); **H** *Paraechinus* cf. *hypomelas* incomplete left mandible (p1, m1, and m2) (Qu: 6/2 Nr:196 AH: IV); **I** *Chondrostoma* sp. left branchial arch (Qu: 6/7 Nr: 743 AH: III); **J** *Malpolon insignitus* trunk vertebra (Qu: 6/9 Nr: 244 AH: VI); **K** *Agamidae* left dentary (Qu: 7/2 Nr: 76 AH: III); **L** *Bufo/Bufotes* sp. right ilium (Qu: 6/9 Nr: 252 AH: III). Qu: quadrant, Nr: register number, AH: archeological horizon

Material NISP = 16. AH VI (NISP = 2), AH Vc (NISP = 3), AH Va (NISP = 1), AH IIIc (NISP = 2), AH IIIb (NISP = 1), AH IIIa (NISP = 4), and AH III (NISP = 3). These remains, all of them corresponding to fragmentary molars, were not identified to the genus level because of their poor preservation and a lack of key characteristics.

Genus Microtus Schrack, 1798.
Microtus sp.

Material NISP = 24. Molars from *Microtus* were found in AH VI (NISP = 4), AH Vc (NISP = 1), AH IIIb (NISP = 11), and AH III (NISP = 8).

Description and discussion Our material can only be attribute to genus level as they exhibit the basic morphology and characteristics for the *Microtus* genus, consisting of an anterior cap (AC) with five alternating and closed triangles. The second triangle (counting from the posterior end of the tooth) is not as wide (labiolingually) as the first (Bell and Bever 2006; López-García 2011).

Habitat and distribution Due to the high diversity of species (about 62 are placed within this genus and are distributed across North America, Europe, and Asia) and habitats, it is not possible to attribute a specific habitat or distribution for this genus (Musser and Carleton 2005).

Microtus cf. *irani.*

Material NISP = 1. The only remain belonging to this species corresponds to a left m1 from AH IVc.

Description and discussion Four buccal and five lingual reentrant angles with a posterior lobe, seven triangles, and an AC characterize the *Microtus* m1 (Kryštufek and Vohralík 2009).

Table 3 Identified taxa from Ghar-e Boof from layer VI to layer V (MP), from layer IVd to layer IVc (transition period), and from layer IVb to layer III (UP Rostamian). All values correspond to NISP (number of identified specimens)

Order	Taxon	Middle Paleolithic (MP)						Transition		Upper Paleolithic (UP)							Total
		(81–45 ka)						(48–45 ka)		Rostamian (42–35 ka)							
		VI	Vd	Vc	Vb	Va	V	IVd	IVc	IVb	IVa	IV	IIIc	IIIb	IIIa	III	
Chiroptera	Chiroptera indet															2	**2**
Eulipothyphla	Erinaceidae													1		2	**3**
	Paraechinus cf. *hypomelas*				1							8				4	**13**
Lagomorpha	*Ochotona* cf. *rufescens*								3								**3**
Rodentia	Arvicolinae indet	2		3		1							2	1	4	3	**16**
	Microtus sp.	4		1										11		8	**24**
	Microtus cf. *irani*								1								**1**
	Ellobius sp.															3	**3**
	Tatera indica															1	**1**
	Meriones sp.	1	2	4		6	2							18	3	25	**61**
	Meriones libycus	1	3	5									3	10	5	49	**76**
	Meriones vinogradovi	4	9	17		7	4		4			9	15	25	24	194	**312**
	Mus musculus															4	**4**
Reptilia	Agamidae indet			1	4	4	1	2	4	5	6	15	8	8		5	**63**
	Lacertidae indet											1					**1**
	M. insignitus	1			1											5	**7**
	Viperidae indet					1										1	**2**
	Ophidia indet				1		1									2	**4**
Amphibia	*Bufo/Bufotes* sp.			4	5	3						2	1	20	4	24	**63**
	Anura indet								1		1			2		8	**12**
Teleostei	Leuciscinae													8	1	1	**10**
	Chondrostoma sp.															1	**1**
Aves (small)	Passeriformes	4	2	2	7	4		3	10	8	1	14	9	4		5	**73**
Total		**17**	**16**	**37**	**19**	**26**	**8**	**5**	**23**	**13**	**8**	**49**	**38**	**108**	**41**	**347**	**755**

In *M. irani*, triangles T1–T5 are closed, but T6–T7 are open and not parallel with one another (Rey-Rodríguez et al. 2021).

Habitat and distribution The Persian vole is common in grasslands from Iran to the Caucasus (Karami et al. 2016).

Genus *Ellobius* Fischer, 1814.
Ellobius sp.

Material NISP = 3. These specimens were recovered from AH III and correspond to a maxilla fragment showing just a left M3 and a fragmentary right M3. We did not distinguish specimens to species level due to the lack of discriminant key teeth, such as the M1 or m1 (Rey-Rodríguez et al. 2021).

Description and discussion Remains were attributed to this genus by the presence of roots visible in adults. Molars lack cement in the re-entrant angles. Both M3 and m3 are reduced and smaller than the other molars, with three triangles on the labial side and two triangles on the lingual side (Gharkheloo and Kivanç 2003). In Iran, the genus *Ellobius* is currently represented by three species: *E. fuscocapillus*, *E. lutescens*, and *E. talpinus* (Kryštufek and Vohralík 2005; Karami et al. 2016).

Habitat and distribution Mole-voles of the genus *Ellobius* are species specialized for subterranean life (Coşkun 2001; Coşkun and Ulutürk 2003). In general, *Ellobius* species can presently be found in steppes, grasslands, and semi-deserts from Eastern Europe to Central Asia (Kryštufek and Vohralík 2005).

Family Muridae Illiger, 1811.
Subfamily Gerbillinae Gray, 1825.
Genus *Tatera* Latesta, 1882.
Tatera indica Hardwicke, 1807.

Material NISP = 1. We only identified a right lower m1 recovered from AH III.

Description and discussion The Indian gerbil (*Tatera indica*) presents hypsodont molars but to a lesser degree than *Meriones*. The molars in adults consist of a series of plain straight plates, with three transverse plates in the first molars (Kryštufek and Vohralík 2009). The anteroconid in Gerbillinae includes initially three separate elements, exteroantroconid, interoanterioconod, and an accessory cusplet (Denys 2017), the protuconulid. *Tatera* shows the first two isolated cusps on minimally worn molars (Pavlinov 2008).

This gerbil has previously been documented in the MP deposits of Warwasi Cave (Turnbull 1975). According to Hashemi et al. (2006), the taxon is also present in the UP layers of Yafteh Cave, though it is not mentioned in later zooarchaeological studies about the site (see Otte et al. 2007; Mashkour et al. 2009a). In any case, our specimen constitutes the southernmost record of the Indian gerbil in the Zagros.

Habitat and distribution The Indian gerbil is found from Mesopotamia (where it is known in Turkey, Syria, and Iraq), across Iran, Afghanistan, and Pakistan, to India and Sri Lanka (Kryštufek and Vohralík 2009). *T. indica* is the only species of this genus currently present in Iran (Karami et al. 2016). The species lives in steppe and desert habitats of eastern, central, and southern Iran. The Indian gerbil is less adapted to desert life than other gerbils and cannot tolerate frost (Kryštufek and Vohralík 2009; Karami et al. 2016).

Genus Meriones, Illiger 1811.
Meriones sp.

Material NISP = 61. The molars from *Meriones* were not attribute to the species level because they were fragmentary or had no diagnostic characteristics They were recovered from AH VI (NISP = 1), AH Vd (NISP = 2), AH Vc (NISP = 4), AH Va (NISP = 6), AH V (NISP = 2), AH IIIb (NISP = 18), AH IIIa (NISP = 3), and AH III (NISP = 25).

Description and discussion Typical morphology of *Meriones* includes semihypsodont molars with prismatic enamel triangles linked by a longitudinal crest and no trace of cusps (Dianat et al. 2017; Rey-Rodríguez et al. 2021). Although there are several species belonging to the genus *Meriones*, only some of them currently live in the southern Zagros Mountains (i.e., *M. crassus*, *M. persicus*, *M. hurrianae*, *M. lybicus*, and *M. vinogradovi*; Karami et al. 2016).

Habitat and distribution The distribution of the genus *Meriones* encompasses North Africa, Central Asia, Transcaucasia, Turkey, and Pakistan (Yiğit et al. 2003; Darvish 2011; Darvish et al. 2014; Stoetzel et al. 2017). Its preferred habitats are clay and sandy deserts (Kryštufek and Vohralík 2009).

Meriones libycus Lichtenstein, 1823.

Material NISP = 76. Molars and mandibles of this species were recovered from AH VI (NISP = 1), AH Vd (NISP = 3), AH Vc (NISP = 5), AH IIIc (NISP = 3), AH IIIb (NISP = 10), AH IIIa (NISP = 5), and AH III (NISP = 49).

Description and discussion We provisionally attributed these specimens to the Libyn jird, but will investigate this further due to the lack of this species in our reference collection. Despite this, the Ghar-e Boof specimens attributed to *M. lybicus* show the typical morphology of the taxa, including semi-hypsodont molars with prismatic enamel triangles linked by a longitudinal crest and with no trace of cusps (Pavlinov 2008; Kryštufek and Vohralík 2009). We could distinguish *M. lybicus* from *M. vinogradovi* using the first lower molar (m1), since in occlusal view, the anteroconid shows an ascendent oblique elongation, but in *M. lybicus*, it is more narrow and flattened than in *M. vinogradovi.* The paraflexus-protoflexus and the metaflexus-hypoflexus pairs are more or less parallel in both species but it is clear that in *M. libycus*, the pairs are closer to each other than in *M. vinogradovi.* The second lower molar (m2) is also a key tooth to distinguish both species. *M. vinogradovi* presents an H-shaped m2, while in *M. libycus*, this molar is much more oblique (Mamkhair et al. 2007; Pavlinov 2008; Kryštufek and Vohralík 2009).

If confirmed, the presence of the Libyan jird at Ghar-e Boof would constitute the first record of this taxon during the MP in the Zagros Mountains. Until now, archeologists have only reported Libyan jird remains in the UP deposits of Yafteh Cave (Otte et al. 2007; Mashkour et al. 2009a).

Habitat and distribution The Libyan jird is widely distributed, ranging from North Africa through Arabia, Jordan, Iraq, Syria, Transcaucasia, Iran, Turkmenistan, Afghanistan, Pakistan, and Kazakhstan to Xinjiang, in Western China (Kryštufek and Vohralík 2009). Overall, this species is well-adapted to arid conditions and inhabits mostly vegetated arid landscapes, including steppes, semi-deserts, and deserts, but is also associated with clay, loess, gravel, sandy, or hard soil substrates (Kryštufek and Vohralík 2009). Nevertheless, the Libyan jird prefers dry and exposed places (Pavlinov et al. 1990). In Iran, the species is distributed widely throughout the country, but lives mostly on Saxaul shrublands and the edges of cultivation fields and avoids

Hyrcanian forests, high mountains, and coastal areas (Karami et al. 2016).

Meriones vinogradovi Heptner, 1931.

Material NISP = 308. We identified Vinogradov's jird molars, maxillae and mandibles in AH VI (NISP = 4), AH Vd (NISP = 9), AH Vc (NISP = 17), AH Va (NISP = 7), AH V (NISP = 4), AH IVc (NISP = 4), AH IV (NISP = 9), AH IIIc (NISP = 15), AH IIIb (NISP = 25), AH IIIa (NISP = 24), and AH III (NISP = 194).

Description and discussion As mentioned previously, *M. libycus* can be distinguished from *M. vinogradovi* by using both the M/m1 and the M/m2 as key teeth. As a main characteristic, we observed in the m1 a less flattened AC and more distance between the paraflexus and protoflexus, which is also present between the metaflexus and protoflexus. Moreover, *M. vinogradovi* shows a typical H-shaped m2, unlike *M. lybicus* (Pavlinov 2008; Kryštufek and Vohralík 2009).

The Vinogradov's jirds from our assemblage represent the first and oldest record of the taxon in the MP of the Zagros. So far, it has only been documented in the UP sequence of Yafteh Cave (Otte et al. 2007; Mashkour et al. 2009a).

Habitat and distribution Presently, this species shows a range largely restricted to Transcaucasia and northern Iran, including also Syria and adjacent Turkey, but the fossil history of Vinogradov's jird has not yet been well-documented (Kryštufek and Vohralík 2009). In Iran, the species is most common in the northwestern part of the country, and its typical habitats comprise cool semideserts and high elevation steppes (Kryštufek and Vohralík 2009). Furthermore, it requires deep soil for burrowing. Vinogradov's jird prefers dry soils, and it does not occur on sands and on substrates of rocky debris (Kryštufek and Vohralík 2009).

Genus *Mus* Linnaeus, 1785.
Mus musculus Linnaeus, 1785.

Material NISP = 4. A complete right hemi-mandible was recovered from AH III, containing all three molars (m1–m3).

Description and discussion In our sample, the m1 shows the key characteristics for distinguishing this genus: the dental ends of mesial and central cusps on first lower molars fuse early and the mesiolabial cusp is small. The anterior half of the m1 also has a symmetrical X pattern formed at the anterior portion of the tooth (Siahsarvie and Darvish 2008; Rey-Rodríguez et al. 2020). Previously, in the Zagros, archeologists have documented this taxon in the MP and UP layers of Kaldar Cave (Bazgir et al. 2017; Rey-Rodríguez et al. 2020).

Habitat and distribution Currently, the house mouse (*M. musculus*) is spread worldwide, living in close association with humans as a commensal animal, but it is also found in the wild (Firouz 2005; Karami et al. 2016). In Iran, the species is distributed throughout the whole country, with the exception of completely dry areas like the Dasht-e Kavir and the Dasht-e Lut, both located in the middle of the Iranian Plateau (Karami et al. 2016).

Order Eulipotyphla Waddell et al., 1999.
Family Erinaceidae Fischer, 1814.

Material NISP = 3. The material comprises the distal epiphysis of a humerus, a small mandibular fragment, and an isolated molar recovered in AH IIIb (NISP = 1) and AH III (NISP = 2). Due to their fragmentary conditions and the lack of modern Iranian Erinaceidae taxa in our comparative collection, it was not possible to attribute them to genus or species.

Genus *Paraechinus* Trouessart, 1879.
Paraechinus cf. *hypomelas* Brandt, 1836.

Material NISP = 13. The specimens consist of incomplete mandibles, with and without teeth, found in AH Vb (NISP = 1), AH IV (NISP = 8), and AH III (NISP = 4). The most complete mandible was from AH IV, which has the p1, m1, and m2 in situ.

Description and discussion Today, four species of hedgehog are present in Iran: *Erinaceus concolor*, *Hemiechinus auritus*, *Paraechinus aethiopicus*, and *Paraechinus hypomelas* (Harrison and Bates 1991; Firouz 2005; Karami et al. 2016). The morphological characteristics of the mandible, such as the angle (close to 90°) between the ramus and the mandible body and the distribution of the cusps for m2 and m1 (Yusefi 2002; Yusefi et al. 2016), fit for the attribution of the Brandt's hedgehog (*P. hypomelas*).

If our identification of these remains as Brandt's hedgehog is correct, then it would be the first appearance of this taxon in the Paleolithic record of the Zagros Mountains. However, other species from the Erinaceidae family have been reported for this region. Archeologists found European hedgehogs (*Erinaceus europaeus*) or just *Erinaceus* sp. in the Late Pleistocene-Holocene levels of Wezmeh Cave (Mashkour et al. 2009b), in the UP layers of Gelimgoush

Cave (Heydari-Guran et al. 2021b), and in the Epipaleolithic deposits of Palegawra Cave (Reed and Braidwood 1960; Turnbull and Reed 1974). Moreover, the long-eared hedgehog (*Hemiechinus auritus*) has also been documented in Palegawra (Turnbull and Reed 1974), and tentatively in some of the Pleistocene sites from the Khorramabad region studied by Hole and Flannery (1967). Finally, Bazgir et al. (2014) reported indeterminate Erinaceidae remains from the Pleistocene deposits of Ghamari Cave.

Habitat and distribution Brandt's hedgehog has been reported across Iran, except in northern forested areas and other northwestern regions of the country. This species usually lives in deserts and the foothills of steppe areas (Karami et al. 2016).

Order Chiroptera Blumenbach, 1779.

Material NISP = 2. Only two specimens of chiroptera were found in our assemblage, which consist of two distal fragments of humeri, one in AH IV, and another in AH III. Due to the wide diversity of different genera belonging to this order in Iran (e.g., *Eptisicus*, *Hipposideros*, *Hypsugo*, *Myotis*, *Miniopterus*, *Nyctinomus*, *Nyctalus*, *Otonycteris*, *Pipistrellus*, *Rhinolophus*, *Rhinopoma*, *Tadarida*, *Vespertilio*, to name just a few; Karami et al. 2016), and the lack of Iranian bats in modern comparative collections, it was not possible to classify the remains further.

Squamate reptiles

Order Squamata Oppel, 1811.
Family Agamidae Gray, 1827.

Material NISP = 63. Except for AHs VI, Vd, and IIIa, dentaries belonging to this family are present throughout the entire sequence: AH Vc (NISP = 1), AH Vb (NISP = 4), AH Va (NISP = 4), AH V (NISP = 1), AH IVd (NISP = 2), AH IVc (NISP = 4), AH IVb (NISP = 5), AH IVa (NISP = 6), AH IV (NISP = 15), AH IIIc (NISP = 8), AH IIIb (NISP = 8), and AH III (NISP = 5). The main characteristic of the Agamidae dentaries is the presence of an acrodont dentition showing a general triangular shape and the teeth are laterally flattened (Blain 2009). Once again, based on the wide diversity of this family in Iran and the lack of specimens in modern comparative collections, we could not determine the Ghar-e Boof specimens to genus or species level. Several genera are present in Iran, such as *Calotes*, *Laudakia*, *Paralaudakia*, *Phrynocephalus*, and *Trapelus*, with each of the genera containing several species (Mozaffari et al. 2016).

Family Lacertidae Oppel, 1811.

Material NISP = 1. We only found one fragmentary trunk vertebra that belongs to the family Lacertidae, recovered from AH IV, but a more precise identification was not possible. Overall morphology of this vertebra is consistent with an attribution to this family excluding other groups of Squamata such as Agamidae or Ophidia.

Suborder Ophidia Linnaeus, 1758.

Material NISP = 4. Here, we include very fragmentary trunk vertebrae from AH Vb (NISP = 1), AH V (NISP = 1), and AH III (NISP = 2).

Family Lamprophiidae Fitziger, 1843.
Genus *Malpolon* Fitzinger, 1826.
Malpolon insignitus Geoffroy St. Hilarire, 1809.

Material NISP = 7. Isolated trunk vertebrae were present in AH VI (NISP = 1), AH Vb (NISP = 1), and AH III (NISP = 5).

Description and discussion We attributed these vertebrae to the Eastern Montpellier snake (*M. insignitus*) on the basis of the haemal keel, which is thin and sharp before the condyle (Bendrey et al. 2020). This is the first record of *M. insignitus* during the MP in the Zagros Mountains. Previously, Mashkour et al. (2009b) had only identified the Western Montpellier snake (*M. monspessulanus*) in Wezmeh Cave. The authors, probably used to the old taxonomy when they studyied those remains. Our current knowledge about the distribution of species of the genus *Malpolon* dictates that the species *M. monspessulanus* is not distributed eastward beyond northwestern Italy and central Algeria, so its identification outside of this region is not correct nowadays and the individuals considered before to be *M. monspessulanus* are now attributed to the new species *M. insignitus* (Mozzaffari et al. 2016).

Habitat and distribution The Eastern Montpellier snake is widely distributed across Eurasia (Mozaffari et al. 2016). The species lives in diverse types of habitats, such as forest, shrublands, grasslands, foothills, rocky areas, and semi-desert (Firouz 2005; Mozaffari et al. 2016).

Family Viperidae Oppel, 1811.

Material NISP = 2. We only identified two isolated trunk vertebrae as Viperidae, one from AH Va and another one from AH III. Although the shape of the caudal area of the postzygapophysis is typical for the genus *Vipera* (Markert 1978; Blain 2009), we could not attribute these specimens with confidence to the genus level. The remains show poor preservation and there is a lack of Iranian taxa in the modern comparative collections. Moreover, the family shows a great diversity in Iran, with 13 different species belonging to the genera *Cerastes*, *Echis*, *Eristocophis*, *Gloydius*, *Macrovipera*, *Montivipera*, *Pseudocerastes*, and *Vipera* (Mozaffari et al. 2016).

Amphibians

Order Anura Duméril, 1806.

Material NISP = 12. Here, we included several fragmentary postcranial elements such as vertebrae, humeri, and ilium that lack discriminant traits. We found indeterminate Anura specimens in AH IVc (NISP = 1), AH IVa (NISP = 1), AH IIIb (NISP = 2), and AH III (NISP = 8).

Family Bufonidae Gray, 1825.
Genus *Bufo/Bufotes* Garsault, 1764.
Bufo/Bufotes sp.

Material NISP = 63. Most of the toad (*Bufo/Bufotes* sp.) remains that correspond to ilia and humeri were present in AH Vc (NISP = 4), AH Vb (NISP = 5), AH Va (NISP = 3), AH IV (NISP = 2), AH IIIc (NISP = 1), AH IIIb (NISP = 20), AH IIIa (NISP = 4), and AH III (NISP = 24).

Description and discussion For anurans, the ilium is widely considered to be the single best element upon which to base fossil identifications when isolated bones are all that are available (Bever 2005). The *Bufo/Bufotes* genus determination is based on the absence of a dorsal crest and the presence of an upper tuberosity that is flat and exhibits a rounded dorsal edge (Blain 2009). In Iran, there are several species that belong to the genus *Bufo/Bufotes*, such as *B. bufo*, *B. eichwaldi*, *B. kavirensis*, *B. luristanicus*, *B. oblongus*, *B. olivaceus*, *B. stomaticus*, *B. surda*, and *B. viridis* (Yousefi-Siahkalroodi et al. 2013). Due to this wide diversity, and the lack of Iranian toads in our comparative collection, it was not possible to attribute the remains recovered at Ghar-e Boof to the species level.

Habitat and distribution *Bufo/Bufotes* represent the most numerous and wide spread genus of amphibians in Iran, most likely because of their ecological tolerance (Firouz 2005). Overall, amphibians are very dependent on humid habitats (Blain et al. 2008); however, toads have a particularly dry skin through which water is not easily lost, enabling them to live and survive in more arid areas than other amphibians (Firouz 2005). Therefore, although most toads need to have access to water resources and thus inhabit areas near marshes, shallow ponds, streams, and rivers, they can also live in meadows, rocky areas, and dry areas (Yousefi-Siahkalroodi et al. 2013).

Fish

Order Cypriniformes Bleeker, 1859.
Family Leusciscinae Bonaparte, 1835.

Material NISP = 10. All of these specimens correspond to precaudal and caudal vertebrae from AH IIIb (NISP = 8), AH IIIa (NISP = 1), and AH III (NISP = 1). We could not identify the remains up to the genus or species level because of the lack of Iranian taxa in our comparative collection, as well as the wide diversity of the family Leuciscinae in Iran (Keivany et al. 2016).

Genus *Chondrostoma* Agassiz, 1832.
Chondrostoma sp.

Material NISP = 1. This genus is represented in our assemblage by just a left pharyngeal arch fragment from AH III.

Description and discussion We determined this branchial arch as nase (*Chondrostoma* sp.) based on the compressed hook shape of the branchial teeth and the presence of just one tooth row (Escala and Miranda 2002). Currently, only two species are presently living in Iran: *C. cyri* and *C. regium* (Keivany et al. 2016). However, due to the lack of these species in our comparative collection, as well as the fragmentary state of this specimen, we could not attribute it to either of the two species.

Our study represents the first record of this genus in a Paleolithic site of the Zagros. Overall, fish remains in MP and UP Iranian sites are very rare. So far, archeologists have only reported the presence of cyprinids and chubs (*Leuciscus* sp.) in Yafteh Cave (Otte et al. 2007; Mashkour et al. 2009a) and some undetermined fish remains in Palegawra Cave, which still need to be analyzed (Asouti et al. 2020).

Habitat and distribution Kura undermouth (*C. cyri*) is located exclusively in the Caspian Sea basin (Aras River) and lives mainly in streams and rivers. As for the Mesopotamian nase (*C. regium)*, it is more widely distributed and is present in the Tigris (Karun, Marun, Bazoft, Karkheh), Isfahan (Zayandehrud River), and Fars (Kor River) basins. The Mesopotamian nase lives in lakes, reservoirs, and rivers with stone grounds and still waters (Keivany et al. 2016).

Small birds

Order Passeriformes Linnaeus, 1758.

Material NISP = 73. The small bird assemblage of Ghar-e Boof consists mostly of postcranial elements such as humeri, tibiotarsus, tarsmetatarsus, or vertebrae recovered from almost all layers, except for AHs V and IIIa: AH VI (NISP = 4), AH Vd (NISP = 2), AH Vc (NISP = 2), AH Vb (NISP = 7), AH Va (NISP = 4), AH IVd (NISP = 3), AH IVc (NISP = 10), AH IVb (NISP = 8), AH IVa (NISP = 1), AH IV (NISP = 14), AH IIIc (NISP = 9), AH IIIb (NISP = 4), and AH III (NISP = 5). In Iran, the order Passeriformes encompasses more than 200 species (Kaboli et al. 2016). Due to the great diversity of species and the lack of Iranian taxa in our collection, we could not go deeper in the taxonomical classification of these remains. Therefore, this material would be considered a subject of study for future researchers.

Taxonomic remarks

In the MP sequence of Ghar-e Boof (Table 3, Fig. 3), the most abundant identified taxa are jirds (*Meriones* sp. and *M. vinogradovi*, with a few examples of *M.* cf. *lybicus*). Among other genera and species of micromammals, we also documented the presence of voles (*Microtus* sp.), mole-voles (*Ellobius* sp.), and Brandt's hedgehog (*Paraechinus* cf. *hypomelas)*. Moreover, we identified squamate reptiles and amphibians, such as agamids, lizards, vipers, Eastern Montpellier snake (*M. insignitus*), toad (*Bufo/Bufotes* sp.), and other indeterminate Anura (Table 3).

Except for AH V, small birds or Passeriformes were recorded throughout the entire MP sequence. Overall, rodents are well-represented in AHs VI to V, with the exception of AH Vb. However, they are practically missing in AHs IVd and IVc, and also in AHs IVb to IV. The drastic reduction of rodents corresponds with the transition period between the MP and the beginning of the early UP Rostamian techno-complex (Heydari et al. 2021; see Table 1). The only small mammals recovered in these layers are the Afghan pika (*O.* cf. *rufescens*, NISP = 3), the Persian vole (*M.* cf. *irani,* NISP = 1), and the Libyan jird (*M.* cf. *lybicus*, NISP = 4), all of them in AH IVc, along with a few squamate reptiles and amphibians (agamids, lizards, toads, and indeterminate Anura) and small birds.

In the early UP Rostamian layers of Ghar-e Boof, the majority of the rodents reappear in AH IIIc (Table 3). From AH IIIc upwards, the small vertebrate assemblage is once again dominated by jirds (*Meriones* sp. and *M. vinogradovi*, *M.* cf. *libycus*) followed by voles (*Microtus* sp.), mole-voles (*Ellobius* sp.), Indian gerbil (*T. indica*), and the house mouse (*M. musculus*). Alongside these rodents, we also recorded insectivores, including the Brandt's hedgehog (*P.* cf. *hypomelas*), and other indeterminate Erinaceidae and bats. Regarding squamate reptiles, amphibians, and small birds, we did not observe any apparent changes with previous horizons. However, for the first time, we documented fish remains in AHs IIIb to III, represented by indeterminate cyprinids and nase (*Chondrostoma* sp.).

Taphonomic observations

According to our preliminary observations of different degrees of digestion in our assemblage of micromammals and *Bufo/Bufotes* remains (mostly very light or light; < 20% of the bone surface is damaged), the possible predator responsible for part of the accumulation could be a category 1 predator such as the Barn owl (*Tyto alba*, Fernández-Jalvo et al. 2016). This species, with a generalist diet in areas where prey is scarce, is currently present in the area. Barn owls are also cavity nesters and are sedentary, indicating that their prey spectrum is assumed to be a good representation of the ecosystem in which they are present (Kaboli et al. 2016). No mechanical deformation, breakage, or polishing on the bone surface is present in cranial or postcranial elements (Fernández-Jalvo et al. 2016; Frontini et al. 2021).

We also document the presence of one individual in layer III in anatomical connection (skull, mandibles, and cervical vertebrae) likely indicating in situ mortality, although some birds of prey such as the Eurasian eagle owl could produce pellets with skulls in connection with mandibles (Andrews 2006; Fernández-Jalvo et al. 2016). In this case, the presence of cervical vertebrae in anatomical connection and lack of digestion marks on teeth further indicates that the animals were not introduced to the site by predators. Other microvertebrates seemed to have accumulated similarly, such as agamids, which can die of thermal stress during hibernation (Rastegar-Pouyani and Torki 2007). Bite marks, crush marks, or digestive marks were also absent on the fish remains, which means that carnivores or birds can be ruled out as accumulative agents for fish specimens (Nicholson 1993).

In terms of burning, we recovered just a dozen burnt remains, all of them from the upper layers of the sequence (AH III). All of these specimens show stage 3 of thermal discoloration, characterized by blackening across the entire bone surface. This stage indicates a fire temperature from 500 to < 700 °C (Cáceres et al. 2002).

In general, our observations are preliminary and further ongoing taphonomic studies will provide further data about the origin of the microvertebrate accumulation and post-depositional modifications.

Paleoenvironmental reconstructions

We present the results of our paleoenvironmental reconstructions obtained with the habitat weighting method in Fig. 4. These data, based exclusively on micromammals, indicate that the paleoenvironment of Ghar-e Boof was mainly characterized by warm, arid conditions, with the presence of

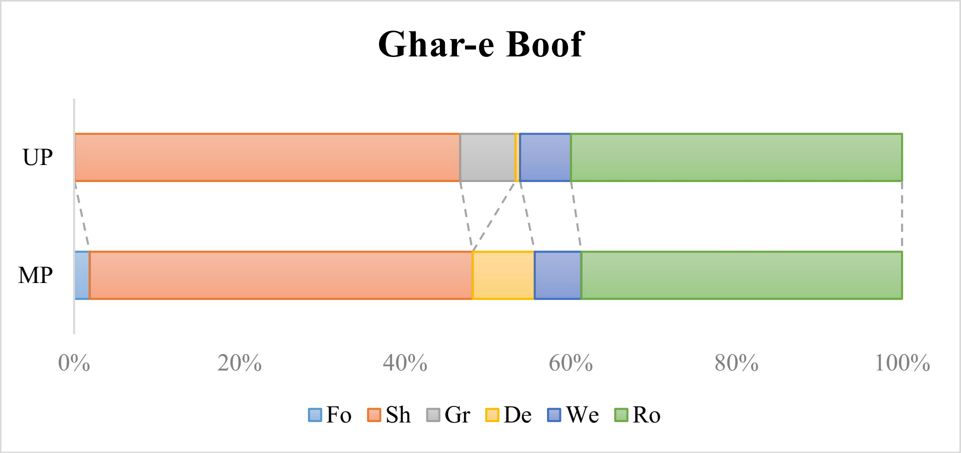

Fig. 4 Results of the habitat weighting method for MP and UP layers based on NISP. Forest (Fo), shrubland (Sh), grassland (Gr), desert (De), wetland (We), and rocky (Ro)

shrublands and rocky terrain. These environmental conditions are mostly derived from the predominance of Vinogradovi's jird throughout the entire stratigraphic sequence (Tables 2 and 3). The results also provide evidence of wetlands and permanent water sources close to the site, which is inferred from the presence of Lybian jird in both MP and UP layers and the house mouse in the UP. To a lesser extent, the surrounding landscape of the cave included grasslands, open forests, and desert or semi-desert areas, though their relative proportions fluctuated between the MP and UP (Fig. 4).

Although desert and semi-desert conditions decrease during the UP, there is also an increase in grassland-adapted species, in parallel with a decline in forest habitats (Fig. 4). Overall, our data seem to suggest a slight increase in aridity at Ghar-e Boof during the UP in comparison to the MP.

Some squamate reptiles, amphibians, and fish support the general paleoenvironmental conditions inferred from small mammal taxa. Among all the squamate reptiles recovered at Ghar-e Boof, we were only able to identify the Eastern Montpellier snake (*M. insignitus*) to the species level, while we classified the rest to family (Agamidae, Lacertidae, and Viperidae). The Eastern Montpellier snake is not a good paleoenvironmental indicator, since it inhabits diverse types of habitats (i.e., forest, shrublands, grasslands, rocky areas, and semi-deserts, Firouz 2005; Mozaffari et al. 2016). However, most Viperidae and Agamidae taxa in Iran live in warm, rocky outcrops, while there are some species that can be found near small bushes, or in arid, semi-desert, or desert areas (Firouz 2005; Mozaffari et al. 2016). Toads (*Bufo/Bufotes* sp.) in the assemblages suggest the presence of meadows and wetlands, such as marshes and ponds (Yousefi-Siahkalroodi et al. 2013). Moreover, the recovery and identification of fish remains, such as Leuciscinae cyprinids and nase, reflect the proximity of the cave to rivers with rocky beds and still waters (Keivany et al. 2016). As mentioned above, Ghar-e Boof is located about 200 m away from the Solak seasonal stream. Besides this stream, the Dasht-e Rostam region is drained by the Fahliyan River, with a perennial flow, and the Shiv stream, also seasonal and contains more than 50 springs (Conard and Ghasidian 2011; Heydari-Guran 2014). Therefore, despite the predominance of warm, arid conditions during most of the MP and UP at the site, hunter-gatherers had access to permanent and abundant water resources during most of the year.

Discussion

Ghar-e Boof: paleoenvironmental reconstructions and archeological implications

Our results provide new data for a better understanding of the paleoenvironmental context of Ghar-e Boof based on microvertebrates. The combination of data belonging to the micromammals, reptiles, amphibians, and fish record is an important tool to characterize the MP-UP landscape around Ghar-e Boof as dominated by warm, arid conditions, with the presence of shrublands and rocky terrain. Amphibians and fish also indicated the presence of water sources. Available archaeobotanical and zooarchaeological data describe a similar landscape characterized by dry/arid conditions with the presence mostly of grass and scrubland (Baines et al. 2014), inhabited by sheep/goat and gazelles (Mata-González et al. 2022).

A second goal of this study was to assess chronologically whether the cultural and/or demographic shifts documented at Ghar-e Boof correlate with local environmental fluctuations. Find densities of lithic artifacts were low in AHs IVd and IVc (Conard and Zeidi 2019; Heydari et al. 2021), so any cultural attribution to either the MP or UP has to be made with caution. However, these layers lack characteristic components associated with the Zagros UP technocultural complexes, such as Arjeneh points and perforated shells, which indeed have been observed in the subsequent upper layers (AHs IVb–IV and above; Heydari et al. 2021).

Whereas OSL ages for AH IVd fall in the range of 48–45 kya, AHs IV to IVa have been dated between 42 and 40 kya (Heydari et al. 2021). As a result, in the same study, Heydari and colleagues suggested that AHs IVc–IVd represent the period between the MP and the Rostamian, while AHs IVb–IV correspond to the onset of the UP at Ghar-e Boof and in the Zagros Mountains as a whole. Based on the analysis of lithic artifacts, Bretzke and Conard (2017) hypothesized that the early UP occupation in the southern Zagros might have been related to a displacement of small groups carrying MP industries. There is the question as to whether paleoenvironmental fluctuations contributed to such a cultural and/or demographic replacement at Ghar-e Boof or in the Dasht-e Rostam region more broadly. Sample size is relatively small for AHs IVd to IV in comparison with other MP and UP layers. Nonetheless, the analysis of species presence/absence, along with the discussion of their habitat preferences and requirements, also allows us to draw qualitative paleoenvironmental inferences for these layers. In general, as mentioned above, rodents (mostly murids) are well-represented in AHs VI to V (MP) and AHs IIIc to III (UP). However, one of the most striking results of our study is that during the shift from the MP to the UP (AHs IVd to IV, Table 3), we document a temporary drastic reduction of rodents and the first and only record of Afghan pika (*O.* cf. *rufescens*) at the site occurs in AHs IVc.

Although some authors associate remains of lagomorphs with the presence of large birds of prey (Redpath et al. 2009; Lloveras et al. 2009a; Lloveras et al. 2017), our preliminary taphonomic observations would indicate that only the barn owl (*T. alba*) could be the main accumulating agent of at least part of the microvertebrate assemblage in Ghar-e Boof, excluding the activity of large birds of prey. Archeologists have interpreted the presence of pikas as a possible sign of colder climatic conditions and rugged, open landscapes (Turnbull and Reed 1974; Laplana et al. 2015; Kandel et al. 2017). The drastic reduction of rodents and the presence of the Afghan pika could indicate colder and/or drier conditions than today (Laplana et al. 2015). In other studies, remains of pikas are only recovered from northern sites in Zagros Mountains such as Warwasi Cave (Turnbull 1975) or Yafteh Cave (Mashkour et al. 2009a). Thus, the available data indicate a transitionary time period with colder and/or drier conditions between MP and UP (AHs IVd–IV), which seems to correlate with a change in the techno-cultural industries recovered at Ghar-e Boof.

Our results would support a plausible scenario in which scattered groups of MP hunter-gatherers had to face harsher environmental conditions, visiting Ghar-e Boof very sporadically until their disappearance from the Dasht-e Rostam region ca. 48–45 kya. Chronological investigations carried out at the site have suggested the arrival of AMHs ca. 45–42 kya (Becerra-Valdivia et al. 2017; Heydari et al. 2021). This shift was accompanied by a major technological change and the rise of symbolic artifacts, such as personal ornaments (Bretzke and Conard 2017; Conard and Zeidi 2019; Heydari et al. 2021). Despite the continuity of relative cold, arid conditions and an open landscape until 40–39 kya, AMHs were able to populate the intermountain valleys of the southern Zagros Mountains, possibly thanks to new and more efficient hunting technologies as indicated by the predominance of bladelets in the early UP Rostamian assemblages (Bretzke and Conard 2017). After the temporary cold phase, we observe an increase in occupation intensity at Ghar-e Boof during the early UP, reflecting more frequent visits to the site, longer occupation periods, and/or even larger human populations spread across the region (Mata-González et al. 2022). It is likely that relatively better and more stable environmental conditions led to a more intense use of Ghar-e Boof a few millennia after the initial arrival of AMHs, as we recently hypothesized (Mata-González et al. 2022).

Ghar-e Boof microvertebrate record in the context of the Zagros Mountains

In Table 4, we compare the identified species from Ghar-e Boof with other MP and UP small vertebrate assemblages recovered in the Zagros Mountains, including Kaldar Cave (Bazgir et al. 2017; Rey-Rodríguez et al. 2020, 2021), Shanidar Cave (Perkins 1964; Tilby et al. 2022), Warwasi Cave (Turnbull 1975), Yafteh Cave (Hashemi et al. 2006; Otte et al. 2007; Mashkour et al. 2009a), and Palegawra Cave (Turnbull and Reed 1974; Asouti et al. 2020).

In addition to small vertebrates having the potential to inform us about local paleoenvironmental conditions, the establishment of inter-site comparisons, along with the combination of different sets of paleoenvironmental data, can also provide a better understanding of regional- and trans-regional population dynamics and human habitat preferences. It is worth noting that microvertebrate remains have also been reported in Gar Arjeneh, Kunji Cave, Pa-Sangar and Ghamari Cave (Hole and Flannery 1967; Bazgir et al. 2014), and Wezmeh Cave (Mashkour et al. 2009b). Nonetheless, these assemblages are excluded from our comparisons because either the available species lists include very few taxa, as is the case of Ghamari Cave (Hole and Flannery 1967; Bazgir et al. 2014), or there is evidence of disturbances, such as at Wezmeh Cave (Mashkour et al. 2009b).

The most striking difference between the MP small vertebrate assemblages of Kaldar Cave, Shanidar Cave, Warwasi Cave, and Ghar-e Boof is the relatively high richness of micromammals observed at Kaldar Cave in comparison with the other two sites, although it could be related to sample size bias. Rey-Rodríguez et al. (2020) reported 10 different genera of rodents, some of them even with more than one species (i.e., Persian vole, *M. irani*; social vole, *M. socialis*;

Table 4 MP-UP Zagros Mountains sites with microvertebrate lists. GB, Ghar-e Boof (present study); KC, Kaldar Cave (Bazgir et al. 2017; Rey-Rodríguez et al. 2020, 2021); WC, Warwasi Cave (Turnbull 1975); SH, Shanidar Cave (Tilby et al. 2022); YC, Yafteh Cave (Hashemi et al. 2006; Otte et al. 2007; Mashkour et al. 2009a); PC, Palegawra Cave (Turnbull and Reed 1974; Asouti et al. 2020). Clades: 1, Rodentia; 2, Insectivora and Eulipotyphla; 3, Lagomorpha; 4, Amphibia; 5, Reptilia; 6, Teleostei

Clade	Taxon	MP				UP				EP	
		GB	KC	WC	SH	GB	KC	YC	WC	PC	WC
1	*Allactaga* sp.		+				+	+	+		
	Allactaga cf. *williamsi/euphratica*							+			
	Apodemus sp.		+		+		+				
	Apodemus cf. *flavicollis*		+				+				
	Arvicola cf. *terrestris* (=*amphibius*)				+					+	
	Arvicola terretris (=*amphibius*)							+			
	Calomyscus bailwardi				+			+			
	Chionomys nivalis		+				+	+			
	Cricetinae		+				+	+			
	Cricetulus cf. *migratorius*									+	
	Cricetulus migratorius		+				+				
	Ellobius sp.		+		+	+	+	+			
	Ellobius cf. *fuscocapillus*			+					+	+	+
	Ellobius fuscocapillus		+				+				
	Ellobius cf. *lutescens*							+			
	Ellobius lutescens		+				+				
	Meriones sp.	+	+			+	+	+	+	+	+
	Meriones cf. *persicus*		+		+		+		+	+	+
	Meriones cf. *libycus*	+				+					
	Meriones libycus							+			
	Meriones vinogradovi	+				+		+			
	Mesocricetus sp.		+	+			+			+	
	Mesocricetus cf. *auratus*			+							
	Mesocricetus brandti		+				+				
	Microtus sp.	+	+			+	+	+			+
	Microtus cf. *socialis*							+			+
	Microtus socialis		+		+		+			+	
	Microtus guentheri						+				
	Microtus irani		+								
	Mus cf. *musculus*		+		+	+	+				
	Myomimus sp.		+								
	Spalax leucodon									+	
	Tatera cf. *indica*			+							
	Tatera indica					+		+			
2	Chiroptera					+				+	
	Crocidura cf. *suaveolens*				+						
	Erinaceidae	+				+					
	Erinaceus sp.									+	
	Erinaceus europaeus									+	
	Hemiechinus auritus									+	
	Paraechinus cf. *hypomelas*	+				+					
3	*Ochotona* cf. *rufescens*	+		+					+	+	
	Ochotona rufescens							+			
4	Anura indet	+	+			+					
	Bufo/Bufotes sp.	+	+			+	+			+	
	Bufo/Bufotes viridis									+	

Table 4 (continued)

Clade	Taxon	MP				UP				EP	
		GB	KC	WC	SH	GB	KC	YC	WC	PC	WC
5	Agamidae	+	+			+					
	Colubrinae						+				
	Elapidae						+				
	Eryx sp.		+				+				
	Gekkonidae						+				
	Lacertidae		+			+	+				
	Malpolon insignitus	+				+					
	Pseudopus sp.						+				
	Scincidae						+				
	Viperidae	+	+			+	+				
6	Teleostei					+		+		+	
	Cyprinidae							+			
	Leusciscinae					+		+			
	Leuciscus sp.							+			
	Chondrostoma sp.					+					

Southern mole-vole, *E. fuscocapillus*; and Transcaucasian mole-vole, *E. lutescens*). Kaldar Cave is also rich in squamate reptiles and amphibians, though so far only toad (*Bufo/Bufotes* sp.) and sand boa (*Eryx* sp.) were identified to the genus level, while the rest were assigned to family (Bazgir et al. 2017). Despite that, the local environmental conditions were similar at the four sites. Like the situation at Ghar-e Boof, the small vertebrate assemblage of Kaldar Cave indicates that during the MP, the surrounding landscape of the site was characterized by dry, open steppe with some vegetation cover and active water resources nearby, but lower temperatures and more arid conditions than today (Bazgir et al. 2017; Rey-Rodríguez et al. 2020). Turnbull (1975) also argued that Warwasi Rockshelter had a rocky, open environment, covered sparsely with bushes, and with colder and drier conditions than at present. Tilby et al. (2022) observed similar drier and colder conditions at Shanidar Cave during the MP, although the authors also indicate relatively warm, wet conditions at the base of the sequence.

As for the UP, species representation at Kaldar and Warwasi were more or less the same as the MP, with a few exceptions: first, Persian jird (*Meriones* cf. *persicus*) is only present in the UP record of Warwasi (Turnbull 1975); second, mouse-tailed dormouse (*Myomimus* sp.) and Persian vole (*M. irani*) were not reported in the UP layer of Kaldar, whereas archeologists recorded Günter's vole (*M. guentheri*), which were absent in the MP (Rey-Rodríguez et al. 2020); and finally, the UP sequence of Kaldar also show a greater diversity of squamate reptiles (Bazgir et al, 2017). However, Turnbull (1975) did not mention any environmental shifts during the complete stratigraphic sequence of Warwasi (from the MP to the Epipaleolithic). Likewise, Rey-Rodríguez et al. (2020) did not observe any major paleoenvironmental and paleoclimatic changes, though the MP was slightly colder and drier. The UP small mammal assemblages of Yafteh Cave also show strong similarities with Ghar-e Boof, including the presence of Lybian jird (*M. libycus*), Vinogradov's jird (*M. vinogradovi*), Indian gerbil (*Tatera indica*), voles (*Microtus* sp.), and mole voles (*Ellobius* sp.) (Hashemi et al. 2006; Otte et al. 2007; Mashkour et al. 2009a). Indeed, archeologists have suggested a landscape composed of arid lowlands, piedmont and cool uplands, and some woodlands (Otte et al. 2007). The Epipaleolithic deposits of Palewgara Cave (Turnbul and Reed 1974) have also yielded small vertebrate remains, which indicate a steppe environment, with colder temperatures than today in northern Iraq (Turnbull and Reed 1974). Recently, Asouti et al. (2020) re-excavated the site and confirmed previous environmental data, highlighting the human exploitation of grasslands and shrublands, and some sparsely forested areas.

In addition, there are fish remains at Yafteh (indeterminate cyprinids and *Leuciscus* sp.), which seem to have been accumulated by raptors and/or carnivores, but archeologists do not completely rule out a possible anthropogenic origin as a result of fishing activities (Otte et al. 2007; Mashkour et al. 2009a). Similarly, it is possible that the fish remains at Ghar-e Boof were accumulated anthropogenically, as there are no bite or digestion marks implicating raptors and/or carnivores in the accumulation of the remains.

In general, paleoenvironmental reconstructions drawn on the basis of small vertebrate analyses from MP and UP sites in Zagros support other paleoenvironmental data obtained from sediment cores and archaebotanical studies (i.e., van Zeist and Bottema 1977; Wasylikowa 2005; Djamali et al. 2008a, 2011; Baines et al. 2014; Fiacconi and Hunt 2015; Allúe et al. 2018). Therefore, both MP and UP humans inhabited and exploited mosaic landscapes with relatively similar environmental conditions across different regions of the Zagros Mountains.

The number of sites in the Zagros with both well-dated MP and UP deposits has increased considerably during the last few years (Becerra-Valdivia et al. 2017; Heydari et al. 2021; Heydari-Guran et al. 2021a, b). Nevertheless, Kaldar Cave represents the only site at which archeologists have evaluated the possible influence of paleoenvironmental conditions on cultural changes in Neanderthal and AMH populations (Rey-Rodríguez et al. 2020), though they did not find any major environmental or climatic changes during the MP and UP.

The small vertebrate assemblages of Ghar-e Boof indicate a relatively short phase with colder and/or drier environmental conditions during the shift from the MP to UP. The palynological study of sediment cores from Lake Urmia (northern Zagros), along with loess sequences from the Basin of Persepolis (southern Zagros), have documented several environmental and climatic changes during the Late Pleistocene (Kehl et al. 2005; Djamali et al. 2008a, 2008b). For instance, Lake Urmia shows evidence of an increase in lake-level corresponding to the middle part of last glacial period (MIS 3), suggesting lower evaporation rates caused by a decrease in summer temperatures (Djamali et al. 2008b). Thus, the MP and early UP deposits of Ghar-e Boof could reflect changes in the local environmental signal.

Our results are quite similar in comparison with the taphonomic analysis of Kaldar Cave. Rey-Rodríguez et al. (2020) observed that the predation activity was the origin of at least part of the accumulation of the microvertebrate remains in this site. The authors hypothesized that a category 3 predator, such as the tawny owl (*Strix aluco*) or the Eurasian eagle owl (*Bubo bubo*), accumulated the remains. Based on our samples, a category 1 predator such as the Barn owl (*Tyto alba*) could be the accumulation agent of at least part of the assemblage in Ghar-e Boof. In Shanidar Cave, the results are different and Tilby et al. (2022) observed a constant presence of digestion marks, a fact that would indicate an important accumulation of the remains by birds of prey. The authors also highlighted a gradual increase in rockfall damage towards the upper layers of the site, indicating a slight shift produce by a relatively wet, warm condition in the lower levels. In Shanidar Cave (Tilby et al. 2022), like in Ghar-e Boof, there are also some burnt specimens present, suggesting proximity to hearths, although those remains appear sporadically mixed with the majority of unburnt bones. In terms of taphonomy, further quantitative analyses would need to be conducted to more thoroughly clarify the origin of the microvertebrate accumulation in Ghar-e Boof.

Conclusions

Our study represents the first taxonomic analysis of the small vertebrate assemblages from the MP and early UP sequence of Ghar-e Boof, along with paleoenvironmental reconstructions. We recovered and studied an NISP of 755 of micromammals, squamate reptiles, amphibians, fish, and small birds. Among these taxa, this study shows the first record of Brandt's hedgehog (*P.* cf. *hypomelas*) and nase (*Chondrostoma* sp.) in a Paleolithic locality of the Zagros Mountains, the southernmost record of the Indian gerbil (*T. indica*) and the Afghan pika (*O.* cf. *rufescens*) of this region, and, finally, the first record of two jird species (*M.* cf. *libycus* and *M. vinogradovi*) in the MP of the southern Zagros.

The results of our paleoenvironmental reconstructions suggest a landscape mainly characterized by warm, arid conditions, with dry, open meadows, a rocky terrain, and water sources close to the site during most of the sequence. Alongside the strategic location of Ghar-e Boof within the Dasht-e Rostam region, these environmental conditions favored frequent visits to the site, which provided hominins access to different terrestrial and aquatic, plant, and animal resources (Mata-González et al. 2022).

During the shift from the MP to the UP, we document a short period with colder and/or drier conditions, based on the presence of the Afghan pika and the temporary drastic reduction of rodents. This cold and relatively dry phase seems to correlate with a change in the techno-cultural record at Ghar-e Boof, which might reflect a population shift and the arrival of AMHs. Adverse environmental conditions during the shift from the MP to UP appear to have affected MP hominins in the region. During this period of environmental change, groups occupied the site sporadically. Despite the presence of relatively cold, arid conditions, which lasted until ca. 40–39 kya, AMHs were able to spread across the intermountain valleys of the southern Zagros Mountains, possibly due to more efficient hunting technologies (Bretzke and Conard, 2017). Ongoing archaeobotanical analyses will soon allow us to test this hypothesis further. At present, the microvertebrate record provides the most reliable insights into the environmental conditions that prevailed during the late MP and early UP of the southern Zagros, a period of radical change in hominin population dynamics and cultural adaptations.

Acknowledgements Many people deserve thanks for their contributions in this study. We are grateful to the editors and the anonymous reviewers for providing constructive feedback that improved our manuscript. The authors would like to thank the Iranian Center for Archaeological Research (ICAR) and the Research Institute of Cultural Heritage and Tourism (RICHT). We are thankful to all members of the TISARP team for their contribution during the excavation, water-screening, and management of the recovered material, especially Saman Hamzavi. We also express our gratitude to Dr. Hugues-Alexandre Blain, Dr. Elisa Luzi, Dr. Iván Rey-Rodríguez, and Dr. Yusefi for their comments and suggestions.

Author contribution A. Blanco-Lapaz and M. Mata-González analyzed the microvertebrate assemblage. B.M. Starkovich, N.J. Conard, and M. Zeidi provided archeological and geological context. The manuscript was written by A. Blanco-Lapaz and M. Mata-González. All authors contributed to all sections of the manuscript.

Funding MMG is the beneficiary of a research grant awarded to NJC from the Ministerium für Wissenschaft, Forschung und Kunst Baden-Württemberg as part of the Evolution of Cultural Modernity Project at the University of Tübingen. Excavations at Ghar-e Boof were funded by the Deutsche Forschungsgemeinschaft (DFG) grant CO 226/30–1. We would like to thank the ROCEEH, SHEP, and members of the University of Tübingen who supported us during our work.

Declarations

Competing interests The authors declare no competing interests.

References

Allúe E, Expósito I, Tumung L, Ollé A, Bazgir B (2018) Early evidence of *Prunus* and *Prunus* cf. a*mygdalus* from Palaeolithic sites in the Khorramabad valley, western Iran. CR Palevol 17:335–345

Andrews P (1990) Owls, caves and fossils: predation, preservation, and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset. The University of Chicago Press, Chicago, UK, p 231

Andrews P (2006) Taphonomic effects of faunal impoverishment and faunal mixing. Palaeogeogr, Palaeclimatol, Palaeoecol 241:572–589

Andrews P, O'Brien EM (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. J Zool 251:205–231

Asouti E, Baird D, Kabukcu C, Swinson K, Martin L, García-Suárez A, Jenkins E, Rasheed K (2020) The Zagros Epipalaeolithic revisited: new excavations and ^{14}C dates from Palegawra cave in Iraqi Kurdistan. PLoS ONE 15(9):e0239564

Avery D (2007) Micromammals as palaeoenvironmental indicators of the southern African quaternary. Trans Royal Soc South Afr 62(1):17–23

Baines JA, Riehl S, Conard NJ, Zeidi M (2014) Upper Palaeolithic archaeobotany of Ghar-e Boof cave, Iran: a case study in site disturbance and methodology. Archaeol Anthropol Sci 7:245–256

Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC (1993) Handbook of avian anatomy, 2nd edn. Massachusetts, Cambridge, p 775

Bazgir B, Otte M, Tumung L, Ollé A, Deo SG, Joglekar P, López-García JM, Picin A, Davoudi D, van der Made J (2014) Test excavations and initial results at the Middle and Upper Paleolithic sites of Gilvaran, Kaldar, Ghamari Caves and Gar Arjene Rockshelter, Khorramabad Valley, Western Iran. CR Palevol 13:511–525

Bazgir B, Ollé A, Tumung L, Becerra-Valdivia L, Douka K, Higham T, van der Made J, Picin A, Saladié P, López-García JM, Blain HA, Allué E, Fernández-García M, Rey-Rodríguez I, Arceredillo D, Bahrololoumi F, Azimi M, Otte M, Carbonell E (2017) Understanding the emergence of modern humans and the disappearance of Neanderthals: insights from Kaldar Cave (Khorramabad Valley, Western Iran). Sci Rep 7:43460

Becerra-Valdivia L, Douka K, Comeskey D, Bazgir B, Conard NJ, Marean CW, Ollé A, Otte M, Tumung L, Zeidi M, Higham TFG (2017) Chronometric investigations of the Middle to Upper Paleolithic transition in the Zagros Mountains using AMS radiocarbon dating and Bayesian regression modelling. J Hum Evol 109:57–69

Bell C, Bever GS (2006) Description and significance of the *Microtus* (Rodentia: Arvicolinae) from the type Irvington fauna, Alameda County, California. J Vertebr Paleontol 26(2):371–380

Belmaker M, Hovers E (2011) Ecological change and the extinction of the levantine Neanderthals: implications from a diachronic study of micromammals from Amud cave, Israel. Quat Sci Rev 30:319–3209

Bendrey R, Van Neer W, Bailon S, Rofes J, Herman J, Morlin M, Moore T (2020) Animal remains and humananimal-environment realationships at Early Neolithic Bestansur and Shimshara. In: Matthews R, Matrrhews W, Raheem KR, Richardson A (eds) The early neolithic of the eastern fertile crescent: Excavations at Bestansur and Shimshara, Iraqui Kurdistan. Central Zagros Archaeological Project CZAP Reports Volume 2, pp 311–352

Bever GS (2005) Variation in the ilium of North American *Bufo* (Lissamphibia: Anura) and its implications for species-level identification of fragmentary anuran fossils. J Vertebr Paleontol 25(3):548–560

Biton R, Bailon S, Birkenfeld M, Bridault A, Khalaily H, Valla FR, Rabinovich R (2021) The anurans and squamates assemblage form Final Natufian Eynan (Ain Mallaha, Israel) with an emphasis on snake-human interactions. PLoS ONE 16(2):e0247283

Blain HA (2009) Contribution de la paléoherpétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocènce du climat et du paysage du Pliocènce supérieur au Pléistocènce moyen d'Espagne. Treballs Del Museu De Geologia De Barcelona 16:39–170

Blain HA, Bailon S, Cuenca-Bescós G (2008) The Early-Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. Palaeogeogr Palaeclimatol Palaeoecol 261:177–192

Blain HA, Bailon S, Cuenca-Bescós G, Arsuaga JL, Bermúdez de Castro JM, Carbonell E (2009) Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. J Hum Evol 56:55–65

Blanco-Lapaz A, Martínez-Monzón A, Blain H-A, Cuenca-Bescós G (2021) Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record. Palaeogeogr Palaeoclimatol Palaeoecol 574(2):11044

Boivin N, Fuller DQ, Dennell R, Allaby R, Petraglia MD (2013) Human dispersal across diverse environments of Asia during the Upper Pleistocene. Quatern Int 300:32–47

Bretzke K, Conard NJ (2017) Not just a crossroad: population dynamics and changing material culture in southwestern Asia during the Late Pleistocene. Curr Anthropol 58(17):449–462

Cáceres I, Bravo P, Esteban M, Expósito I, Saladié P (2002) Fresh and heated bones breakage. An experimental approach. In: De Renzi M, Pardo M, Belinchón M, Peñalver E, Montoya P, Márquez-Aliaga A (eds) Current topics on taphonomy and fossilization, Special Issue International Conference Taphos 2002. 3rd Meeting on Taphonomy and Fossilization: 471–479

Čermák S, Obuch J, Benda P (2006) Notes on the genus *Ochotona* in the Middle East (Lagomorpha: Ochotonidae). Lynx 37:51–66

Churchill SE, Franciscus RB, McKean-Peraza HA, Daniel JA, Warren BR (2009) Shanidar 3 Neanderthal rib puncture wound and Paleolithic weaponry. J Hum Evol 57:163–178

Conard NJ, Ghasidian E (2011) The Rostamian cultural group and the taxonomy of the Iranian Upper Paleolithic. In: Conard N, Drechslerr P, Morales A (eds) Between sand and sea: the archaeology and human ecology of southwestern Asia. Kerns Verlag, Tübingen, pp 33–52

Conard NJ, Zeidi M (2019) New research on the Palaeolithic occupation of Ghar-e Boof, Fars Province. Archaeol Spring 2:1–10

Conard NJ, Ghasidian E, Heydari S, Zeidi M (2006) Report on the 2005 survey of the Tübingen-Iranian Stone Age Research Project in the provinces of Esfahan, Fars and Kohgiluyeh-Boyerahmad. In: Azarnoush M (ed) Archaeological reports 5. ICAR, Tehran, pp 9–34

Conard NJ, Ghasidian E, Heydari S, Naderi R, Zeidi M (2007) The 2006 season of the Tübingen-Iranian Stone Age Research Project in the provinces of Fars and Markazi. In: Fazeli H (ed) 9th Annual Report of Archaeological Organisation. ICAR, Tehran, pp 43–67

Coşkun Y (2001) On distribution, morphology and biology of the mole vole, *Ellobius lutescens* Thomas, 1897 (Mammalia: Rodentia) in eastern Turkey. Zool Middle East 23:5–12

Coşkun Y, Ulutürk S (2003) Observations on the mole vole, *Ellobius lutescens* Thomas 1897, (Mammalia: Rodentia) in Turkey. Turk J Zool 27:81–87

Cowgill LW, Trinkaus E, Zeder MA (2007) Shanidar 10: a Middle Paleolithic immature distal lower limb from Shanidar Cave, Iraqi Kurdistan. J Hum Evol 53:213–233

Darvish J (2011) Morphological comparison of fourteen species of the genus *Meriones* Illiger, 1811 (Rodentia: Gerbillinae) from Asia and North Africa. Iran J Anim Biosystematic 7:49–74

Darvish J, Mohammadi Z, Mahmoudi A, Siahsarvie R (2014) Faunistic and taxonomic study of rodents from northwestern Iran. Iran J Anim Bisoyst 10:119–136

Delfino M (2004) The Middle Pleistocene herpetofauna of Valdemino Cave (Liguria, North-Western Italy). Herpetol J 14:113–128

Denys C (2017) Subfamily Deomynae, Gerbillinae, Ieimacomynae, Iophimynae species accounts. In: Wilson DE, Lacher TE, Mittermeier RA (eds) Handbook of the mammals of the world, vol 7. Rodents II. Lynx Edicions, Barcelona, pp 598–650

Dianat M, Darvish J, Cornett R, Aliabadian M, Nicolas V (2017) Evolutionary history of the Persian Jird, *Meriones persicus*, based on genetics, species distribution modelling and morphometric data. J Zool Syst Evol Res 55:29–45

Djamali M, de Beaulieu JL, Shah-Hosseini M, Andrieu-Ponel V, Ponel P, Amini A, Akhani H, Leroy SAG, Stevens L, Lahijani H, Brewer S (2008) A Late Pleistocene long pollen record from Lake Urmia, NW Iran. Quatern Res 69:413–420

Djamali M, Kürschner H, Akhani H, de Beaulieu JL, Amini A, Andrieu-Ponel V, Ponel P, Stevens L (2008) Palaeoecological significance of the spores of the liverwort *Riella* (Riellaceae) in a late Pleistocene long pollen record from the hypersaline Lake Urmia, NW Iran. Rev Palaeobot Palynol 152:66–73

Djamali M, Biglari F, Abdi K, Andrieu-Ponel V, de Beaulieu JL, Mashkour M, Ponel P (2011) Pollen analysis of coprolites from a late Pleistocene-Holocene cave deposit (Wezmeh Cave, west Iran): insights into the late Pleistocene and late Holocene vegetation and flora of the central Zagros Mountains. J Archaeol Sci 38:3394–3401

Escala MC, Miranda R (2002) Guía de Identificación de restos óseos de los ciprínidos presentes en España. Escamas, opérculos, cleitros y arcos faríngeos. Serie Zoología 28:1–239

Evans EMN, Van Couvering JAH, Andrews P (1981) Palaeoecology of Miocene sites in western Kenya. J Hum Evol 10:99–116

Fernández-Jalvo Y, Avery DM (2015) Pleistocene micromammals and their predators at Wonderwerk Cave, South Africa. Afr Archaeol Rev 32:752–791

Fernández-Jalvo Y, Andrews P, Denys C, Sesé C, Stoetzel E, Marin-Monfort D, Pesquero D (2016) Taphonomy for taxonomists: implications of predation in small mammal studies. Quat Sci Rev 139:138–157

Fiacconi M, Hunt CO (2015) Pollen taphonomy at Shanidar Cave (Kurdish Iraq): an initial evaluation. Rev Palaeobot Palynol 223:87–93

Field JS, Petraglia MD, Mirazón-Lahr M (2006) The southern dispersal hypothesis and the South Asian archaeological record: examination of dispersal routes through GIS analysis. J Anthropol Archaeol 26:88–108

Firouz E (2005) The complete fauna of Iran. Tauris & Co Ltd, London, p 322

Frontini R, Roselló-Izquierdo E, Morales-Muñiz A, Denys C, Guillaud E, Fernández-Jalvo Y, Pesquero-Fernández MD (2021) Compression and digestion as agents of vertebral deformation in Sciaenidae, Merlucidae and Gadidae remains: an experimental study to interpret archaeological assemblages. J Archaeol Method Theory. https://doi.org/10.1007/s10816-021-09527-5

Gharkheloo M, Kivanç E (2003) A study on the morphology, karyology and distribution of *Ellobius* Fischer, 1814 (Mammalia: Rodentia) in Iran. Turk J Zool 27(4):281–292

Ghasidian E (2014) The Early Upper Paleolithic occupation at Ghar-e Boof Cave: a reconstruction of cultural tradition in the southern Zagros Mountains of Iran. Kerns Verlag, Tübingen, p 304

Ghasidian E, Bretzke K, Conard NJ (2017) Excavations at Ghar-e Boof in the Fars Province of Iran and its bearing on models for the evolution of the upper Paleolithic in the Zagros Mountains. J Anthropol Archaeol 47:33–49

Ghasidian E, Heydari-Guran S, Mirazón-Lahr M (2019) Upper Paleolithic cultural diversity in the Iranian Zagros Mountains and the expansion of modern humans into Eurasia. J Hum Evol 132:101–118

Grayson DK (1984) Quantitative zooarchaeology. Academic Press, Orlando, p 202

Gromov IM, Erbajeva MA (1995) The mammals of Russia and adjacent territories: lagomorphs and rodents. Russian Academy of Sciences, Zoological Institute, St. Petersburg, p 522

Harrison DL, Bates PJJ (1991) The mammals of Arabia. Harrison Zoological Museum, Sevenoaks, p 354

Hashemi N, Darvish J, Mashkour M, Biglari F (2006) Rodents and lagomorphs remains from late Pleistocene and early Holocene caves and rockshelter sites in the Zagros region, Iran. Iran J Anim Biosyst 2(1):25–33

Heydari M, Mahdavi A (2009) The survey of plant species diversity and richness between ecological species groups (Zagros Ecosystem, Ilam). J Appl Sci 9(4):745–751

Heydari M, Guérin G, Zeidi M, Conard NJ (2021) Bayesian luminescence dating at Ghar-e Boof, Iran, provides a new chronology for Middle and Upper Paleolithic in the southern Zagros. J Hum Evol 151:102926

Heydari-Guran S (2014) Paleolithic landscapes of Iran. BAR international series, Oxford, p 296

Heydari-Guran S, Ghasidian E (2020) Late Pleistocene hominin settlement patterns and population dynamics in the Zagros Mountains: Kermanshah region. Archaeol Res Asia 21:100161

Heydari-Guran S, Benazzi S, Talamo S, Ghasidian E, Hariri N, Oxilia G, Asiabani S, Azizi F, Naderi R, Safaierad HJJ, Foley RA, Mirazón-Lahr M (2021a) The discovery of an in situ Neanderthal remain in the Bawa Yawan Rockshelter, West-Central Zagros Mountains, Kermanshah. Plos ONE 16(8):e0253708

Heydari-Guran S, Douka K, Higham T, Münzel SC, Deckers K, Hourshid S, Nadari R, Asiabani S, Ghasidian E (2021b) Early Upper Palaeolithic occupation at Gelimgoush Cave, Kermanshah; West-Central Zagros mountains of Iran. J Archaeol Sci Report 38:103050

Hole F, Flannery KV (1967) The prehistory of southwestern Iran: a preliminary report. Proc Prehist Soc 33:147–206

Ikeda J (1979) Preliminary report of an archaeological survey in Arsanjan Area, Fars Province, Iran, 1977. Kyoto University, Kyoto

Kaboli M, Aliabadian M, Tohidifar M, Hashemi A, Musavi SB, Roselaar CC (2016) Atlas of birds of Iran. Department of Environment of Iran, Tehran, p 617

Kandel AW, Gasparyan B, Allué E, Bigga G, Bruch AA, Cullen VL, Frahm E, Ghukasyan R, Gruwier B, Jabbour F, Miller CE, Taller A, Vardazaryan V, Vasilyan D, Weissbrod L (2017) The earliest evidence for Upper Paleolithic occupation in the Armenian Highlands at Aghitu-3 Cave. J Hum Evol 110:37–68

Karami M, Ghadirian T, Faizolahi K (2016) The atlas of mammals of Iran. Iran Department of the Environment, Tehran, p 292

Kehl M, Frechen M, Skowronek A (2005) Paleosols derived from loess and loess-like sediments in the Basin of Persepolis, Southern Iran. Quatern Int 140–141:135–149

Keivany Y, Nasri M, Abbasi K, Abdoli A (2016) Atlas of inland water fishes of Iran. In: Daneshgahi J, Branch K (eds) Biodiversity and Wildlife Division of Iranian Department of Environment, Teheran, p 186

Kessler JE (2015) Osteological guide of songbirds from Central Europe. Ornis Hungarica 23(2):62–155

Kryštufek B, Vohralík V (2005) Mammals of Turkey and Cyprus. Rodentia I: Sciuridae, Dipodidae, Gliridae, Arvicolinae. University of Primorska, Science and Research Centre Koper, Koper, p 292. https://doi.org/10.1644/10-MAMM-R-221.1

Kryštufek B, Vohralík V (2009) Mammals of Turkey and Cyprus, Rodentia II: Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae. University of Primorska, Science and Research Centre Koper, Koper, Castoridae, p 374

Laplana C, Sevilla P, Arsuaga JL, Arriaza MC, Baquedano E, Pérez-González A, López-Martínez N (2015) How far into Europe did pikas (Lagomorpha: Ochotonidae) go during the Pleistocene? New Evidence from Central Iberia. PlosOne 10(11):e0140513

Lapparent FD, Bailon S, Augé ML, Rage JC (2020) Amphibians and reptiles from the Neogene of Afghanistan. Plazi.org taxonomic treatments database. Geodiversitas. https://doi.org/10.5252/geodiversitas2020v42a22

Lloveras L, Cosso A, Solé J, Claramunt-López B, Nadal J (2017) Taphonomic signature of Golden eagles (*Aquila chrysaetos*) on bone prey remains. Hist Biol. https://doi.org/10.1080/08912963.2017.1319830

Lloveras L, Moreno-García M, Nadal J (2009) The eagle owl (*Bubo bubo*) as a leporid remains accumulator. Taphonomic analysis of modern rabbit remains recovered from nests of this predator. Int J J Osteoarchaeol 19:573–592

Lloveras L, Moreno-García M, Nadal J (2009) Butchery, cooking and human consumption marks on rabbit (*Oryctolagus cuniculus*) bones: an experimental study. Journal of Taphonomy 7:179–201

López-García JM (2011) Los micromamíferos del Pleistoceno superior de la Península Ibérica: Evolución de la diversidad taxonómica y cambios paleoambientales y paleoclimáticos. Editorial Académica Española, Tarragona, p 416

Lyman RL (2008) Quantitative paleozoology. In: Cambridge Manuals in Archaeology. Cambridge University Press, New York, p 388

Mamkhair H, Samara FF, Shehab AH (2007) Morphological characteristics of the Libyan Jird, *Meriones libycus* Lichtenstein, 1823 (Rodentia: Gerbillinae), in Syria. Zool Middle East 42(1):37–46. https://doi.org/10.1080/09397140.2007.10638244

Markert D (1978) Erstmalige verwengund quartärer reptilreste bei paleökologischen rekonstruktionsversuchen am beispiel des oberen Donauraumes um die wende Pleistozän/Holozän. Archaeologica Venatoria, Tübingen, p 97

Mashkour M, Radu V, Mohaseb A, Hashemi N, Otte M, Shidrang S (2009a) The Upper Paleolithic faunal remains from Yafteh cave (central Zagros) 2005 campaign. A preliminary study. In: Otte M, Biglari F, Jaubert J (eds) Le Paleolithique D'Iran. Archaeopress, Oxford, pp 73–85

Mashkour M, Moncho H, Trinkaus E, Reyss JL, Biglari F, Bailon S, Heydari S, Abdi K (2009b) Carnivores and their prey in the Wezmeh Cave (Kermanshah, Iran): a late refuge in the Zagros. Int J Osteoarchaol 19:678–694

Mata-González M, Starkovich BM, Zeidi M, Conard NJ (2022) New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains). Quatern Sci Rev 279:107350

Medina ME, Teta P, Rivero D (2012) Burning damage and small-mammal human consumption in Quebrada del Real 1 (Córdoba, Argentina): an experimental approach. J Archaeol Sci 39:737–743

Mostafavi H, Reza-Merhabian A, Teimori A. Shafizade-Moghadam H. Kambouzia J (2021) The ecology and modelling of the freshwater ecosystems in Iran. In: Jawad LA (Ed.), Tigris and Euphrates Rivers: their environment from headwaters to mouth. Aquat Ecol Ser 11:1143–1200

Mozaffari O, Kamali K, Fahimi H (2016) The atlas of reptiles of Iran. Department of Environment of Iran, Tehran, p 361

Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic reference. Johns Hopkins University Press, pp 894–1531

Nicholson RA (1993) An investigation into the effects on fish bone on passage through the human gut: some experiments and comparisons with archaeological material. Circaea 10:38–51

Noroozi J, Talebi A, Doostmohammadi M, Bagheri A (2020) The Zagros Mountain range. In: Noroozi J (eds) Plant biogeography and vegetation of high mountains of Central and South-West Asia. Plant and Vegetation. 17:185–214

Oppenheimer S (2009) The great arc of dispersal of modern humans: Africa to Australia. Quat Int 202:2–13

Otte M, Biglari F, Flas D, Shidrang S, Zwyns N, Mashkour M, Naderi R, Mohaseb A, Hashemi N, Darvis J, Radu V (2007) The Aurignacian in the Zagros region: new research at Yafteh Cave, Lorestan. Iran Antiquity 81:82–96

Pavlinov I (2008) A review of phylogeny and classification of Gerbillinae (Mammalia: Rodentia). Moscow University Publishing, Moscow, p 74

Pavlinov I, Dubrovsky YA, Rossolimo OL, Potapova EG (1990) Gerbils of the world. Nauka, Moscow, p 363

Perkins D (1964) Prehistoric fauna from Shanidar, Iraq. Science 144(3226):1565–1566

Piperno M (1972) Jahrom, a Middle Palaeolithic site in Fars, Iran. East West 22:183–197

Piperno M (1974) Upper Paleolithic caves in southern Iran, preliminary report. East West 24:9–13

Pomeroy E, Mirazón-Lahr M, Crivellaro F, Farr L, Reynolds T, Hunt CO, Barker G (2017) Newly discovered Neanderthal remains from Shanidar Cave, Iraqi Kurdistan, and their attribution to Shanidar 5. J Hum Evol 111:102–118

Pomeroy E, Bennett P, Hunt CO, Reynolds T, Farr L, Frouin M, Holman J, Lane R, French C, Barker G (2020) New Neanderthal remains associated with the 'flower burial' at Shanidar Cave. Antiquity 94(373):11–26

Rastegar-Pouyani N, Torki F (2007) Spermatogenesis without spermiogenesis in *Laudakia caucasia* (Reptilia: Agamidae): the role of hibernation. Iran J Anim Biosyst 3(1):37–42

Redpath S, Clarke R, Madders M, Thirgood SJ (2009) Assessing raptor diet: comparing pellets, prey remains, and observational data at Hen Harrier nests. Condor 103:184–188

Reed CA, Braidwood RJ (1960) Toward the reconstruction of the environmental sequence of northern Iraq. Stud Anc Oriental Civiliz 31:169–174

Rey-Rodríguez I, López-García JM, Blain HA, Stoetzel E, Denys C, Fernández-García M, Tumung L, Ollé BB (2020) Exploring the landscape and climatic conditions of Neanderthals and anatomically modern humans in the Middle East: the rodent assemblage from the late Pleistocene of Kadar Cave (Khorramabad Valley, Iran). Quatern Sci Rev 236(2):106278

Rey-Rodríguez I, Arnaud J, López-García JM, Stoetzel E, Denys C, Cornette R, Bazgir B (2021) Distinguish between three modern *Ellobius* species (Rodentia, Mammalia) and identification of fossil *Ellobius* from Kaldar Cave (Iran) using geometric morphometric analyses of the first lower molar. Palaentol Electron 24(1):01. https://doi.org/10.26879/1122palaeo-electronica.org/content/2021/3265-ellobius-and-gmm

Rhodes SE, Walker MJ, López-Jiménez A, López-Martínez M, Hber-Uriarte M, Fernánez-Jalvo Y, Chazan M (2016) Fire in the Early Palaeolithic: Evidence from burnt small mammal bones at Cueva Negra del Estrecho del Río Quñipar, Murcia, Spain. J Archaeol Sci Rep 9:427–436

Rosenberg MS (1979) Eshkaft-e Gavi (The Malyan Project), Iran. J Br Inst Persian Stud 17:148–149

Rosenberg MS (1985) Report on the 1978 sondage at Eshkaft-e Gavi, Iran. J Br Inst Persian Stud 23:51–62

Rosenberg MS (1988) Paleolithic settlement pattern in the Marv Dasht, Fars Province, Iran. Unpublished Ph.D. dissertation. University of Pennsylvania, p 798

Scott JE, Marean CW (2009) Paleolithic hominin remains from Eshkaft-e Gavi (southern Zagros Mountains, Iran): description, affinities, and evidence for butchery. J Hum Evol 57:248–259

Shipman P, Foster G, Shoeninger M (1984) Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. J Archaeol Sci 11(4):307–325

Shoaee MJ, Vahdati-Nasab H, Petraglia MD (2021) The Paleolithic of the Iranian Plateau: hominin occupation history and implications for human dispersals across southern Asia. J Anthropol Archaeol 62:101292

Siahsarvie R, Darvish J (2008) Geometric morphometric analysis of Iranian wood mice of the genus *Apodemus* (Rodentia, Muridae). Mammalia 72:109–115

Solecki, RS (1958) The Baradostian industry and the Upper Palaeolithic in the near east. Unpublished PhD dissertation. Columbia University, p 174

Solecki RS (1963) Prehistory in Shanidar Valley northern Iraq. Science 139:179–193

Stiner MC, Kuhn SL, Weiner S, Bar-Yusef O (1995) Differential burning, recrystallization and fragmentation of archaeological bone. J Archaeol Sci 22:223–237

Stoetzel E, Cornette R, Lalis A, Nicolas V, Cucchi T, Denys C (2017) Systematics and evolution of the *Meriones shawii/grandis* complex (Rodentia, Gerbillinae) during the Late Quaternary in northwestern Africa: exploring the role of the environmental and anthropogenic changes. Quat Scien Rev 164:199–216

Tesakov AS (2016) Early middle Pleistocene *Ellobius* (Rodentia, Cricetidae, Arvicolinae) from Armenia. Russian Journal of Theriology 15(2):151–158

Tilby E, Miracle P, Barker G (2022) The microvertebrates of Shanidar Cave: preliminary taphonomic findings. Quaternary 5:4. https://doi.org/10.3390/quat5010004

Trinkaus E (1983) The Shanidar Neanderthals. Academic Press, New York, p 502

Trinkaus E (2018) Pleistocene human remains from Iran. In: Biglari F, Shidrang S, Mashkour M (eds) The Pleistocene archaeology of the Iranian Plateau, Iraq and the Caucasus. National Museum of Iran, Tehran, pp 53–63

Trinkaus E, Biglari F (2006) Middle Paleolithic human remains from Bisitun Cave. Iran Paléorient 32:105–111

Trinkaus E, Villotte S (2017) External auditory exostoses and hearing loss in the Shanidar 1 Neanderthal. PLoS ONE 12(10):e0186684

Trinkaus E, Biglari F, Mashkour M, Monchot H, Reyss JL, Rougier H, Heydari S, Abdi K (2008) Late Pleistocene human remains from Wezmeh Cave, western Iran. Am J Phys Anthropol 135:371–378

Tsanova T (2013) The beginning of the Upper Paleolithic in the Iranian Zagros. A taphonomic approach and techno-economic comparison of Early Baradostian assemblages from Warwasi and Yafteh (Iran). J Hum Evol 65:39–64

Turnbull F (1975) The mammalian fauna of Warwasi rock shelter. West-Central Iran Fieldiana 33(8):141–155

Turnbull PF, Reed CA (1974) The fauna from the terminal Pleistocene of Palegawra Cave, a Zarzian occupation site in northeastern Iraq. Fieldiana. 63(3):81–146

Vahdati-Nasab H, Clark GA, Torkamandi S (2013) Late Pleistocene dispersal corridors across the Iranian Plateau: a case study from Mirak, a Middle Paleolithic site on the northern edge of the Iranian Central Desert (Dasht-e Kavir). Quatern Int 300:267–281

van Zeist W, Bottema S (1977) Palynological investigations in western Iran. Palaeohistoria 19:19–85

Walker MJ, Anesin D, Angelucci DE, Avilés-Fernández A, Berna F, Buitrago-López A, Fernández-Jalvo Y, Haber-Uriarte M, López-Jiménez A, López-Martínez M, Martín-Lerma I, Ortega-Rodrigáñez J, Polo-Camacho JL, Rhodes SE, Richter D, Rodríguez-Estrella T, Schwenninger JL, Skinner AR (2015) Findings, context, and significance of combustión at the late Early Pleistocene Palaeolithic site of Cueva Negra del Estrecho del Río Quípar (Caravaca de la Cruz, Spain). Antiquity 90(351):571–589

Wasylikowa K (2005) Palaeocology of Lake Zeribar, Iran, in the Pleniglacial, Lateglacial and Holocene, reconstructed from plant macrofossils. Holocene 15(5):720–735

Wójcik J (2002) The comparative osteology of the humerus in European thrushes (Aves: *Turdus*) including a comparison with other similarly sized genera of passerine birds- preliminary results. Acta Zool Cracov 45:369–381

Yiğit N, Çolak E, Sözen M, Özkurt Ş (2003) A study on the geographical distribution along with habitat aspects of rodent species in Turkey. Bonn Zool Bull 50:355–368

Yousefi-Siahkalroodi S, Saeedi H, Sadat-Behfar M, Fallahi R, Izadian M (2013) Atlas of amphibians of Iran. Department of Environment of Iran, Tehran

Yusefi GH (2002) Taxonomic study of the Brandt's hedgehog *Paraechinus hypomelas* (three islands and one mainland populations). MSc thesis, Shahid Beheshti Universit

Yusefi GH, Kiabi BH, Khalatbari L, Faizolahi K, Monteiro NM (2016) Morphological analysis of Brandt's hedgehog *(Paraechinus hypomelas)* reflects the isolation history of Persian

Gulf islands and has implications for taxonomy. Biol J Lin Soc 119(2):497–510

Zanolli C, Biglari F, Mashkour M, Abdi K, Monchot H, Debue K, Mazurier A, Bayle P, Leyur ML, Rougier H, Trinkaus E, Macchiarelli R (2019) A Neanderthal from the Central Western Zagros, Iran. Structural reassessment of the Wezmeh 1 maxillary premolar. J Human Evol 135:102643

Zeidi M, Conard NJ (2019) The fourth season of excavation at Ghar-e Boof, Rostam County, Fars Province. In: Shirazi RA (ed) 16th Annual Symposium of the Iranian Archaeology. Iranian Center for Archaeological Research, Tehran, pp 234–238 ((**in Farsi**))

Zeidi M, McCall B, Khosrowzadeh A (2006) Survey of Dasht-e Rostam-e Yek and Dasht-e Rostam-e Do. In: Potts DT, Roustaei K (eds) The Mamasani Archaeological Project Stage One: a report on the first two seasons of the ICAR – University of Sydney Expedition to the Mamasani District, Fars Province, Iran. Iranian Center for Archaeological research, Tehran, pp 147–168

APPENDIX 2

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran). Quat. Sci. Rev. 279, 107350. https://doi.org/10.1016/j.quascirev.2021.107350.

Submitted to the journal: 13 October 2021.

Accepted: 17 December 2021.

Quaternary Science Reviews 279 (2022) 107350

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran)

Mario Mata-González [a, *], Britt M. Starkovich [a, b], Mohsen Zeidi [b, c], Nicholas J. Conard [a, b, c]

[a] Institute for Archaeological Sciences, University of Tübingen, Hölderlinstr. 12, 72074, Tübingen, Germany
[b] Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstr. 12, 72074, Tübingen, Germany
[c] Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Schloss Hohentübingen, D-72070, Tübingen, Germany

ARTICLE INFO

Article history:
Received 13 October 2021
Received in revised form
14 December 2021
Accepted 17 December 2021
Available online 29 January 2022

Handling Editor: Donatella Magri

Keywords:
Rostamian
Zagros Mountains
Zooarchaeology
Subsistence strategies
Prey choice
Small game
Site occupation intensity

ABSTRACT

Ghar-e Boof is a Paleolithic cave site in Iran, known for being the type locality for the early Upper Paleolithic (UP) Rostamian lithic industries. Defining the Rostamian cultural group has significant archaeological implications for the Zagros Mountains. First, it highlights the cultural diversity of the UP in the Zagros. Second, it evinces a more complex scenario for the spread of anatomically modern humans (AMHs) across Southwest Asia. Despite this, little is known about human subsistence strategies during the Rostamian. In this paper, we present the results of a zooarchaeological analysis that allows us to reconstruct prey choice, transport decisions, and carcass processing at Ghar-e Boof. Wild sheep/goat was the main prey at the site, but other taxa such as partridges, tortoises, and gazelles represented important dietary supplements. Mortality data indicate that Rostamian hunters primarily targeted prime-aged adult ungulates. Anatomical representation also shows that there was no selective transport of animal carcasses to the site, so hunting activities most likely took place nearby. Although many specimens in the assemblage were covered by thick concretions, the presence of cut marks demonstrates defleshing, filleting, dismemberment, and even the removal of internal organs of prey. Percussion impacts and cone fractures also suggest the processing of bones for marrow. Chronologically, moving from the oldest to the youngest layers, there is a decrease in large game in parallel with a progressive increase in small, fast-moving animals. Following the prey choice model of optimal foraging theory, this diachronic variation might track regional resource stress or an increase in hunting pressure. Our results, along with the analysis of lithic artifacts and changes in the rates of sedimentation during the Rostamian sequence, indicate an increase in occupation intensity through time. Thus, the archaeological record of Ghar-e Boof and the ubiquity of UP sites across the Dasht-e Rostam region most probably reflect population growth within a few millennia after the arrival of AMHs.

1. Introduction

The Zagros Mountains, situated near the junction of Africa, Europe, and western Asia, are a vast chain of mountains that extend between Iran, Iraq, and Turkey. From an archaeological standpoint, the region likely represented a crossroad used by archaic and modern humans as they were leaving Africa and expanding into Europe and Asia. Due to this strategic location, numerous survey and excavation projects have been carried out in the Iranian Zagros Mountains starting in the early twentieth century (i.e., Garrod, 1930, 1957; Coon, 1951; Braidwood and Howe, 1960; Hole and Flannery, 1967; Solecki, 1958, 1963; Piperno, 1972, 1974; Ikeda, 1979; Rosenberg, 1979, 1985, 1988). However, the Islamic Revolution of 1979 and the war between Iraq and Iran (1980–1988) stopped most field work in the region (Vahdati Nasab et al., 2013). Fortunately, the new century has led to renewed archaeological investigations (Roustaei et al., 2002, 2006; Conard et al., 2006, 2007; Otte et al., 2007; Bazgir et al., 2014), which have provided valuable information for our understanding of cultural traditions, human settlement dynamics, and environmental conditions in the Zagros during the Late Pleistocene.

Most of the archaeological studies in the Zagros Mountains have focused on the systematic description of lithic assemblages in order to understand the spatial and temporal patterning of the material

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* Corresponding author.
E-mail address: mario.mata-gonzalez@student.uni-tuebingen.de (M. Mata-González).

https://doi.org/10.1016/j.quascirev.2021.107350
0277-3791/

culture (Conard and Ghasidian, 2011), especially during the Middle Paleolithic (MP) to the UP transition. Based on the available radiocarbon dates, the onset of the UP in the Zagros Mountains dates to 45–40 ka cal. BP (Becerra-Valdivia et al., 2017; Heydari et al., 2021). The early UP lithic industries in the Zagros, characterized by a preponderance of blades and burins, were named Baradostian after the description of the lithic assemblages recovered at Shanidar by Solecki (1958, 1963). Based on strong similarities between the Baradostian and the European and Levantine Aurignacian, some authors have considered the Baradostian a regional variant of the Aurignacian (Olszewski and Dibble, 1994; Olszewski, 1999; Otte and Kozłowski, 2007; Shidrang, 2018). Scholars assume that this cultural tradition is associated with Anatomically Modern Humans (AMHs), though UP human remains are scarce in the Zagros (Otte et al., 2011). Known human remains from the region consist of a premolar, found in the Baradostian levels of Gar Arjeneh (Trinkaus, 2018); another tooth specimen, recovered from the Baradostian layers of Warwasi (Tsanova, 2013); and ten remains (a molar, four cranial specimens, a patella, a pelvic fragment, the diaphysis of a clavicle and two long-bone fragments), which derive from at least four individuals, from the UP and Epipaleolithic deposits of Eshkaft-e Gavi (Scott and Marean, 2009).

After four campaigns of intense archaeological field work, Ghar-e Boof is considered one of the most promising and richest UP sequences in the Zagros Mountains. At first, based on the presence of small bladelet tools and cores, excavators thought that the lithic assemblage might represent an Epipaleolithic industry (Conard and Ghasidian, 2011); however, radiocarbon and luminescence dates situate the assemblage in the range of 42–35 ka cal. BP (Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017; Heydari et al., 2021). Comparisons of Ghar-e Boof lithic artifacts with other Baradostian/early UP lithic assemblages from the northern and central Zagros highlight the particularities of the Ghar-e Boof lithic industries, as do surface finds recovered at other sites of the Dasht-e Rostam region, precisely because of the predominance of diminutive bladelet artifacts within them. Consequently, a new cultural group was defined: the Rostamian (Conard and Ghasidian, 2011; for further details, see Ghasidian, 2014; Ghasidian et al., 2017; for criticisms, see also Olszewski, 2017). Thus, the identification and description of the Rostamian cultural group provided two major scientific contributions to the understanding of the Paleolithic record of the Zagros: 1) it demonstrated that the geographical region contains greater variability and more local cultural groups than previously thought (Conard and Ghasidian, 2011; Ghasidian, 2014); and 2) this cultural diversity indicates chronologically deeper and spatially more complex processes and scenarios for the migration of modern human populations over southwestern Asia (Ghasidian et al., 2017, 2019).

Despite these contributions, little is known about the socioeconomic adaptations and foraging conditions of the UP populations that inhabited the southern Zagros. Therefore, we present here the first comprehensive zooarchaeological study of the entire Rostamian sequence of Ghar-e Boof. This study addresses several research questions, which primarily cover the following four points:

1) Bone taphonomy: which taphonomic processes altered or affected the preservation of the faunal remains? Were humans the primary agents of bone accumulation and/or modification?
2) Diet breadth: which species are present at the site? Are there patterns in prey selection? How does species abundance change through time?
3) Transport decisions: what decisions did past hunters make when transporting animals or different portions of animal to the site? Did they transport complete carcasses to the cave? Or did they preferentially target meat- or fat-rich elements?
4) Butchery strategies and carcass processing: how did humans exploit animal carcasses at Ghar-e Boof?

In order to answer these questions, and to assess and interpret the faunal assemblage and its archaeological implications for the Rostamian, we use optimal foraging theory, which is based on the assumption that organisms make decisions that provide the greatest nutritional return and enhance their reproductive success in order to maximize their fitness in a specific environment (Stephens and Krebs, 1986).

2. Ghar-e Boof – site background

2.1. Regional setting

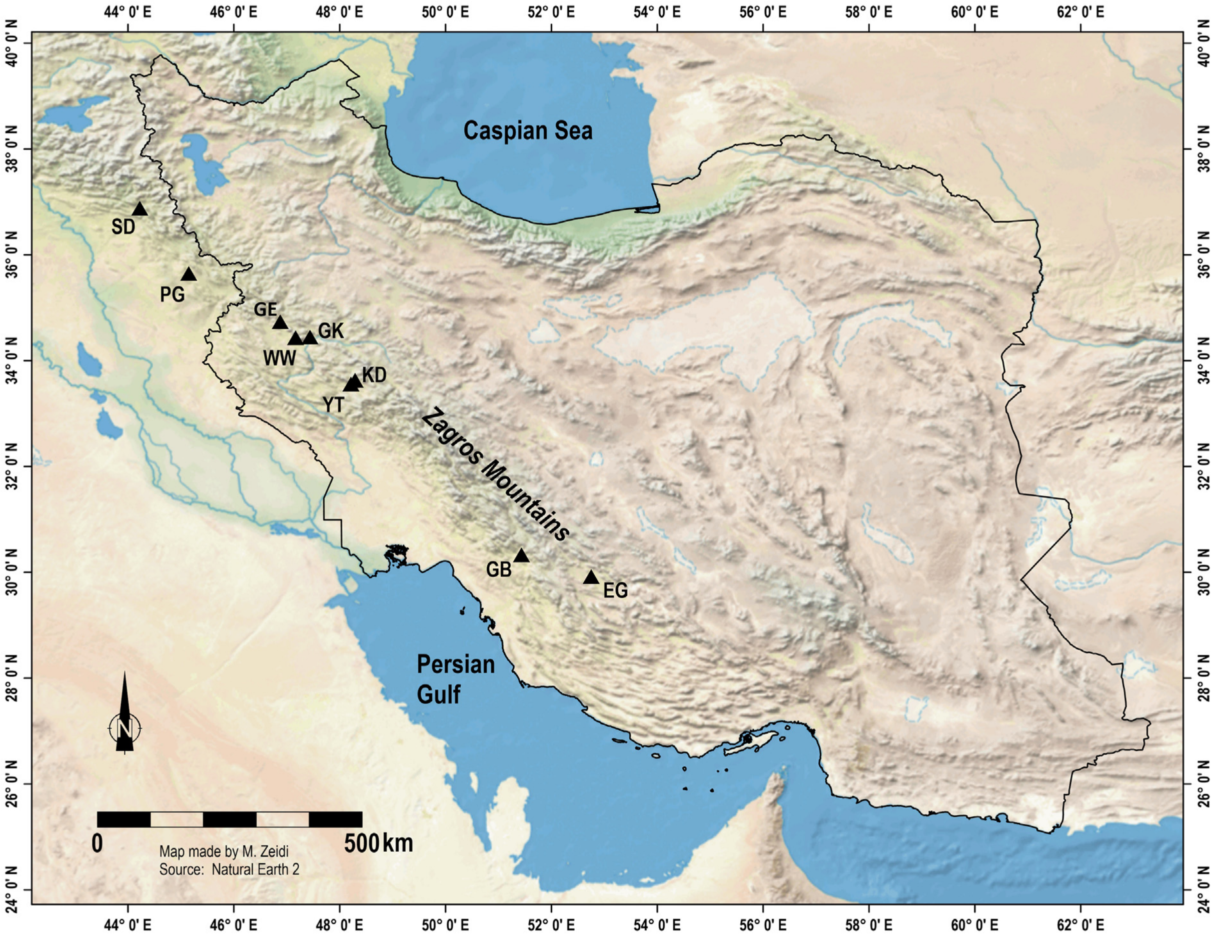
The Dasht-e Rostam region is located in the northwestern part of the Fars Province (southern Zagros Mountains, Iran), at the junction of the Mesopotamian plain and the southernmost mountains of the Zagros chain (Fig. 1). The Persian Gulf is about 140 km to the west. The topography of the region is complex, forming natural east-west and north-south corridors (Heydari-Guran, 2015; Ghasidian et al., 2017). The Dasht-e Rostam region is drained by three rivers: the Fahliyan, with a perennial flow, and the Solak and Shiv streams, which are seasonal (Conard and Ghasidian, 2011; Heydari-Guran, 2014). The bottom of the basin contains thick accumulations of Holocene sediments and most of its lands are dedicated to agricultural production. Because of this, archaeological research focused on the hills and mountains surrounding the Dasht-e Rostam region (Conard and Ghasidian, 2011). The mountains range from 700 to 2500 m.a.s.l., and their geological composition consists of limestone, dolomite and argillaceous limestone, which formed between the Jurassic and the Oligocene, and between the Miocene to the Pleistocene (Heydari-Guran, 2014).

Today, the Dasht-e Rostam region is characterized by an arid to semi-arid climate, with cold, wet winters and warm, dry summers (Bobek, 1968; Ganji, 1968). The region is located in the mild temperate zone of the Zagros where the average annual temperature is ca. 15–25 °C and the mean annual precipitation can exceed ca. 500 mm (Roustaei et al., 2006). The extant vegetation in the southern Zagros region is dominated by patches of oak (*Quercus persica*) forests. At lower altitudes, the oak-woodland turns into a more open, steppe landscape, composed of scattered shrubs and trees, such as pistachio (*Pistacia atlantica*) and almond (*Amygdalus scoparia*) (Roustaei et al., 2006).

Ghar-e Boof (N 30.2839°, E 51.4352°) is located in the Yagheh Sangar, a narrow pass that separates the southeastern and northwestern halves of the Dasht-e Rostam region (Fig. 2a). As many other geomorphological features in the landscape of Fars Province, the cave is formed in limestone by karstic and other erosional activities (Jamali et al., 2015). Ghar-e Boof lies at an altitude of 905 m.a.s.l., it has an area of about 60 m^2, and it opens toward the north (Conard and Ghasidian, 2011). In addition, its strategic location in the Yagheh Sangar provides a panoramic view of the Dasht-e Rostam region and it is only 200 m away from the Solak seasonal stream. Thus, Ghar-e Boof would have most likely been a very attractive place for past hunter-gatherers (Conard and Ghasidian, 2011; Ghasidian, 2014).

2.2. Excavation history

In 2004, the Tübingen-Iranian Stone Age Research Project (TISARP) was founded with the goal of carrying out numerous seasons of survey and excavation focusing on the Paleolithic



Map made by M. Zeidi
Source: Natural Earth 2

Fig. 1. Location of Ghar-e Boof (GB) in the Zagros Mountains, along with some other sites with UP sequences for which zooarchaeological data are available: EG = Eshkaft-e Gavi; YT = Yafteh Cave; KD = Kaldar Cave; WW = Warwasi; GK = Ghar-e Khar; GE = Gelimgoush Cave; PG = Palegawra Cave; SD = Shanidar Cave. Figure by M. Zeidi.

archaeological record of Iran (Conard et al., 2006, 2007, 2009; Zeidi et al., 2006; Conard and Ghasidian, 2011; Ghasidian, 2014; Heydari-Guran, 2014; Ghasidian et al., 2017; Conard and Zeidi, 2019). Based on surface finds, the TISARP team has identified more than 120 archaeological sites. Among those sites, one of the most promising was Ghar-e Boof, or 'the Owl's Cave' in Persian. It was originally known as Eshkaft-e Yagheh Sangar, and it was discovered and recorded for the first time in 1997 by Mr. R. Nowroozi, a member of the Fars cultural heritage office (Nowroozi, 1997). An Iranian-Australian team also visited the site in 2003, while the TISARP team did so in 2005 (Conard et al., 2006; Zeidi et al., 2006). Besides the abundance of lithic artifacts on the surface, Ghar-e Boof showed potential for excavation due to its seemingly well preserved deposits. Numerous large boulders in front of the site trapped the sediments within the cave and prevented erosion (Fig. 2b and c, Conard and Ghasidian, 2011).

The TISARP team, under the direction of Nicholas J. Conard and Mohsen Zeidi, has conducted a total of four seasons of excavation at Ghar-e Boof: 2006, 2007, 2015, and 2017. During this period, excavators documented a long occupation sequence that spans from the MP to the Islamic period (Conard et al., 2007; Conard and Ghasidian, 2011; Conard and Zeidi, 2019; Zeidi and Conard, 2019; Heydari et al., 2021). The excavation extends over an area of 18 square meters, running from the entrance (north) towards the back wall of the cave (south), and over 6 m deep (Fig. 2c; Conard and Ghasidian, 2011; Heydari et al., 2021). Each square meter was divided into 50 cm sub-squares and excavators worked by digging *Abträge*, which followed the slope of the sediments instead of horizontal spits (Conard and Zeidi, 2019). They also plotted lithic artifacts and organic remains in three dimensions, and recorded the orientation for elongated finds (Conard and Zeidi, 2019). Archaeologists first floated sediments and then water screened them through five and two mm mesh (Conard and Zeidi, 2019). This facilitated the recovery of even small finds, including botanical and faunal remains, beads, and micro-lithics and debitage (Conard et al., 2007; Conard and Ghasidian, 2011; Conard and Zeidi, 2019). Overall, we recovered large amounts of lithic artifacts and more than 5000 identifiable faunal remains, including macro and micro vertebrates.

2.3. *Stratigraphy, cultural sequence, and chronology*

The archaeological sequence of Ghar-e Boof is divided into six archaeological horizons (AH) and 13 sub-horizons (Fig. 3). The uppermost AHs (I and II) correspond to Holocene silts and ash deposits. Excavators recovered pieces of chipped flint and other Pleistocene artifacts from AHs I and II. Nevertheless, they usually appeared accompanied by pottery sherds, metal, and glass artifacts from the Islamic period, which confirm the use of the cave during historic times (Conard and Ghasidian, 2011). The radiocarbon analysis of a grain of barley from AH IIb yielded an approximate age of 1250 cal. BP (Baines et al., 2014; Ghasidian, 2014). As we documented many diagnostic Zarzian (Epipaleolithic) lithic artifacts from AH IIa and IIb, this grain was probably intrusive from the

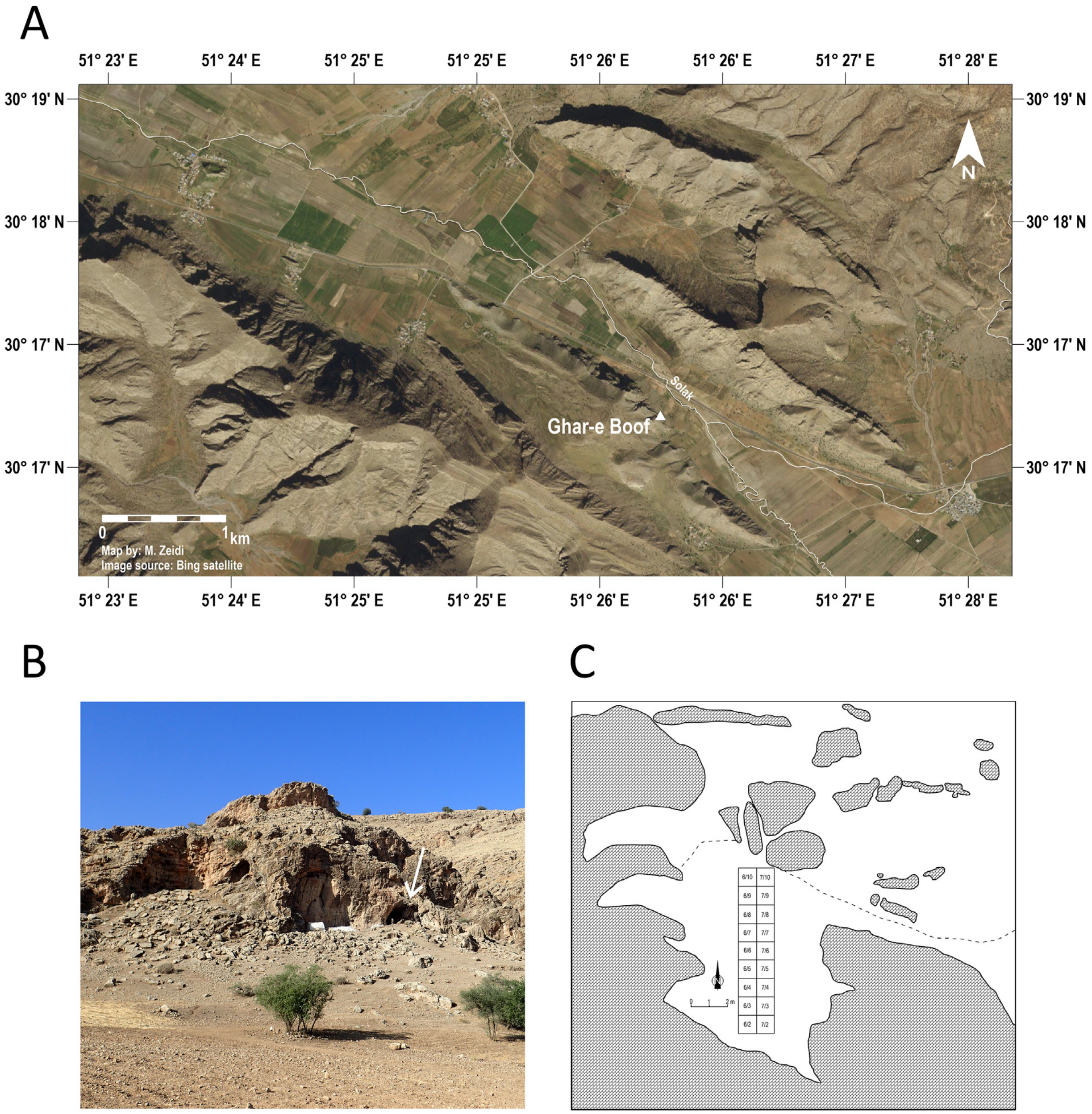


Fig. 2. Ghar-e Boof: a) Satellite view of the Dasht-e Rostam region and location of the site (figure by M. Zeidi); b) View of the entrance of cave (white arrow; photo by N. J. Conard, 2017); c) General plan and location of the excavation area (modified after Conard and Ghasidian, 2011).

uppermost layers. In addition, small, backed triangles and numerous thumbnail scrapers were recovered at the top of AH III. These artifacts most likely postdate the main Rostamian deposits and may also be part of an Epipaleolithic assemblage (Conard and Zeidi, 2019).

The early UP horizons begin with AH III. The stratigraphic complex of AH III-IIIc yielded about 95% of the total lithic artifacts recovered at Ghar-e Boof, and they show great homogeneity from a cultural standpoint. The Rostamian lithic assemblage is characterized by small bladelet artifacts and abundant small platform cores, mostly made on radiolarian-chert cobbles from local rivers, and includes all phases of the lithic reduction sequence (Fig. 4; Conard and Ghasidian, 2011; Ghasidian, 2014). The micromorphology of these layers also indicates considerable anthropogenic input, with evidence for the combustion of wood and an increase in the sedimentation rate due to frequent human occupation of the site (Schilt, 2011). These archaeological horizons have also yielded a large record of animal and botanical remains, and archaeobotanical studies have suggested that part of this assemblage might be the result of plant use by humans during the Rostamian (Baines et al., 2014). From AH IV downward, the find density diminishes considerably and the deposits are mostly of geogenic origin (Conard and Ghasidian, 2011; Schilt, 2011). Nevertheless, in AH IV, excavators documented a few features that resemble hearths and suggest brief occupations of the cave (Conard and Zeidi, 2019). In addition, lithic artifacts from AH IV-IVb show strong similarities with the upper horizons, so they probably belong to the same Rostamian cultural tradition, though the knapping sequences are less complete (Ghasidian, 2014; Conard and Zeidi, 2019). Radiocarbon dates place AH III-IIIc at 39–35 ka cal. BP and AH IV-IVb at 42–40 ka cal. BP (Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017; calibrated dates from Ghasidian et al., 2019).

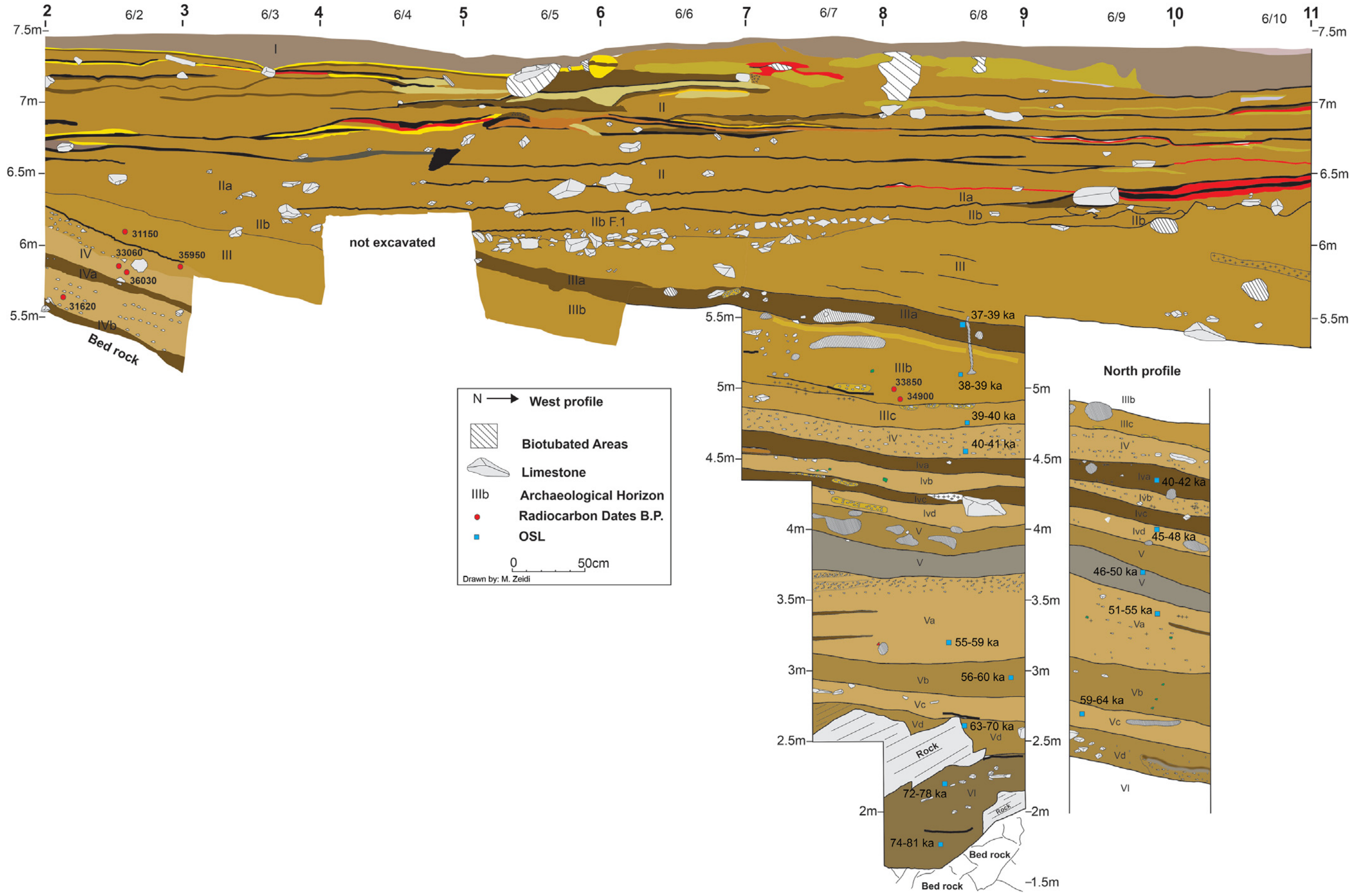


Fig. 3. Ghar-e Boof. Stratigraphic sequence: west profile and part of the north. Figure by M. Zeidi.

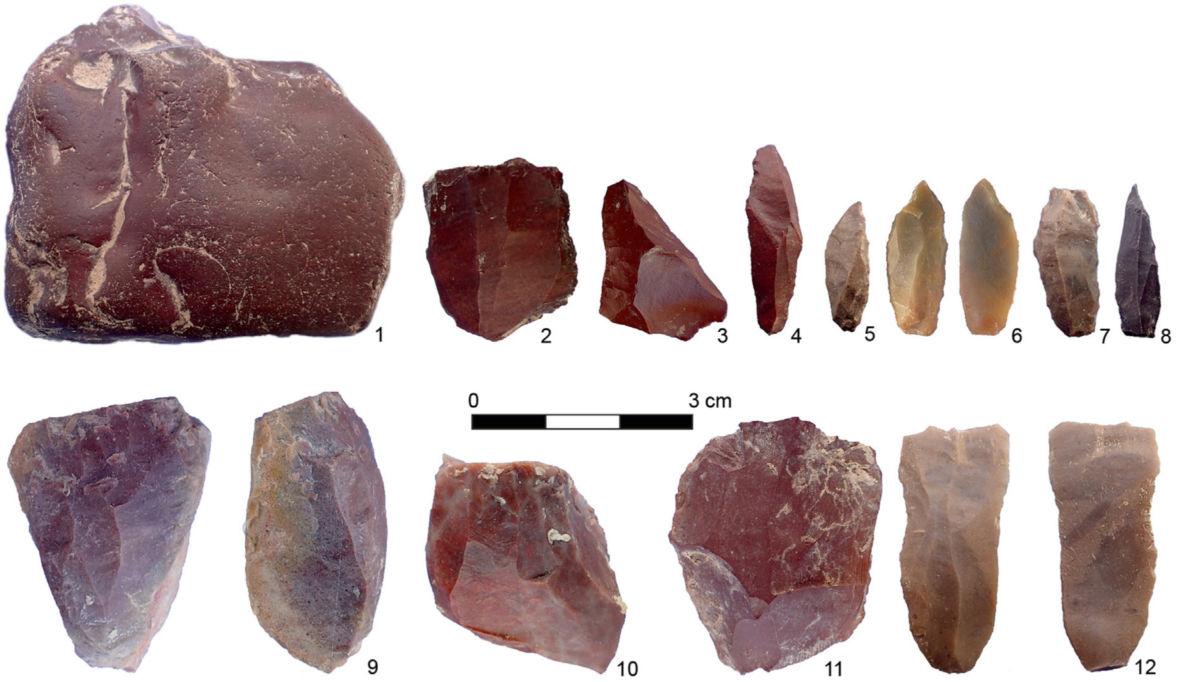


Fig. 4. Ghar-e Boof. Selection of Rostamian lithic artifacts and raw materials recovered from AHs IIIa and IIIb, quadrant 6/8: radiolarian-chert nodule (1), bladelet cores (2, 9 and 10), retouched flake (3), retouched bladelets (4 and 7), backed bladelet (5), retouched bladelet/perforator (6), backed bladelet/point (8), flake/blade core (11), and retouched blade (12). Figure adapted from Conard and Zeidi (2019).

OSL ages agree with the published ^{14}C dates and confirm the attribution of the Rostamian to the early UP (Heydari et al., 2021). Thus, Ghar-e Boof is currently one of the oldest UP assemblages in the Zagros Mountains (Becerra-Valdivia et al., 2017; Heydari et al., 2021).

The analysis of lithic artifacts recovered during the 2015 and 2017 campaigns is still ongoing, though a preliminary examination indicates that the lowermost AHs IVc-d, V, and VI contain MP industries. However, the find densities are very low and they may reflect short, sporadic human occupations at the site (Bretzke and Conard, 2017; Conard and Zeidi, 2019; Zeidi and Conard, 2019). Recent OSL dates for these horizons yielded ages between 81 and 45 ka (68% CI; Heydari et al., 2021).

It is important to mention that archaeologists identified bio-galleries in all horizons. Some of them appear to have formed recently; for example, in AH III most bio-galleries were hollow voids (Conard and Zeidi, 2019). When bio-galleries were filled, they normally consisted of gray homogenized sediments from AH II and were therefore relatively easy to differentiate. However, sometimes bio-galleries were found filled with sediments which were hard to identify and distinguish from the intact deposits (i.e., AH IIIa and IIIb). Nonetheless, whenever possible, archaeologists separated the sediments from the bio-galleries and removed them from in-situ sediments, though a minor degree of mixing may have occurred (Conard and Zeidi, 2019).

3. Material and methods

In this paper, we include a sample of 3137 identified faunal specimens from the Rostamian horizons of Ghar-e Boof (from AH III to AH IVb). Due to time constraints, we were not able to quantify unidentifiable specimens, but a conservative estimate of those would be approximately 14,000 bone fragments. Heydari-Guran (2014) described a small amount of faunal material, but our study is the first to analyze the entire assemblage of the UP sequence.

For the taxonomic and anatomical identifications, we used the comparative zooarchaeological collection at the University of Tübingen, along with the assistance of zooarchaeological guides when necessary (Boessneck, 1963; Halstead and Collins, 2002; Payne, 1985; Zeder and Lapham, 2010; and other unpublished electronic faunal manuals). All specimens were identified as precisely as possible. We analyzed the material following standard zooarchaeological methods (Binford, 1984; Grayson, 1984; Stiner, 1994, 2005; Lyman, 1994, 2008; Reitz and Wing, 2008). Most identifiable specimens were identified to genus or species, whereas fragments with less diagnostic features were assigned to body size categories (Stiner, 2005). The main counting unit in this study is number of identified specimens (NISP; Lyman, 2008). From NISP, we derived minimum number of elements (MNE) by counting all complete and fragmentary specimens with unique bone landmarks and how often they occur in each AH for a specific species or body size category (Binford, 1984). In this case, we also took side and age into account for the calculation of MNE. We calculated minimum number of individual (MNI) values by taking into consideration the most common element and side by taxon (Grayson, 1984; Lyman, 1994, 2008), and reported them here to allow comparisons with other Paleolithic faunal assemblages from the Zagros Mountains (e.g., Evins, 1982); however, our analysis is based on NISP. Finally, we evaluated changes in species representation using Cochran's test of linear trend (Cannon, 2001). Because relative abundance values are weighted by sample size, this chi-square test is sensitive to small sample sizes, and it results in lower rates of Type I and Type II statistical errors than other correlation-based methods (Cannon, 2001).

In order to determine the main agent of accumulation and/or modification (carnivores versus hominins) and post-depositional processes, we examined bone surface damage with a 10x hand lens. When needed, we used a binocular microscope for higher resolution examination of such modifications. Following Behrensmeyer (1978) and Fisher (1995), we documented natural surface modifications and weathering, such as cracks, flaking and exfoliation. In addition, we recorded the presence of root etching, chemical weathering, and sediment concretions. Other observations that we documented for each specimen were carnivore and rodent gnawing, tooth wear, epiphyseal fusion, butchery damage, and burning (Payne, 1973; Stiner, 1990, 1994, 2005; Stiner et al., 1995; Zeder, 2006). Among the evidence of butchery damage we included cut marks, percussion impacts, and green/fresh bone fractures (Johnson, 1985; Gifford-Gonzalez, 1989; Lyman, 1994). We photographed all specimens presented in this study as figures with a Keyence VHX-500FD digital microscope, with 5x to 40x magnification, depending on the given taphonomic damage or modification of interest.

Although the bones are well preserved, many faunal remains were recovered encased in sediment crusts, presumably made of calcium carbonate (Conard and Zeidi, 2019). These concretions obscured bone surfaces and hampered taxonomic identifications. In order to remove sediment crusts and make the bones easier to analyze, we followed a strict cleaning protocol when necessary. The sediment concretions were moistened by applying ethanol with cellulose and then were left to dry. Once dried, the specimens were cleaned with a small bamboo rod, though the removal of extremely thick concretions required the use of surgical tools, especially scalpels. On some occasions, the mechanical cleaning was accompanied by the gentle and controlled removal of concretions with cellulose to avoid sediment particles from damaging or scratching the bone surfaces. After the partial or complete elimination of sediment crusts, ethanol was once again applied to the bone surfaces with a cotton swab and they were left to dry. Though the removal of sediment concretions facilitated our taxonomic identification, in many cases, the concretions damaged the bone surfaces, making taphonomic modifications impossible to see. Although there were specimens in which cut marks and cone/percussion fractures were visible despite the concretions (Fig. 5), it is likely that modifications, regardless of their taphonomic agent, are underestimated.

Finally, there is variation in sample size between layers. This is partially due to the excavation strategy followed at Ghar-e Boof; for instance, archaeologists dug AH III in almost the complete excavation area, while they only reached AH IIIc, IVa, and IVb in two quadrants (Conard and Ghasidian, 2011; Conard and Zeidi, 2019). Because of this, some of our analyses are only applied to layers with a large enough sample size. In other cases, we combined all the Rostamian layers to have a more robust sample.

3.1. Density-mediated attrition

Density-mediated attrition or bone loss occurs because less structurally dense elements are more easily affected than compact bones by mechanical or chemical processes, such as carnivore gnawing, weathering damage and sediment compaction (Binford and Bertram, 1977; Marean and Spencer, 1991; Lyman, 1994; Fisher, 1995; Marean and Frey, 1997). In order to understand if density-mediated attrition has affected the faunal remains recovered from Ghar-e Boof, we calculated bone survivorship following Lyman (1994) and compared it to bone density values from photon densitometry measurements. We use sheep/goat (*Ovis/Capra*) elements from Ghar-e Boof because they are the most common taxa found in the assemblage. For this analysis, we combined sheep/goat elements with specimens identified as medium ungulates because

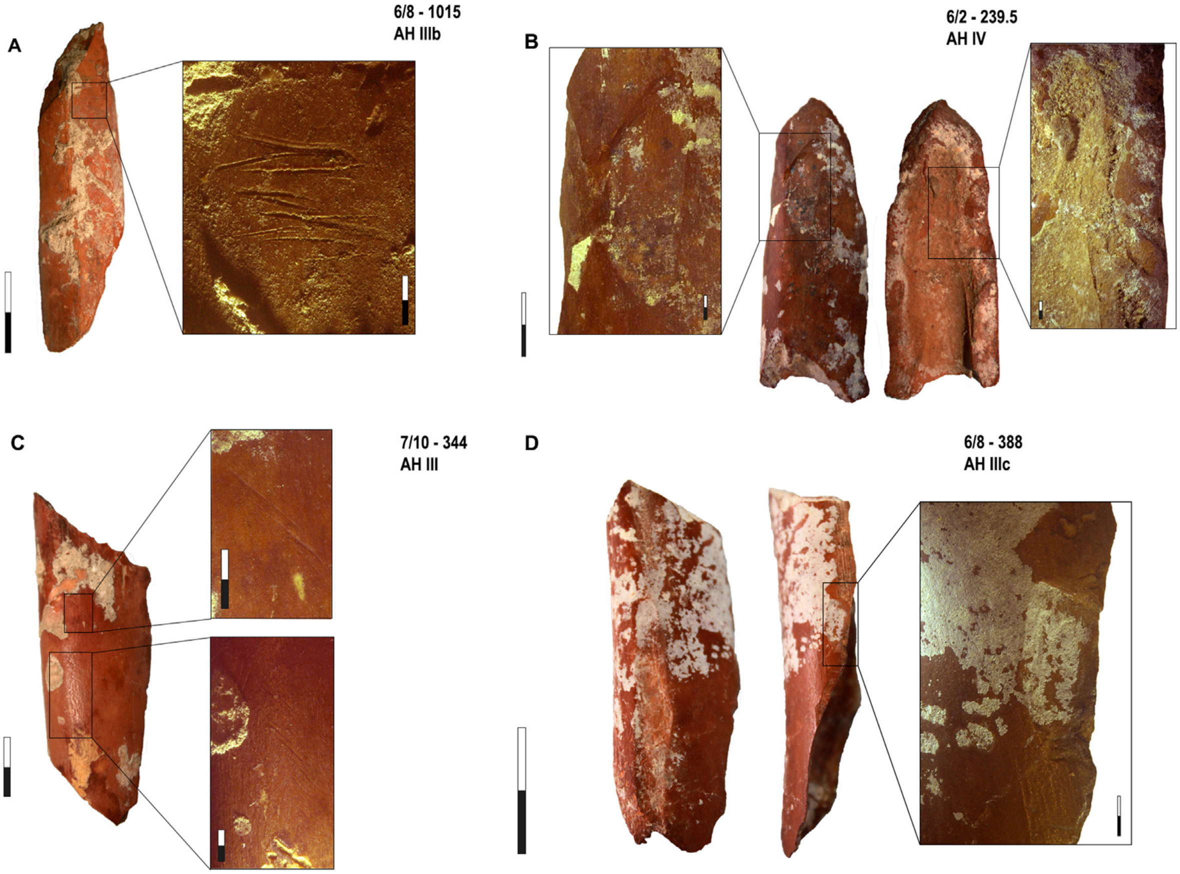


Fig. 5. Ghar-e Boof. Medium ungulate remains with visible anthropogenic modifications despite being partly covered with concretions: tibiae with cut marks (a) and cone fractures (b); and humeri with cut marks (c) and with a percussion impact (d). All of these specimens also have split/spiral fractures. Scale: general view = 20 mm; closer-up view = 2 mm. Figure by A. Blanco-Lapaz.

they most likely belong to one of these species. Due to its similarities to wild sheep/goat, we applied density standards from domestic sheep (*Ovis aries*) (Lyman, 1994). We used a Spearman's rank-order correlation in R Studio for testing possible relationship between survivorship and bone density values. Due to sample size limitations, this test was only applied to AHs III and IIIb.

As a second method for analyzing density-mediated attrition in all the Rostamian layers, we also examined the ratio of tooth- and cranium-based MNE values (Stiner, 1994). When people transport a carcass to a site, we expect teeth to remain with the skull. This should lead to a 1:1 ratio between the most common tooth and the most common skull element (Stiner, 1994). Bones are more susceptible to attritional process than teeth because they are much less structurally dense (Lyman, 1994; Hillson, 2005). Consequently, if tooth-based MNE values are considerably higher than bone-based MNE values, this would indicate that attritional process might have affected the assemblage. In order to provide a more robust sample, all the ungulate taxa were combined in this analysis.

3.2. Prey age selection

Prey mortality patterns can inform us about several aspects of past human forager lifeways, such as hunting strategies, population densities, and resource intensification. We addressed these questions by providing data on tooth eruption and wear for wild sheep and goat (Payne, 1973), and long bone fusion for caprines and medium ungulates (Zeder, 2006). Following Stiner (1990, 1994), we recorded tooth eruption and wear based on eight different possible wear stages. We used the mandibular deciduous fourth premolar (dp4) and the fourth permanent premolar (p4), whose combination represents the complete lifetime of caprines (Stiner, 1990).

We applied the three-cohort system, following Stiner (1990, 1994), to determine prey age selection among Rostamian foragers at Ghar-e Boof. We grouped tooth wear stages into three age classes. While the juvenile class encompasses only deciduous teeth, we classified permanent teeth as prime-aged and old adults (Stiner, 1990). Teeth with no occlusal wear to medium wear were collapsed into the prime-aged category, and medium-advanced and advanced wear stages were considered old adults. We plotted the three age cohorts on a triangular graph with a 95% confidence interval following Weaver et al. (2011), superimposed on zones mathematically defined by Discamps and Costamagno (2015). Although sheep/goat-adapted zoning for ternary diagrams are not available, Discamps and Costamagno (2015) also developed a non-taxon-specific graph considering ethological and ontological data of different taxa. Due to the constraints of small sample sizes for each particular layer, we combined all the UP horizons together to have a more robust sample.

3.3. Transport decisions: body part representation and evenness

The analysis of body part representation at an archaeological site is useful for understanding prey transport decisions or how far foragers had to go to hunt (O'Connell et al., 1990; Broughton, 1999; Cannon, 2003; Nagaoka, 2005; Faith and Gordon, 2007; Saladié et al., 2011). To assess body part representation, we grouped the ungulate skeleton into nine anatomical regions following Stiner (1991). Within each anatomical region, we calculated minimum animal units (MAU) by dividing the observed MNE by the expected MNE for each element in a complete skeleton (Binford, 1978) and also for each anatomical region (Stiner, 1991). Selective transport of elements or anatomical regions, or even diachronic changes in transport decisions, are usually reflected in the evenness or uniformity of MAU across those elements or anatomical regions (Faith and Gordon, 2007). Here we measured skeletal evenness with the reciprocal of Simpson's index, which is also expressed as 1/D and calculated as $1/\Sigma(\rho_i)^2$ (Simpson, 1949; Lyman, 2008), where Σ is the number of anatomical regions in a skeleton and ρ is the proportion of MAU for a particular i anatomical region. A perfectly even distribution of the different anatomical regions results in an evenness of 9 (the total number of anatomical regions defined by Stiner, 1991), while values approach 1 as evenness decreases.

Table 1
Ghar-e Boof. Spearman's rank-order correlation values for the relationship between bone mineral density and percent survivorship for sheep/goat and medium ungulates. Bone density and survivorship values are included in Tables A.1 and A.2.

AH	n	r_s	p
AH III	43	0.43	0.004
AH IIIb	29	0.53	0.003

Table 2
Ghar-e Boof. Ratios between ungulate tooth-based and bone-based MNE values by AH. All ungulate taxa are included for a more robust dataset.

Archaeological horizon	Tooth MNE	Bone MNE	Tooth/bone MNE
AH III	12	17	0.7
AH IIIa	1	3	0.3
AH IIIb	7	11	0.6
AH IIIc	2	5	0.4
AH IV	1	4	0.3
AH IVa	2	7	0.3
AH IVb	3	2	1.5

4. Results

4.1. Taphonomic processes

4.1.1. Density-mediated attrition

It is important to first establish the extent to which density-mediated attrition affected faunal remains, before interpreting changes in prey choice or butchery and transport strategies. The results of the Spearman's rank-order correlation between bone density values and percent survivorship (%MAU) for AHs III and IIIb are presented in Table 1. In both horizons, there is a positive correlation between bone density values and percent survivorship for sheep/goat and medium ungulate remains. However, when we examine the ratio of tooth-to bone-based MNE values for all of the Rostamian AHs, including those with samples too small for the previous analysis, most layers have lower tooth-based MNE values as compared to skull elements (Table 2).

4.1.2. Bone taphonomy

Table 3 shows the frequencies of natural modifications on faunal remains recovered at Ghar-e Boof by layer. A little over two percent of the specimens were completely crushed due to sediment compaction, preventing more precise identification. In addition, 37.4% of the total remains were partially or entirely covered by thick concretions. Surface weathering damage, such as linear cracks and exfoliation, is quite uncommon, being visible on less than 0.8% of the total specimens. Likewise, root etching is also rare (0.6%). However, chemical weathering affected the assemblage to a greater extent, with 38.2% of specimens displaying irregular etched scars and/or spots. Evidence of carnivore or rodent gnawing is rare (1.8% and 2.1%, respectively) in our assemblage.

4.2. Prey choice

4.2.1. Species representation and relative abundances

Total NISP counts and their relative proportions for all species by layer are found in Table 4 (MNI values are included in Table A.3). The most commonly identified species is wild goat (*Capra aegagrus*) and sheep/goat, followed by tortoise (*Testudo* sp.), chukar partridge

Table 3
Ghar-e Boof. Frequencies of sedimentological alterations, weathering damage and gnawing observed on faunal specimens by AH.

	III		IIIa		IIIb		IIIc		IV		IVa		IVb		Total	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Sedimentological alterations																
None	711	53.4	170	59.9	468	67.8	186	63.3	126	66.0	151	64.5	82	74.5	1894	60.4
Bone covered or partially covered by sediment crust	583	43.8	107	36.0	207	30.0	100	34.0	65	34.0	83	35.5	28	25.5	1173	37.4
Sediment Crushing	37	2.8	10	3.4	15	2.2	8	2.7	0	0.0	0	0.0	0	0.0	70	2.2
Total	1331	100.0	287	100.0	690	100.0	294	100.0	191	100.0	234	100.0	110	100.0	3137	100.0
Weathering[a]																
None	822	68.3	195	72.0	318	49.7	143	50.7	110	64.7	123	55.4	67	64.4	1778	61.4
Fine linear cracks only	3	0.3	0	0.0	2	0.3	0	0.0	2	1.1	1	0.5	2	1.9	10	0.4
Fine cracks, some “open”	1	0.1	0	0.0	0	0.0	0	0.0	0	0.0	1	0.5	0	0.0	2	0.1
Many cracks, most “open”	0	0.0	0	0.0	0	0.0	1	0.4	0	0.0	0	0.0	0	0.0	1	<0.1
Some exfoliation	0	0.0	1	0.4	0	0.0	0	0.0	0	0.0	2	0.9	1	1.0	4	0.1
Advanced exfoliation	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.5	0	0.0	1	<0.1
Chemical weathering	376	31.3	76	28.0	317	49.6	140	49.7	67	37.9	94	42.3	36	34.6	1106	38.2
Root etching	6	0.5	0	0.0	5	0.8	0	0.0	1	0.6	3	1.4	1	1.0	16	0.6
Total	1203	100.0	271	100.0	639	100.0	282	100.0	177	100.0	222	100.0	104	100.0	2898	100.0
Gnawing[a]																
None	1168	97.1	260	95.9	630	98.6	270	95.7	174	98.3	192	86.5	92	88.5	2786	96.1
Carnivore damage	21	1.7	8	3.0	6	0.9	6	2.1	1	0.6	3	1.4	6	5.8	51	1.8
Rodent	14	1.2	3	1.1	3	0.5	6	2.1	2	1.1	27	12.2	6	5.8	61	2.1
Total	1203	100.0	271	100.0	639	100.0	282	100.0	177	100.0	222	100.0	104	100.0	2898	100.0

[a] Tooth elements are excluded.

Table 4
Ghar-e Boof. Number of identified specimens (NISP) and relative proportions (%) by AH for each taxon or body size group.

Taxon	III		IIIa		IIIb		IIIc		IV		IVa		IVb		Total	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Ungulate																
Small ungulate	68	5.1	9	3.1	34	4.9	14	4.8	6	3.1	12	5.1	2	1.8	145	4.6
Gazelle (*Gazella* sp.)	34	2.6	9	3.1	18	2.6	5	1.7	6	3.1	6	2.6	1	0.9	79	2.5
Small/medium ungulate	100	7.5	8	2.8	40	5.8	21	7.1	11	5.8	15	6.4	2	1.8	197	6.3
Gazelle/goat (*Gazella/Capra*)	1	<0.1	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	2	0.1
Medium ungulate	439	33.0	89	31.1	216	31.3	113	38.4	54	28.3	95	40.6	51	46.4	1057	33.7
Sheep (*Ovis* sp.)	19	1.4	3	1.1	7	1.0	2	0.7	3	1.6	6	2.6	1	0.9	41	1.3
Wild goat (*Capra aegagrus*)	95	7.1	23	8.0	50	7.2	6	2.0	8	4.2	10	4.3	7	6.4	199	6.3
Sheep/goat (*Ovis/Capra*)	105	7.9	22	7.7	63	9.1	23	7.8	6	3.1	27	11.5	2	1.8	248	7.9
Medium/large ungulate	11	0.8	2	0.7	5	0.7	0	0.0	1	0.5	4	1.7	0	0.0	23	0.7
Large ungulate	11	0.8	6	2.1	11	1.6	5	1.7	2	1.1	15	6.4	2	1.8	52	1.7
Red deer (*Cervus elaphus*)	0	0.0	0	0.0	4	0.6	1	0.3	0	0.0	0	0.0	0	0.0	5	0.2
Wild pig (*Sus scrofa*)	3	0.2	0	0.0	2	0.3	2	0.7	0	0.0	1	0.4	1	0.9	9	0.3
Equid (*Equus* sp.)	1	<0.1	0	0.0	0	0.0	0	0.0	0	0.0	1	0.4	0	0.0	2	0.1
Large/very large ungulate	3	0.2	0	0.0	1	0.2	0	0.0	1	0.5	2	0.9	2	1.8	9	0.3
Very large ungulate	2	0.2	0	0.0	1	0.2	0	0.0	0	0.0	4	1.7	0	0.0	7	0.2
Wild cattle (*Bos primigenius*)	1	<0.1	0	0.0	0	0.0	0	0.0	0	0.0	1	0.4	0	0.0	2	0.1
Carnivore																
Small carnivore	0	0.0	0	0.0	3	0.4	0	0.0	0	0.0	0	0.0	0	0.0	3	0.1
Wild Cat (*Felis* sp.)	2	0.2	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	3	0.1
Red fox (*Vulpes vulpes*)	4	0.3	0	0.0	2	0.3	1	0.3	0	0.0	0	0.0	0	0.0	7	0.2
Large carnivore	2	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	0.1
Small mammals																
Indet. Erinaceidae	2	0.2	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	3	0.1
Brandt's Hedgehog (*Paraechinus* cf. *hypomelas*)	4	0.3	0	0.0	0	0.0	0	0.0	8	4.2	0	0.0	0	0.0	12	0.4
Reptile																
Tortoises (*Testudo* sp.)	115	8.6	41	14.3	22	3.2	28	9.5	52	27.2	23	9.8	11	10.0	292	9.3
Fish																
Indet. Leuciscinae	1	<0.1	1	0.4	8	1.2	0	0.0	0	0.0	0	0.0	0	0.0	10	0.3
Nase (*Chondrostoma* sp.)	1	<0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	<0.1
Birds																
Small birds	5	0.4	0	0.0	4	0.6	9	3.1	14	7.3	1	0.4	8	7.3	41	1.3
Medium birds	199	15.0	55	19.1	160	23.1	50	17.0	17	8.9	8	3.4	17	15.5	506	16.1
Partridge (*Alectoris* cf. *chukar*)	92	6.9	16	5.6	31	4.5	8	2.7	2	1.1	3	1.3	3	2.7	155	4.9
Dove (Cf. *Streptopelia/Columba*)	2	0.2	0	0.0	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	3	0.1
Large birds	9	0.7	2	0.7	4	0.6	4	1.4	0	0.0	0	0.0	0	0.0	19	0.6
Huge birds	0	0.0	1	0.4	0	0.0	2	0.7	0	0.0	0	0.0	0	0.0	3	0.1
Total	1331	100.0	287	100.0	690	100.0	294	100.0	191	100.0	234	100.0	110	100.0	3137	100.0

(*Alectoris* cf. *chukar*), gazelle (*Gazella* sp.), and sheep (*Ovis* sp.). Other species of large and very large ungulates were recorded in the assemblage, such as wild pig (*Sus scrofa*), red deer (*Cervus elaphus*), equid (*Equus* sp.), and wild cattle (*Bos primigenius*), but they are uncommon. Similarly, carnivores were rare at Ghar-e Boof, with just two identified species: red fox (*Vulpes vulpes*) and wild cat (*Felis* sp.). The assemblage also includes a small number of Brandt's hedgehog (*Paraechinus* cf. *hypomelas*), dove (cf. *Streptopelia/Columba*), and fish remains (indeterminate Leuciscinae and a nase, *Chondrostoma* sp.).

We present the relative species representation for large game relative to small game, and small, slow-moving relative to small, fast-moving game in Fig. 6 (data from Tables 4 and 5). Cochran's test of linear trend indicates that there is a statistically significant increase of small game over time ($X^2_{\text{trend}} = 6.61$, $p = 0.01$). There is also a significant increase through time of small, fast-moving game relative to small, slow-moving animals ($X^2_{\text{trend}} = 25.35$, $p = < 0.0001$). However, though significant, in both cases X^2_{trend} values for temporal trends are low.

4.2.2. Prey age

Tripolar plots of mortality data indicate that Rostamian hunters targeted mainly prime-aged adult ungulates, though there is a mild deviation towards a living-structure or non-selective pattern (juvenile-prime-old) (Fig. 7). Table 6 shows epiphyseal fusion data for sheep/goat and medium ungulates. Although the sample size is small for some of the selected skeletal elements, first phalanges, second phalanges, and distal metapodials indicate that more than 70% of caprines survived to be sub-adults. We also identified a medium ungulate fetal scapula in AH III.

4.3. Anatomical profiles

Fig. 8 depicts the representation of the different anatomical body parts for caprines/medium ungulates by AH. Almost all anatomical regions are present in most of the layers, with two exceptions: first, horns were only recorded in AH IV; second, there are neck elements in all the layers, but not in AH IV. Although the sample size varies between AHs, some patterns are apparent. Overall, medium ungulates are represented mainly by head parts and limb elements, whereas there is an underrepresentation of neck and axial elements, and horns. Skeletal evenness (1/D) is found in Table 7. The distribution of the different body parts is moderately even, and it remains stable through the entire Rostamian sequence (1/D values between 4.48 and 5.75, Fig. 9).

4.4. Butchery and carcass processing

In Fig. 10, we depict absolute values and the relative proportion of unburned and burned (carbonized and calcined) bones. Overall, frequencies of specimens exhibiting burning damage is fairly low. Of our assemblage, 15.2% is burned, while 11.4% is carbonized and

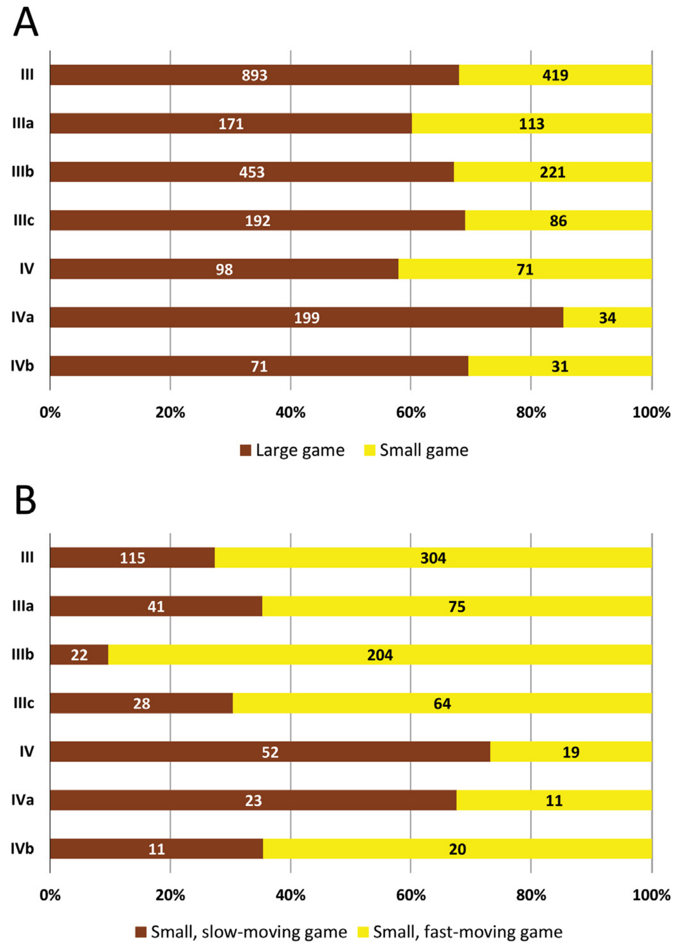


Fig. 6. Ghar-e Boof. Species representation (NISP) for large game relative to small game (a), and small, slow-moving game relative to small, fast-moving game (b). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

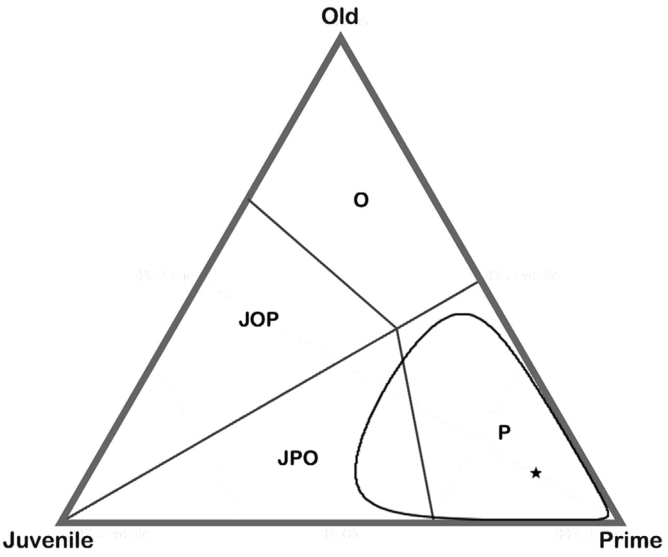


Fig. 7. Ghar-e Boof. Three-cohort mortality profiles for sheep/goat based on the premolar sets (dp4-p4) from the Rostamian sequence (all layers combined). Data from Table A.4.

Table 6

Ghar-e Boof. Percentages of unfused and fused elements. Skeletal elements were selected following Stiner (2005). Elements fuse between 12 and 48 months (Zeder, 2006).

Element	Fusion (months)	MNE (total)	% Unfused	% Fused
P Phalanx 1	12–18	56	30	70
P Phalanx 2	12–18	57	21	79
D Tibia	18–30	2[a]	50	50
D Metapodial	18–30	30	20	80
D Calcaneus	30–48	4[a]	50	50
P Femur	30–48	8[a]	25	75
D Radius	30–48	4[a]	50	50

[a] Small sample sizes.

Table 5

Ghar-e Boof. Prey body-size groups and their relative proportions by AH.

Taxon[a]	*III*		*IIIa*		*IIIb*		*IIIc*		*IV*		*IVa*		*IVb*		*Total*	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Very large ungulate	3	0.3	0	0.0	1	0.2	0	0.0	0	0.0	5	2.4	0	0.0	9	0.3
Large ungulate	15	1.2	6	2.2	17	2.7	8	3.0	2	1.3	17	8.0	3	3.1	68	2.3
Medium ungulate	658	54.6	137	49.5	336	52.6	144	54.6	71	45.5	138	65.1	61	62.2	1545	54.2
Small ungulate	102	8.5	18	6.5	52	8.2	19	7.2	12	7.7	18	8.5	3	3.1	224	7.9
Large carnivore	2	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	0.1
Small carnivore	6	0.5	0	0.0	6	0.9	1	0.4	0	0.0	0	0.0	0	0.0	13	0.5
Small, slow-moving	115	9.5	41	14.8	22	3.4	28	10.6	52	33.3	23	10.9	11	11.2	292	10.3
Small, fast-moving	304	25.2	75	27.2	204	32.0	64	24.2	19	12.2	11	5.2	20	20.4	697	24.5
Total	1205	100.0	277	100.0	638	100.0	264	100.0	156	100.0	212	100.0	98	100.0	2850	100.0

[a] Prey body-size groups are as follows: very large ungulate (wild cattle), large ungulate (red deer, wild pig and equids), medium ungulate (sheep/goat), small ungulate (gazelle), small carnivore (fox/cat sized), small, slow-moving game (tortoises), small, fast-moving game (medium -Galliformes/Columbiformes-, large -small raptors-, and huge -large raptors-birds, and fish).

3.8% is calcined. The proportion of burned specimens changes little over the chronological sequence, though there is a slight increase in the uppermost layers (AHs IIIa and III).

Frequencies of butchery damage are presented in Table 8. The most common types of damage are splits and spiral fractures (27% for the overall faunal assemblage, with more than 20% in almost all of the AHs). Transverse fractures are far less abundant (8%). Both types of fractures can occur when fresh bones are broken for marrow extraction. Frequencies of cut marks and impact damage (including cone fractures), are fairly low (6.4% and 4.1%, respectively). Cut marks and percussion impacts were documented on bone specimens belonging to all the different body size groups of ungulates, from small to very large. We also recorded cut marks on bird, tortoise and carnivore remains (Fig. 11).

To take a closer look at carcass butchery strategies of the most common prey groups, we present frequencies of cut marks and

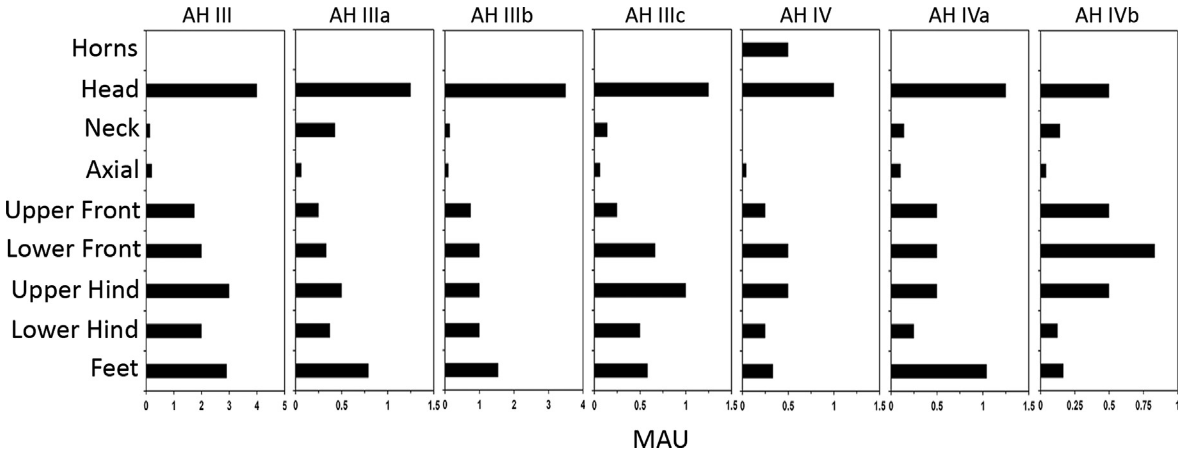


Fig. 8. Ghar-e Boof. MAU for each skeletal region of sheep/goat and medium ungulates by AH. Data from Tables A.5-11.

Table 7
Ghar-e Boof. Skeletal evenness (reciprocal of Simpson's index, expressed as 1/D) across anatomical regions by AH.

Archaeological horizon	1/D
AH III	5.75
AH IIIa	5.42
AH IIIb	4.48
AH IIIc	5.39
AH IV	5.73
AH IVa	5.27
AH IVb	5.23

percussion impacts by element for medium ungulates in Fig. 12. All the UP horizons were combined in order to have a more representative sample. Meat-bearing and lower limb elements, such as the humerus, femur, innominate, radius and tibia, have high frequencies of cut marks (between 16.7 and 26.0%; Fig. 12a). Cut marks on carpals, tarsals, mandibles, and metapodials are fairly common (between 7.8 and 13.3%), and we also recorded cuts on some phalanges, skull elements, and ulnae, but to a lesser extent (1.7–6.7%). Furthermore, we found a medium ungulate rib specimen with cut marks on its ventral surface (Fig. 13). Regarding marrow processing, frequencies of percussion impacts seem to be higher in long-bone elements with high-marrow content, such as the tibia, femur, metacarpals, and humerus (Table 9 and Fig. 12b). However, the sample size is not large enough to statistically confirm this relationship. In addition, some phalanges, examples of elements with small marrow cavities, also preserve impacts. Finally, we identified 5 fragments of bone tools (Table 8) that complement the small number of organic tools reported by Conard and Zeidi (2019).

5. Discussion and conclusions

Overall, the results of our analyses indicate there are two taphonomic alterations that affected a large number of the faunal remains recovered at Ghar-e Boof. First, several bone specimens present irregular etched scars and/or spots. We interpreted this as chemical weathering and/or corrosion, and it seems to have been caused by some kind of acid due to diagenetic processes and the decomposition of organic materials in the direct burial context of the bones (Fernández-Jalvo and Andrews, 2016). Indeed, the micromorphological study of thin sections from AHs III and IV revealed that part of the site was covered by a vegetated surface, while in some areas there is evidence of bird or bat guano (Schilt, 2011). Second, many specimens were covered by thick mineral concretions, presumably made of calcium carbonate (Conard and Zeidi, 2019). Ghar-e Boof is a small-shallow cave, and, during field work at the site, excavators observed that when there is heavy rain in the Dasht-e Rostam region, accompanied with strong winds, rain can enter the cave. The percolation of water through the sediments

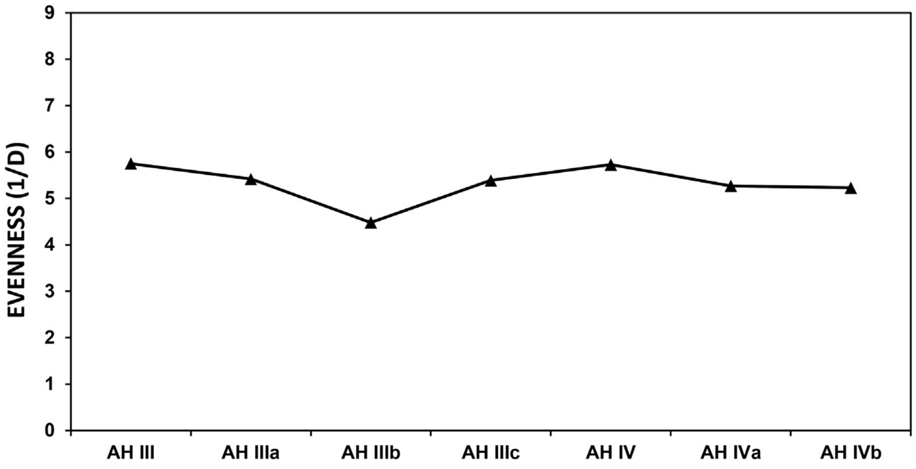


Fig. 9. Ghar-e Boof. Evenness (reciprocal of Simpson's index, expresses as 1/D) for the different medium ungulate anatomical regions by AH. Data from Table 7.

Fig. 10. Ghar-e Boof. NISP count and relative proportion of unburned and burned (carbonized/calcined) bones by AH. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 8
Ghar-e Boof. Butchery damage on faunal specimens by AH. Tooth remains are excluded.

Butchery damage	*III*		*IIIa*		*IIIb*		*IIIc*		*IV*		*IVa*		*IVb*		*Total*	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Cone/impact fracture	27	2.2	7	2.6	35	5.5	23	8.1	5	2.8	13	5.9	10	9.6	120	4.1
Transverse fracture	110	9.1	19	7.0	53	8.3	30	10.6	15	8.4	20	9.0	8	7.7	255	8.8
Split/spiral fracture	291	24.2	68	25.0	202	31.6	76	26.9	44	14.7	71	32.0	39	37.5	791	27.3
Cut marks	59	4.9	19	7.0	36	5.6	17	6.0	20	11.2	25	11.3	10	9.6	186	6.4
Bone tools	2	0.2	0	0.0	1	0.2	1	0.4	0	0.0	0	0.0	1	1.0	5	0.2
Total	1203	100.0	272	100.0	639	100.0	283	100.0	179	100.0	222	100.0	104	100.0	2902	100.0

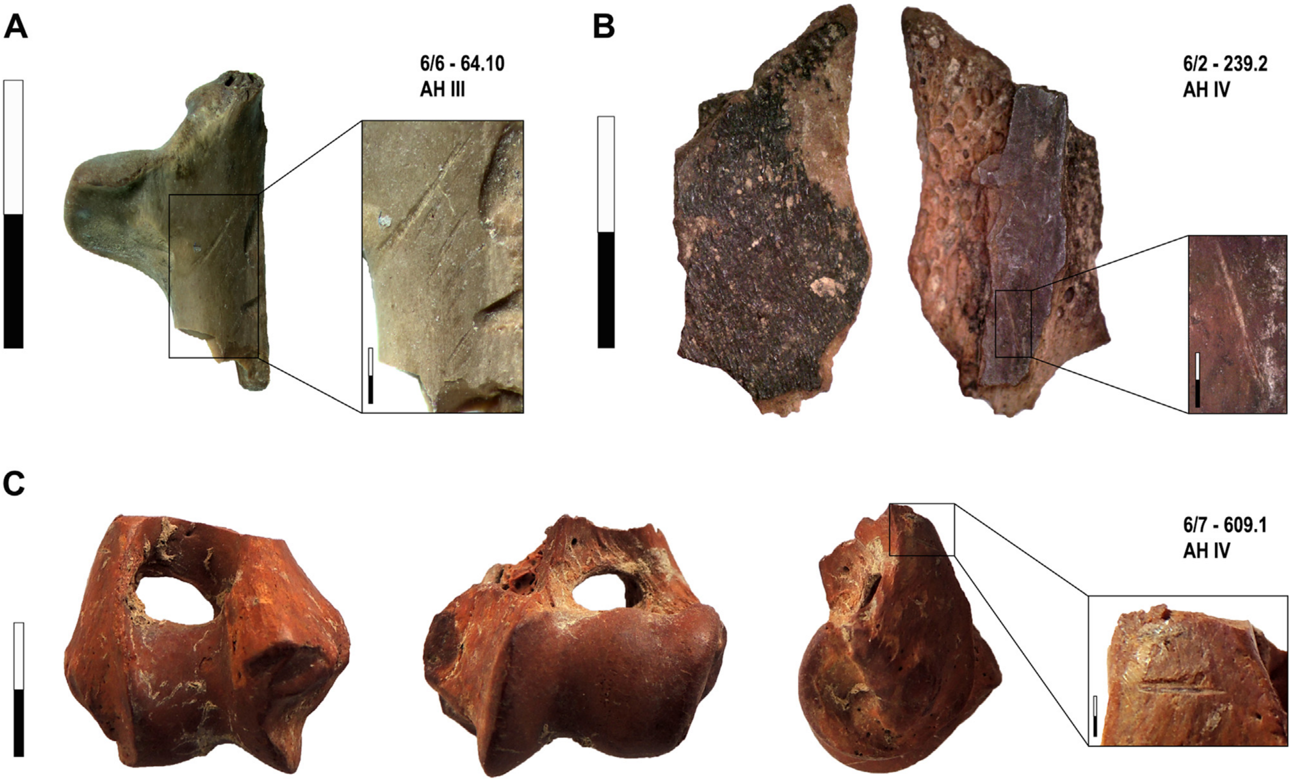


Fig. 11. Ghar-e Boof. Cut marks on small game remains: a) proximal epiphysis of bird scapula; b) tortoise-shell fragment; c) distal epiphysis of red fox humerus. Scale: general view = 10 mm; closer-up view = 1 mm. Figure by A. Blanco-Lapaz.

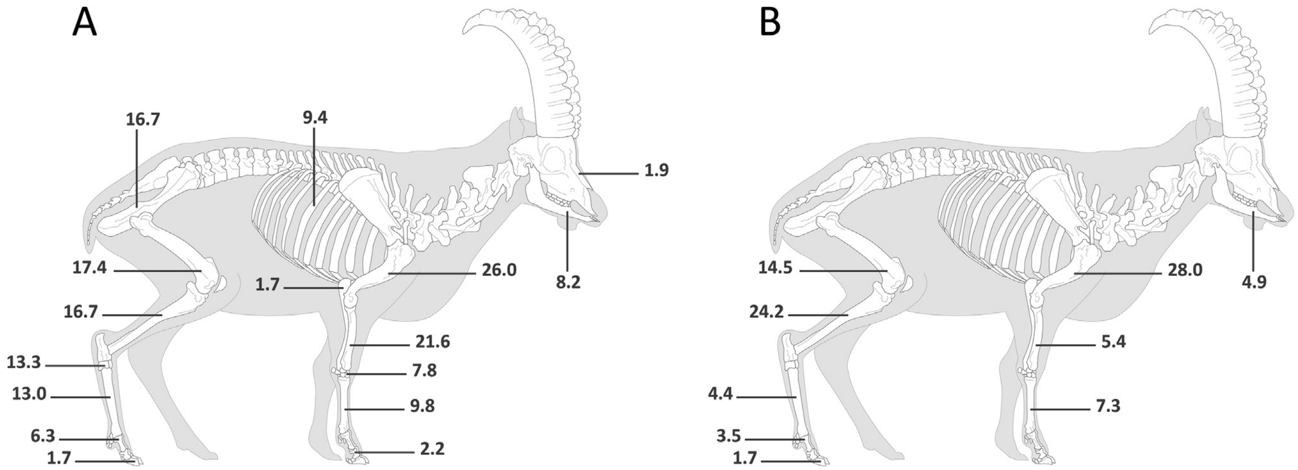


Fig. 12. Ghar-e Boof. Frequencies (%) of cut marks (a) and percussion impacts (b) on medium ungulate specimens by element for the Rostamian sequence (all layers combined). Data from Tables A.12 and A.13. Goat skeleton drawn by M. Coutureau (© 2015 ArcheoZoo.org).

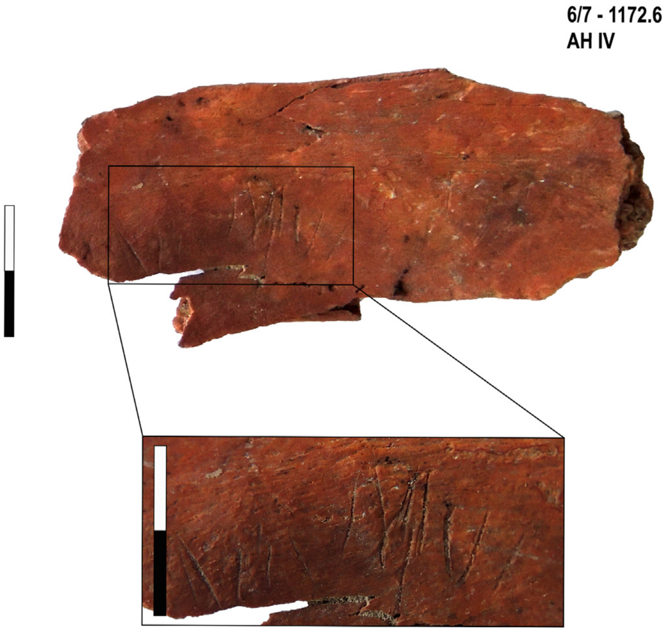


Fig. 13. Ghar-e Boof. Medium ungulate rib fragment with cut marks on the ventral surface. Scale: general view and closer-up view = 10 mm. Figure by A. Blanco-Lapaz.

Table 9
Ghar-e Boof. Medium ungulate specimens (N) with percussion impacts (cones, opposite cones and impacts) by element and their relative proportion (%) from all layers combined, along with the Marrow Index (MI; values for sheep from Binford, 1978:27).

Elements	*N*	*%*	*MI*
Metatarsal	1	4.4	117.67
Tibia	16	24.2	88.50
Metacarpal	3	7.3	67.39
Radius	2	5.4	52.12
Femur	10	14.5	47.30
Humerus	14	28.0	34.90
First phalanx	5	3.5	33.77
Second phalanx	0	0.0	25.11
Calcaneus	0	0.0	23.11
Mandible	3	4.9	10.35
Innominate	0	0.0	9.57
Scapula	0	0.0	6.23
Third phalanx	1	1.7	1.00
Total	55	8.5	

could be the reason why bones were encased by sediment crusts. These concretions obscured the identification of bone surface modifications. As we mentioned previously, sediment concretions were removed and cleaned when possible; nevertheless, they damaged the surface of many specimens. Despite this, the high frequency of split/spiral and transverse fractures, tool impacts, and cut marks indicates that the faunal assemblage of Ghar-e Boof can provide reliable information for reconstructing past human behavior and animal economies.

Overall, there is a good fidelity between the accumulation of bones by humans and the archaeological record. Evidence of carnivore damage and rodent gnawing are uncommon, so they were probably not the main agents of bone accumulation and/or modification at the site. Weathering damage and root etching is also rare, which fits with our expectations about an assemblage from a rockshelter. Although specimens with burning damage are more common than those with gnawing or weathering damage, their relative proportions are still fairly low and they display little change over the UP sequence. Our results also show positive correlations between bone density values and percent survivorship for sheep/goat and medium ungulate remains in AHs III and IIIb. However, a correlation between bone survivorship and density values do not indicate the biasing agent of bone loss (non-human vs. human processes; Beaver, 2004). Bone survivorship could potentially reflect human transport decisions, instead of attrition (Stiner, 1994, 2002; Lyman, 1994, 2008; Beaver, 2004). Despite that, the higher proportion of ungulate cranial bone-based MNEs in comparison with tooth-based MNEs suggest that density-mediated attrition played a minor role in shaping this assemblage, and the general patterns observed in our taxonomic and anatomical study most likely reflect human subsistence strategies.

5.1. Human subsistence strategies during the Rostamian

Our zooarchaeological study indicates that the main prey at Ghar-e Boof was sheep/goat. If we assume that specimens classified as medium ungulates were probably also caprines, then they comprise more than half of the total remains in this assemblage. The presence of cut marks on bird and tortoise bones demonstrates that small game animals were also eaten by humans. Though there is no direct evidence at Ghar-e Boof, it is also possible that birds were exploited for reasons other than food. For instance, several studies have suggested the use of feathers in Paleolithic contexts and their possible role in the symbolic repertoire of people (e.g., Finlayson et al., 2012; Blasco et al., 2019). Moreover, gazelles, and to a much lesser extent, pigs, red deer, horses, cattle, and fish were also part of the human diet. Along with legumes, which were presumably collected by people (Baines et al., 2014), the faunal remains highlight that Rostamian foragers had a diverse diet that included a mix of terrestrial, aquatic, animal and plant resources. In addition, the low frequencies of carnivore gnawing on the faunal specimens indicate that the site was occupied mainly by humans and it was not used extensively as a carnivore den. Although carnivores were rare at Ghar-e Boof, the documentation of a fox specimen with cut marks support the human exploitation of carnivores for meat and/or fur.

The animal species found at Ghar-e Boof also provide new insights that improve our understanding of the foraging and environmental conditions during the early UP of the southern Zagros Mountains. All the ungulate species from the site are extant in Iran, therefore we can infer their ecological niches and habitat requirements based on their present-day distribution (Evins, 1982; Firouz, 2005; Otte et al., 2007; Karami et al., 2016). The habitat surrounding the site is characterized by piedmonts and craggy-rocky slopes, and based on the dominance of sheep/goat, people were probably hunting nearby or at least in the local area that has such an environment (Baskin and Danell, 2003; Firouz, 2005; Genov et al., 2009). Although wild goats mainly prefer rocky-mountainous areas, they can also be found in dry-arid lowlands and open steppe landscapes (Roberts, 1977; Schaller, 1977; Genov et al., 2009). An open steppe is also indicated by the presence of gazelles, equids, and cattle. In spite of being less common, red deer and wild pig suggest the existence of some open woodlands (Firouz, 2005; Karami et al., 2016). A preliminary study of the archaeobotanical remains of Ghar-e Boof shows a balance of rocky, wet, and steppe plants (Baines et al., 2014). The presence of legumes/vetches, such as *Lathyrus*/*Vicia* and *Medicago*, and perennial herbs (i.e., *Polygonum*), native to the Mediterranean, indicate temperate climatic conditions (Baines et al., 2014). The analysis of the small vertebrate assemblage of Ghar-e Boof is still ongoing; nonetheless, for the UP horizons we have already identified several genera of micromammals, such as jird (*Meriones* spp.), vole (*Microtus* sp.), mole vole (*Ellobius* sp.), along with toad (Bufonidae), agamid lizard (Agamidae), and lamprophiid snake (Lamprophiidae). Therefore, the paleoenvironmental context drawn from this study supports the archaeobotanical and small-vertebrate data, which suggests a landscape dominated by warm, arid conditions, with open, dry meadows and rocky terrain, and some nearby water sources (Baines et al., 2014).

Prey mortality data are quite limited because of the available sample size for UP horizons, thus any interpretations must be made with caution. It seems than Rostamian hunters focused on prime-aged adult ungulates, though both dental wear and bone fusion data show some overlap with non-selective hunting. Prime-age-focused harvesting is ecologically unique to the human species, having developed since at least 400 ka BP (Stiner et al., 2011), and is consistently documented through the MP and UP in southwestern Asia (Kersten, 1987; Speth and Tchernov, 1998; Yeshurun et al., 2007; Asouti et al., 2020). Targeting prime-aged adult ungulates is considered to yield higher fat return rates on average than hunting juveniles (Stiner, 1994). Furthermore, the focus on prime-adult prey implies controlled procurement by hunting bands, which must involve social, cooperative labor and a planned use of the space (Stiner, 1990). The strategic location of Ghar-e Boof and many other rockshelters in the Yagheh Sangar, the narrow pass that separates the southeastern and northwestern halves of Dasht-e Rostam region, provided past foragers with an extraordinary panoramic view of the landscape, which allowed occupants to observe prey crossing the valley and to intercept them at predetermined points (Conard and Ghasidian, 2011; Ghasidian, 2014; Heydari-Guran, 2014). The overlap with non-selective pattern might also be interpreted as the result of ambush hunting, with the possibility of using landscape trapping strategies (Wright and Miller, 1976; Stiner, 1990; Zhang et al., 2010).

Several ethnographic and archaeological studies have illustrated how skeletal element representation reflects patterns of carcass transport, based on the nutritional values of different skeletal portions or particular elements and their corresponding tissues, as well as the travel distances between kill sites and campsites (Binford, 1978; Bunn et al., 1988; O'Connell et al., 1988, 1990; Lupo, 2006). Overall, body part representation for medium ungulates during the UP points to foragers transporting whole carcasses to the site. This also suggest that caprines were hunted nearby. Following the central place foraging model, hunting over short distances requires lower energetic costs in terms of handling time, enabling the transport of complete carcasses, even of large prey, to the site (Cannon, 2003).

Evenness values for anatomical profiles remain relatively stable through the entire Rostamian sequence. Despite small sample sizes in some of the layers and their limitations to correctly differentiating between different carcass transport strategies (Faith and Gordon, 2007), it seems that foragers were using Ghar-e Boof as a campsite and transporting animal carcasses there in a similar way over the course of several millennia. Nevertheless, our data show an underrepresentation of horns, neck and axial elements. Although the ratio of tooth cranial-to tooth-based MNE values is higher, it is still possible that the underrepresentation of neck and axial elements indicates some degree of density-mediated attrition. Indeed, less structurally dense elements, such as ribs and vertebrae could be more easily affected by sediment compaction and chemical leaching (Binford and Bertram, 1977; Marean and Spencer, 1991; Lyman, 1994; Fisher, 1995; Marean and Frey, 1997; Faith and Gordon, 2007). An alternative explanation would be the in-field abandonment of most of the neck and axial elements before transport (Starkovich, 2017). The underrepresentation of horns, on the other hand, probably reflects an identification bias. Both male and female caprines have horns, though their size differs significantly (Schaller, 1977). However, when highly fragmented, caprine horns may lack diagnostic morphological features and they frequently overlap in size with those of small-bodied ungulates, such as gazelles. As a result, we classified most horn fragments recovered at Ghar-e Boof as small/medium ungulates.

While our faunal assemblage is not very informative regarding prey sex composition, the preservation of a fetal scapula in AH III confirms that Rostamian foragers also hunted at least one pregnant caprine. The fetal scapula may also suggest humans occupied the site at least during late winter and/or early spring, since sheep and goats give births during spring (Korshunov 1994; Karami et al., 2016). Beyond this, we found little evidence to determine the seasonal timing of the occupation of Ghar-e Boof.

Despite the underrepresentation of anthropogenic modifications due to sediment concretions and/or chemical weathering, cut marks, percussion impacts, and different types of fractures allow us to reconstruct butchery strategies and bone processing at Ghar-e Boof. Cut marks located on meat-bearing elements reflect defleshing, filleting and dismembering activities, whereas those located on carpals, tarsals, metapodials and phalanges, among others, might be more associated with the disarticulation and skinning of carcasses (Binford, 1981; Lyman, 1987; Galán and Domínguez-Rodrigo, 2013; Soulier and Costamagno, 2017). Finally, a rib specimen presents cut marks on its ventral surface, probably caused by the exploitation of animal organs (Yravedra et al., 2010, 2012). Moreover, ethnographic and archaeological studies have demonstrated that hunter-gatherers preferentially accessed within-bone nutrients based on their energetic yields (Binford, 1978; Jones and Metcalfe, 1988; Saint-Germain, 1997; Cregg-Madrigal, 2004; Bar-Oz and Munro, 2007). Here we interpret percussion impacts and cone fractures as direct evidence for marrow extraction. In this assemblage, these modifications seem to be more common on long-bone elements with high-marrow content. Within-bone nutrients exploitation could also explain the relatively high frequencies of split/spiral and transverse fractures on long bone elements. All these markers also suggest the importance of marrow processing for the occupants of Ghar-e Boof.

5.2. Evidence of resource intensification or changes in site occupation intensity?

Within optimal foraging theory, the prey choice model ranks food items by taking into account the cost of acquiring a given resource, its handling time, and its nutritional benefits (Stephens and Krebs, 1986; Kelly, 1995; Pianka, 2000). According to the model, foragers pursue the highest-return resources, turning to low-return foods only when high-return resources are scarce or not available (Kelly, 1995; Pianka, 2000). Previous ethnographic studies have found that large mammal or ungulate prey are generally high-ranked by hunter-gatherers (Broughton, 1994; Broughton et al., 2011; Hames and Vickers, 1982; Kelly, 1995; among others). Small-bodied taxa, on the other hand, are normally considered low-ranked (Broughton, 1994); however, small prey also presents variation in return rates (Stiner et al., 1999, 2000; Munro, 2004; Steele and Klein, 2009). For instance, slow or sessile animals, such as tortoises and limpets, can be collected very easily by foragers, and, therefore, have relatively high return rates due to their low capture costs (Stiner et al., 1999, 2000; Munro, 2004). In contrast, small, fast-moving animals, such hares, partridges, and fish, have lower caloric returns and higher capture costs because of their predator escape strategies. Moreover, hunting small, fast game taxa also requires the cooperation of larger groups of people or a greater technological investment to make nets or snares (Madsen and Schmitt, 1998; Stiner et al., 1999, 2000; Lupo and Schmitt, 2002). A shift from high-return ungulate prey to low-return small prey could indicate resource depletion and increased hominin hunting pressures. Therefore, the application of the prey choice model allows us to make predictions about decisions people made in the past, how people behaved and how they optimized their foraging efforts, based on the relative proportions of high-versus low-ranked prey animals (Stephens and Krebs, 1986; Kelly, 1995; Pianka, 2000).

Our results show that there is a decrease in large game through time in tandem with a progressive increase of small, fast-moving game, mostly partridges. This is a pattern that has been documented at several other UP sites in Eurasia, mainly in the Mediterranean Basin (Morales et al., 1998; Stiner et al., 1999, 2000; Aura Tortosa et al., 2002; Munro, 2004; Speth and Clark, 2006; Kuhn et al., 2009; Stutz et al., 2009; Stiner, 2009; Stiner and Munro, 2011; Starkovich, 2012, 2014, 2017; Munro et al., 2016; Napierala et al., 2017; Yeshurun et al., 2019; Sadhir et al., 2020). In most cases, this pattern has been interpreted as an increase in hunting pressure and site occupation intensity, though other scholars have attributed certain shifts in prey representation to changes in environmental conditions and resource availability (Jones, 2012). Unfortunately, paleoenvironmental studies are very scarce in the Zagros Mountains, though the available information indicates that animal communities and environmental conditions remained relatively stable during the Late Pleistocene in the region (Otte et al., 2007; Bazgir et al., 2017; Rey-Rodríguez et al., 2020). Thus, the most plausible explanation for changes in species representation at Ghar-e Boof is regional hunting pressure and resource stress. However, although the p values of the Cochran's test of linear trend are significant, X^2_{trend} values are notably low, which suggests that these changes in species representation are relatively subtle. How can we interpret these results then? Is there any other evidence for an increase in hunting pressures? How intensively were Rostamian foragers exploiting animal resources and using the site?

As mentioned above, AHs III-IIIc are very rich in artifacts. The lithic assemblages for these layers include all phases of the reduction sequence (Ghasidian, 2014). As one moves downward in the stratigraphy, the density of finds decreases, and the lithic assemblages found in AHs IV-IVb show less complete reduction sequences (Ghasidian, 2014; Conard and Zeidi, 2019). The presence of Arjeneh points and perforated shells, along with OSL dates, support the attribution of these layers to the early UP (Heydari et al., 2021). Thus, on the basis of lithic artifacts and find densities, it seems that at the onset of the UP, AMHs used the site in an ephemeral manner. Over the course of a few millennia, Rostamian people spent longer periods at Ghar-e Boof. The richer number and variety of artifacts documented in the uppermost layers might also indicate that they performed more varied activities through time (Conard and Zeidi, 2019). Moreover, the analysis of the micromorphology of AHs III and IV shows that the sedimentation rate seems to increase due in part to more frequent human occupations of the site (Schilt, 2011). While AH IV mainly consists of natural sediments, AH III is characterized by high anthropogenic input (Schilt, 2011).

Taking everything together, there is evidence to suggest an increase in site occupation intensity throughout the UP, which concurrently might have resulted in higher hunting pressures and resource stress in the surrounding area of the site. Nevertheless, the term ‘site occupation intensity’ not only comprises length of stay and frequency of visits, but also resident population size (Munro, 2004), though differentiating between these factors is extremely difficult. For instance, the increase in site occupation intensity might be caused by a family group of ten individuals living at the cave for a few days, or by a smaller group staying there several weeks. In addition, the high density of UP sites in the Dasht-e Rostam region (Conard and Ghasidian, 2011; Ghasidian, 2014; Heydari-Guran, 2014) may suggest larger human populations spread across the entire valley. The fact that Rostamian people most likely hunted near the site during the whole sequence could also indicate that increasing travel distances were not possible due to territorial circumscriptions as a result of larger populations in the region (e.g., Starkovich, 2017). Therefore, the increase in site occupation intensity observed at Ghar-e Boof could be caused by any, or even all, of the abovementioned factors.

5.3. Ghar-e boof and the Upper Paleolithic zooarchaeological record of the Zagros Mountains

The long geographic extension of the Zagros Mountains (over 1800 km from northwest to southeast) and the extreme variation in elevation (from ca. 600 to more than 4000 m.a.s.l.) make this area a very complex geographic and ecological system, with multiple, diverse microenvironments. The faunal record of Ghar-e Boof not only provides a unique opportunity for reconstructing local foraging conditions and human subsistence strategies in the Dasht-e Rostam region, but also for improving our understanding of larger regional phenomena regarding the expansion and adaptation of AMHs across the Zagros. Baradostian (UP) and Zarzian (Epipaleolithic) sites located in the southern, central, and northern regions of the mountain range offer an interesting comparison for Ghar-e Boof. Scholars have published zooarchaeological data for

Table 10
Archaeological sites with UP and Epipaleolithic sequences for which zooarchaeological data are available, including their cultural affiliations, techno-typological characteristics and dating. Some of the archaeological sites also preserve MP and Epipaleolithic horizons, but we have mainly focused on UP faunal assemblages, with a few exceptions.

Chronological Periods	Cultural affiliations	Techno-typological characteristics	Sites	Dates (yr. cal BP)	References
Epipaleolithic	Zarzian	Backed bladelets, microlithic bladelets, and thumbnail scrapers	Palegawra Cave	19.6–13 ka	Asouti et al. (2020)
UP & Epipaleolithic	Zarzian & Baradostian-like industries	NA[a]	Eshkaft-e Gavi	NA[a]	Rosenberg (1985); Scott and Marean (2009); Hodgkins and Marean (2017)
UP	Baradostian[b]	Burin, blade and bladelet technology, with a strong emphasis on the production of flakes	Ghar-e Khar	NA[a]	Hesse (1989); Shidrang et al. (2016)
			Warwasi	NA[a]	Braidwood and Howe (1960); Turnbull (1975); Olszewski (1993); Olszewski and Dibble (1994); Otte and Kozłowski (2007); Tsanova (2013)
			Yafteh Cave	38.8–33.5 ka	Hole and Flannery (1967); Otte and Kozłowski (2007); Otte et al. (2007, 2011); Mashkour et al. (2009); Tsanova (2013); Becerra-Valdivia et al. (2017)
			Gelimgoush Cave	42-33 ka	Heydari-Guran et al. (2021)
			Shanidar	43.2–39.6 ka & 35–28.7 ka	Solecki (1958, 1963); Perkins (1964); Hole and Flannery (1967); Evins (1982); Solecki and Solecki (1993); Becerra-Valdivia et al. (2017)
			Kaldar Cave	54.4–46 ka & 38.6–36.7 ka	Bazgir et al. (2014, 2017); Becerra-Valdivia et al. (2017)
	Rostamian	Predominance of diminutive bladelet tools and small platform cores	Ghar-e Boof	42-35 ka	Conard and Ghasidian (2011); Ghasidian (2014); Becerra-Valdivia et al. (2017); Ghasidian et al. (2017, 2019); Heydari et al. (2021)

[a] NA (Not Applicable and/or Not Available).

[b] There are also arguments that some early UP and UP assemblages from the west-central Zagros show a significant degree of regional variability, representing tentatively a different, independent techno-cultural tradition. For further details, see Ghasidian (2019) and Heydari-Guran et al. (2021).

Shanidar, Warwasi, Yafteh Cave, Eshkaft-e Gavi, Ghar-e Khar, Kaldar Cave, Gelimgoush Cave, and Palegawra Cave (Table 10; Perkins, 1964; Hole and Flannery, 1967; Turnbull, 1975; Evins, 1982; Hesse, 1989; Otte et al., 2007, Mashkour et al., 2009; Bazgir et al., 2017; Hodgkins and Marean, 2017; Asouti et al., 2020; Heydari-Guran et al., 2021).

Overall, patterns for anatomical part representation, carcass processing, and mortality profiles are similar to those found at Ghar-e Boof, indicating the transport of whole carcasses to campsites for the exploitation of meat and marrow (Evins, 1982; Hodgkins and Marean, 2017; Asouti et al., 2020), while mortality data mostly fall either within the range of a non-selective pattern (Shanidar and Ghar-e Khar; Evins, 1982; Hesse, 1989) or one focused primarily on prime-aged adults (Palegawra Cave, Asouti et al., 2020). In addition, the taxonomic representation from the above mentioned UP sites show similar relative species abundances, with wild sheep/goat as the main prey followed by gazelles, equids, red deer, wild pig, and cattle (Perkins, 1964; Evins, 1982; Hesse, 1989; Otte et al., 2007; Hodgkins and Marean, 2017). Ghar-e Boof only differs from the faunal assemblages of Warwasi and Palegawra, which are dominated by equids, though sheep/goats are still represented in high proportions (Turnbull, 1975; Asouti et al., 2020). Considering just ungulates recovered at several sites dated between the MP and the Epipaleolithic, Hodgkins and Marean (2017) found no clear temporal trend in species representation and they highlighted the low species diversity observed at the Zagros Paleolithic localities as a consequence of the local high-elevation environments.

When analyzing the dietary spectrum of past foragers, possible changes in species abundance, and signals of an intensified use of habitats, archaeologists must take into account that Paleolithic humans did not only rely on large game species, but also on small animals. Small prey, such as tortoises and partridges, have much more variation than ungulates regarding their life histories and predator escape characteristics (Stiner et al., 1999, 2000; Stiner, 2001). At Ghar-e Boof, small game comprises almost 35.0% of the total faunal assemblage by NISP. In fact, partridges and medium birds represent the second most abundant prey group after medium ungulates. Currently, there are very few comparative zooarchaeological and taphonomic studies of UP collections from the Zagros Mountains that include both large and small game species. Recently, Asouti et al. (2020) have suggested that tortoises presumably played an important role in human subsistence at Palegawra Cave during the Epipaleolithic. Tortoise remains have also been reported in the UP horizons of Kaldar and Yafteh Cave (Mashkour et al., 2009; Bazgir et al., 2017), though with the exception of a burned epiplastron of tortoise from Kaldar Cave, no anthropogenic modifications have been published. We found the same situation with respect to bird remains. A few indeterminate birds were recovered at Ghar-e Khar, Kaldar, Yafteh, and Palegawra caves (Hesse, 1989; Mashkour et al., 2009; Bazgir et al., 2017; Asouti et al., 2020), but taphonomic information is not available. The only exception is Gelimgoush Cave (west-central Zagros), where recently Heydari-Guran et al. (2021) documented a raven specimen with a cut mark dated to 35–34 ka cal. BP. Moreover, Mashkour et al. (2009) noted that hares were a relatively important component of human diets at Yafteh Cave during the UP. Finally, although there is evidence that suggests a non-human accumulation of fish by raptors and/or carnivores, Otte et al. (2007) did not exclude the possibility of human fishing activities at Yafteh Cave. Despite limited archaeological evidence for small game exploitation in the Zagros in terms of anthropogenic modifications, experimental studies have demonstrated that it is possible for humans to process and disarticulate medium birds, such as doves and pigeons, with their bare hands and without any additional tools (Val et al., 2016).

The change in species abundance, with a decrease in large game relative to small game during the Rostamian sequence at Ghar-e Boof, in parallel with an increase in difficult-to-procure small game, represents a unique pattern in the zooarchaeological record of the Zagros Mountains. Contemporary early UP sites in the Levant show similar trends (Stiner et al., 1999; Stiner, 2009; Yeshurun et al., 2019), which may indicate hunting pressure, resource stress, and/or greater occupation intensity as a result of increasing population densities in southwestern Asia during the early UP. Recent archaeological research in Iran, especially in the Dasht-e Rostam, Kermanshah, and Khorramabad regions (southern and west-central Zagros, respectively; Conard et al., 2006, 2007, 2009; Conard and Ghasidian, 2011; Ghasidian, 2014: Heydari-Guran, 2014; Bazgir et al., 2014, 2017; Heydari-Guran and Ghasidian, 2017, 2020; Ghasidian et al., 2017; Conard and Zeidi, 2019), have increased our understanding of settlement patterns and population dynamics during the Late Pleistocene. In comparison to MP assemblages, the high densities of Rostamian and Baradostian industries, in certain regions and habitats of the Zagros, demonstrates a generalized population growth throughout the early UP (Ghasidian et al., 2019; Heydari-Guran and Ghasidian, 2020).

In summary, AMHs spread across the Zagros Mountains between ca. 45–40 ka cal. BP (Becerra-Valdivia et al., 2017; Heydari et al., 2021), where they had to adapt to new and diverse environmental conditions (Boivin et al., 2013). The Zagros have heterogeneous topography and numerous microenvironments, so UP hunter-gatherers adopted diverse cultural adaptations and subsistence strategies in different landscapes (Ghasidian et al., 2019; Heydari-Guran and Ghasidian, 2020). Our results suggest that in the southernmost part of this mountain range, the Dasht-e Rostam region offered a landscape where humans could not only observe and hunt ungulates, but also had access to a variety of food items, including terrestrial, aquatic, animal and plant resources. At the onset of the UP, Ghar-e Boof was either occupied by small groups, or was used very sporadically; however, within less than 3 millennia, there was an increase in occupation intensity. This increase in site use after the arrival of AMHs, along with the ubiquity of early UP Rostamian sites across the entire Dasht-e Rostam region most probably reflects population growth. We hypothesize that this phenomenon might have corresponded with more favorable environmental conditions, though more data are needed. The faunal record is also consistent with larger human population densities, which seem to have resulted in more intensive exploitation of animal prey regionally. Thus, the Rostamian cultural and faunal record of Ghar-e Boof represents a key reference for establishing future regional comparisons with other areas of the Zagros Mountains and southwestern Asia.

Author contributions

Regarding the contributions of the authors, M.M.G. and B.M.S. designed the research and analyzed the faunal assemblage, while all the authors have contributed in the writing, review and editing of the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We would like to thank the Iranian Center for Archaeological Research (ICAR), the Research Institute of Cultural Heritage and Tourism (RICHT), and all members of the TISARP team for their support during fieldwork, especially Saman and Sasan Hamzavi. We are very thankful to Ángel Blanco-Lapaz for sorting, cleaning and restoring the faunal remains presented in this study. He also photographed all the specimens with taphonomic modifications included here and created Figs. 4, 10 and 12. Thanks to Flora Schilt for sharing with us her research about the micromorphology of Ghar-e Boof. We are also grateful to Siah Beattie, Elisa Luzi, Susanne C. Münzel, along with the editor and two anonymous reviewers for their constructive comments that improved our paper. This work was funded by a grant to M.M.G. from the Ministerium für Wissenschaft, Forschung und Kunst Baden-Württemberg as part of the Evolution of Cultural Modernity Project at the University of Tübingen. M.M.G. was also a beneficiary of a research fellowship from the Dr. Daniel Schuhmann Foundation. Excavations at Ghar-e Boof were funded by the Deutsche Forschungsgemeinschaft (DFG) grant CO 226/30–1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2021.107350.

References

Asouti, E., Baird, D., Kabukcu, C., Swinson, K., Martin, L., García-Suárez, A., Jenkins, E., Rasheed, K., 2020. The Zagros Epipalaeolithic revisited: new excavations and ^{14}C dates from Palegawra cave in Iraqi Kurdistan. PLoS One 15 (9), e0239564.

Aura Tortosa, J.E., Villaverde Bonilla, V., Pérez Ripoll, M., Martínez Valle, R., Guillem Calatayud, P., 2002. Big game and small prey: Paleolithic and Epipaleolithic economy from Valencia (Spain). J. Archaeol. Method Theory 9, 215–268.

Baines, J.A., Riehl, S., Conard, N.J., Zeidi, M., 2014. Upper Palaeolithic archaeobotany of Ghar-e Boof cave, Iran: a case study in site disturbance and methodology. Archaeol. Anthropol. Sci. 7, 245–256.

Bar-Oz, G., Munro, N.D., 2007. Gazelle bone marrow yields and Epipalaeolithic carcass exploitation strategies in the southern Levant. J. Archaeol. Sci. 34, 946–956.

Baskin, L., Danell, K., 2003. Ecology of Ungulates: a Handbook of Species in Eastern Europe and Northern and Central Asia. Springer-Verlag, Berlin, Heidelberg.

Bazgir, B., Otte, M., Tumung, L., Ollé, A., Deo, S.G., Joglekar, P., López-García, J.M., Picin, A., Davoudi, D., van der Made, J., 2014. Test excavations and initial results at the Middle and Upper Paleolithic sites of Gilvaran, Kaldar, Ghamari caves and Gar Arjene rockshelter, Khorramabad Valley, western Iran. C. R. Palevol 13, 511–525.

Bazgir, B., Ollé, A., Tumung, L., Becerra-Valdivia, L., Douka, K., Higham, T., van der Made, J., Picin, A., Saladié, P., López-García, J.M., Blain, H.A., Allué, E., Fernández-García, M., Rey-Rodríguez, I., Arceredillo, D., Bahrololoumi, F., Azimi, M., Otte, M., Carbonell, E., 2017. Understanding the emergence of modern humans and the disappearance of Neanderthals: insights from Kaldar Cave (Khorramabad Valley, western Iran). Sci. Rep. 7, 43460.

Beaver, J.E., 2004. Identifying necessity and sufficiency relationships in skeletal-part representation using fuzzy-set theory. Am. Antiq. 69 (1), 131–140.

Becerra-Valdivia, L., Douka, K., Comeskey, D., Bazgir, B., Conard, N.J., Marean, C.W., Ollé, A., Otte, M., Tumung, L., Zeidi, M., Higham, T.F.G., 2017. Chronometric investigations of the Middle to Upper Paleolithic transition in the Zagros Mountains using AMS radiocarbon dating and Bayesian age modelling. J. Hum. Evol. 109, 57–69.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–160.

Binford, L.R., 1978. Nunamiut Ethnoarchaeology. Academic Press, New York.

Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.

Binford, L.R., 1984. Butchering, sharing, and the archaeological record. J. Anthropol. Archaeol. 3, 235–257.

Binford, L.R., Bertram, J.B., 1977. Bone frequencies and attritional processes. In: Binford, L.R. (Ed.), For Theory Building in Archaeology. Academic Press, New York, pp. 77–156.

Blasco, R., Rosell, J., Sánchez-Marco, Gopher, A., Barkai, R., 2019. Feathers and food: human-bird interactions at Middle Pleistocene Qesem Cave, Israel. J. Hum. Evol. 136, 102653.

Boessneck, J., 1963. Osteological differences between sheep (*Ovis aries* Linné) and goat (*Capra hircus* Linné). In: Brothwell, D., Higgs, E. (Eds.), Science in Archaeology: a Comprehensive Survey of Progress and Research, first ed. Thames and Hudson, London, pp. 333–358.

Bobek, H., 1968. Vegetation. In: Fisher, W.B. (Ed.), The Cambridge History of Iran, vol.

1: The land of Iran. Cambridge University Press, Cambridge, pp. 280–293.

Boivin, N., Fuller, D.Q., Dennell, R., Allaby, R., Petraglia, M.D., 2013. Human dispersal across diverse environments of Asia during the Upper Pleistocene. Quat. Int. 300, 32–47.

Braidwood, R.J., Howe, B., 1960. Prehistoric Investigations in Iraqi Kurdistan. University of Chicago Press, Chicago.

Bretzke, K., Conard, N.J., 2017. Not just a crossroad: population dynamics and changing material culture in southwestern Asia during the Late Pleistocene. Curr. Anthropol. 58 (S17), S449–S462.

Broughton, J.M., 1994. Declines in mammalian foraging efficiency during the Late Holocene, San Francisco Bay, California. J. Anthropol. Archaeol. 13, 37–401.

Broughton, J.M., 1999. Resource Depression and Intensification during the Late Holocene. San Francisco Bay: Evidence from the Emeryville Shellmound. University of California Press, Berkeley.

Broughton, J.M., Cannon, M.D., Bayham, F.E., Byers, D.A., 2011. Prey body size and ranking in zooarchaeology: theory, empirical evidence, and applications from the Northern Great Basin. Am. Antiq. 76, 403–428.

Bunn, H.T., Bartram Jr., L.E., Kroll, E.M., 1988. Variability in bone assemblage formation from Hadza hunting, scavenging, and carcass processing. J. Anthropol. Archaeol. 7, 412–457.

Cannon, M.D., 2001. Archaeofaunal relative abundance, sample size, and statistical methods. J. Archaeol. Sci. 28, 185–195.

Cannon, M.D., 2003. A model of central place forager prey choice and an application to faunal remains from the Mimbres Valley, New Mexico. J. Anthropol. Archaeol. 22, 1–25.

Conard, N.J., Ghasidian, E., 2011. The Rostamian cultural group and the taxonomy of the Iranian Upper Palaeolithic. In: Conard, N.J., Drechsler, P., Morales, A. (Eds.), Between Sand and Sea: the Archaeology and Human Ecology of South-Western Asia. Kerns Verlag, Tübingen, pp. 33–52.

Conard, N.J., Zeidi, M., 2019. New research on the Paleolithic occupation of Ghar-e Boof, Fars Province. J. Iranian Center Archaeol. Res. 2, 7–16.

Conard, N.J., Ghasidian, E., Heydari, S., Zeidi, M., 2006. Report on the 2005 survey of the Tübingen Iranian Stone Age Research Project in the Provinces of Esfahan, Fars and Kohgiluyeh-Boyerahmad. In: Azarnoush, M. (Ed.), Archaeological Reports 5. ICAR, Tehran, pp. 9–34.

Conard, N.J., Ghasidian, E., Heydari, S., Naderi, R., Zeidi, M., 2007. The 2006 season of the Tübingen-Iranian Stone Age Research Project in the Provinces of Fars and Markazi. In: Fazeli, H. (Ed.), 9th Annual Report of Archaeological Organisation. ICAR, Tehran, pp. 43–67.

Conard, N.J., Ghasidian, E., Heydari-Guran, S., 2009. The open-air Late Paleolithic site of Bardia and the Paleolithic occupation of the Qaleh Gusheh Sand Dunes, Esfahan Province, Iran. In: Otte, M., Biglari, F., Jaubert, J. (Eds.), Iran Paleolithic/Le Paléolithique D'Iran. BAR International Series, Oxford, pp. 141–154.

Coon, C.S., 1951. Cave Explorations in Iran, 1949. University Museum, University of Pennsylvania, Philadelphia.

Cregg-Madrigal, T., 2004. The derivation and application of white-tailed deer utility indices and return rates. J. Taphon. 2 (4), 185–200.

Discamps, E., Costamagno, S., 2015. Improving mortality profile analysis in zooarchaeology: a revised zoning for ternary diagrams. J. Archaeol. Sci. 58, 62–76.

Evins, M.A., 1982. The fauna from Shanidar Cave: Mousterian wild goat exploitation in northeastern Iraq. Paléorient 8, 37–58.

Faith, J.T., Gordon, A.D., 2007. Skeletal element abundances in archaeofaunal assemblages: economic utility, sample size, and assessment of carcass transport strategies. J. Archaeol. Sci. 34, 872–882.

Fernández-Jalvo, Y., Andrews, P., 2016. Atlas of Taphonomic Identifications. Springer, New York.

Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J.J., Bortolotti, G.R., Finlayson, G., Sánchez-Marco, A., Giles-Pacheco, F., Rodríguez-Vidal, J., Carrión, J.S., Fa, D.A., Rodríguez-Llanes, J.M., 2012. Birds of a feather: Neanderthal exploitation of raptors and corvids. PLoS One 7 (9), e45927.

Firouz, E., 2005. The Complete Fauna of Iran. Tauris & Co Ltd, London.

Fisher, J.W.J., 1995. Bone surface modifications in zooarchaeology. J. Archaeol. Method Theory 2, 7–68.

Galán, A.B., Domínguez-Rodrigo, M., 2013. An experimental study of the anatomical distribution of cut marks created by filleting and disarticulation on long bone ends. Archaeometry 55, 1132–1149.

Ganji, M.H., 1968. Climate. In: Fisher, W.B. (Ed.), The Cambridge History of Iran, vol. 1: The Land of Iran. Cambridge University Press, Cambridge, pp. 212–249.

Garrod, D.A.E., 1930. The Paleolithic of southern Kurdistan: excavations in the caves of Zarzi and Hazar Merd. Bull. Am. Sch. Prehist. Res. 6, 8–43.

Garrod, D., 1957. Notes sur le Paléolithique Supérieur du Moyen Orient. Bull. Soc. Prehist. Fr. 54, 439–445.

Ghasidian, E., 2014. Early Upper Palaeolithic Occupation at Ghar-E Boof Cave: a Reconstruction of Cultural Traditions in Southern Zagros Mountains of Iran. Kerns Verlag, Tübingen.

Ghasidian, E., 2019. Rethinking the Upper Palaeolithic of the Zagros Mountains. PaleoAnthropology 2019, 240–310.

Ghasidian, E., Bretzke, K., Conard, N.J., 2017. Excavations at Ghar-e Boof in the Fars Province and its bearing on models for the evolution of the Upper Paleolithic in the Zagros. J. Anthropol. Archaeol. 47, 33–49.

Ghasidian, E., Heydari-Guran, S., Mirazón-Lahr, M., 2019. Upper Paleolithic cultural diversity in the Iranian Zagros Mountains and the expansion of modern humans into Eurasia. J. Hum. Evol. 132, 101–118.

Genov, P., Georgiev, G., Georgiev, V., 2009. Persian wild goat (*Capra aegagrus* Erxleben) –Biology, ecology and possibilities for its re-introduction in Bulgaria. Biotechnol. Biotechnol. Equip. 23(SE), 341–342.

Gifford-Gonzalez, D.P., 1989. Ethnographic analogues for interpreting modified bones: some cases from East Africa. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, University of Maine, Orono, pp. 179–246.

Grayson, D.K., 1984. Quantitative Zooarchaeology. Academic Press, Orlando.

Halstead, P., Collins, P., 2002. Sorting the sheep from the goats: morphological distinctions between the mandibles and mandibular teeth of adult *Ovis* and *Capra*. J. Archaeol. Sci. 29, 545–553.

Hames, R., Vickers, W., 1982. Optimal diet breadth theory as a model to explain variability in Amazonian hunting. Am. Ethnol. 9, 358–378.

Heydari, M., Guérin, G., Zeidi, M., Conard, N.J., 2021. Bayesian luminescence dating at Ghar-e Boof, Iran, provides new chronology for Middle and Upper Paleolithic in the southern Zagros. J. Hum. Evol. 151, 102926.

Heydari-Guran, S., 2014. Paleolithic Landscapes of Iran. BAR international series, Oxford.

Heydari-Guran, S., 2015. Tracking Upper Pleistocene human dispersals into the Iranian Plateau: a geoarchaeological model. In: Sanz, N. (Ed.), Human Origin Sites and the World Heritage Convention in Eurasia, Heads 4, vol. 6. United Nations Educational, Scientific and Cultural Organization (UNESCO) Office, Paris, France and Ciudad de México, D.F., Mexico, pp. 40–53.

Heydari-Guran, S., Ghasidian, E., 2017. The MUP Zagros Project: tracking the Middle-Upper Palaeolithic transition in the Kermanshah region, West-Central Zagros, Iran. Antiquity 91, 1–7.

Heydari-Guran, S., Ghasidian, E., 2020. Late Pleistocene hominin settlement patterns and population dynamics in the Zagros Mountains: Kermanshah region. Archaeological Res. Asia 21, 100161.

Heydari-Guran, S., Douka, K., Higham, T., Münzel, S.C., Deckers, K., Hourshid, S., Nadari, R., Asiabani, S., Ghasidian, E., 2021. Early Upper Palaeolithic occupation at Gelimgoush Cave, Kermanshah; West-Central Zagros mountains of Iran. J. Archaeol. Sci.: Report 38, 103050.

Hesse, B., 1989. Paleolithic faunal remains from Ghar-i Khar, western Iran. In: Crabtree, P.J., Campana, D., Ryan, K. (Eds.), Early Animal Domestication and its Cultural Context. MASCA, the University Museum of Archaeology and Anthropology. University of Pennsylvania, Philadelphia, pp. 37–45.

Hillson, S., 2005. Teeth. Cambridge University Press, Cambridge.

Hodgkins, J.M., Marean, C.W., 2017. New information from old excavations: a comparative analysis of Paleolithic zooarchaeological assemblages from the Zagros Mountains. In: Biglari, F., Mashkour, M., Shidrang, S. (Eds.), The Pleistocene Archaeology of the Iran and Neighboring Regions. National Museum of Iran Paleolithic Studies Series, No. 1. National Museum of Iran, Tehran.

Hole, F., Flannery, K.V., 1967. The Prehistory of southwestern Iran: a preliminary report. Proc. Prehist. Soc. 33, 147–206.

Ikeda, J., 1979. Preliminary Report of an Archaeological Survey in Arsanjan Area, Fars Province, Iran, 1977. Kyoto University, Kyoto.

Jamali, M., Moghimi, E., Jafarpour, Z.A., 2015. Geomorphology of karst features of Shiraz City and Arjan Plain and development limitations. Int. J. Environ. Eng. 9 (1), 25–31.

Johnson, E., 1985. Current developments in bone technology. In: Schiffer, M.B. (Ed.), Advances in Archaeological Method and Theory, vol. 8. Academic Press, New York, pp. 157–235.

Jones, E.L., 2012. Upper Paleolithic rabbit exploitation and landscape patchiness: the Dordogne vs. Mediterranean Spain. Quat. Int. 264, 52–60.

Jones, K.T., Metcalfe, D., 1988. Bare bones archaeology: bone marrow indices and efficiency. J. Archaeol. Sci. 15, 415–423.

Karami, M., Ghadirian, T., Faizolahi, K., 2016. The Atlas of Mammals of Iran. Department of Environment of Iran, Tehran.

Kelly, R.L., 1995. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. Smithsonian Institution Press, Washington.

Kersten, A.M.P., 1987. Age and sex composition of Epipalaeolithic fallow deer and wild goat from Ksar 'Akil. Palaeohistoria 29, 119–131.

Korshunov, V.M., 1994. Ecology of the bearded goat (*Capra aegagrus* Ersleben 1777) in Turkmenistan. In: Fet, V., Atamuradov, K.I. (Eds.), Biogeography and Ecology of Turkmenistan. Monographiae Biologicae, vol. 72. Springer, Dordrecht, pp. 231–246.

Kuhn, S.L., Stiner, M.C., Güleç, E., Özer, I., Yılmaz, H., Baykara, I., Açıkkol, A., Goldberg, P., Martínez Molina, K., Ünay, E., Suata-Alpaslan, F., 2009. The early Upper Paleolithic occupations at Üçağızlı Cave (Hatay, Turkey). J. Hum. Evol. 56, 87–113.

Lupo, K., 2006. What explains the carcass field processing and transport decisions of contemporary hunter-gatherers? Measures of economic anatomy and zooarchaeological skeletal part representation. J. Archaeol. Method Theory 20, 420–447.

Lupo, K., Schmitt, D.M., 2002. Upper Paleolithic net-hunting, small prey exploitation and women's work effort: a view from the ethnographic and ethnoarchaeological record of the Congo Basin. J. Archaeol. Method Theory 9, 147–179.

Lyman, R.L., 1987. Archaeofaunas and butchery studies: a taphonomic perspective. Adv. Archaeol. Method Theory 10, 249–337.

Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge.

Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge Manuals in Archaeology. Cambridge University Press, New York.

Madsen, D.B., Schmitt, D.N., 1998. Mass collecting and the diet breadth model: a

Great Basin Example. J. Archaeol. Sci. 25, 445–455.

Marean, C.W., Spencer, L.M., 1991. Impact of carnivore ravaging on zooarchaeological measures of element abundance. Am. Antiq. 56, 645–658.

Marean, C.W., Frey, C.J., 1997. Animal bones from caves to cities: reverse utility curves as methodological artefacts. Am. Antiq. 62, 698–711.

Mashkour, M., Radu, V., Mohaseb, A., Hashemi, N., Otte, M., Shidrang, S., 2009. The Upper Paleolithic faunal remains from Yafteh cave (central Zagros) 2005 campaign. A preliminary study. In: Otte, M., Biglari, F., Jaubert, J. (Eds.), Le Paleolithique D'Iran. Archaeopress, Oxford, pp. 73–85.

Morales, A., Roselló, E., Hernández, F., 1998. Late Upper Paleolithic subsistence strategies in southern Iberia: Tardiglacial faunas from Cueva de Nerja (Málaga, Spain). Eur. J. Archaeol. 1, 9–50.

Munro, N.D., 2004. Zooarchaeological measures of hunting pressure and occupation intensity in the Natufian. Curr. Anthropol. 45, S5–S33.

Munro, N.D., Kennerty, M., Meier, J.S., Samei, S., al-Nahar, M., Olszewski, D.I., 2016. Human hunting and site occupation intensity in the Early Epipaleolithic of the Jordanian western highlands. Quat. Int. 396, 31–39.

Nagaoka, L., 2005. Declining foraging efficiency and moa carcass exploitation in southern New Zealand. J. Archaeol. Sci. 32, 1328–1338.

Napierala, H., Kandel, A.W., Conard, N.J., 2017. Small game and shifting subsistence patterns from the Upper Palaeolithic to the Natufian at Baaz rockshelter, Syria. In: Mashkour, M., Beech, M. (Eds.), Archaeozoology of the Near East 9. Proceedings of the 9th Conference of the ASWA (AA) Working Group: Archaeozoology of Southwest Asia and Adjacent Areas. Oxbow books, Oxford and Philadelphia, pp. 2–9.

Nowroozi, R., 1997. Archaeological Survey of Prehistoric Localities in Nourabad Mmasani Plain. Unpublished Master thesis. University of Tehran (in Farsi).

O'Connell, J.F., Hawkes, K., Blurton-Jones, N., 1988. Hadza hunting, butchering, and bone transport and their archaeological implications. J. Anthropol. Res. 44, 113–161.

O'Connell, J.F., Hawkes, K., Blurton-Jones, N., 1990. Reanalysis of large mammal body part transport among the Hadza. J. Archaeol. Sci. 17, 301–316.

Olszewski, D.I., 1993. The Late Baradostian occupation at Warwasi rockshelter, Iran. In: Olszewski, D., Dibble, H. (Eds.), The Paleolithic Prehistory of the Zagros-Taurus. The University Museum, University of Pennsylvania, Philadelphia, pp. 186–206.

Olszewski, D.I., 1999. The early Upper Paleolithic in the Zagros Mountains. In: Davis, W., Charles, R. (Eds.), Dorothy Garrod and the Progress of the Paleolithic. Oxbow books, Oxford, pp. 167–180.

Olszewski, D.I., 2017. Assessing patterning in the Upper Paleolithic and Epipaleolithic at Warwasi, Iran. Int. J. Soc. Iranian Archaeol. 3, 1–12.

Olszewski, D.I., Dibble, H.L., 1994. The Zagros Aurignacian. Curr. Anthropol. 35, 68–75.

Otte, M., Kozłowski, J.K., 2007. L'Aurignacien du Zagros, vol. 118. ERAUL, Liège.

Otte, M., Biglari, F., Flas, D., Shirdang, S., Zwyns, H., Mashkour, M., Naderi, R., Mohased, A., Hashemi, N., Darvish, J., Radu, V., 2007. The Aurignacian in the Zagros region: new research at Yafteh cave, Lorestan, Iran. Antiquity 81, 82–96.

Otte, M., Shidrang, S., Zwyns, N., Flas, D., 2011. New radiocarbon dates for the Zagros Aurignacian from Yafteh cave, Iran. J. Hum. Evol. 61, 340–346.

Payne, S., 1973. Kill-off patterns in sheep and goats: the mandibles from Aşvan Kale. Anatol. Stud. 23, 81–303.

Payne, S., 1985. Morphological distinctions between the mandibular teeth of young sheep, *Ovis*, and goats, *Capra*. J. Archaeol. Sci. 12, 139–147.

Perkins, D.J., 1964. Prehistoric fauna from Shanidar, Iraq. Science 144, 1565–1566.

Pianka, E.R., 2000. Evolutionary Ecology, sixth ed. Addison Wesley Education Publishers, Inc., Benjamin/Cummings, San Francisco.

Piperno, M., 1972. Jahrom, a Middle Palaeolithic site in Fars, Iran. East and West 22, 183–197.

Piperno, M., 1974. Upper Paleolithic caves in southern Iran, preliminary report. East and West 24, 9–13.

Reitz, E.J., Wing, E.S., 2008. In: Zooarchaeology, 2nd ed. Cambridge University Press, Cambridge.

Rey-Rodríguez, I., López-García, J.M., Blain, H.A., Stoetzel, E., Denys, C., Fernández-García, Tumung, L., Ollé, A., Bazgir, B., 2020. Exploring the landscape and climatic conditions of Neanderthals and anatomically modern humans in the Middle East: the rodent assemblage from the late Pleistocene of Kaldar Cave (Khorramabad Valley, Iran). Quat. Sci. Rev. 236, 106278.

Roberts, T.J., 1977. The Mammals of Pakistan. Ernest Benn Limited, London.

Rosenberg, M.S., 1979. Eshkaft-e Gavi (The Malyan Project), Iran. Journal of the British Institute of Persian Studies 17, 148–149.

Rosenberg, M.S., 1985. Report on the 1978 sondage at Eshkaft-e Gavi, Iran. Journal of the British Institute for Persian Studies 23, 51–62.

Rosenberg, M.S., 1988. Paleolithic Settlement Pattern in the Marv Dasht, Fars Province, Iran. Unpublished Ph.D. dissertation. University of Pennsylvania, USA.

Roustaei, K., Biglari, F., Heydari-Guran, S., Vahdati Nasab, H., 2002. New research on the Palaeolithic of Lurestan, west Central Iran. Antiquity 76, 19–20.

Roustaei, K., Alamdari, A., Petrie, C.A., 2006. Landscape and environment in Mamasani. In: Potts, D.T., Roustaei, K. (Eds.), The Mamasani Archaeological Project Stage One: a Report on the First Two Seasons of the ICAR – University of Sydney Expedition to the Mamasani District, Fars Province, Iran. Iranian Center for Archaeological research, Tehran, pp. 147–168.

Sadhir, S., al-Hahar, M., Olszewski, D.I., Petrillo, A., Munro, N.D., 2020. Human hunting adaptations at Wadi Madamagh, Jordan at the peak of the Last Glacial Maximum. J. Archaeol. Sci.: Report 34, 102661.

Saint-Germain, C., 1997. The production of bone broth: a study in nutritional exploitation. Anthropozoologica 25–26, 153–156.

Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Cáceres, I., Vallverdú, J., Rosell, J., Bermúdez de Castro, J.M., Carbonell, E., 2011. Carcass transport decisions in *Homo antecessor* subsistence strategies. J. Hum. Evol. 61, 425–446.

Schaller, G.B., 1977. Mountain Monarchs, Wild Sheep and Goats of the Himalaya. University of Chicago Press, Chicago.

Schilt, F.C., 2011. Micromorphology of Upper Paleolithic and Historic Sediments from Boof Cave, Iran. Unpublished Master's Thesis. Eberhard-Karls Universität Tübingen, Germany.

Scott, J.E., Marean, C.W., 2009. Paleolithic hominin remains from Eshkaft-e Gavi (southern Zagros Mountains, Iran): description, affinities, and evidence for butchery. J. Hum. Evol. 57, 248–259.

Shidrang, S., 2018. The Middle to Upper Paleolithic transition in the Zagros: the appearance and evolution of the Baradostian. In: Nishiaki, Y., Akazawa, T. (Eds.), The Middle and Upper Paleolithic Archeology of the Levant and beyond. Springer International Publishing, Singapore, pp. 133–156.

Shidrang, S., Biglari, F., Bordes, J.G., Jaubert, J., 2016. Continuity and change in the late Pleistocene lithic industries of the Central Zagros: a typo-technological analysis of lithic assemblages from Ghar-e Khar Cave, Bisetun, Iran. Archaeol. Ethnol. Anthropol. Eurasia 44 (1), 27–38.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

Solecki, R.S., 1958. The Baradostian Industry and the Upper Palaeolithic in the Near East Unpublished Ph.D. dissertation. Columbia University, USA.

Solecki, R.S., 1963. Prehistory in Shanidar Valley northern Iraq. Science 139, 179–193.

Solecki, R.S., Solecki, R.L., 1993. The pointed tools from the Mousterian occupations of Shanidar Cave, northern Iraq. In: Olszewski, D., Dibble, H. (Eds.), The Paleolithic Prehistory of the Zagros-Taurus. The University Museum of Archaeology and Anthropology. University of Pennsylvania, Philadelphia, pp. 119–146.

Soulier, M.C., Costamagno, S., 2017. Let the cutmarks speak! Experimental butchery to reconstruct carcass processing. J. Archaeol. Sci.: Report 11, 782–802.

Speth, J.D., Tchernov, E., 1998. The role of hunting and scavenging in Neanderthal procurement strategies: new evidence from Kebara Cave (Israel). In: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), Neanderthals and Modern Humans in West Asia. Plenum Press, New York, pp. 223–239.

Speth, J.D., Clark, J.L., 2006. Hunting and overhunting in the Levantine Late Middle Palaeolithic. Before Farming 3, 1–42.

Starkovich, B.M., 2012. Intensification of small game resources at Klissoura Cave 1 (Peloponnese, Greece) from Middle Paleolithic to Mesolithic. Quat. Int. 264, 17–31.

Starkovich, B.M., 2014. Optimal foraging, dietary change, and site use during the Paleolithic at Klissoura Cave 1 (southern Greece). J. Archaeol. Sci. 52, 39–55.

Starkovich, B.M., 2017. Paleolithic subsistence strategies and changes in site use at Klissoura Cave 1 (Peloponnese, Greece). J. Hum. Evol. 111, 63–84.

Steele, T.E., Klein, R.G., 2009. Late Pleistocene subsistence strategies and resource intensification in Africa. In: Hublin, J.J., Richards, M.P. (Eds.), The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence. Springer Science + Business Media B. V., New York, pp. 113–126.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Monographs in Behavior and Ecology. Princeton University Press, Princeton.

Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of hominid predatory adaptations. J. Anthropol. Archaeol. 9, 305–351.

Stiner, M.C., 1991. Food procurement and transport by human and non-human predators. J. Archaeol. Sci. 18, 455–482.

Stiner, M.C., 1994. Honor Among Thieves: a Zooarchaeological Study of Neandertal Ecology. Princeton University Press, Princeton.

Stiner, M.C., 2001. Thirty years on the "Broad Spectrum Revolution" and Paleolithic demography. Proc. Natl. Acad. Sci. U.S.A. 98, 6993–6996.

Stiner, M.C., 2002. On *in situ* attrition and vertebrate body part profiles. J. Archaeol. Sci. 29, 979–991.

Stiner, M.C., 2005. The Faunas of Hayonim Cave, Israel: a 200,000 Year Record of Paleolithic Diet, Demography, and Society. In: Peabody Museum of Archaeology and Ethnology, vol. 48. American School of Prehistoric Research Bulletin, Cambridge, Massachusetts. Harvard University.

Stiner, M.C., 2009. Prey choice, site occupation intensity & economic diversity in the Middle – early Upper Palaeolithic at the Üçağızlı Caves, Turkey. Before Farming 3, 1–20.

Stiner, M.C., Munro, N.D., 2011. On the evolution of diet and landscape during the Upper Paleolithic through Mesolithic at Franchti Cave (Peloponnese, Greece). J. Hum. Evol. 60, 618–636.

Stiner, M.C., Weiner, S., Bar-Yosef, O., Kuhn, S.L., 1995. Differential burning, fragmentation and preservation of archaeological bone. J. Archaeol. Sci. 22, 223–237.

Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E., Bar-Yosef, O., 1999. Paleolithic population growth pulses evidenced by small animal exploitation. Science 283, 190–194.

Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small-game use, the Broad-Spectrum Revolution, and Paleolithic demography. Curr. Anthropol. 41, 39–73.

Stiner, M.C., Gopher, A., Barkei, R., 2011. Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. J. Hum. Evol. 60, 213–233.

Stutz, A.J., Munro, N.D., Bar-Oz, G., 2009. Increasing the resolution of the Broad Spectrum Revolution in the southern Levantine Epipaleolithic (19–12 ka). J. Hum. Evol. 56, 294–306.

Trinkaus, E., 2018. Pleistocene human remains from Iran. In: Biglari, F., Shidrang, S., Mashkour, M. (Eds.), The Pleistocene Archaeology of the Iranian Plateau, Iraq and the Caucasus. National Museum of Iran, Tehran, pp. 53–63.

Tsanova, T., 2013. The beginning of the Upper Paleolithic in the Iranian Zagros. A taphonomic approach and techno-economic comparison of early Baradostian assemblages from Warwasi and Yafteh (Iran). J. Hum. Evol. 65, 39–64.

Turnbull, P., 1975. The mammalian fauna of Warwasi Rock Shelter, West-Central Iran. Fieldiana Geol. 33, 141–155.

Vahdati Nasab, H., Clark, G.A., Torkamandi, S., 2013. Late Pleistocene dispersal corridors across the Iranian Plateau: a case study from Mirak, a Middle Paleolithic site on the northern edge of the Iranian Central desert (Dasht-e kavir). Quat. Int. 300, 267–281.

Val, A., de la Peña, P., Wadley, L., 2016. Direct evidence for human exploitation of birds in the Middle Stone Age of South Africa: the example of Sibudu Cave, KwaZulu-Natal. J. Hum. Evol. 99, 107–123.

Weaver, T.D., Boyko, R.H., Steele, T.E., 2011. Cross-platform program for likelihood-based statistical comparisons of mortality profiles on a triangular graph. J. Archaeol. Sci. 38, 2420–2423.

Wright, G.A., Miller, S.J., 1976. Prehistoric hunting of New World wild sheep: implications for the study of sheep domestication. In: Cleland, C.E. (Ed.), Cultural Change and Continuity. New York Academic Press, New York, pp. 293–318.

Yeshurun, R., Bar-Oz, G., Weinstein-Evron, M., 2007. Modern hunting behavior in the early Middle Paleolithic: faunal remains from Misliya cave, Mount Carmel, Israel. J. Hum. Evol. 53 (6), 656–677.

Yeshurun, R., Schneller-Pels, N., Barzilai, O., Marder, O., 2019. Early Upper Paleolithic subsistence in the Levant: zooarchaeology of the Ahmarian-Aurignacian sequence at Manot Cave, Israel. J. Hum. Evol. 102619.

Yravedra, J., Domínguez-Rodrigo, M., Santonja, M., Pérez-González, A., Panera, J., Rubio-Jara, S., Baquedano, E., 2010. Cut marks on the Middle Pleistocene elephant carcass of Áridos 2 (Madrid, Spain). J. Archaeol. Sci. 37, 2469–2476.

Yravedra, J., Rubio-Jara, S., Panera, J., Uribelarrea, D., Pérez-González, A., 2012. Elephants and subsistence. Evidence of the human exploitation of extremely large mammal bones from the Middle Palaeolithic site of PRERESA (Madrid, Spain). J. Archaeol. Sci. 39, 1063–1071.

Zeder, M.A., 2006. Reconciling rates of long bone fusion and tooth eruption and wear in sheep (*Ovis*) and goat (*Capra*). In: Ruscillo, D. (Ed.), Recent Advances in Ageing and Sexing Animal Bones. Proceedings of the 9th Conference of the International Council of Archaeozoology. Oxbow Books, Oxford, pp. 87–118. Durham, August 2002.

Zeder, M.A., Lapham, H.A., 2010. Assessing the reliability of criteria used to identify postcranial bones in sheep, *Ovis*, and goats, *Capra*. J. Archaeol. Sci. 37, 2887–2905.

Zeidi, M., Conard, N.J., 2019. The fourth season of excavation at Ghar-e Boof, Rostam County, Fars Province. In: Shirazi, R.A. (Ed.), 16th Annual Symposium of the Iranian Archaeology. Iranian Center for Archaeological Research, Tehran, pp. 234–238 (in Farsi).

Zeidi, M., McCall, B., Khosrowzadeh, A., 2006. Survey of Dasht-e Rostam-e Yek and Dasht-e Rostam-e Do. In: Potts, D.T., Roustaei, K. (Eds.), The Mamasani Archaeological Project Stage One: a Report on the First Two Seasons of the ICAR – University of Sydney Expedition to the Mamasani District, Fars Province, Iran. Iranian Center for Archaeological research, Tehran, pp. 147–168.

Zhang, Y., Stiner, M.C., Dennell, R., Wang, C., Zhang, S., Gao, X., 2010. Zooarchaeological perspectives on the Chinese Early and Late Paleolithic from the Ma'anshan site (Guizhou, South China). J. Archaeol. Sci. 37, 2066–2077.

Appendices

Scan site	BMD	MNE Observed	MNE Expected	MAU	MNI	% Survivorship
AC1	0.26	2	2	1.00	5	0.20
AS1	0.54	4	2	2.00	5	0.40
AS2	0.63	4	2	2.00	5	0.40
AS3	0.60	4	2	2.00	5	0.40
AT1	0.07	0	1	0.00	5	0.00
AT2	0.11	0	1	0.00	5	0.00
AT3	NA*	0	1	0.00	5	0.00
AX1	0.13	0	1	0.00	5	0.00
AX2	0.14	0	1	0.00	5	0.00
AX3	NA*	0	1	0.00	5	0.00
CA1	0.43	2	2	1.00	5	0.20
CA2	0.58	1	2	0.50	5	0.10
CA3	0.56	1	2	0.50	5	0.10
CA4	0.43	1	2	0.50	5	0.10
CE1	0.12	2	5	0.40	5	0.08
CE2	0.13	0	5	0.00	5	0.00
DN1	NA*	3	2	1.50	5	0.30
DN2	NA*	2	2	1.00	5	0.20
DN3	NA*	5	2	2.50	5	0.50
DN5	NA*	2	2	1.00	5	0.20
DN6	NA*	4	2	2.00	5	0.40
DN7	NA*	3	2	1.50	5	0.30
DN8	NA*	2	2	1.00	5	0.20
FE1	0.28	3	2	1.50	5	0.30
FE2	0.16	0	2	0.00	5	0.00
FE3	0.20	0	2	0.00	5	0.00
FE5	0.24	2	2	1.00	5	0.20
FE6	0.22	2	2	1.00	5	0.20
HU1	0.13	0	2	0.00	5	0.00
HU2	0.22	0	2	0.00	5	0.00
HU4	0.37	3	2	1.50	5	0.30
HU5	0.34	5	2	2.50	5	0.50
IL1	0.23	0	2	0.00	5	0.00
IL2	0.47	0	2	0.00	5	0.00
IS1	0.49	2	2	1.00	5	0.20
IS2	0.11	0	2	0.00	5	0.00
LU1	0.26	3	7	0.43	5	0.09
LU2	0.22	3	7	0.43	5	0.09
LU3	NA*	1	14	0.07	5	0.01
MC1	0.40	4	2	2.00	5	0.40
MC2	0.55	4	2	2.00	5	0.40
MC4	0.54	8	2	4.00	5	0.80
MC5	0.38	8	2	4.00	5	0.80

Table A.1. Ghar-e Boof, AH III. Survivorship values for sheep/goat and medium ungulates. Density values from Lyman (1994) for domestic sheep (*Ovis aries*).

Scan site	BMD	MNE Observed	MNE Expected	MAU	MNI	% Survivorship
MC6	0.50	8	2	4.00	5	0.80
MR1	0.43	3	2	1.50	5	0.30
MR2	0.53	3	2	1.50	5	0.30
MR4	0.51	2	2	1.00	5	0.20
MR5	0.31	4	2	2.00	5	0.40
MR6	0.39	4	2	2.00	5	0.40
P11	0.43	22	8	2.75	5	0.55
P12	0.40	24	8	3.00	5	0.60
P13	0.55	35	8	4.38	5	0.88
P21	0.34	29	8	3.63	5	0.73
P22	0.39	25	8	3.13	5	0.63
P23	0.42	23	8	2.88	5	0.58
P31	0.30	19	8	2.38	5	0.48
PA1	0.44	0	2	0.00	5	0.00
PU1	0.45	0	2	0.00	5	0.00
PU2	0.25	0	2	0.00	5	0.00
RA1	0.35	2	2	1.00	5	0.20
RA2	0.36	2	2	1.00	5	0.20
RA4	0.19	1	2	0.50	5	0.10
RA5	0.21	2	2	1.00	5	0.20
RI1	NA*	2	26	0.08	5	0.02
RI2	NA*	4	26	0.15	5	0.03
RI3	NA*	2	26	0.08	5	0.02
RI5	NA*	4	26	0.15	5	0.03
SC1	0.20	0	1	0.00	5	0.00
SC2	0.16	0	1	0.00	5	0.00
SP1	0.25	2	2	1.00	5	0.20
SP2	0.33	2	2	1.00	5	0.20
TH1	0.24	0	13	0.00	5	0.00
TH2	0.19	3	13	0.23	5	0.05
TI1	0.16	0	2	0.00	5	0.00
TI2	0.20	0	2	0.00	5	0.00
TI4	0.36	1	2	0.50	5	0.10
TI5	0.28	2	2	1.00	5	0.20
UL1	0.28	0	2	0.00	5	0.00
UL2	0.26	0	2	0.00	5	0.00
UL3	NA*	1	2	0.50	5	0.10

NA* (Not available).

Table A.1. Continued.

Scan site	BMD	MNE Observed	MNE Expected	MAU	MNI	% Survivorship
AC1	0.26	1	2	0.50	3	0.17
AS1	0.54	0	2	0.00	3	0.00
AS2	0.63	0	2	0.00	3	0.00
AS3	0.6	0	2	0.00	3	0.00
AT1	0.07	0	1	0.00	3	0.00
AT2	0.11	0	1	0.00	3	0.00
AT3	NA*	0	1	0.00	3	0.00
AX1	0.13	0	1	0.00	3	0.00
AX2	0.14	0	1	0.00	3	0.00
AX3	NA*	0	1	0.00	3	0.00
CA1	0.43	1	2	0.50	3	0.17
CA2	0.58	1	2	0.50	3	0.17
CA3	0.56	0	2	0.00	3	0.00
CA4	0.43	0	2	0.00	3	0.00
CE1	0.12	0	5	0.00	3	0.00
CE2	0.13	2	5	0.40	3	0.13
DN1	NA*	1	2	0.50	3	0.17
DN2	NA*	3	2	1.50	3	0.50
DN3	NA*	5	2	2.50	3	0.83
DN5	NA*	2	2	1.00	3	0.33
DN6	NA*	2	2	1.00	3	0.33
DN7	NA*	0	2	0.00	3	0.00
DN8	NA*	1	2	0.50	3	0.17
FE1	0.28	0	2	0.00	3	0.00
FE2	0.16	0	2	0.00	3	0.00
FE3	0.2	0	2	0.00	3	0.00
FE5	0.24	0	2	0.00	3	0.00
FE6	0.22	0	2	0.00	3	0.00
HU1	0.13	1	2	0.50	3	0.17
HU2	0.22	0	2	0.00	3	0.00
HU4	0.37	3	2	1.50	3	0.50
HU5	0.34	2	2	1.00	3	0.33
IL1	0.23	0	2	0.00	3	0.00
IL2	0.47	0	2	0.00	3	0.00
IS1	0.49	0	2	0.00	3	0.00
IS2	0.11	0	2	0.00	3	0.00
LU1	0.26	1	7	0.14	3	0.05
LU2	0.22	1	7	0.14	3	0.05
LU3	NA*	0	14	0.00	3	0.00
MC1	0.4	5	2	2.50	3	0.83
MC2	0.55	5	2	2.50	3	0.83
MC4	0.54	2	2	1.00	3	0.33
MC5	0.38	4	2	2.00	3	0.67
MC6	0.5	2	2	1.00	3	0.33
MR1	0.43	2	2	1.00	3	0.33
MR2	0.53	2	2	1.00	3	0.33
MR4	0.51	0	2	0.00	3	0.00

Table A.2. Ghar-e Boof, AH IIIb. Survivorship values for sheep/goat and medium ungulates. Density values from Lyman (1994) for domestic sheep (*Ovis aries*).

Scan site	BMD	MNE Observed	MNE Expected	MAU	MNI	% Survivorship
MR5	0.31	2	2	1.00	3	0.33
MR6	0.39	2	2	1.00	3	0.33
P11	0.43	16	8	2.00	3	0.67
P12	0.4	9	8	1.13	3	0.38
P13	0.55	16	8	1.88	3	0.63
P21	0.34	14	8	1.75	3	0.58
P22	0.39	15	8	1.88	3	0.63
P23	0.42	20	8	2.50	3	0.83
P31	0.3	13	8	1.63	3	0.54
PA1	0.44	0	2	0.00	3	0.00
PU1	0.45	0	2	0.00	3	0.00
PU2	0.25	0	2	0.00	3	0.00
RA1	0.35	0	2	0.00	3	0.00
RA2	0.36	0	2	0.00	3	0.00
RA4	0.19	1	2	0.50	3	0.17
RA5	0.21	2	2	1.00	3	0.33
RI1	NA*	1	26	0.04	3	0.01
RI2	NA*	0	26	0.00	3	0.00
RI3	NA*	0	26	0.00	3	0.00
RI5	NA*	1	26	0.04	3	0.01
SC1	0.2	0	1	0.00	3	0.00
SC2	0.16	0	1	0.00	3	0.00
SP1	0.25	0	2	0.00	3	0.00
SP2	0.33	0	2	0.00	3	0.00
TH1	0.24	0	13	0.00	3	0.00
TH2	0.19	2	13	0.15	3	0.05
TI1	0.16	0	2	0.00	3	0.00
TI2	0.2	0	2	0.00	3	0.00
TI4	0.36	0	2	0.00	3	0.00
TI5	0.28	0	2	0.00	3	0.00
UL1	0.28	0	2	0.00	3	0.00
UL2	0.26	1	2	0.50	3	0.17
UL3	NA*	1	2	0.50	3	0.17

NA* (Not available).

Table A.2. Continued.

	III		*IIIa*		*IIIb*		*IIIc*		*IV*		*IVa*		*IVb*		*Total*	
Taxon	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Ungulate																
Small ungulate	68	NA*	9	NA	34	NA	14	NA	6	NA	12	NA	2	NA	145	NA
Gazelle (*Gazella* sp.)	34	2	9	1	18	1	5	1	6	1	6	1	1	1	79	8
Small/medium ungulate	100	NA	8	NA	40	NA	21	NA	11	NA	15	NA	2	NA	197	NA
Gazelle/goat (*Gazella/Capra*)	1	1	0	0	1	1	0	0	0	0	0	0	0	0	2	2
Medium ungulate	439	NA	89	NA	216	NA	113	NA	54	NA	95	NA	51	NA	1057	NA
Sheep (*Ovis* sp.)	19	2	3	1	7	1	2	1	3	1	6	1	1	1	41	8
Wild goat (*Capra aegagrus*)	95	5	23	1	50	3	6	1	8	1	10	1	7	1	199	13
Sheep/goat (*Ovis/Capra*)	105	3	22	1	63	2	23	1	6	1	27	1	2	1	248	10
Medium/large ungulate	11	NA	2	NA	5	NA	0	NA	1	NA	4	NA	0	NA	23	NA
Large ungulate	11	NA	6	NA	11	NA	5	NA	2	NA	15	NA	2	NA	52	NA
Red deer (*Cervus elaphus*)	0	0	0	0	4	1	1	1	0	0	0	0	0	0	5	2
Wild pig (*Sus scrofa*)	3	1	0	0	2	1	2	1	0	0	1	1	1	1	9	5
Horse (*Equus* sp.)	1	1	0	0	0	0	0	0	0	0	1	1	0	0	2	2
Large/very large ungulate	3	NA	0	NA	1	NA	0	NA	1	NA	2	NA	2	NA	9	NA
Very large ungulate	2	NA	0	NA	1	NA	0	NA	0	NA	4	NA	0	NA	7	NA
Wild cattle (*Bos primigenius*)	1	1	0	0	0	0	0	0	0	0	1	1	0	0	2	2
Carnivore																
Small carnivore	0	NA	0	NA	3	NA	0	NA	0	NA	0	NA	0	NA	3	NA
Wild Cat (*Felis* sp.)	2	1	0	0	1	1	0	0	0	0	0	0	0	0	3	2
Red fox (*Vulpes vulpes*)	4	1	0	0	2	1	1	1	0	0	0	0	0	0	7	3
Large carnivore	2	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	2	NA
Small mammals																
Indet. Erinaceidae	2	NA	0	NA	1	NA	0	NA	0	NA	0	NA	0	NA	3	NA
Brandt’s Hedgehog (*Paraechinus* cf. *hypomelas*)	4	1	0	0	0	0	0	0	8	1	0	0	0	0	12	2
Reptile																
Tortoises (*Testudo* sp.)	115	2	41	1	22	1	28	1	52	1	23	1	11	1	292	8
Fish																
Indet. Leuciscinae	1	NA	1	NA	8	NA	0	NA	0	NA	0	NA	0	NA	10	NA
Nase (*Chondrostoma* sp.)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Birds																
Small birds	5	NA	0	NA	4	NA	9	NA	14	NA	1	NA	8	NA	41	NA
Medium birds	199	NA	55	NA	160	NA	50	NA	17	NA	8	NA	17	NA	506	NA
Partridge (*Alectoris* cf. *chukar*)	92	11	16	2	31	4	8	2	2	1	3	2	3	1	155	23
Dove (Cf. *Streptopelia/ Columba*)	2	2	0	0	1	1	0	0	0	0	0	0	0	0	3	3
Large birds	9	NA	2	NA	4	NA	4	NA	0	NA	0	NA	0	NA	19	NA
Huge birds	0	NA	1	NA	0	NA	2	NA	0	NA	0	NA	0	NA	3	NA
Total	1331	35	287	7	690	18	294	10	191	7	234	10	110	7	3137	94

NA* (Not Applicable).

Table A.3. Ghar-e Boof. Number of identified species (NISP) and Minimum Number of Individuals (MNI) by AH for each taxa.

Dental set used for ageing sequence	Young	Prime	Old	MNE
dLP4-LP4	1	8	1	10
dLP4-LM3	1	8	0	9

Table A.4. Ghar-e Boof. Comparison of mortality pattern results in three-cohort format based on premolar sets versus premolar-molar series of the low jaws of sheep/goat (all AHs combined).

Elements	MNE in skeleton	NISP	MNE	MAU
Horn	2	0	0	0
1/2 Cranium	2	20	9	4.5
Mandible	2	20	7	3.5
Atlas	1	0	0	0.0
Axis	1	0	0	0.0
Cervical	5	3	1	0.2
Thoracic	13	6	2	0.2
Lumbar	6	8	2	0.3
Sacrum	1	0	0	0.0
Rib	26	14	4	0.2
Innominate	2	3	2	1.0
Scapula	2	4	3	1.5
Humerus	2	22	4	2.0
Radius	2	13	2	1.0
Ulna	2	4	2	1.0
Metacarpal	2	17	8	4.0
Femur	2	31	6	3.0
Patella	2	2	2	1.0
Tibia	2	31	6	3.0
Astragalus	2	4	4	2.0
Calcaneum	2	3	2	1.0
Metatarsal	2	7	4	2.0
Phalanx 1	8	56	25	3.1
Phalanx 2	8	37	26	3.3
Phalanx 3	8	20	19	2.4
Total	107	325	140	40.2

Table A.5. Ghar-e Boof, AH III. NISP, MNE and MAU values for sheep/goat and medium ungulate body parts, alongside a standard goat skeleton. Horizontal lines indicates grouping for anatomical regions.

Elements	MNE in skeleton	NISP	MNE	MAU
Horn	2	0	0	0
1/2 Cranium	2	3	3	1.5
Mandible	2	7	2	1
Atlas	1	1	1	1
Axis	1	1	1	1
Cervical	5	2	1	0.2
Thoracic	13	0	0	0
Lumbar	6	1	1	0.2
Sacrum	1	0	0	0
Rib	26	2	1	0.04
Innominate	2	1	1	0.5
Scapula	2	0	0	0
Humerus	2	3	1	0.5
Radius	2	0	0	0
Ulna	2	0	0	0
Metacarpal	2	4	2	1
Femur	2	3	1	0.5
Patella	2	2	2	1
Tibia	2	4	2	1
Astragalus	2	0	0	0
Calcaneum	2	0	0	0
Metatarsal	2	3	1	0.5
Phalanx 1	8	12	6	0.8
Phalanx 2	8	10	7	0.9
Phalanx 3	8	7	6	0.8
Total	107	66	39	12.4

Table A.6. Ghar-e Boof, AH IIIa. NISP, MNE and MAU values for sheep/goat and medium ungulate body parts, alongside a standard goat skeleton. Horizontal lines indicates grouping for anatomical regions.

Elements	MNE in skeleton	NISP	MNE	MAU
Horn	2	0	0	0
1/2 Cranium	2	10	8	4
Mandible	2	16	6	3
Atlas	1	0	0	0
Axis	1	0	0	0
Cervical	5	2	1	0.2
Thoracic	13	3	2	0.2
Lumbar	6	2	1	0.2
Sacrum	1	0	0	0
Rib	26	3	1	0.04
Innominate	2	1	1	0.5
Scapula	2	0	0	0
Humerus	2	11	3	1.5
Radius	2	7	2	1
Ulna	2	4	1	0.5
Metacarpal	2	9	3	1.5
Femur	2	14	2	1
Patella	2	0	0	0
Tibia	2	15	4	2
Astragalus	2	0	0	0
Calcaneum	2	2	2	1
Metatarsal	2	7	2	1
Phalanx 1	8	31	12	1.5
Phalanx 2	8	28	12	1.5
Phalanx 3	8	14	13	1.6
Total	107	179	76	22.2

Table A.7. Ghar-e Boof, AH IIIb. NISP, MNE and MAU values for sheep/goat and medium ungulate body parts, alongside a standard goat skeleton. Horizontal lines indicates grouping for anatomical regions.

Elements	MNE in skeleton	NISP	MNE	MAU
Horn	2	0	0	0
1/2 Cranium	2	5	3	1.5
Mandible	2	4	2	1
Atlas	1	0	0	0
Axis	1	0	0	0
Cervical	5	1	1	0.2
Thoracic	13	1	1	0.08
Lumbar	6	1	1	0.2
Sacrum	1	0	0	0
Rib	26	7	1	0.04
Innominate	2	0	0	0
Scapula	2	0	0	0
Humerus	2	4	1	0.5
Radius	2	6	2	1
Ulna	2	1	1	0.5
Metacarpal	2	3	1	0.5
Femur	2	7	2	1
Patella	2	1	1	0.5
Tibia	2	4	1	0.5
Astragalus	2	2	2	1
Calcaneum	2	0	0	0
Metatarsal	2	4	1	0.5
Phalanx 1	8	11	5	0.5
Phalanx 2	8	4	3	0.4
Phalanx 3	8	6	6	0.8
Total	107	71	35	10.7

Table A.8. Ghar-e Boof, AH IIIc. NISP, MNE and MAU values for sheep/goat and medium ungulate body parts, alongside a standard goat skeleton. Horizontal lines indicates grouping for anatomical regions.

Elements	MNE in skeleton	NISP	MNE	MAU
Horn	2	1	1	0.5
1/2 Cranium	2	2	2	1
Mandible	2	6	2	1
Atlas	1	0	0	0
Axis	1	0	0	0
Cervical	5	0	0	0
Thoracic	13	0	0	0
Lumbar	6	1	1	0.2
Sacrum	1	0	0	0
Rib	26	2	1	0.04
Innominate	2	0	0	0
Scapula	2	0	0	0
Humerus	2	3	1	0.5
Radius	2	4	1	0.5
Ulna	2	1	1	0.5
Metacarpal	2	3	1	0.5
Femur	2	4	1	0.5
Patella	2	0	0	0
Tibia	2	4	1	0.5
Astragalus	2	1	1	0.5
Calcaneum	2	0	0	0
Metatarsal	2	0	0	0
Phalanx 1	8	5	2	0.3
Phalanx 2	8	4	4	0.5
Phalanx 3	8	2	2	0.3
Total	107	43	22	7.3

Table A.9. Ghar-e Boof, AH IV. NISP, MNE and MAU values for sheep/goat and medium ungulate body parts, alongside a standard goat skeleton. Horizontal lines indicates grouping for anatomical regions.

Elements	MNE in skeleton	NISP	MNE	MAU
Horn	2	0	0	0
1/2 Cranium	2	12	4	2
Mandible	2	5	1	0.5
Atlas	1	0	0	0
Axis	1	0	0	0
Cervical	5	1	1	0.2
Thoracic	13	2	1	0.08
Lumbar	6	4	2	0.3
Sacrum	1	0	0	0
Rib	26	3	1	0.04
Innominate	2	1	1	0.5
Scapula	2	0	0	0
Humerus	2	4	2	1
Radius	2	6	1	0.5
Ulna	2	3	1	0.5
Metacarpal	2	3	1	0.5
Femur	2	5	1	0.5
Patella	2	0	0	0
Tibia	2	4	1	0.5
Astragalus	2	0	0	0
Calcaneum	2	0	0	0
Metatarsal	2	2	1	0.5
Phalanx 1	8	23	12	1.5
Phalanx 2	8	8	6	0.8
Phalanx 3	8	7	7	0.9
Total	107	93	43	10.8

Table A.10. Ghar-e Boof, AH IVa. NISP, MNE and MAU values for sheep/goat and medium ungulate body parts, alongside a standard goat skeleton. Horizontal lines indicates grouping for anatomical regions.

Elements	MNE in skeleton	NISP	MNE	MAU
Horn	2	0	0	0
1/2 Cranium	2	0	0	0
Mandible	2	3	2	1
Atlas	1	0	0	0
Axis	1	0	0	0
Cervical	5	1	1	0.2
Thoracic	13	1	1	0.08
Lumbar	6	0	0	0
Sacrum	1	0	0	0
Rib	26	1	1	0.04
Innominate	2	0	0	0
Scapula	2	0	0	0
Humerus	2	3	2	1
Radius	2	1	1	0.5
Ulna	2	2	2	1
Metacarpal	2	2	2	1
Femur	2	5	1	0.5
Patella	2	1	1	0.5
Tibia	2	4	1	0.5
Astragalus	2	0	0	0
Calcaneum	2	0	0	0
Metatarsal	2	0	0	0
Phalanx 1	8	4	2	0.3
Phalanx 2	8	1	1	0.1
Phalanx 3	8	1	1	0.1
Total	107	30	19	6.8

Table A.11. Ghar-e Boof, AH IVb. NISP, MNE and MAU values for sheep/goat and medium ungulate body parts, alongside a standard goat skeleton. Horizontal lines indicates grouping for anatomical regions.

	III		IIIa		IIIb		IIIc		IV		IVa		IVb		Total	
Element	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Unknown long bone	4	3.4	4	12.5	5	8.8	6	18.8	2	20.0	2	15.4	1	9.0	24	9.2
Flat bone	0	0.0	1	100.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	25.0
Unknown metapodial	0	0.0	1	33.3	2	22.2	1	16.7	0	0.0	3	75.0	0	0.0	7	15.9
Unknown carpal/ tarsal	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	33.3	0	0.0	1	25.0
Horn	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Half cranium	0	0.0	0	0.0	1	10.0	0	0.0	0	0.0	0	0.0	0	0.0	1	1.9
Half mandible	1	5.0	0	0.0	1	6.3	0	0.0	3	50.0	0	0.0	0	0.0	5	8.2
Atlas	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Axis	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Cervical vertebra	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Thoracic vertebra	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Lumbar vertebra	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Ribs	1	7.1	0	0.0	0	0.0	2	28.6	0	0.0	0	0.0	0	0.0	3	9.4
Innominate	1	33.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	16.7
Scapula	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Humerus	4	18.2	0	0.0	3	27.3	1	50.0	2	66.7	1	25.0	2	66.7	13	26.0
Radius	0	0.0	0	0.0	1	14.3	1	16.7	3	75.0	2	16.7	1	100.0	8	21.6
Ulna	1	25.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	6.7
Carpals	1	5.6	1	6.3	2	28.6	0	0.0	0	0.0	0	0.0	0	0.0	4	7.8
Metacarpal	2	11.8	1	33.3	0	0.0	0	0.0	0	0.0	0	0.0	1	50.0	4	9.8
Femur	1	3.2	0	0.0	3	21.4	0	0.0	2	50.0	4	80.0	2	40.0	12	17.4
Patella	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Tibia	4	12.9	1	25.0	2	13.3	0	0.0	1	25.0	1	25.0	2	50.0	11	16.7
Tarsals	1	25.0	0	0.0	1	33.3	0	0.0	0	0.0	0	0.0	0	0.0	2	13.3
Astragalus	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Calcaneus	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Metatarsal	1	14.3	1	33.3	1	14.3	0	0.0	0	0.0	0	0.0	0	0.0	3	13.0
Sesamoids	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	14.3	1	0.6
First phalanx	3	5.4	0	0.0	5	16.1	0	0.0	0	0.0	1	4.4	0	0.0	9	6.3
Second phalanx	0	0.0	1	10.0	0	0.0	0	0.0	0	0.0	1	12.5	0	0.0	2	2.2
Third phalanx	0	0.0	0	0.0	1	7.1	0	0.0	0	0.0	0	0.0	0	0.0	1	1.7
Total	25	4.4	11	8.7	28	9.6	11	8.2	13	20.0	16	12.0	10	17.2	114	8.3

Table A.12. Ghar-e Boof. Medium ungulate specimens (NISP) with cut marks by element and their relative proportion (%).

	III		IIIa		IIIb		IIIc		IV		IVa		IVb		Total	
Element	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Unknown long bone	10	9.4	2	6.3	9	15.8	8	25.0	1	10.0	2	15.4	2	18.1	34	13.0
Flat bone	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Unknown metapodial	1	5.9	0	0.0	0	0.0	1	17.7	0	0.0	1	25.0	0	0.0	3	6.8
Horn	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Half cranium	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Half mandible	0	0.0	0	0.0	3	18.8	0	0.0	0	0.0	0	0.0	0	0.0	3	4.9
Atlas	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Axis	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Cervical vertebra	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Thoracic vertebra	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Lumbar vertebra	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Ribs	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Innominate	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Scapula	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Humerus	4	18.2	1	33.3	1	9.0	4	100.0	1	33.0	1	25.0	2	66.7	14	28.0
Radius	1	7.7	0	0.0	0	0.0	0	0.0	1	25.0	0	0.0	0	0.0	2	5.4
Ulna	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Carpals	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Metacarpal	0	0.0	0	0.0	1	11.1	1	33.3	0	0.0	0	0.0	1	50.0	3	7.3
Femur	3	9.7	1	33.3	3	21.4	2	28.6	0	0.0	1	20.0	0	0.0	10	14.5
Patella	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Tibia	4	12.9	1	25.5	2	13.3	3	75.0	1	25.0	2	50.0	3	75.0	16	24.2
Tarsals	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Astragalus	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Calcaneus	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Metatarsal	0	0.0	0	0.0	1	14.2	0	0.0	0	0.0	0	0.0	0	0.0	1	4.4
First phalanx	0	0.0	0	0.0	4	12.9	0	0.0	0	0.0	0	0.0	1	25.0	5	3.5
Second phalanx	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Third phalanx	1	5.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	1.7
Total	24	4.2	5	3.9	24	8.2	19	14.1	4	6.2	7	5.3	9	15.0	92	6.7

Table A.13. Ghar-e Boof. Medium ungulate specimens (NISP) with percussion impacts (cones, opposite cones and impacts) by element and their relative proportion (%).

APPENDIX 3

Mata-González, M., Starkovich, B.M., Zeidi., M., Conard, N.J., 2023. Evidence for diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros). Sci. Rep. 13, 19006. https://doi.org/10.1038/s41598-023-45974-8.

Submitted to the journal: 31 May 2023.

Accepted: 26 October 2023.

Published online: 3 November 2023.

www.nature.com/scientificreports

scientific reports

OPEN

Evidence of diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros)

Mario Mata-González[1,2]✉, Britt M. Starkovich[1,3], Mohsen Zeidi[3,4] & Nicholas J. Conard[1,3,4]

Although Middle Paleolithic (MP) hominin diets consisted mainly of ungulates, increasing evidence demonstrates that hominins at least occasionally consumed tortoises, birds, leporids, fish, and carnivores. Until now, the MP zooarchaeological record in the Zagros Mountains has been almost exclusively restricted to ungulates. The narrow range of hominin prey may reflect socioeconomic decisions and/or environmental constraints, but could also result from a research bias favoring the study of large prey, since archaeologists have undertaken no systematic taphonomic analyses of small game or carnivores in the region. Here, we report on the first comprehensive taphonomic analysis of an MP faunal assemblage from Ghar-e Boof (~ 81–45 kyr), a Late Pleistocene site in the southern Zagros of Iran. Anthropogenic bone surface modifications point to hominins as the main agent of accumulation. Hominins preyed primarily on ungulates, particularly wild goat. However, we also found evidence for MP hominin exploitation of carnivores and tortoises at the site. Although small game represents only a minor portion of the diet, our results suggest that the hunting behavior of MP hominins in the Zagros was more diverse than previously thought, similar to what we find elsewhere in Eurasia.

The reconstruction of past hominin diets and subsistence strategies constitutes one of the primary goals of zooarchaeological studies since it informs us about how hominins adapted to and interacted with different environments. There is a general consensus among archaeologists that the animal component of the diet and foraging spectrum of Neanderthals and other Middle Paleolithic (MP) hominins was mainly dominated by ungulates or large game species across most of Eurasia[1–10]. Nevertheless, there has been an increasing body of evidence that demonstrates the hominin exploitation of tortoises[10–15], birds[16–21], leporids[22–25], fish[26,27], and small and large carnivores[21,28,29] during the MP (for a more detailed synthesis of the available evidence and latest updates, see[30] and references therein). Independently if small game and carnivore taxa were systematically[18–20,22,24] or sporadically[15,21,23,28] collected or exploited when MP hominins encountered them while foraging, their presence in the zooarchaeological record allows us to better understand and assess crucial aspects of hominin socioeconomics, behavioral variability, and hunting capabilities.

Within the prey choice model of optimal foraging theory, small game is normally considered low-ranked prey in comparison to high-ranked, large game[5,11,12] (but see[31]). However, small animals with low capture or handling costs, such as slow-moving tortoises or sessile shellfish, have higher net yields relative to small, fast-moving game[5,11,12]. As a result, tortoises might have represented higher-ranked and easy-to-catch resources collected by foragers of different ages and sexes[32,33]. On the other hand, leporids, birds, and fish are quick, and more difficult-to-catch animals, that generally have lower caloric yields[5,11,12]. Moreover, economic decisions to include small game in the diet can be related to environmental constraints and prey availability[22,25,30], which directly affects the encounter rate[34]. From a technological standpoint, hunting small, fast-moving game may require the use of trapping techniques, such as nets and snares[19,25], or more efficient procurement methods (e.g., mass collecting[31,35]), which, in turn, can reduce capture costs and increase overall return rates[11,12,31,35].

[1]Institute for Archaeological Sciences, University of Tübingen, Hölderlinstr. 12, 72074 Tübingen, Germany. [2]Department of Anthropology, University of Connecticut, Unit 1176, 354 Mansfield Road, Storrs, CT 06269, USA. [3]Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstr. 12, 72074 Tübingen, Germany. [4]Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Schloss Hohentübingen, 72070 Tübingen, Germany. ✉email: mario.mata-gonzalez@student.uni-tuebingen.de

Besides the dietary use of small game[19,20,22,23], archaeologists have suggested that MP hominins might have also exploited rabbits for pelts[25] and birds for feathers[16–18,20], the latter of which has been interpreted as an indicator of symbolic behavior. Since both large carnivores and MP hominins were top predators within the ecosystems that they lived, the documentation of carnivore remains in the zooarchaeological record can shed light on the interspecific competition for food resources, landscape and space use, and predatory-prey relationships[36,37]. Cut-marked carnivore bones associated with defleshing and skinning activities indicate the active exploitation of carnivores by MP hominins, not only for the acquisition of food but also fur[21,28,29].

The Zagros Mountains represent a key geographic region in southwestern Asia for the study of human evolution and cultural and behavioral adaptations during the MP, especially because of their heterogeneous topography and high environmental diversity[38]. However, although important archaeological sites in the Zagros have yielded animal bones in direct association with lithic artifacts or even hominin remains (Fig. 1), up until now the MP zooarchaeological record in the region is almost exclusively restricted to ungulate species[4,39–49]. The only exception is Shanidar Cave, where Evins[42] proposed that land tortoise might have had an important supplementary economic value for hominins, based on the continuous occurrence of this taxon throughout the MP sequence, its higher frequency in relation to other species, and the presence of burned shell fragments. Overall, the presumably narrow range of hominin prey deduced from previous studies[42,43,47,48] may reflect socioeconomic decisions (e.g., a focus on high-ranked, large game to maximize energetic returns[5,11,12]). Alternatively, some scholars suggest that in the Zagros Mountains the narrow exploitation of ungulate taxa, mostly caprines, was due to environmental constraints[48]. Nevertheless, the predominance of ungulates in MP zooarchaeological assemblages could also be the result of research bias, caused by a disproportionate study of large prey by zooarchaeologists[4,43–46,48,49], especially since zooarchaeologists have undertaken no systematic taphonomic analyses of small game nor carnivores in the Zagros region. Therefore, further investigations are still required.

Here, we present the first results of a comprehensive taphonomic analysis of the MP faunal assemblage from Ghar-e Boof, dated between ca. 81–45 kyr (OSL dates[50]). The main goals of our study are: (1) to determine whether hominins were the primary agents of bone accumulation or modification at the site, and identify

Figure 1. Location of Ghar-e Boof (1) in Southwest Asia and in the Zagros region, along with other Late Pleistocene sites with MP sequences mentioned in the text: Eshkaft-e Gavi (2), Kunji Cave (3), Kaldar Cave (4), Wezmeh Cave (5), Bisotun Cave (6), Warwasi Rockshelter (7), Ghar-e Khar (8), Kobeh Cave (9), Bawa Yawan Rockshelter (10), Shanidar Cave (11), Tamtama Cave (12). Map created by QGIS 3.10.12 (https://www.qgis.org/).

other post-depositional processes that might have affected and altered the preservation of the zooarchaeological remains; and (2) to reconstruct and evaluate hominin prey choice and subsistence strategies during the MP. In this paper, we not only confirm that hominins were the main accumulation agent, but we also report direct evidence for MP hominin exploitation of carnivores and tortoises in the region. Although caprines represented the main prey and food resources exploited at Ghar-e Boof, we demonstrate that the hunting behavior of MP hominins in the Zagros was more diverse than previously thought.

Geographical, archaeological, and chronological setting

Ghar-e Boof (N 30.2839°, E 51.4352°) is located in the Dasht-e Rostam region, in the northwest of Fars Province (southern Zagros Mountains, Iran, Fig. 2a). The topography of the region is heterogenous, with mountains ranging between 700 to 2500 m.a.s.l., and numerous plains and river valleys, which represent natural east–west and north–south corridors[51,52]. Formed in limestone and with an area of about 60 m^2, the cave lies at an altitude of 905 m.a.s.l., and its entrance faces north[53] (Fig. 2b). The valley bottom is currently situated approximately 190 m directly downslope from Ghar-e Boof, and a seasonal stream, the Solak River, runs ~ 200 m away towards the northeast. Ghar-e Boof was discovered in 1997 by R. Nowroozi, a member of the Fars cultural heritage office[54], though the site was originally named Eshkaft-e Yagheh Sangar. The Tübingen-Iranian Stone Age Research Project Team visited Ghar-e Boof in 2005 for the first time, documenting and collecting numerous lithic artifacts on the surface of the site, and assessing its archaeological potential[55,56]. The first excavations were carried out in 2006 and 2007, co-directed by N. J. Conard and M. Zeidi[57], while another two seasons of excavation took place in 2015 and 2017[58,59].

The excavation at Ghar-e Boof has an area of 18 m^2 (2 by 9 m), extending from near the entrance of the site to the back wall, across its north–south axis[53] (Fig. 2c). The overall stratigraphic sequence consists of ca. 6 m of well-stratified deposits[50], characterized mostly by ashy silts and silty sediments with limestone clasts of different sizes. These sediments derive primarily from aeolian processes and the effects of gravity, which includes rocks and silts detached from the cave walls and roof[60]. The hominin occupation of the site spans from the MP or MIS5a to the historical period (Table S1[61], and references therein).

Archaeologists identified six main geological and archaeological horizons (AH)s, and 13 sub-horizons (Fig. 2d). Moving from the top downward, the stratigraphic sequence begins with Holocene deposits (AHs I and II). In these layers, pottery sherds, metal, and glass artifacts from historical periods were recovered along with some Epipaleolithic-Upper Paleolithic (UP) artifacts[53]. AHs IIa and IIb mainly consist of Epipaleolithic (Zarzian) lithic artifacts, but a radiocarbon date and a few pottery sherds have evidenced some disturbance with the upper sediments[62]. The undisturbed Pleistocene deposits start with AH III. The early UP sequence spans from AH III to IVb, and radiocarbon and OSL dates situated this entire stratigraphic complex at the range of 42–35 kyr cal. BP[50,53,62,63]. The early UP lithic artifacts recovered at Ghar-e Boof constitute the assemblage type used for defining the Rostamian cultural group in the southern Zagros[53]. The main characteristic of the Rostamian technocomplex is the predominance of diminutive bladelets, retouched bladelet tools, and small platform cores made on radiolarian-chert cobbles[53,58,64]. Besides lithic artifacts, archaeologists also documented combustion features and personal ornaments, such as perforated shells and teeth[53,58]. Our zooarchaeological data indicate that, during the early UP, Ghar-e Boof was primarily occupied by humans and used as a campsite, while the presence of carnivores at the cave was extremely rare[65]. In addition, the faunal record shows Rostamian foragers preyed mostly on caprines for meat and marrow, but there is also evidence for the exploitation of a great variety of animal taxa, including small- to very-large-bodied ungulates (i.e., gazelles, wild pigs, red deer, equids, and wild cattle), tortoises, birds, and carnivores[65].

AH IVd yielded an OSL date of 48–45 kyr[50], but at present, we cannot confidently ascribe AHs IVc and IVd to either the MP or UP because of low find densities. Nonetheless, both layers lack characteristic artifacts of the UP techno-cultural repertoire in the Zagros, such as perforated shells and Arjeneh points, which were recovered in AHs IV to IVb despite having similar low find densities[50]. Consequently, AHs IVc and IVd have been tentatively assigned to either the MP[66], or to the MP–UP transition[50]. The MP deposits have only been excavated so far in three quadrants (6/7, 6/8, and 7/7), which are located towards the central-northern part of the excavation area. Moving downwards, the OSL chronology for AHs V to Vc falls in the range of 63–46 kyr, while AH VI spans between 81 and 72 kyr (68% credible interval[50]). Although the analysis of MP lithic artifacts is still ongoing, preliminary observations indicate a technology focused on the production of flakes and diverse scrapers, in stark contrast with the UP Rostamian industries documented at Ghar-e Boof[50,59,66]. The presence of Levallois reduction techniques is currently still unclear due to the low find densities[66]. Overall, the MP record of Ghar-e Boof likely reflects short-term hominin occupations or even low populations in the Dasht-e Rostam region during the MP[58,66]. Finally, most lithic artefacts preserved sharp edges, and it seems they were recovered in their primary position.

Paleoenvironmental data inferred from the small vertebrate record of Ghar-e Boof, including small mammals, reptiles, amphibians, and fish, show that during most of the Late Pleistocene, the landscape around the site was mainly dominated by warm, arid conditions with dry, open meadows, shrublands and rocky terrain, and water sources nearby[61]. The sample size for small vertebrates is relatively small for some layers and environmental interpretations must be drawn with caution. However, the presence of Afghan pika (*Ochotona* cf. *rufescens*) in AH IVc, along with a decrease in the number of rodents between AHs IVd and IV, may suggest a short phase with slightly lower temperatures and/or drier conditions[61]. Finally, hominin remains have not been unearthed at Ghar-e Boof so far. Nonetheless, there is a general agreement among archaeologists and paleoanthropologists regarding the association of early/initial UP sites in the Zagros exclusively with Anatomically Modern Humans (AMH)s[47,50,64,66–68], though AMH skeletal remains are very rare in the region[69–71]. As for the MP, several sites also yielded Neanderthal or Neanderthal-like remains, such as Shanidar Cave[39,72–78], Bisotun Cave[79], Wezmeh

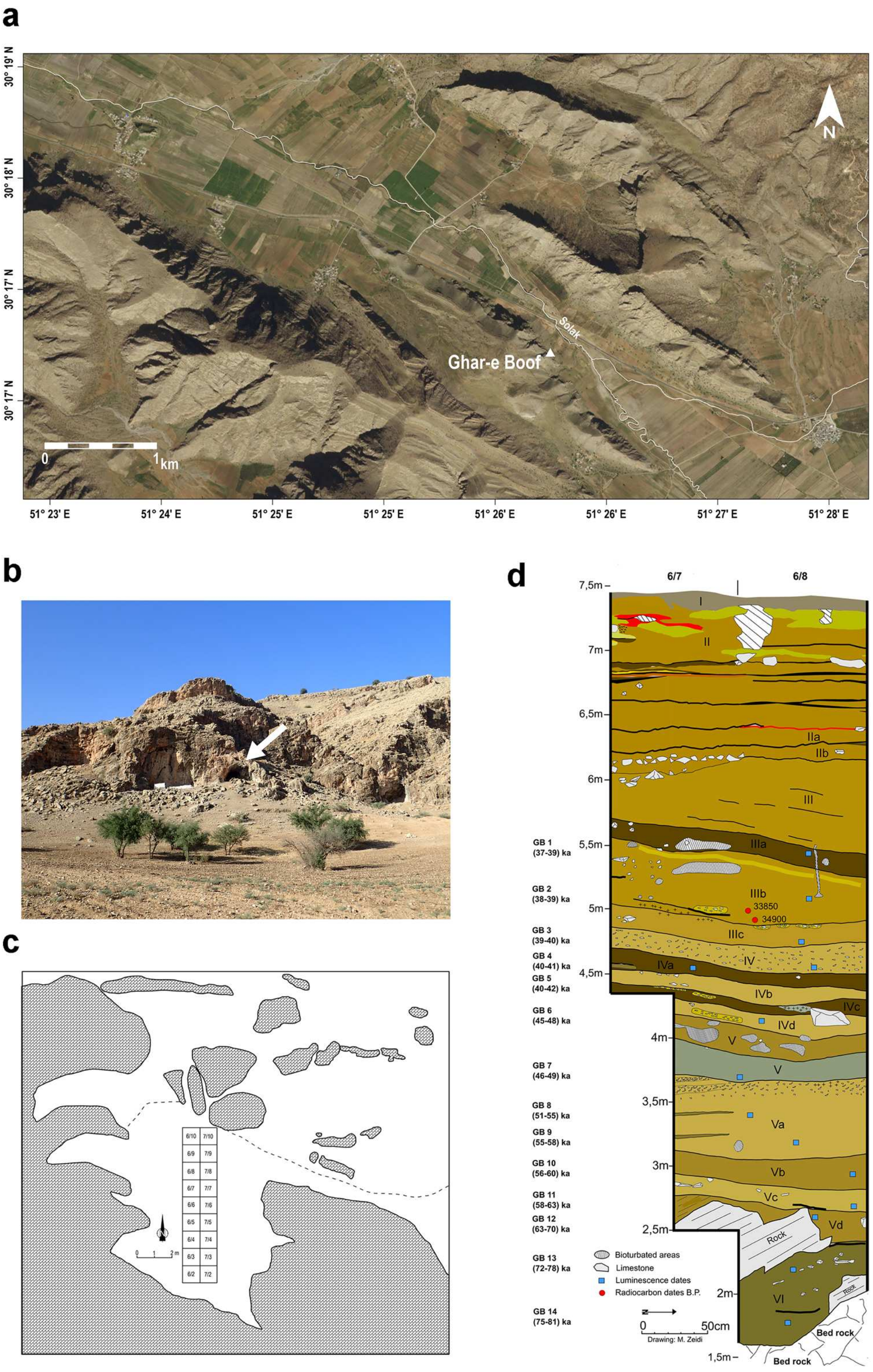


Figure 2. Ghar-e Boof: (**a**) location of the cave in the Dasht-e Rostam region, Iran (satellite view; map created by QGIS 3.10.12, https://www.qgis.org/); (**b**) general view of the entrance of the site (white arrow); (**c**) Schematic representation of the interior of the cave and location of the excavation area divided by quadrants (created by Inkscape 0.92.4, https://inkscape.org; and modified from[53]; dotted line indicates the dripline); (**d**) chrono-stratigraphic sequence (west profile; some of the OSL dates were obtained for the north profile, see[50], but we included them here at approximate locations within the west profile in order to offer a comprehensive view of the chronology).

Cave[80] and Bawa Yawan Rockshelter[81]. However, the complex paleoanthropological record from the MP in southwestern Asia, especially in the southern Levant, indicates early dispersals of AMHs to the region[82–84], along with the presence of Neanderthals[85,86]. In the absence of hominin remains in MP sites, both Neanderthals and AMHs could still be considered as plausible makers of MP assemblages[50,87].

Data presentation and results

In this paper, we examine a sample of 941 identified specimens (Table 1; Table S2) recovered from eight layers (AHs IVc to VI) at Ghar-e Boof, ranging from ca. 81 kyr to 45 kyr[50]. Although the faunal assemblage is primarily dominated by ungulates (NISP = 710), we also present the skeletal element representation and anthropogenic modifications of carnivores (NISP = 7), tortoises (NISP = 161), and medium and large bird (NISP = 63) remains in order to assess the complete animal foraging spectrum of MP hominins at the site, beyond just ungulate/large game hunting. Our sample does not include small mammals (rodents, pikas, and insectivores), amphibians, squamate reptiles (agamid lizards and snakes) and small birds (Passeriformes), since the accumulation of these taxa at the site was most likely the result of non-hominin predator activities or natural death[61].

Species representation

More than 75% of the MP faunal assemblage of Ghar-e Boof consists of ungulates, from small to very large taxa. The ungulate assemblage is dominated by caprines (*Ovis*/*Capra*), but mostly wild goat (*Capra aegagrus*), followed by gazelle (*Gazella* sp.). We also documented small numbers of wild pig (*Sus scrofa*), red deer (*Cervus elaphus*), equid (*Equus* sp.), and wild cattle (*Bos primigenius*). As for small game, the most common species-specific identification is tortoise (*Testudo* sp.), and species-specific designations for birds are restricted exclusively to partridge (*Alectoris* cf. *chukar*). However, the medium bird category encompasses other Galliformes and Columbiformes for which taxonomic identifications are not yet available, and large birds (small raptors) are also present. Carnivores are very rare, represented by red fox (*Vulpes vulpes*) and a large felid, probably leopard (*Panthera* cf. *pardus*).

Skeletal element representation and bone surface modifications

Figure S1 shows the representation of each skeletal region for caprines and medium ungulates by AH (data from Table S3). Despite the sample sizes, a few patterns are evident: (1) head and limb body segments are present in all layers, and in particular, heads are the most well-represented anatomical parts; (2) we did not record any horns identified as caprine or assigned to the category "medium ungulate"; (3) neck and axial elements were not recovered from most layers, and when documented, they are visibly underrepresented; and (4) feet are also relatively rare throughout the entire MP sequence. Furthermore, correlations between skeletal elements by percentage of minimum animal units (%MAU) for all AHs combined and food utility[88] and standard food utility[89] indices are not statistically significant (Table S4 and S5). Instead, there are positive and statistically significant correlations between %MAU and marrow[88] and unsaturated marrow[90] indices respectively. Regarding the analysis of density-mediated attrition, we present ratios of ungulate tooth- to skull bone-based minimum number of elements (MNEs) by layer in Table S6. Most layers show higher cranial-based MNEs in comparison to tooth-based MNEs. There a few layers with very small sample sizes, yet they have an even ratio. Lower tooth-relative to cranial

AH	**IVc**		**IVd**		**V**		**Va**		**Vb**		**Vc**		**Vd**		**VI**		**Total**	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Ungulates																		
Subtotal ungulates	56	69.1	13	76.5	71	69.6	168	69.7	98	68.1	83	71.6	28	68.3	193	97.0	710	75.5
Carnivores																		
Red fox (*Vulpes vulpes*)	0	0.0	0	0.0	0	0.0	1	0.4	0	0.0	0	0.0	0	0.0	0	0.0	1	0.1
Large carnivore	0	0.0	0	0.0	0	0.0	1	0.4	0	0.0	0	0.0	0	0.0	0	0.0	1	0.1
Leopard (*Panthera cf. pardus*)	0	0.0	1	5.9	4	3.9	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	5	0.5
Subtotal carnivores	0	0.0	1	5.9	4	3.9	2	0.8	0	0.0	0	0.0	0	0.0	0	0.0	7	0.7
Reptiles																		
Tortoise (*Testudo* sp.)	8	9.9	2	11.8	23	22.6	57	23.7	34	23.6	27	23.3	10	24.4	0	0.0	161	17.1
Birds																		
Medium birds	11	13.6	0	0.0	3	2.9	12	5.0	9	6.3	6	5.2	3	7.3	5	2.5	49	5.2
Partridge (*Alectoris* cf. *chukar*)	5	6.2	1	5.9	1	1.0	1	0.4	3	2.1	0	0.0	0	0.0	1	0.5	12	1.3
Large birds	1	1.2	0	0.0	0	0.0	1	0.4	0	0.0	0	0.0	0	0.0	0	0.0	2	0.2
Subtotal birds	17	21.0	1	5.9	4	3.9	14	5.8	12	8.3	6	5.2	3	7.3	6	3.0	63	6.7
Total	81	100.0	17	100.0	102	100.0	241	100.0	144	100.0	116	100.0	41	100.0	199	100.0	941	100.0

Table 1. MP faunal assemblages from Ghar-e Boof. Number of identified specimens (NISP) and relative proportions (%) by AH for each taxon or body size group. The category "ungulates" includes all body size groups, from small to very large ungulates, which are represented by gazelle, wild sheep, wild goat, red deer, wild pig, equid, and wild cattle (for more details, see Table S2).

bone-based MNE values or an even ratio is the opposite of what we would expect if density-mediated attrition had influenced the faunal remains from Ghar-e Boof.

We recorded different types of bone surface modifications on the MP faunal remains recovered at Ghar-e Boof, such as sedimentological alterations, weathering and gnawing (Table S7). The most extreme damage documented in the assemblage is crushing by sediment compaction, but just less than two percent of the total remains were crushed. However, 21.2% of the total specimens were partly or completely covered by sediment concretions. Surface weathering is rare, affecting 2.5% of the bone remains. In this case, weathering damage is limited to the presence of fine linear cracks, some of them open (weathering stages 1 and 2), and none of the specimens are splintered or have surfaces with fibrous or rough textures (stages 3 to 5, after[91]). Root etching is very uncommon as well (1.1%), and none of the specimens are rounded or abraded. In contrast, chemical weathering is quite frequent, with 32.9% of the total bone specimens showing irregular etched scars and/or spots (Fig. S2). Frequencies of carnivore tooth marks and rodent gnawing are very low (1.2% and 3.0% respectively, Fig. S3; nevertheless, these frequencies would be slightly higher, 2.6% and 3.2%, if we consider specimens that were potentially gnawed, but for which the observed damage is not unequivocal).

Overall, burning damage occurs with fairly low intensity (Fig. S4): 6.8% of the bone assemblage is burned. Among the burned specimens, 5.8% are carbonized (stages 1 to 3) and only 1.0% are calcined (stages 4 to 6, after[92]). There is no apparent temporal change in the proportion of burned remains and burning intensity over the stratigraphic sequence. Anthropogenic modifications on bone specimens recovered at Ghar-e Boof which are associated with butchery and carcass processing activities comprise green (split/spiral and transverse) fractures, impact damage, cut marks, and bone tools (Table S8; Fig. 3). Overall, the most frequent types of damage are splits and spiral fractures, documented on more than 40.0% of the total bone assemblage. The proportion of transverse fractures, instead, is much lower (6.5% of the assemblage). Moreover, cut-marked bones are particularly abundant (20.7% of the entire assemblage), while impact damage (including cone fractures, opposite cones, and percussion impacts) is also not uncommon (8.5%). On ungulates, cut marks are more common on meat-bearing and lower limb elements (i.e., ribs, femora, humeri, radii and tibiae, Table S9). However, we also recorded cut marks on other elements, such as crania, mandibles, ulnae, metatarsals, and phalanges, and on a calcaneus, a scapula, and an astragalus. Likewise, impact damage is almost exclusively restricted to long-bone elements with high-marrow content, such as metatarsals, tibiae, femora, humeri, radii, and a mandible. One exception is an impact mark on the scapula of an aurochs, which also exhibits longitudinal scraping (Fig. S5). Finally, we identified a small number of bone retouchers (N = 6, Fig. S6), made on medium-bodied ungulate long-bone shaft fragments, along with some other potential bone tools.

Table 2 shows the skeletal element representation by NISP for carnivores and small game taxa. Regarding carnivores, we recorded two cranial remains: an upper molar of a red fox, and an indeterminate canine of a large carnivore (Table S10; the latter specimen was highly damaged and a more precise taxonomic identification was not possible). The rest of the carnivore bones are postcranial elements, all of them identified as cf. leopard. We documented an appendicular element (distal epiphysis of a right radius), and four complete phalanges (three first phalanges and a second phalanx). All postcranial elements are fully fused and therefore belonged to an adult individual. Despite the small number of carnivore postcranial elements in our assemblage, all of them preserve cut-marks (Table 3; Fig. 4). Moreover, a radius and two first phalanges are partially carbonized (stages 1–2), and the radius also exhibits a green fracture.

The tortoise assemblage is mostly dominated by shell specimens (91.9%), comprised of both carapace and plastron fragments (Table 2; Table S10). In Fig. 5, we show some examples of tortoise specimens exhibiting burning and butchery damage. Aside from ungulates, tortoise is the taxon with the highest number of burned specimens recovered from the MP sequence of Ghar-e Boof (NISP = 18, Table 3), though burning is exclusively restricted to shell fragments. Fifteen of them were carbonized (stages 1–3), while just three were calcined (4–5). Likewise, green fractures were equally abundant and limited to carapace and plastron specimens. Other types of butchery damage were uncommon, but we documented three shell fragments with percussion impacts and another four specimens (two shell fragments and two appendicular long bones) that were cut-marked and/or scratched. Bird remains consist predominantly of long bones elements. Phalanges, cranial, and axial elements are underrepresented. None of the bird bones shows evidence of burning, and we did not find unambiguous anthropogenic modifications, such as cut marks. Green fractures are the only type of damage that might have been caused by hominins, though other agents of bone accumulation or modification (e.g., carnivores) cannot be excluded. We recorded six bird specimens (three tibiotarsi, one femur, one ulna, and one undiagnostic piece of a long bone) that exhibit either transverse or split/spiral breakages. However, the absence of carnivore damage on bird remains likewise does not allow us to rule out hominins as potential accumulators.

Discussion and conclusions

In general, the results of our taphonomic analysis indicate that post-depositional bone surface alterations, such as weathering and root etching, are infrequent, which is expected in the protected environment of a cave[93], and in agreement with the overall pattern documented previously in the UP sequence of Ghar-e Boof[65]. The absence of rounding or abrasion damage in our assemblage also support the hypothesis that bone specimens were found in primary position, or at least, they were not considerably displaced horizontally by water, wind or trampling. Nevertheless, a considerable proportion of the bone specimens were either partially or completely covered by sediment concretions, or affected by chemical weathering. These mineral concretions are presumably made of calcium carbonate and are most likely caused by the percolation of water through the sediments[58,65]. In our analysis, we used the term chemical weathering to describe irregular etched scars or spots on the surface of bones. The observed chemical weathering is probably the result of biological or geochemical actions[93], for example, due to the presence of guano[60] or the decomposition of organic materials in the burial context of the faunal remains[65].

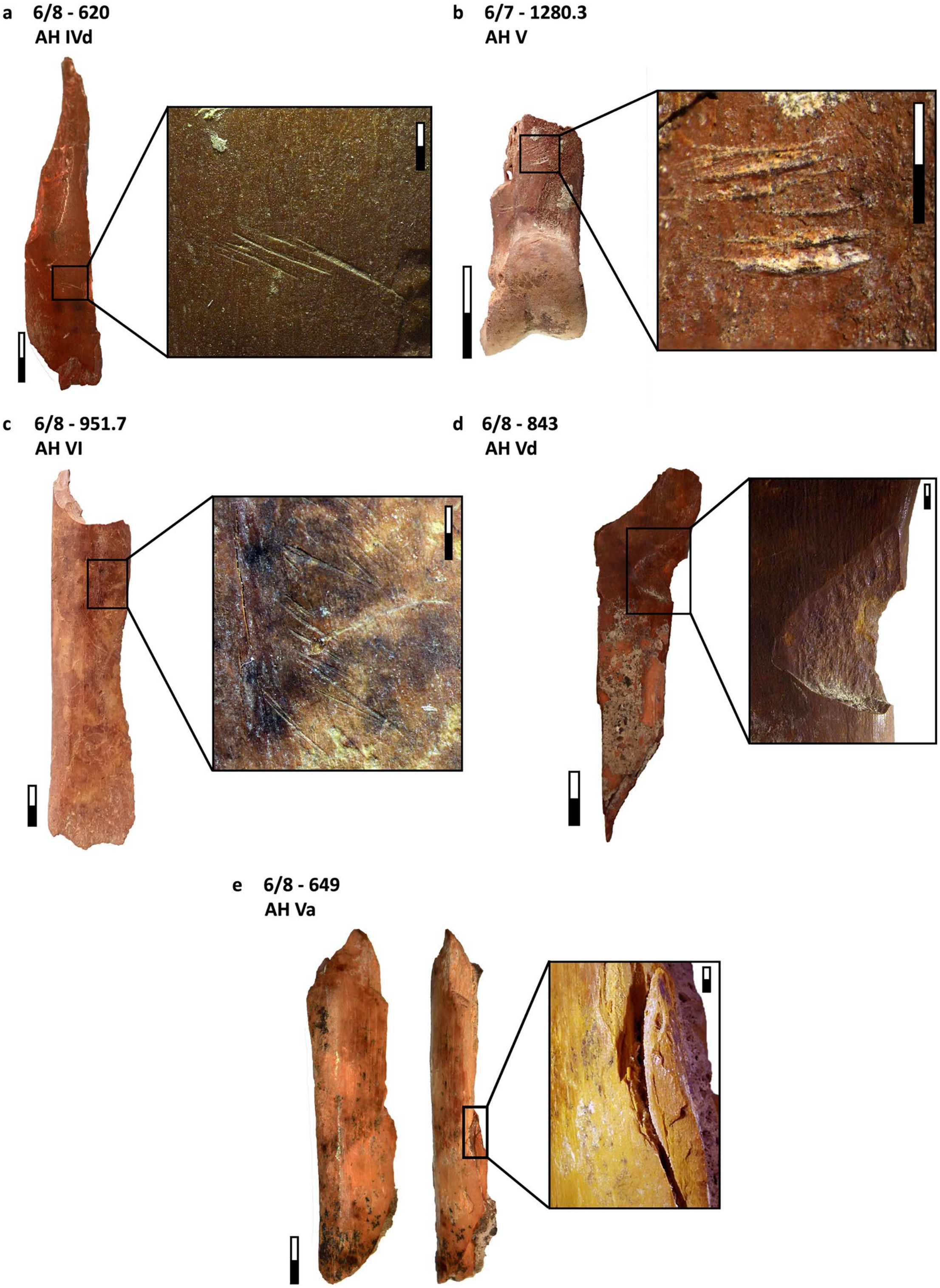


Figure 3. MP ungulate remains from Ghar-e Boof with anthropogenic modifications: (**a**) medium/large ungulate long bone shaft fragment with cut marks; (**b**) wild goat second phalanx with cut marks; (**c**) medium ungulate tibia heavily cut-marked; (**d**) medium ungulate tibia exhibiting an opposite cone fracture; and (**e**) medium ungulate radius with a cone fracture, in which the negative bone flake still remains attached. All these specimens also present green (split/spiral) fractures. Scale: general view = 10 mm; closer-up view = 2 mm.

Taxon	Total NISP	Cranial	Axial	Appendicular	Phalanges	Shell fragments	Others
Carnivores							
Red fox (*Vulpes vulpes*)	1	1	0	0	0	NA	0
Large carnivore	1	1	0	0	0	NA	0
Leopard (*Panthera* cf. *pardus*)	5	0	0	1	4	NA	0
Reptiles							
Tortoise (*Testudo* sp.)	161	0	1	12	0	148	0
Birds							
Medium birds	49	3	9	24	12	NA	1
Partridge (*Alectoris* cf. *chukar*)	12	0	0	12	0	NA	0
Large birds	2	0	0	1	1	NA	0
Total	231	5	10	50	17	148	1

Table 2. MP carnivore and small game remains from Ghar-e Boof. Skeletal element representation by anatomical region and NISP. All archaeological layers are combined. Data from Table S6. *NA* not applicable.

Taxon	Anatomical regions	Burning	Green fractures	Percussion damage	Cut marks
Leopard	Appendicular	1 (100.0%)	1 (100.0%)	0	1 (100.0%)
	Phalanges	2 (50.0%)	0	0	4 (100.0%)
Tortoise	Axial	0	0	0	0
	Appendicular	0	0	0	2 (16.7%)
	Shell fragments	18 (12.2%)	18 (12.2%)	3 (2.0%)	2 (1.4%)
Birds	Cranial	0	0	0	0
	Axial	0	0	0	0
	Appendicular	0	6 (16.2%)	0	0
	Phalanges	0	0	0	0
	Others	0	0	0	0
Total		21 (9.1%)	25 (10.8%)	3 (1.3%)	9 (3.9%)

Table 3. MP carnivore and small game remains from Ghar-e Boof. Anthropogenic modifications on bone specimens (by NISP and %NISP). Carnivore dental elements are not included.

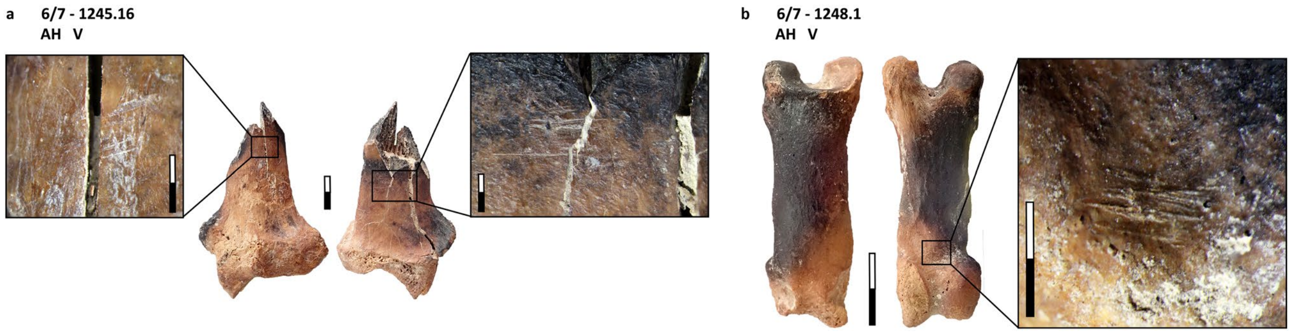


Figure 4. Cf. leopard remains from the MP sequence of Ghar-e Boof, which have cut marks and burning: (**a**) distal epiphysis of a radius, with cut marks located on both the anterior and posterior surfaces of the preserved shaft, and most of them are transverse, but few are also diagonal; and (**b**) first phalanx with a cluster of short and transverse cut marks in the palmar/plantar side, near the distal epiphysis.

Although both sediment concretions and chemical weathering might have obscured or even obliterated other taphonomic modifications, the relatively high proportion of green fractures, tool marks, and burning point to hominins as the main accumulating agent. Carnivore damage and rodent gnawing are rare in our assemblage, suggesting that carnivores and rodents played a minor role in the accumulation or alteration of the bones at the site. Based on the ratios of ungulate tooth- to skull bone-based MNEs, density-mediated attrition does not appear to have impacted the bone assemblage. Therefore, the faunal record of Ghar-e Boof has the potential to offer new information on hominin prey choice and subsistence strategies in the Zagros during the MP, not only including evidence for hunting and butchering ungulates, but also, at least occasionally, carnivores and small game.

During the MP at Ghar-e Boof, hominins preyed primarily on ungulates, which represent more than 75% of the identified animal specimens in the assemblage. Within the ungulate category, the most common prey

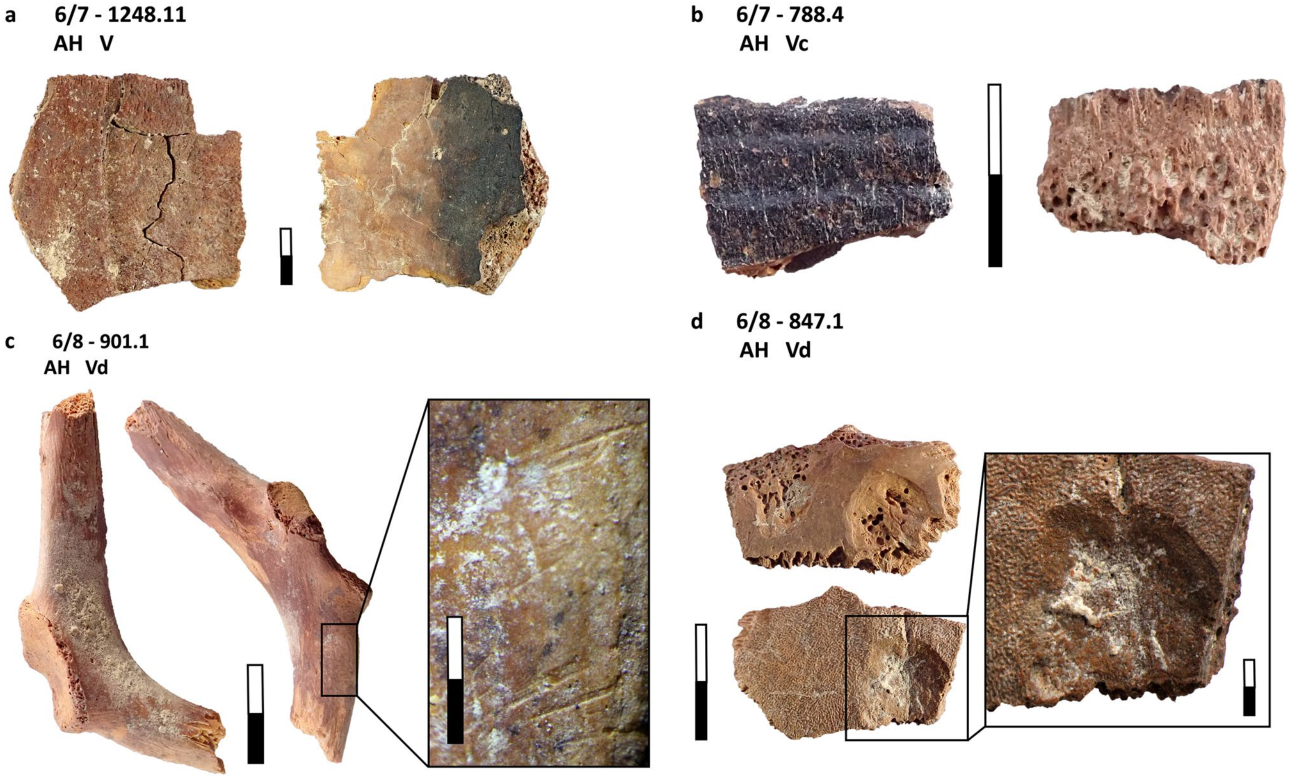


Figure 5. MP tortoise remains from Ghar-e Boof with anthropogenic modifications: (**a**) burnt plastron fragment; (**b**) burnt carapace shell fragment; (**c**) cut-marked scapula; (**d**) plastron fragment with a percussion impact.

was medium-bodied ungulates, including sheep/goat, but mostly wild goat. If we assume that most specimens identified as medium ungulates were most likely caprines too, then they constituted almost 60% of the animal component of the hominin diet. Hominins also hunted small ungulates such as gazelles, which are relatively abundant at Ghar-e Boof, and to a much lesser extent, we documented equid, wild pig, red deer, and wild cattle.

The analysis of skeletal element representation of caprines and medium ungulates show that our assemblage is mostly dominated by head, upper and lower limb elements, whereas horns and neck, axial and foot body segments are rare at the site. An underrepresentation of structurally weak elements, such as ribs and vertebrae, could track density-mediated attrition (e.g.,[94]). However, we feel confident that skeletal profiles mostly reflect transport practices and economic decisions for two reasons: (1) most AHs present a higher cranial-based MNEs in comparison to tooth-based MNEs; if there were density-mediated attrition, we should expect an overrepresentation of teeth, which are more resistant to attritional processes than bone due to their mineral composition[1,94]; (2) phalanges, which represent relatively dense elements[94], are also uncommon. As a result, even if a minor degree of in-situ attrition might have occurred, we suggest that the MP occupants of Ghar-e Boof did not transport complete ungulate carcasses to the cave, abandoning in the kill sites most horns, and neck, axial and foot elements. Additionally, we have found positive and statistically significant correlations between %MAU and marrow and unsaturated marrow utility indices, which points to the preferential transportation of elements with high quantities of marrow and unsaturated fatty acids[88,90,95] to the cave.

Overall, anthropogenic modifications on ungulate remains, such as cut marks, impact damage, and green breaks demonstrate that MP hominins exploited ungulates and butchered and processed their carcasses for meat and marrow[96–99]. Our taphonomic analysis shows that cut marks are relatively more frequent on meat-bearing and lower limb elements, including ribs, femora, humeri, radii, and tibiae. Experimental and ethnoarchaeological studies indicate that cut marks located on the above-mentioned elements are mostly associated with defleshing, filleting, and dismembering activities[96,98,99]. We also recorded cut marks on elements with relatively low utility values, which are more related to the disarticulation, skinning, and tendon removal of ungulate carcasses[96,98,99]. Moreover, most of the impact damage is located on long-bone elements with relatively high-marrow content[88,90,95]. Therefore, impact damage, along with the relatively large number of green (split/spiral and transverse) fractures, definitely suggest not only that long bones were broken when fresh through dynamic loading with hammerstones[94,97], but also that marrow processing and the consumption of within-bone nutrients played an important economic role for MP hominins at Ghar-e Boof. Finally, we recorded six bone retouchers, which seem to have been used to retouch stone flakes.

Recently, based on the small vertebrate assemblage recovered from Ghar-e Boof, Blanco-Lapaz et al.[61] suggested that during the Late Pleistocene the surrounding landscape of the site was mainly dominated by warm and arid conditions, open, dry meadows and shrublands, and rocky terrain, with some nearby water sources. Wild goats mostly live in piedmonts and craggy-rocky slopes, but they can also inhabit dry lowlands and steppe landscapes[100,101]. Therefore, as we suggested for the UP zooarchaeological assemblage of Ghar-e Boof[65], the predominance of caprines and medium ungulates, along with gazelles and small-bodied ungulates, could indicate that MP hominins were likely hunting near the site, or at least locally where those environments were present. On the other hand, according to the prey choice model from optimal foraging theory, hunter-gatherers are expected to maximize their foraging efforts and energetic return rates by targeting high-ranked resources, such as ungulate prey, which provide the greatest nutritional benefits per hunting episode (i.e.[5,11,12,33], and references therein). Optimality models predict that foragers would only turn to low-return animal resources when high-ranked prey decline or are no longer available[12,33]. If we consider caprines as high-ranked prey in the Zagros Mountains in comparison to other types of resources (e.g., small, fast-moving game), then a narrow diet, with a focus on caprines, would mean that MP hominin groups in the region were able to meet most of their daily caloric demands with high-ranked prey[5]. This narrow economic focus on medium ungulates during the MP could only have been maintained due to short-term, sporadic hominin occupations at the site, or low population densities[3,5]. In fact, our team previously suggested that Ghar-e Boof was occupied ephemerally by hominins based on the low find densities recovered from the MP deposits[58,66], which consequently may also reflect low population densities or small population groups living in the southern Zagros region during the MP.

Regarding small game, the documentation of anthropogenic marks and burning damage on tortoise specimens demonstrate that hominins collected and processed tortoises for dietary purposes. We observed no signs of carnivore or raptor damage. Instead, green fractures and percussion impacts indicate that tortoise shells were broken and crushed with stone tools, while cut marks and scratches are associated with the defleshing and removal of meat, viscera, and ligaments[14,15]. The observed burning pattern on tortoise remains does not seem to be caused by accidental exposure to fire: (1) we only documented burning damage on shell fragments, and it appears to be restricted, with a few exceptions, to the outside surfaces of the shells, which most archaeologists have interpreted as evidence for in-shell roasting of tortoises on a fire[13,15,42,102]; (2) tortoise specimens display higher instances of burning compared to other taxa[13]; and (3) some of the shell fragments are also calcined, which is rarely accidental, since calcination of faunal remains takes place with direct exposure to live coals[92]. In addition, based on the relative abundance of tortoises throughout most of the MP sequence of Ghar-e Boof, we suggest that tortoises most likely constituted important dietary supplements. Although in general small game animals yield relatively low return rates, slow or sessile small game taxa, such as tortoises, are very easy to collect, and therefore, represent high-ranked resources because of their low capture costs[5,11,12]. The relative proportion of tortoises seems to vary little throughout time, or at least, there is no visible chronological trend. Since tortoises are susceptible to human overexploitation due to their slow maturation rates and population recovery[5,11,12], it seems that the MP hominins that inhabited Ghar-e Boof did not exert great harvesting pressure on tortoises, which again could point to an ephemeral occupation of the site or small population groups in the region.

Carnivore remains are uncommon in the MP sequence of Ghar-e Boof. We only recorded an upper molar of a red fox, an indeterminate canine of a large carnivore, and five postcranial elements (one radius and four phalanges), which were identified as cf. leopard. Despite the small number of carnivore specimens in the assemblage, all the postcranial elements exhibit anthropogenic modifications, demonstrating the hominin exploitation of carnivores at Ghar-e Boof during the MP. These postcranial remains were recovered in a relatively small area and in close proximity to each other between the upper part of AH V, and the bottommost part of AH IVd (see Table S2 and comments). In addition, all these specimens are completely fused and have similar sizes. They probably belonged to a single adult individual, which indicates that the exploitation of carnivore resources at Ghar-e Boof represents a rare and isolated event. The observed butchery pattern on the radius and phalanges is consistent with the damage caused during disarticulation and skinning actions[103,104], and therefore, we suggest the processing and use of carnivore pelts by MP foragers at the site. Burning damage on carnivore remains could be related to the direct exposure of bones to fire after carcass processing[104], or to a pelt discarding event[105], though, in this case, we cannot rule out indirect or accidental burning (e.g.,[92]). Hominins could have had access to carnivore fur through active hunting or scavenging of recently dead animals[29]. If the latter was the case, skinning for fur retrieval is a task that humans can only accomplish shortly after an animal dies (from ca. an hour to maximum of one day depending on climatic conditions), or the hair will "slip" from the hide and it will be ruined[29,106,107]. The small sample size of carnivore remains and the absence of meat-bearing elements in the assemblage potentially biases our interpretation toward skin procurement, but we do not exclude the possibility that MP foragers, on occasion, consumed carnivore meat, since it seems unlikely that they would waste fresh meat due to its nutritional value[107]. In any case, the documentation of both carnivore tooth marks on ungulate remains and anthropogenic modifications on carnivore bones recovered at Ghar-e Boof provide compelling evidence for direct and indirect carnivore-hominin interactions in the southern Zagros Mountains.

Finally, any interpretations regarding the main agent responsible for the accumulation of birds must be made with caution. In our study, we did not find unequivocal evidence for an anthropogenic origin of the bird remains recovered from the MP sequence of Ghar-e Boof, yet the most common species at the site are those that tend to be exploited by hominin foragers. Most of the bird specimens identified in the assemblage correspond to medium-sized birds, probably Columbiformes or Galliformes. However, more precise taxonomic identifications (either genus or species) were not possible for several reasons: some specimens do not present diagnostic features; there is a high diversity of birds currently distributed across modern-day Iran and southwestern Asia[108]; and we only had access to few Iranian taxa in our comparative collection. Columbiformes, such as rock doves and other pigeons, inhabit stony and rocky environments, and even breed and shelter inside caves[108]. It is possible that some bird remains come from animals that died naturally in the cave, as suggested recently for some of the small vertebrate taxa recovered at the site[61]. However, Galliformes, particularly Chukar partridges, do not live in caves[108]. A small number of medium bird or partridge specimens exhibit green fractures, indicating that the bones might have been broken by predators. On the one hand, we did not record carnivore damage on bird remains, which allows us to consider hominins as potential accumulators. On the other hand, experimental studies have demonstrated that humans can deflesh and disarticulate bird carcasses using their bare hands without the assistance of any tools[109]. Thus, the absence of cut marks on bird specimens at Ghar-e Boof does not necessarily mean that MP hominins did not exploit or consume bird resources occasionally. Following the prey choice model, small, fast-moving, or difficult-to-catch animals, such as partridges, usually provide lower caloric return rates because they have higher capture and processing costs than large game or small, slow-moving taxa[5,11,12,35]. Under the purported low population densities and hunting pressures attested in the southern Zagros during the MP, hominins were able to have a narrow diet dominated by high-ranked food resources, while low-ranked birds might have been either completely ignored or represented very sporadic contributions to the total meat intake[3,5,11,12].

During the last decades, the reconstruction of dietary and subsistence strategies of MP hominins have benefited considerably from the improvement and standardization of modern excavation techniques (e.g., systematic water-sieving of sediments or use of ≤ 2 mm mesh, which allow archaeologists to recover even the smallest faunal remains[22,25]). In addition, there have been an increasing number of detailed taphonomic-oriented analyses that have focused on different classes of faunal remains present in archaeological assemblages (i.e.[15,19,21,22,25]). Some scholars have proposed that Neanderthals habitually exploited small, fast-moving animals, such as leporids and birds[18–20,22,24]. However, the systematic use of small, quick animals is still rare in the MP record of Eurasia[3,22], and it might only have been a feasible foraging strategy at some localities due to their unique environmental conditions or the availability of small prey[20,22,25,30,34]. In most cases, the zooarchaeological evidence points to sporadic use of small, fast-moving game and carnivores[21,23,28]. Nevertheless, the acquisition and exploitation of diverse prey highlight the high plasticity, variability, and complex foraging skills of MP hominins throughout Eurasia.

The majority of examples of hominin utilization of diverse types of prey during the MP, especially small, fast-moving taxa, have been documented at southwestern European sites[18–26,30]. Overall, the available data are comparatively scarce in southwestern Asia, and most of the evidence comes from the northern and southern Levant. Besides a narrow focus on large game hunting, in this region, MP hominins favored the exploitation of small, slow-moving game species, such as shellfish, land tortoise, and freshwater turtle[2,3,11–14,110,111]. Our analysis of the MP faunal assemblages of Ghar-e Boof shows a similar picture. MP hominins probably met most of their meat and marrow demands with large game animals, while sessile tortoises could be considered important dietary supplements. Instead, birds and carnivores seem to have played a much more marginal role within the animal fraction of the hominin diets. If we use the observed diet breadth as an indicator of hunting pressure and demography[5,11,12], in southwestern Asia, from the eastern rim of the Mediterranean Sea to the southern Zagros Mountains, hominin population densities were consistently low during most of the MP on local and regional scales.

In the Zagros Mountains, archaeologists have published zooarchaeological data for the following Late Pleistocene sites with MP deposits (Fig. 1): Eshkaft-e Gavi[48], Kunji Cave[45,48], Kaldar Cave[47], Warwasi Rockshelter[41], Ghar-e Khar[43], Kobeh Cave[4,44–46,48], and Shanidar Cave[39,40,42,49]. As we mentioned above, the only instance of purported hominin harvesting of tortoises in the region might be Shanidar Cave, on the basis of burning damage and relative species abundances[42]. Other than that, zooarchaeologists have suggested that during the MP hominins targeted ungulates across the Zagros almost exclusively, mostly caprines, along with equids and gazelles, but also red deer, roe deer, wild pig, and wild cattle[4,39,40,42–49]. Overall, the relative species abundances from these MP sites and our analysis are very similar, and a narrow focus on ungulates could reflect both environmental constraints and prey availability[48], as well as socioeconomic decisions linked to the optimization of energetic return rates by targeting primarily high-ranked resources[5,11,12].

Our taphonomic analysis of the MP faunal remains from Ghar-e Boof suggests that tortoises constituted important dietary supplements for hominins, and the occupants of the site only exploited carnivores and possibly birds on occasion. Nonetheless, these results still offer new insights on the diversity and flexibility of foraging behaviors of MP hominins in the Zagros Mountains. Previously, Evins[42] suggested that the lack of tortoises at some Late Pleistocene sites might just attest to local prey availability. However, tortoises (*Testudo* spp.) are flexible in their habitat requirements, and nowadays they can be found throughout the entire range of the Zagros Mountains[112]. Chukar partridges, for example, also inhabit a great variety of habitats across the Zagros, including stony foothills, bush-covered plains, barren terrains and gullies and wadis in arid plains[108]. The ecological flexibility of these two species leads us to suggest that different classes of small game taxa must have been available in the surrounding environments of the above-mentioned sites. Likewise, the taxonomic and taphonomic analyses of the remains recovered at Bisotun Cave, Tamtama Cave, and Wezmeh Cave confirmed these sites were mainly carnivore dens[48,113]. Carnivore remains were also documented at Kobeh Cave and Eshkaft-e Gavi[48], indicating that carnivores were either constant threats, potential resources for hominins, or both. Up to now, it seems that our understanding of hominin diets and subsistence strategies in the Zagros have been partly biased because zooarchaeologists have paid more attention to large game animals[4,43–46,48,49]. In addition, scholars have demonstrated that archaeologists who originally excavated MP sites during the 1950s or 1960s introduced certain biases because excavation standards were different compared to modern practices, they did not have access to technology such as total stations, or did not retain all the faunal remains[48,49]. Recently, new archaeological research projects have focused on re-excavating well-known sites, such as Shanidar Cave[76,77], but also excavating relatively new sites, including Kaldar Cave[47], Ghar-e Boof[58,59] and Bawa Yawan Rockshelter[81], among others, with modern excavation techniques. Further investigations are still required, but the complete recovery of even the smallest faunal remains from these excavations will almost certainly provide us with new evidence to reconstruct more exhaustively the hominin foraging spectrum, and to assess the socioeconomic importance of different types of game during the MP in the Zagros. Meanwhile, the faunal remains from the MP sequence of Ghar-e Boof represent the first evidence of hominin exploitation of small game and carnivores in the southern Zagros Mountains. Even if the use and consumption of some of these taxa were sporadic, our results demonstrate that MP hominins exploited more diverse animals than previously thought in the Zagros region, and is more consistent with what is found in other parts of Eurasia.

Methods summary

Archaeologists excavated Ghar-e Boof by 50 cm sub-squares within each squared meter, and in two to three cm-deep spits or *abträge*, following the slope of the sediments[58]. Both lithic artifacts and organic remains were recorded in three dimensions, along with the orientation for elongated finds[58]. In order to allow the retrieval of even the smallest animal remains, excavators floated all the sediments and water-screened them using superimposed five- and two-mm mesh[58]. We identified taxonomically and anatomically the faunal remains recovered from Ghar-e Boof with the help of the zooarchaeological reference collection of the University of Tübingen. When needed, our identifications were also assisted by osteological atlases and zooarchaeological guides (i.e., for caprines[114,115]; for carnivores[116]; and for tortoises[117]; among others), in combination with other unpublished electronic manuals and images. Number of identified specimens (NISP) is the basic counting unit in this study for estimating taxonomic abundance following Grayson[118]'s and Lyman[94,119]'s definitions. Here, NISP not only includes specimens identified to the lowest possible taxonomic level, such as species, genus, or family, but also fragments with less diagnostic features that we assigned to body size groups (e.g., medium bird or small carnivore[2]). Specimens were recorded following Stiner[120]'s coding system for skeletal elements and portions of elements, with some minor modifications for Aves and Testudines. Although our zooarchaeological analysis is based exclusively on species representation and abundance comparisons by NISP counts and percentages of NISP, we estimated the minimum number of individuals (MNI) and provided them in Table S2, in order to allow comparisons with other Late Pleistocene faunal collections from the Zagros region for which MNI values are available (e.g.,[42,113]). For the quantification of MNI, we considered the most common element, as well as side and age, by taxon[94,118,119], and for each AH.

In order to examine anatomical part representation for the main prey (caprines and medium ungulates), we grouped skeletal elements into nine body regions, which constitute logical portions in terms of butchery and transport decisions[121]. Following Binford[122] and Stiner[121], we calculated MAU by dividing our MNE values by the expected MNE in a complete animal skeleton for each different element and body region. We also complement our analysis of transport and butchery practices with Spearman's rank-order correlation test to examine possible relationships between %MAU (MAUs divided by the highest observed MAU value in our assemblage and then multiplied by 100[119]) and food utility[88], standard food utility[89], marrow[88], and unsaturated marrow[90] indices. Due to small sample sizes, all the caprine and medium ungulate elements recovered from MP sequence were combined. Bone density-mediated attrition was examined by contrasting ungulate tooth- and skull bone-based MNE counts[1]. Considered as a single transportable unit, the head region encompasses both bony and tooth elements that are expected to be brought together to a site, and therefore, the ratio between the most abundant tooth and bone cranial element based on MNE should be nearly 1:1[1]. Because of the differences in mineral composition and structural density, teeth better withstand attritional processes than bones[1,94]. As a result, an overrepresentation of teeth would indicate that density-mediated attrition had affected a faunal assemblage[1]. We combined all ungulate taxa together for each layer in this analysis in order to have a more robust dataset[65].

We analyzed bone surface modifications and fractures to identify the main agent of accumulation or modification of the MP deposits of Ghar-e Boof, and to evaluate other post-depositional processes that may have affected the integrity and the interpretative protentional of the archeofaunal assemblage. All bone specimens were examined with a 10× hand lens. When the analysis of bone surface modifications required higher resolution examination and for photographing the specimens, we used an Olympus SZX7 stereo microscope with a digital camera and a Keyence VHX-500FD digital microscope, which offer magnifications from 4× to 336×, and from 5× to 200× respectively. We distinguished between physical, abiotic, and non-human biological alterations, and anthropogenic modifications. As for non-human alterations, we recorded for each specimen the presence/absence of weathering damage (e.g., cracks, flaking, and exfoliation), root etching, rounding/abrasion, chemical weathering, sedimentological alterations (sediment concretions and crushing), carnivore damage (e.g., tooth marks, crenulation, digestion, and punctures) and rodent gnawing. Our identification of such modifications follows the criteria described by[91,93,97]. Anthropogenic modifications documented for this study include burning, percussion damage, cut marks, bone tools, and green/fresh fractures (following[92–94,97], and references therein). Among the fresh fractures, we differentiated between transverse fractures (those that occur when a bone was broken at a right angle or perpendicular to its long axis) and splits or spiral fractures (which break the bone parallel to the long axis, though spiral fractures also present a helical shape around the circumference of the bone shaft[94,123,124]. Finally, our interpretation of the different anthropogenic modifications and bone fractures (or their absence) are mainly based on ethnographic and experimental studies for ungulate[95,96,98,99], carnivore[103,104], and bird[109] carcasses, and the corresponding observed butchery behaviors, such as skinning, defleshing, dismemberment, and marrow processing.

Data availability

All the data supporting the results and interpretations reported in this paper are available within the main text, figures, and tables or as Supplementary Information. For access to the zooarchaeological assemblages from Ghar-e Boof temporarily housed at the University of Tübingen, the readers may contact the co-directors of the site (N.J.C. and M.Z.).

Received: 31 May 2023; Accepted: 26 October 2023

References

1. Stiner, M. C. *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology* (Princeton University Press, 1994).
2. Stiner, M. C. *The Faunas of Hayonim Cave, Israel: A 200,000 Year Record of Paleolithic Diet, Demography, and Society* (Peabody Museum Press, 2005).
3. Stiner, M. C. An unshakable Middle Paleolithic? Trends versus conservatism in the predatory niche and their social ramifications. *Curr. Anthropol.* **54**, S288–S304. https://doi.org/10.1086/673285 (2013).
4. Marean, C. W. & Kim, S. Y. Mousterian large-mammal remains from Kobeh Cave. Behavioral implications for Neanderthals and early modern humans. *Curr. Anthropol.* **39**, S79–S114. https://doi.org/10.1086/204691 (1998).
5. Stiner, M. C. & Munro, N. D. Approaches to Prehistoric diet breadth, demography, and prey ranking systems in time and space. *J. Archaeol. Method Theory* **9**, 181–214. https://doi.org/10.1023/A:1016530308865 (2002).
6. Adler, D. S., Bar-Oz, G., Belfer-Cohen, A. & Bar-Yosef, O. Ahead of the game: Middle and Upper Palaeolithic hunting behaviors in the southern Caucasus. *Curr. Anthropol.* **47**, 89–118. https://doi.org/10.1086/432455 (2006).
7. Speth, J. D. & Tchernov, E. The Middle Palaeolithic occupations at Kebara Cave in *Kebara Cave, Mt Carmel, Part 1. The Middle and Upper Palaeolithic Archaeology* (eds. Bar-Yosef, O. & Meignen, L.) 165–260 (Peabody Museum Press, 2007).
8. Yeshurun, R., Bar-Oz, G. & Weinstein-Evron, M. Modern hunting behavior in the early Middle Paleolithic: Faunal remains from Misliya Cave, Mount Carmel. *Isr. J. Hum. Evol.* **53**, 656–677. https://doi.org/10.1016/j.jhevol.2007.05.008 (2007).
9. Niven, L. *et al.* Neandertal mobility and large-game hunting: The exploitation of reindeer during the Quina Mousterian at Chez-Pinaud Jonzac (Charente-Maritime, France). *J. Hum. Evol.* **63**, 624–635. https://doi.org/10.1016/j.jhevol.2012.07.002 (2012).
10. Starkovich, B. M. Paleolithic subsistence strategies and changes in site use at Klissoura Cave 1 (Peloponnese, Greece). *J. Hum. Evol.* **111**, 63–84. https://doi.org/10.1016/j.jhevol.2017.04.005 (2017).
11. Stiner, M. C., Munro, N. D., Surovell, T. A., Tchernov, E. & Bar-Yosef, O. Paleolithic population growth pulses evidenced by small animal exploitation. *Science* **283**, 190–194. https://doi.org/10.1126/science.283.5399.190 (1999).
12. Stiner, M. C., Munro, N. D. & Surovell, T. A. The tortoise and the hare: Small-game use, the Broad-Spectrum Revolution, and Paleolithic demography. *Curr. Anthropol.* **41**, 39–79. https://doi.org/10.1086/300102 (2000).
13. Speth, J. D. & Tchernov, E. Middle Paleolithic tortoise use at Kebara Cave (Israel). *J. Archaeol. Sci.* **29**, 471–483. https://doi.org/10.1006/jasc.2001.0740 (2002).
14. Biton, R., Sharon, G., Oron, M., Steiner, T. & Rabinovich, R. Freshwater turtle or tortoise? The exploitation of testudines at the Mousterian site of Nahal Mahanayeem Outlet, Hula Valley, Israel. *J. Archaeol. Sci. Rep.* **14**, 409–419. https://doi.org/10.1016/j.jasrep.2017.05.058 (2017).
15. Nabais, M. & Zilhão, J. The consumption of tortoise among Last Interglacial Iberian Neanderthals. *Quat. Sci. Rev.* **217**, 225–246. https://doi.org/10.1016/j.quascirev.2019.03.024 (2019).
16. Peresani, M., Fiore, I., Gala, M., Romandini, M. & Tagliacozzo, A. Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proc. Natl. Acad. Sci.* **108**, 3888–3893. https://doi.org/10.1073/pnas.1016212108 (2011).
17. Morin, E. & Laroulandie, V. Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS ONE* **7**, e32856. https://doi.org/10.1371/journal.pone.0032856 (2012).
18. Finlayson, C. *et al.* Birds of a feather: Neanderthal exploitation of raptors and corvids. *PLoS ONE* **7**, e45927. https://doi.org/10.1371/journal.pone.0045927 (2012).
19. Blasco, R. *et al.* The earliest pigeon fanciers. *Sci. Rep.* **4**, 5971. https://doi.org/10.1038/srep05971 (2014).
20. Blasco, R., Rosell, J., Rufà, A., Sánchez-Marco, A. & Finlayson, C. Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. *Quat. Int.* **421**, 62–77. https://doi.org/10.1016/j.quaint.2015.10.040 (2016).
21. Gómez-Olivencia, A. *et al.* First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Sci. Rep.* **8**, 10551. https://doi.org/10.1038/s41598-018-28377-y (2018).
22. Cochard, D., Brugal, J.-P., Morin, E. & Meignen, L. Evidence of small fast game exploitation in the Middle Paleolithic of Les Canalettes Aveyron, France. *Quat. Int.* **264**, 32–51. https://doi.org/10.1016/j.quaint.2012.02.014 (2012).
23. Carvalho, M., Pereira, T. & Manso, C. Rabbit exploitation in the Middle Paleolithic at Gruta Nova da Columbeira, Portugal. *J. Archaeol. Sci. Rep.* **21**, 821–832. https://doi.org/10.1016/j.jasrep.2018.09.003 (2018).
24. Morin, E. *et al.* New evidence of broader diets for archaic *Homo* populations in the northwestern Mediterranean. *Sci. Adv.* https://doi.org/10.1126/sciadv.aav9106 (2019).
25. Pelletier, M., Desclaux, E., Brugal, J.-P. & Texier, P.-J. The exploitation of rabbits for food and pelts by last interglacial Neandertals. *Quat. Sci. Rev.* **224**, 105972. https://doi.org/10.1016/j.quascirev.2019.105972 (2019).
26. Zilhão, J. *et al.* Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science* **367**, eaaz7943. https://doi.org/10.1126/science.aaz7943 (2020).
27. Blanco-Lapaz, A., Kitagawa, K. & Kind, C. J. Aquatic resources exploitation during the Palaeolithic in the Swabian Jura based on fish remains from Hohlenstein-Stadel Cave. *Quartär* **68**, 25–38 (2021).
28. Gabucio, M. J., Cáceres, I., Rodríguez-Hidalgo, A., Rosell, J. & Saladié, P. A wildcat (*Felis silvestris*) butchered by Neanderthals in Level O of the Abric Romaní site (Capellades, Barcelona, Spain). *Quat. Int.* **326–327**, 307–318. https://doi.org/10.1016/j.quaint.2013.10.051 (2014).
29. Romandini, M. *et al.* Bears and humans, a Neanderthal tale. Reconstructing uncommon behaviors from zooarchaeological evidence in southern Europe. *J. Archaeol. Sci.* **90**, 71–91. https://doi.org/10.1016/j.jas.2017.12.004 (2018).
30. Blasco, R. *et al.* Small animal use by Neanderthals in *Updating Neanderthals: Understanding Behavioural Complexity in the Late Middle Palaeolithic* (eds. Romagnoli, F., Rivals, F. & Benazzi, S.) 123–143 (Elsevier, 2022). https://doi.org/10.1016/C2019-0-03240-2.
31. Morin, E., Bird, D., Winterhalder, B. & Bliege Bird, R. Deconstructing hunting returns: Can we reconstruct and predict payoffs from pursuing prey?. *J. Archaeol. Method Theory* **29**, 561–623. https://doi.org/10.1007/s10816-021-09526-6 (2022).
32. Kuhn, S. L. & Stiner, M. C. What's a mother to do? The division of labor among Neanderthals and modern humans in Eurasia. *Curr. Anthropol.* **47**, 953–981. https://doi.org/10.1086/507197 (2006).
33. Kelly, R. L. *The Lifeways of Hunter–Gatherers: The Foraging Spectrum* (Cambridge University Press, 2013). https://doi.org/10.1017/CBO9781139176132.
34. Blasco, R. *et al.* Environmental availability, behavioural diversity and diet: A zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quat. Sci. Rev.* **70**, 124–144. https://doi.org/10.1016/j.quascirev.2013.03.008 (2013).
35. Madsen, D. B. & Schmitt, D. N. Mass collecting and the Diet Breadth Model: A Great Basin example. *J. Archaeol. Sci.* **25**, 445–455. https://doi.org/10.1006/jasc.1997.0245 (1998).
36. Stiner, M. C. Competition theory and the case for Pleistocene hominin–carnivore coevolution. *J. Taphon.* **10**, 129–145 (2012).
37. Camarós, E., Münzel, S. C., Cueto, M., Rivals, F. & Conard, N. J. The evolution of Paleolithic hominin–carnivore interaction written in teeth: Stories from the Swabian Jura (Germany). *J. Archaeol. Sci. Rep.* **6**, 798–809. https://doi.org/10.1016/j.jasrep.2015.11.010 (2016).

38. Shoaee, M. J., Vahdati Nasab, H. & Petraglia, M. D. The Paleolithic of the Iranian Plateau: Hominin occupation history and implications for human dispersals across southern Asia. *J. Anthropol. Archaeol.* **62**, 101292. https://doi.org/10.1016/j.jaa.2021.101292 (2021).
39. Solecki, R. S. Prehistory in Shanidar Valley, northern Iraq. *Science* **139**, 179–193. https://doi.org/10.1126/science.139.3551.179 (1963).
40. Perkins, D. Prehistoric fauna from Shanidar, Iraq. *Science* **144**, 1565–1566. https://doi.org/10.1126/science.144.3626.1565 (1964).
41. Turnbull, P. F. The mammalian fauna of Warwasi rock shelter, West-central Iran. *Fieldiana Geol.* **33**, 141–155. https://doi.org/10.5962/bhl.title.5352 (1975).
42. Evins, M. A. The Fauna from Shanidar Cave: Mousterian wild goat exploitation in Northeastern Iraq. *Paléorient* **8**, 37–58. https://doi.org/10.3406/paleo.1982.4308 (1982).
43. Hesse, B. Paleolithic faunal remains from Ghar-i Khar, western Iran in *Early Animal Domestication and its Cultural Context* (eds. Crabtree, P. J., Campana, D. & Ryan, K.) 37–45 (MASCA, the University Museum of Archaeology and Anthropology. University of Pennsylvania, 1989).
44. Marean, C. W. & Frey, C. J. Animal bones from caves to cities: Reverse utility curves as methodological artifacts. *Am. Antiq.* **62**, 698–711. https://doi.org/10.2307/281887 (1997).
45. Cleghorn, N. & Marean, C. W. Distinguishing selective transport and in situ attrition: A critical review of analytical approaches. *J. Taphon.* **2**, 43–68 (2004).
46. Marean, C. W. A critique of the evidence for scavenging by Neandertals and early modern humans: New data from Kobeh Cave (Zagros Mountains, Iran) and Die Kelders Cave 1 Layer 10 (South Africa). *J. Hum. Evol.* **35**, 111–136. https://doi.org/10.1006/jhev.1998.0224 (1998).
47. Bazgir, B. *et al.* Understanding the emergence of modern humans and the disappearance of Neanderthals: Insights from Kaldar Cave (Khorramabad Valley, Western Iran). *Sci. Rep.* **7**, 43460. https://doi.org/10.1038/srep43460 (2017).
48. Hodgkins, J. M. & Marean, C. W. New information from old excavations: A comparative analysis of Paleolithic zooarchaeological assemblages from the Zagros Mountains in *The Pleistocene Archaeology of the Iranian Plateau, Iraq and the Caucasus* (eds. Biglari, F., Mashkour, M. & Shidrang, S.) (National Museum of Iran, 2017).
49. Campana, D. V. & Crabtree, P. Evidence for skinning and craft activities from the Middle Paleolithic of Shanidar Cave, Iraq. *J. Archaeol. Sci. Rep.* **25**, 7–14. https://doi.org/10.1016/j.jasrep.2019.03.024 (2019).
50. Heydari, M., Guérin, G., Zeidi, M. & Conard, N. J. Bayesian luminescence dating at Ghār-e Boof, Iran, provides a new chronology for Middle and Upper Paleolithic in the southern Zagros. *J. Hum. Evol.* **151**, 102926. https://doi.org/10.1016/j.jhevol.2020.102926 (2021).
51. Heydari-Guran, S. *Paleolithic Landscapes of Iran* (BAR International Series, 2014).
52. Heydari-Guran, S. Tracking Upper Pleistocene human dispersals into the Iranian Plateau: A geoarchaeological model in *Human Origin Sites and the World Heritage Convention in Eurasia, Heads 4* (ed. Sanz, N.) vol. 1 40–53 (UNESCO Office, 2015).
53. Conard, N. J. & Ghasidian, E. The Rostamian cultural group and the taxonomy of the Iranian Upper Palaeolithic in *Between Sand and Sea: The Archaeology and Human Ecology of Southwestern Asia* (eds. Conard, N. J., Drechsler, P. & Morales, A.) 33–52 (Kerns Verlag, 2011).
54. Nowroozi, R. *Archaeological Survey of Prehistoric Localities in Nourabad Mmasani Plain* (University of Tehran, 1997) in Farsi.
55. Conard, N. J., Ghasidian, E., Heydari, S. & Zeidi, M. Report on the 2005 survey of the Tübingen Iranian Stone Age Research Project in the Provinces of Esfahan, Fars and Kohgiluyeh-Boyerahmad in *Archaeological Reports 5* (ed. Azarnoush, M.) 9–34 (Iranian Center for Archaeological Research, 2006).
56. Zeidi, M., McCall, B. & Khosrowzadeh, A. Survey of Dasht-e Rostam-e Yek and Dasht-e Rostam-e Do in *The Mamasani Archaeological Project Stage One: A Report on the First Two Seasons of the Iranian Center for Archaeological Research—University of Sydney Expedition to the Mamasani District, Fars Province, Iran* (eds. Potts, D. T. & Roustaei, K.) 147–168 (Iranian Center for Archaeological research, 2006).
57. Conard, N. J., Ghasidian, E., Heydari, S., Naderi, R. & Zeidi, M. The 2006 season of the Tübingen-Iranian Stone Age Research Project in the Provinces of Fars and Markazi in *9th Annual Report of Archaeological Organisation* (ed. Fazeli, H.) 43–67 (Iranian Center for Archaeological Research, 2007).
58. Conard, N. J. & Zeidi, M. New research on the Paleolithic occupation of Ghar-e Boof, Fars Province. *J. Iran. Center Archaeol. Res.* **2**, 7–16 (2019).
59. Zeidi, M. & Conard, N. J. The fourth season of excavation at Ghar-e Boof, Rostam County, Fars Province in *16th Annual Symposium of the Iranian Archaeology* (ed. Shirazi, R. A.) 234–238 (Iranian Center for Archaeological Research, 2019) in Farsi.
60. Schilt, F. C. *Micromorphology of Upper Paleolithic and Historic Sediments from Boof Cave, Iran* (University of Tubingen, 2011).
61. Blanco-Lapaz, A., Mata-González, M., Starkovich, B. M., Zeidi, M. & Conard, N. J. Late Pleistocene environments in the southern Zagros of Iran and their implications for human evolution. *Archaeol. Anthropol. Sci.* **14**, 161. https://doi.org/10.1007/s12520-022-01615-1 (2022).
62. Baines, J. A., Riehl, S., Conard, N. J. & Zeidi, M. Upper Palaeolithic archaeobotany of Ghar-e Boof cave, Iran: A case study in site disturbance and methodology. *Archaeol. Anthropol. Sci.* **7**, 245–256. https://doi.org/10.1007/s12520-014-0191-6 (2015).
63. Becerra-Valdivia, L. *et al.* Chronometric investigations of the Middle to Upper Paleolithic transition in the Zagros Mountains using AMS radiocarbon dating and Bayesian age modelling. *J. Hum. Evol.* **109**, 57–69. https://doi.org/10.1016/j.jhevol.2017.05.011 (2017).
64. Ghasidian, E., Bretzke, K. & Conard, N. J. Excavations at Ghār-e Boof in the Fars Province of Iran and its bearing on models for the evolution of the Upper Palaeolithic in the Zagros Mountains. *J. Anthropol. Archaeol.* **47**, 33–49. https://doi.org/10.1016/j.jaa.2017.03.001 (2017).
65. Mata-González, M., Starkovich, B. M., Zeidi, M. & Conard, N. J. New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran). *Quat. Sci. Rev.* **279**, 107350. https://doi.org/10.1016/j.quascirev.2021.107350 (2022).
66. Bretzke, K. & Conard, N. J. Not just a crossroad: Population dynamics and changing material culture in southwestern Asia during the Late Pleistocene. *Curr. Anthropol.* **58**, S449–S462. https://doi.org/10.1086/694077 (2017).
67. Otte, M., Shidrang, S., Zwyns, N. & Flas, D. New radiocarbon dates for the Zagros Aurignacian from Yafteh cave, Iran. *J. Hum. Evol.* **61**, 340–346. https://doi.org/10.1016/j.jhevol.2011.05.011 (2011).
68. Goder-Goldberger, M. & Malinsky-Buller, A. The initial Upper Paleolithic and its place within the Middle-to-Upper Paleolithic transition of Southwest Asia: What hides behind the curtain of taxonomies? *J. Paleolit. Archaeol.* **5**, 2. https://doi.org/10.1007/s41982-022-00112-0 (2022).
69. Scott, J. E. & Marean, C. W. Paleolithic hominin remains from Eshkaft-e Gavi (southern Zagros Mountains, Iran): Description, affinities, and evidence for butchery. *J. Hum. Evol.* **57**, 248–259. https://doi.org/10.1016/j.jhevol.2009.05.012 (2009).
70. Tsanova, T. The beginning of the Upper Paleolithic in the Iranian Zagros. A taphonomic approach and techno-economic comparison of early Baradostian assemblages from Warwasi and Yafteh (Iran). *J. Hum. Evol.* **65**, 39–64. https://doi.org/10.1016/j.jhevol.2013.04.005 (2013).
71. Trinkaus, E. Pleistocene human remains from Iran in *The Pleistocene Archaeology of the Iranian Plateau, Iraq and the Caucasus* (eds. Biglari, F., Shidrang, S. & Mashkour, M.) 53–63 (National Museum of Iran, 2018).

72. Solecki, R. S. Shanidar IV, a Neanderthal Flower Burial in Northern Iraq. *Science* **190**, 880–881. https://doi.org/10.1126/science.190.4217.880 (1975).
73. Trinkaus, E. *The Shanidar Neandertals* (Academic Press, 1983). https://doi.org/10.1016/C2013-0-11620-0.
74. Cowgill, L. W., Trinkaus, E. & Zeder, M. A. Shanidar 10: A Middle Paleolithic immature distal lower limb from Shanidar Cave, Iraqi Kurdistan. *J. Hum. Evol.* **53**, 213–223. https://doi.org/10.1016/j.jhevol.2007.04.003 (2007).
75. Churchill, S. E., Franciscus, R. G., McKean-Peraza, H. A., Daniel, J. A. & Warren, B. R. Shanidar 3 Neandertal rib puncture wound and paleolithic weaponry. *J. Hum. Evol.* **57**, 163–178. https://doi.org/10.1016/j.jhevol.2009.05.010 (2009).
76. Pomeroy, E. *et al.* Newly discovered Neanderthal remains from Shanidar Cave, Iraqi Kurdistan, and their attribution to Shanidar 5. *J. Hum. Evol.* **111**, 102–118. https://doi.org/10.1016/j.jhevol.2017.07.001 (2017).
77. Pomeroy, E. *et al.* New Neanderthal remains associated with the 'flower burial' at Shanidar Cave. *Antiquity* **94**, 11–26. https://doi.org/10.15184/aqy.2019.207 (2020).
78. Trinkaus, E. & Villotte, S. External auditory exostoses and hearing loss in the Shanidar 1 Neandertal. *PLoS ONE* **12**, e0186684. https://doi.org/10.1371/journal.pone.0186684 (2017).
79. Trinkaus, E. & Biglari, F. Middle Paleolithic Human Remains from Bisitun Cave, Iran. *Paléorient* **32**, 105–111. https://doi.org/10.3406/paleo.2006.5192 (2006).
80. Zanolli, C. *et al.* A Neanderthal from the Central Western Zagros, Iran. Structural reassessment of the Wezmeh 1 maxillary premolar. *J. Hum. Evol.* **135**, 102643. https://doi.org/10.1016/j.jhevol.2019.102643 (2019).
81. Heydari-Guran, S. *et al.* The discovery of an in situ Neanderthal remain in the Bawa Yawan Rockshelter, West-Central Zagros Mountains, Kermanshah. *PLoS ONE* **16**, e0253708. https://doi.org/10.1371/journal.pone.0253708 (2021).
82. Hershkovitz, I. *et al.* Levantine cranium from Manot Cave (Israel) foreshadows the first European modern humans. *Nature* **520**, 216–219. https://doi.org/10.1038/nature14134 (2015).
83. Hershkovitz, I. *et al.* The earliest modern humans outside Africa. *Science* **359**, 456–459. https://doi.org/10.1126/science.aap8369 (2018).
84. Weber, G. W. *et al.* Before the massive modern human dispersal into Eurasia: A 55,000-year-old partial cranium from Manot Cave, Israel. *Quat. Int.* **551**, 29–39. https://doi.org/10.1016/j.quaint.2019.10.009 (2020).
85. Valladas, H. *et al.* TL Dates for the Neanderthal Site of the Amud Cave, Israel. *J. Archaeol. Sci.* **26**, 259–268. https://doi.org/10.1006/jasc.1998.0334 (1999).
86. Been, E. *et al.* The first Neanderthal remains from an open-air Middle Palaeolithic site in the Levant. *Sci. Rep.* **7**, 2958. https://doi.org/10.1038/s41598-017-03025-z (2017).
87. Goring-Morris, A. N. & Belfer-Cohen, A. Noisy beginnings: The initial Upper Palaeolithic in Southwest Asia. *Quat. Int.* **551**, 40–46. https://doi.org/10.1016/j.quaint.2020.01.017 (2020).
88. Emerson, A. M. The role of body part utility in small-scale hunting under two strategies of carcass recovery in *From Bones to Behavior. Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains* (ed. Hudson, J.) 138–155 (Center for Archaeological Investigation. Southern Illinois University, 1993).
89. Metcalfe, D. & Jones, K. T. A reconsideration of animal body-part utility indices. *Am. Antiq.* **53**, 486–504. https://doi.org/10.2307/281213 (1988).
90. Morin, E. Fat composition and Nunamiut decision-making: A new look at the marrow and bone grease indices. *J. Archaeol. Sci.* **34**, 69–82. https://doi.org/10.1016/j.jas.2006.03.015 (2007).
91. Behrensmeyer, A. K. Taphonomic and ecologic information from bone weathering. *Paleobiology* **4**, 150–162. https://doi.org/10.1017/S0094837300005820 (1978).
92. Stiner, M. C., Kuhn, S. L., Weiner, S. & Bar-Yosef, O. Differential burning, recrystallization, and fragmentation of archaeological bone. *J. Archaeol. Sci.* **22**, 223–237. https://doi.org/10.1006/jasc.1995.0024 (1995).
93. Fernandez-Jalvo, Y. & Andrews, P. Atlas of Taphonomic Identifications. *Springer* https://doi.org/10.1007/978-94-017-7432-1 (2016).
94. Lyman, R. L. *Vertebrate Taphonomy* (Cambridge University Press, 1994). https://doi.org/10.1017/CBO9781139878302.
95. Binford, L. R. *Nunamiut Ethnoarchaeology* (Academic Press, 1978).
96. Binford, L. R. *Ancient Men and Modern Myths* (Academic Press, 1981).
97. Fisher, J. W. Bone surface modifications in zooarchaeology. *J. Archaeol. Method Theory* **2**, 7–68. https://doi.org/10.1007/BF02228434 (1995).
98. Galán, A. B. & Domínguez-Rodrigo, M. An experimental study of the anatomical distribution of cut marks created by filleting and disarticulation on long bone ends. *Archaeometry* **55**, 1132–1149. https://doi.org/10.1111/j.1475-4754.2012.00730.x (2013).
99. Soulier, M.-C. & Costamagno, S. Let the cutmarks speak! Experimental butchery to reconstruct carcass processing. *J. Archaeol. Sci. Rep.* **11**, 782–802. https://doi.org/10.1016/j.jasrep.2016.12.033 (2017).
100. Firouz, E. *The Complete Fauna of Iran* (I.B. Tauris & Co. Ltd., 2005). https://doi.org/10.5040/9780755612215.
101. Karami, M., Ghadirian, T. & Faizolahi, K. *The Atlas of Mammals of Iran* (Department of Environment of Iran, 2016).
102. Thompson, J. C. & Henshilwood, C. S. Tortoise taphonomy and tortoise butchery patterns at Blombos Cave, South Africa. *J. Archaeol. Sci.* **41**, 214–229. https://doi.org/10.1016/j.jas.2013.08.017 (2014).
103. Val, A. & Mallye, J.-B. Small carnivore skinning by professionals: Skeletal modifications and implications for the European Upper Palaeolithic. *J. Taphon.* **9**, 221–243 (2011).
104. Crezzini, J., Boschin, F., Boscato, P. & Wierer, U. Wild cats and cut marks: Exploitation of *Felis silvestris* in the Mesolithic of Galgenbühel/Dos de la Forca (South Tyrol, Italy). *Quat. Int.* **330**, 52–60. https://doi.org/10.1016/j.quaint.2013.12.056 (2014).
105. Val, A., Porraz, G., Texier, P.-J., Fisher, J. W. & Parkington, J. Human exploitation of nocturnal felines at Diepkloof Rock Shelter provides further evidence for symbolic behaviours during the Middle Stone Age. *Sci. Rep.* **10**, 6424. https://doi.org/10.1038/s41598-020-63250-x (2020).
106. Boren, J. C. & Hurd, B. J. *How to Prepare Hides, Guide L-101* (New Mexico State University, 2004).
107. Verheijen, I., Starkovich, B. M., Serangeli, J., van Kolfschoten, T. & Conard, N. J. Early evidence for bear exploitation during MIS 9 from the site of Schöningen 12 (Germany). *J. Hum. Evol.* 103294. https://doi.org/10.1016/j.jhevol.2022.103294 (2022).
108. Kaboli, M. *et al. Atlas of Birds of Iran* (Department of Environment of Iran, 2016).
109. Val, A., de la Peña, P. & Wadley, L. Direct evidence for human exploitation of birds in the Middle Stone Age of South Africa: The example of Sibudu Cave, KwaZulu-Natal.*J. Hum. Evol.* **99**, 107–123. https://doi.org/10.1016/j.jhevol.2016.07.007 (2016).
110. Stiner, M. Prey choice, site occupation intensity & economic diversity in the Middle—early Upper Palaeolithic at the Üçağizli Caves, Turkey. *Before Farm.* **3**, 1–20. https://doi.org/10.3828/bfarm.2009.3.3 (2009).
111. Crater Gershtein, K. M., Zaidner, Y. & Yeshurun, R. A campsite on the open plain: Zooarchaeology of Unit III at the Middle Paleolithic site of Nesher Ramla, Israel. *Quat. Int.* **624**, 49–66. https://doi.org/10.1016/j.quaint.2020.01.026 (2022).
112. Mozaffari, O., Kamali, K. & Fahimi, H. *The Atlas of Reptiles of Iran* (Department of Environment of Iran, 2016).
113. Mashkour, M. *et al.* Carnivores and their prey in the Wezmeh Cave (Kermanshah, Iran): A Late Pleistocene refuge in the Zagros. *Int. J. Osteoarchaeol.* **19**, 678–694. https://doi.org/10.1002/oa.997 (2009).
114. Zeder, M. A. & Lapham, H. A. Assessing the reliability of criteria used to identify postcranial bones in sheep, *Ovis*, and goats, *Capra*. *J. Archaeol. Sci.* **37**, 2887–2905. https://doi.org/10.1016/j.jas.2010.06.032 (2010).
115. Zeder, M. A. & Pilaar, S. E. Assessing the reliability of criteria used to identify mandibles and mandibular teeth in sheep, *Ovis*, and goats, *Capra*. *J. Archaeol. Sci.* **37**, 225–242. https://doi.org/10.1016/j.jas.2009.10.002 (2010).

116. Pales, L. & Garcia, M. A. *Atlas Ostéologique pour Servir à l'Identification des Mammifères du Quaternaire II. Tête, Rachis, Ceintures Scapulaire et Pelvienne, Membres: Carnivores, Homme* (Centre National de la Recherche Scientifique, 1981).
117. Hervet, S. Tortues du Quaternaire de France: Critères de détermination, répartition chronologique el géographique. *Mésogée* **58**, 3–57 (2000).
118. Grayson, D. K. *Quantitative Zooarchaeology* (Academic Press, 1984). https://doi.org/10.1016/C2009-0-21855-1.
119. Lyman, R. L. *Quantitative Paleozoology* (Cambridge University Press, 2008). https://doi.org/10.1017/CBO9780511813863.
120. Stiner, M. C. On *in situ* attrition and vertebrate body part profiles. *J. Archaeol. Sci.* **29**, 979–991. https://doi.org/10.1006/jasc.2001.0798 (2002).
121. Stiner, M. C. Food procurement and transport by human and non-human predators. *J. Archaeol. Sci.* **18**, 455–482. https://doi.org/10.1016/0305-4403(91)90038-Q (1991).
122. Binford, L. R. *Faunal Remains from Klasies River Mouth* (Academic Press, 1984).
123. Johnson, E. Current developments in bone technology in *Advances in Archaeological Method and Theory* (ed. Schiffer, M. B.) vol. 8 157–235 (Academic Press, 1985). https://doi.org/10.1016/B978-0-12-003108-5.50010-5.
124. Gifford-Gonzalez, D. P. Ethnographic analogues for interpreting modified bones: Some cases from East Africa in *Bone Modification* (eds. Bonnichsen, R. & Sorg, M. H.) 179–246 (Center for the Study of the First Americans, University of Maine, 1989).

Acknowledgements

Excavations at Ghar-e Boof were supported by a grant from the Deutsche Forschungsgemeinschaft (CO 226/30-1), and the project Role of Culture in Early Expansions of Humans (ROCEEH) of the Heidelberg Academy of Science and Humanities. M.M.-G. was the beneficiary of a research grant awarded to N.J.C. from the Ministerium für Wissenschaft, Forschung und Kunst Baden-Württemberg as part of the Evolution of Cultural Modernity Project at the University of Tübingen. As part of the University of Tübingen-Connecticut (TÜConn) graduate student exchange program, the University of Connecticut's Office of Global Affairs also provided funding for M.M.-G. Senckenberg Centre for Human Evolution and Palaeoenvironment, alongside the University of Tübingen, supported us during our work. The Iranian Center for Archaeological Research (ICAR), and the Research Institute of Cultural Heritage and Tourism (RICHT) granted us permission to excavate and investigate in Iran, and their support is acknowledged here. We are grateful to all members of the Tübingen-Iranian Stone Age Research Project Team, and in particular, Saman Hamzavi, for their contributions and assistance during the excavations, water-screening, and sorting of the recovered material. Special thanks to Ángel Blanco-Lapaz, not only for sorting the identifiable specimens included in this study, but also for creating and assembling Figs. 2 to 5, and Figs. S2, S3, S5 and S6. In addition, we are very thankful to Natalie D. Munro and Nicholas A. Gonzalez for their constructive comments and suggestions on previous versions of this paper. Finally, we acknowledge support from the Open Access Publishing Fund of the University of Tübingen.

Author contributions

M.M.-G., B.M.S., and N.J.C. designed the research. M.M.-G. analyzed the faunal assemblage under the supervision of B.M.S.; N.J.C. and M.Z. directed and carried out excavations at the site, and provided contextual data. M.Z. is the author of Figs. 1, 2a, c and d, while the photo used in Fig. 2b was taken by N.J.C.; M.M.-G. photographed all the general and close-up views of the faunal remains included in Figs. 3, 4, 5, and in the Supplementary Information section (but see Acknowledgments). Finally, M.M.-G. wrote the original manuscript, and all the authors contributed to the review and editing of the paper.

Funding

Open Access funding enabled and organized by Projekt DEAL.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-023-45974-8.

Correspondence and requests for materials should be addressed to M.M.-G.

SUPPLEMENTARY INFORMATION

Evidence of diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros)

Mario Mata-González[1,2*], Britt M. Starkovich[1,3], Mohsen Zeidi[3,4], and Nicholas J. Conard[1,3,4]

[1]Institute for Archaeological Sciences, University of Tübingen, Hölderlinstr. 12, 72074 Tübingen, Germany

[2]Department of Anthropology, University of Connecticut, Unit 1176, 354 Mansfield Road, Storrs, CT, 06269, USA.

[3]Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstr. 12, 72074 Tübingen, Germany

[4]Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Schloss Hohentübingen, D-72070 Tübingen, Germany

*Corresponding author:

E-mail address: mario.mata-gonzalez@student.uni-tuebingen.de

Table S1. Ghar-e Boof. Summary of available stratigraphic information, including sedimentological characteristics, thickness, dating and cultural affiliations by archaeological horizon (AH). Table from Blanco-Lapaz et al.[1] and references therein.

AH	Sedimentological characteristics	Thickness	Dates (yr. BP)	Cultural affiliations
I	Mixed, gray, ashy silts of the surface and subsurface	5 to 20 cm	-	Historical periods (Late Sassanid and Early Islamic)
II	In-situ laminated ashy silt layers of black, red, orange, yellow, gray, white and various brown hues	100 cm		
IIa	Dark brown/gray ashy silts	15 cm		Mainly Epipaleolithic (Zarzian), but pottery sherds still present
IIb	Medium brown ashy silts to a light, gray/brown silts. Massive geogenic layer (IIb.1) of limestone cobles located at the bottom of this AH	10 cm	1,225-1,260 cal.	
III	Homogenous light gray to yellow-brown ashy silts, similar to loess. Ample lateral variation	10 to 70 cm	35,152 ± 368 cal.	Early UP (Rostamian)
IIIa	Medium brown ashy silts	20 cm	-	
IIIb	Light brown ashy silts with alternating gray-black, white-brown, and light brown silts	60 cm	38,994 ± 1419 cal. 39,949 ± 921 cal.	
IIIc	Light brown silts, starting with an irregular cemented crust	20 cm	-	
IV	Light brown silts with small angular fragments of limestone	25 cm	41,355 ± 326 cal.	
IVa	Brown silts with small angular fragments of limestone	15 cm	40 – 42 k	
IVb	Light brown silts, but less rocky than IV and IVa	15 cm	-	
IVc	Fine rocky brown silts	10 cm	-	MP – UP Transition (?)
IVd	Fine rocky light brown silts	15 cm	45 – 48 k	
V	Light brown but less rocky silts, underlaid by a thin dark brown band and then by a medium brown silty sediment	40 cm	46 – 50 k	MP
Va	Mostly light brown silty matrix with many small sharp-edged pieces of limestone, though thin bands of brown silts were observed	60 cm	51 – 55 k 55 – 59 k	
Vb	Still mostly rocky light brown silty matrix, along with red brown silts	25 cm	56 – 60 k	
Vc	Light brown silts	15 cm	59 – 64 k	
Vd	Light brown to yellow brown silts	25 cm	63 – 70 k	
VI	Homogeneous brown to gray-light yellow brown silts, with small limestone clasts, laying over the bedrock	80 cm	72 – 78 k 74 – 81 k	

Table S2. MP faunal assemblages from Ghar-e Boof. Number of identified specimens (NISP) and minimum number of individuals (MNI) by AH for each taxon or body size group.

AH	*IVc*		*IVd*		*V*		*Va*		*Vb*		*Vc*		*Vd*		*VI*		*Total*	
Taxon	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Ungulates																		
Small ungulate	0	NA*	0	NA	4	NA	17	NA	11	NA	5	NA	0	NA	15	NA	52	NA
Gazelle (*Gazella* sp.)	2	1	0	0	1	1	1	1	1	1	0	0	6	1	6	1	17	6
Small/medium ungulate	2	NA	1	NA	2	NA	9	NA	11	NA	9	NA	4	NA	16	NA	54	NA
Medium ungulate	35	NA	7	NA	52	NA	111	NA	57	NA	36	NA	16	NA	112	NA	426	NA
Sheep (*Ovis* sp.)	0	0	0	0	0	0	2	1	4	1	0	0	0	0	0	0	6	2
Wild goat (*Capra aegagrus*)	10	1	0	0	4	1	2	1	1	1	7	1	0	0	9	2	33	7
Sheep/goat (*Ovis/Capra*)	2	1	3	1	4	1	11	1	9	1	23	2	1	1	26	1	79	9
Medium/large ungulate	0	NA	2	NA	0	NA	4	NA	0	NA	0	NA	1	NA	3	NA	10	NA
Large ungulate	3	NA	0	NA	3	NA	10	NA	2	NA	2	NA	0	NA	2	NA	22	NA
Red deer (*Cervus elaphus*)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Wild pig (*Sus scrofa*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Equid (*Equus* sp.)	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Large/very large ungulate	1	NA	0	NA	0	NA	0	NA	0	NA	1	NA	0	NA	1	NA	3	NA
Very large ungulate	0	NA	0	NA	1	NA	1	NA	1	NA	0	NA	0	NA	0	NA	3	NA
Wild cattle (*Bos primigenius*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	1
Carnivores																		
Red fox (*Vulpes vulpes*)	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Large carnivore	0	NA	0	NA	0	NA	1	NA	0	NA	0	NA	0	NA	0	NA	1	NA
Leopard (*Panthera* cf. *pardus*)	0	0	1	1	4	1	0	0	0	0	0	0	0	0	0	0	5	2(1)**
Reptiles																		
Tortoise (*Testudo* sp.)	8	1	2	1	23	1	57	2	34	1	27	1	10	1	0	0	161	8
Birds																		
Medium birds	11	NA	0	NA	3	NA	12	NA	9	NA	6	NA	3	NA	5	NA	49	NA
Partridge (*Alectoris* cf. *chukar*)	5	2	1	1	1	1	1	1	3	1	0	0	0	0	1	1	12	7
Large birds	1	NA	0	NA	0	NA	1	NA	0	NA	0	NA	0	NA	0	NA	2	NA
Total	81	7	17	4	102	6	241	8	144	7	116	4	41	3	199	7	941	46(45)**

*NA (Not Applicable).

**Although we have documented Leopard's remains in AHs IVd and V, all of them were recovered relatively close to each other, just in the transition between these 2 layers, within an interval of 7 cm in depth. Therefore, they may belong to just 1 individual, instead of 2.

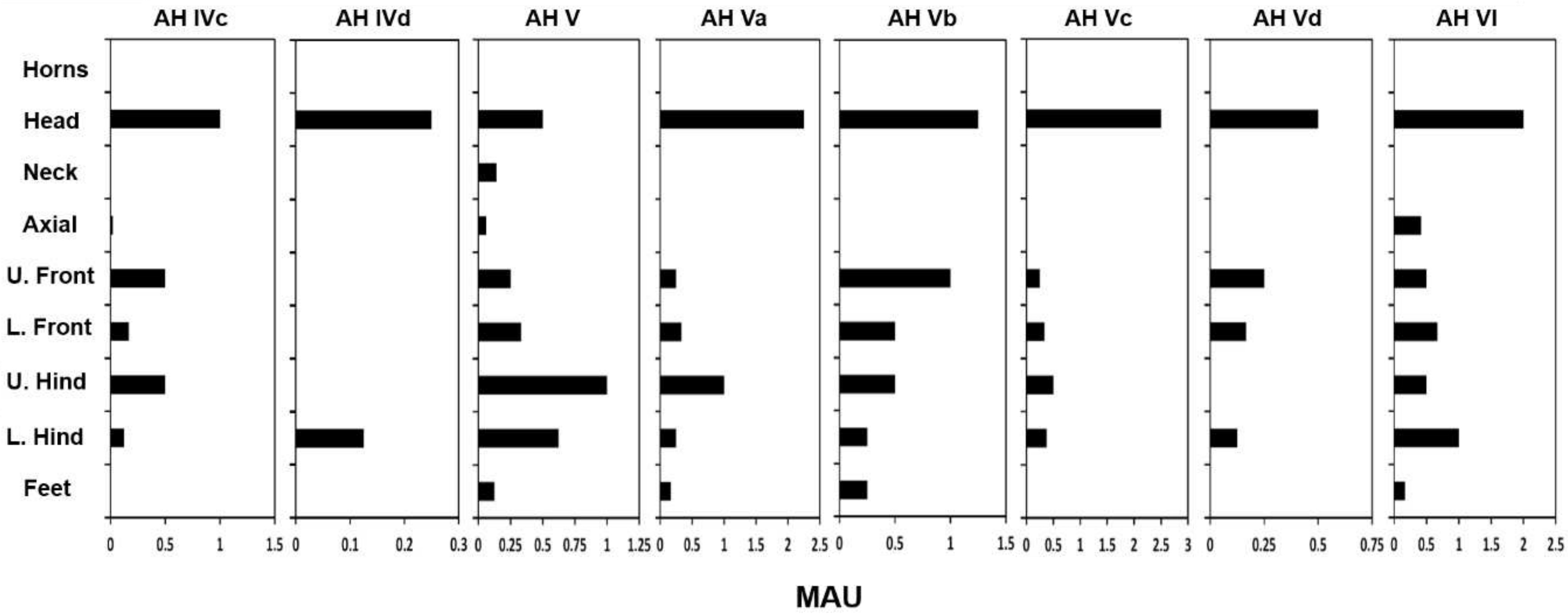


Fig. S1. MP faunal assemblages from Ghar-e Boof. MAU values for each skeletal region of caprines/medium ungulates by AH. Data from Table S4.

Table S3. MP faunal assemblages from Ghar-e Boof. NISP, MNE and MAU counts for caprine/medium ungulate skeletal elements and by AH. As a comparison, the data are presented along with a standard goat skeleton (*). Horizontal lines indicate the elements that encompasses each anatomical region.

	ST*	IVc			IVd			V			Va			Vb			Vc			Vd			VI		
Elements	MNE	NISP	MNE	MAU	NISP	MNE	MAU	NISP	MNE	MAU	NISP	MNE	MAU	NISP	MNE	MAU	NISP	MNE	MAU	NISP	MNE	MAU	NISP	MNE	MAU
Horn	2	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
1/2 Cranium	2	4	3	1.5	1	1	0.5	1	1	0.5	8	7	3.5	5	4	2.0	8	8	4.0	2	2	1.0	8	7	3.5
1/2 Mandible	2	1	1	0.5	0	0	0.0	2	1	0.5	2	2	1.0	2	1	0.5	4	2	1.0	0	0	0.0	5	1	0.5
Atlas	1	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Axis	1	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Cervical	5	0	0	0.0	0	0	0.0	1	1	0.2	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Thoracic	13	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Lumbar	6	0	0	0.0	0	0	0.0	1	1	0.17	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	1	1	0.2
Sacrum	1	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Rib	26	3	1	< 0.1	0	0	0.0	1	1	< 0.1	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	1	1	< 0.1
Innominate	2	0	0	0.0	0	0	0.0	1	1	0.5	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Scapula	2	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	1	1	0.5	0	0	0.0	0	0	0.0	0	0	0.0
Humerus	2	6	2	1.0	0	0	0.0	3	1	0.5	5	1	0.5	5	3	1.5	2	1	0.5	2	1	0.5	6	2	1.0
Radius	2	1	1	0.5	0	0	0.0	5	1	0.5	12	1	0.5	3	1	0.5	1	1	0.5	1	1	0.5	9	2	1.0
Ulna	2	0	0	0.0	0	0	0.0	3	1	0.5	2	1	0.5	2	1	0.5	1	1	0.5	0	0	0.0	4	1	0.5
Metacarpal	2	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	1	1	0.5	0	0	0.0	0	0	0.0	1	1	0.5
Femur	2	1	1	0.5	0	0	0.0	5	2	1.0	11	2	1.0	1	1	0.5	1	1	0.5	0	0	0.0	6	1	0.5
Patella	2	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Tibia	2	4	1	0.5	0	0	0.0	9	3	1.5	14	1	0.5	7	1	0.5	7	2	1.0	2	1	0.5	18	5	2.5
Astragalus	2	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0
Calcaneum	2	0	0	0.0	0	0	0.0	1	1	0.5	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	2	2	1.0
Metatarsal	2	0	0	0.0	1	1	0.5	1	1	0.5	3	1	0.5	1	1	0.5	1	1	0.5	0	0	0.0	3	1	0.5
Phalanx 1	8	0	0	0.0	0	0	0.0	3	2	0.3	1	1	0.1	4	3	0.4	0	0	0.0	0	0	0.0	4	2	0.3
Phalanx 2	8	0	0	0.0	0	0	0.0	2	1	0.1	4	3	0.4	2	2	0.3	0	0	0.0	0	0	0.0	2	2	0.3
Phalanx 3	8	0	0	0.0	0	0	0.0	0	0	0.0	2	2	0.3	1	1	0.1	0	0	0.0	0	0	0.0	0	0	0.0
Total	107	20	10	-	2	2	-	39	19	-	64	22	-	35	21	-	25	17	-	7	5	-	70	29	-

Table S4. MP faunal assemblages from Ghar-e Boof. NISP, MNE, MAU and %MAU for caprines/medium ungulates by element (for a more robust sample, we combined all the MP AHs), alongside MNEs for a standard goat skeleton (ST goat), Foot Utility Index (FUI; from[2]), standard Food Utility Index (sFUI; from[3]), Marrow Index (MI; from[2]), and Unsaturated Marrow Index (UMI; from[4]).

Elements	MNE ST Goat	NISP	MNE	MAU	%MAU	FUI	sFUI*	MI	UMI
Horn	2	0	0	0.0	0.0	NA**	1.0	NA	NA
Cranium***	2	37	33	16.5	100.0	25.3	9.1	NA	NA
Hemimandible	2	16	8	4.0	24.2	NA	31.1	NA	NA
Atlas	1	0	0	0.0	0.0	9.1	10.2	0.0	NA
Axis	1	0	0	0.0	0.0	9.1	10.2	0.0	NA
Cervical	5	1	1	0.2	1.2	38.6	37.1	0.0	NA
Thoracic	13	0	0	0.0	0.0	47.4	47.3	0.0	NA
Lumbar	6	2	2	0.3	1.8	45.1	33.1	0.0	NA
Sacrum	1	0	0	0.0	0.0	NA	NA	NA	NA
Rib	26	5	3	0.1	0.6	62.3	51.6	0.0	NA
Sternum	1	0	0	0.0	0.0	32.4	66.6	0.0	NA
Innominate	2	1	1	0.5	3.0	34.7	49.3	3.9	NA
Scapula	2	1	1	0.5	3.0	27.5	44.7	1.3	NA
Humerus	2	29	11	5.5	33.3	27.5	40.8	79.8	22.8
Radius	2	32	8	4.0	24.2	19.2	23.0	58.9	26.3
Ulna	2	12	5	2.5	15.2	NA	NA	NA	NA
Metacarpal	2	2	2	1.0	6.1	6.5	8.1	17.3	19.6
Carpals	12	3	3	0.3	1.8	10.7	12.7	0.0	0.9
Femur	2	25	8	4.0	24.2	100.0	100.0	87.0	34.0
Patella	2	0	0	0.0	0.0	NA	NA	NA	NA
Tibia	2	61	14	7.0	42.4	57.7	53.5	100.0	51.1
Astragalus	2	0	0	0.0	0.0	30.0	27.7	0.0	0.9
Calcaneum	2	3	3	1.5	9.1	30.0	27.7	0.0	2.6
Metatarsal	2	10	6	3.0	18.2	16.1	17.5	21.1	46.5
Tarsals	8	1	1	0.1	0.6	30.0	27.7	0.0	0.9
Phalanx 1	8	12	8	1.0	6.1	8.8	8.6	3.5	3.7
Phalanx 2	8	10	8	1.0	6.1	8.8	8.6	3.5	1.8
Phalanx 3	8	3	3	0.4	2.4	8.8	8.6	3.5	0.9

*We evaluated long bones as whole elements, so for sFUI we averaged the values provided by Metcalfe and Jones[3] for distal and medial epiphyses.

**NA (Not Applicable).

***MNE values for crania were also estimated for both left and right sides separately, and that is why the "cranium" of a standard goat skeleton has "2 MNEs".

Table S5. Ghar-e Boof. Spearman's rank-order correlation values for the relationship %MAU and utility indices. Data from Table S4.

Utility indices	*n*	r_s	*p*
FUI	23	-0.070	0.751
sFUI	25	0.053	0.803
MI	22	0.864	< 0.001*
UMI	13	0.906	< 0.001*

*Asterisks indicate statistically significant correlations.

Table S6. Middle Paleolithic faunal assemblages of Ghar-e Boof. Ratios between ungulate tooth and bone-based MNE by AH. All ungulate taxa are included for a more robust dataset.

AH	Tooth MNE	Bone MNE	Tooth:bone MNE
IVc	2	4	0.5
IVd	1	1	1.0
V	1	1	1.0
Va	1	10	0.1
Vb	2	9	0.2
Vc	3	10	0.3
Vd	1	2	0.5
VI	3	9	0.3

Table S7. MP faunal assemblages from Ghar-e Boof. Frequencies of sedimentological alterations, weathering damage and gnawing documented on faunal specimens by AH.

AH	*IVc*		*IVd*		*V*		*Va*		*Vb*		*Vc*		*Vd*		*VI*		*Total*	
Type of damage	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Sedimentological alterations																		
None	58	71.6	16	94.1	63	61.8	185	76.8	109	75.7	66	56.9	32	78.1	196	98.5	725	77.1
Sediment concretions	23	28.4	1	5.9	39	38.2	55	22.8	33	22.9	36	31.0	9	22.0	3	1.5	199	21.2
Sediment Crushing	1	1.2	0	0.0	0	0.0	1	0.4	2	1.4	14	12.1	0	0.0	0	0.0	18	1.9
Total	81	100.0	17	100.0	102	100.0	241	100.0	144	100.0	116	100.0	41	100.0	199	100.0	941	100.0
Weathering*																		
None	32	44.4	6	40.0	62	64.6	157	69.5	87	65.4	70	77.8	30	90.9	95	56.6	539	64.7
Fine linear cracks	0	0.0	0	0.0	0	0.0	4	1.8	0	0.0	2	2.2	0	0.0	3	1.8	9	1.1
Fine cracks, some "open"	0	0.0	0	0.0	3	3.1	3	1.3	2	1.5	0	0.0	0	0.0	4	2.4	12	1.4
Chemical weathering	39	54.2	8	53.3	32	33.3	63	27.9	44	33.1	18	20.0	3	9.1	68	40.5	275	33.0
Root etching	2	2.8	2	13.3	2	2.1	0	0.0	1	0.8	0	0.0	0	0.0	2	1.2	9	1.1
Total	72	100.0	15	100.0	96	100.0	226	100.0	133	100.0	90	100.0	33	100.0	168	100.0	833	100.0
Gnawing*																		
None	68	94.4	13	86.7	79	82.3	221	97.8	131	98.5	88	97.8	33	100.0	153	91.1	786	94.4
Carnivore bite marks	1	1.4	0	0.0	3	3.1	0	0.0	0	0.0	0	0.0	0	0.0	6	3.6	10	1.2
Potential carnivore bite marks	1	1.4	0	0.0	3	3.1	2	0.9	1	0.7	0	0.0	0	0.0	5	3.0	12	1.4
Rodent gnawing	2	2.7	2	13.3	12	112.5	3	1.3	1	0.7	1	1.1	0	0.0	4	2.4	25	3.0
Potential rodent gnawing	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	1.1	0	0.0	1	0.6	2	0.2
Possibly digested	0	0.0	0	0.0	0	0.0	0	0.0	1	0.7	0	0.0	0	0.0	0	0.0	1	0.1
Total	72	100.0	15	100.0	96	100.0	226	100.0	133	100.0	90	100.0	33	100.0	168	100.0	833	100.0

*Tooth elements are excluded from these analyses.

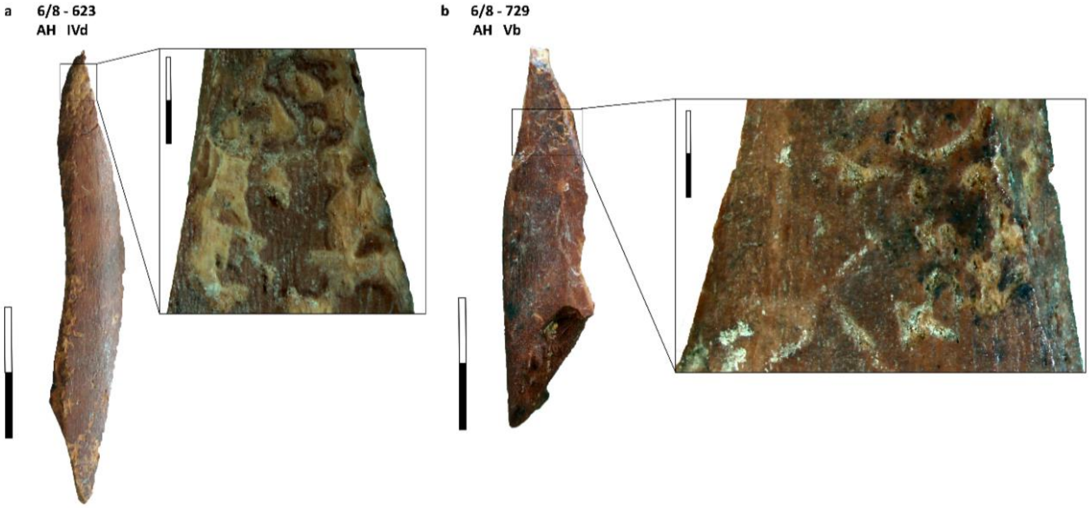


Fig. S2. MP faunal remains from Ghar-e Boof exhibiting chemical weathering: a) medium-bodied ungulate long bone shaft fragment; and b) medium ungulate tibia. Scale: general view = 10 mm; closer-up view = 2 mm.

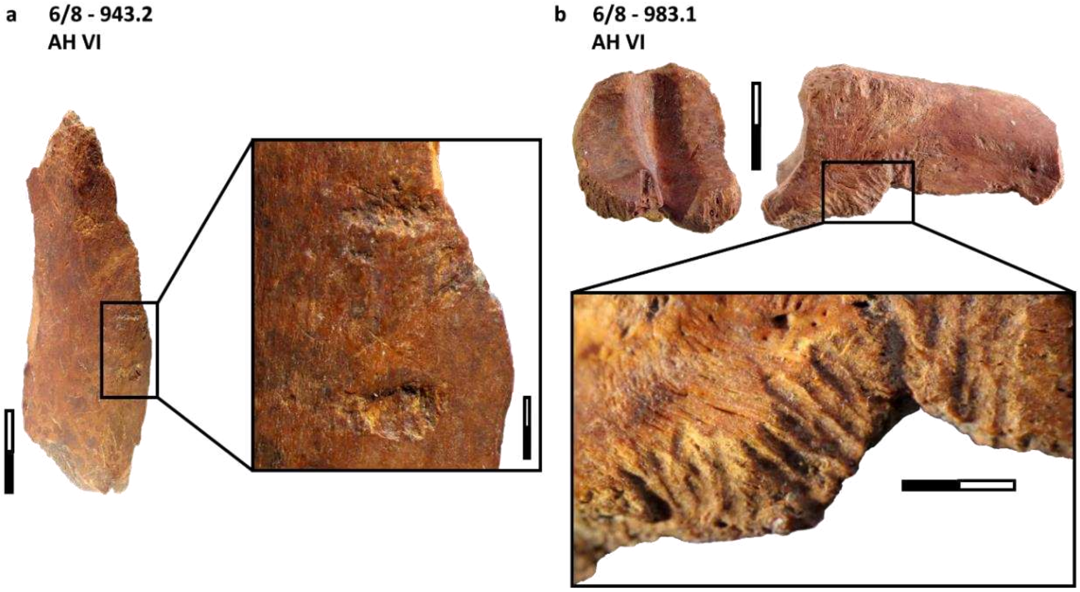


Fig. S3. MP faunal remains from Ghar-e Boof: a) medium-bodied ungulate long bone shaft fragment with carnivore bite marks; b) wild goat first phalanx with rodent gnawing. Scale: general view = 10 mm; closer-up view = 2 mm.

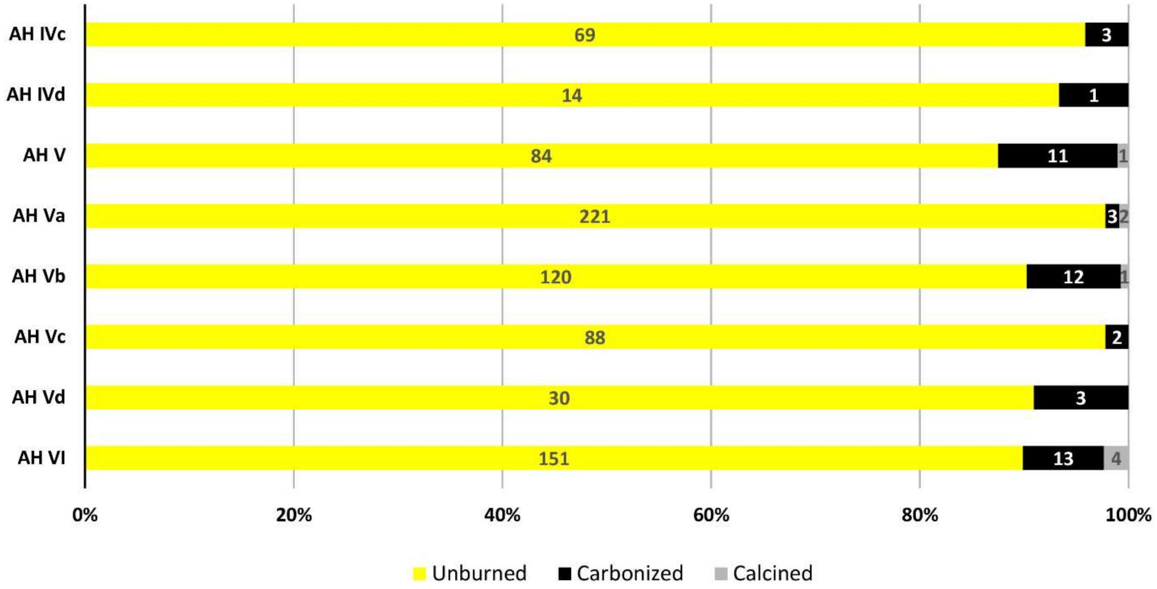


Fig. S4. MP faunal assemblages from Ghar-e Boof. NISP count and %NISP of unburned and burned (carbonized/calcined) bones by AH.

Table S8. MP faunal assemblages from Ghar-e Boof. Butchery damage on faunal specimens by AH. Tooth remains are excluded.

Butchery damage	*IVc*		*IVd*		*V*		*Va*		*Vb*		*Vc*		*Vd*		*VI*		*Total*	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Impact damage	8	11.1	1	6.7	3	3.1	16	7.1	8	6.0	9	10.0	6	18.2	20	11.9	71	8.5
Potential impact damage	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	6.1	1	0.6	3	0.4
Transverse fracture	6	8.3	0	0.0	8	8.3	10	4.4	14	10.5	5	5.6	0	0.0	11	6.6	54	6.5
Split/spiral fracture	26	36.1	8	53.3	33	34.4	98	43.4	47	35.3	35	38.9	10	30.3	89	53.0	346	41.5
Cut marks	6	8.3	4	26.7	19	19.8	48	21.2	21	15.8	11	12.2	4	12.1	57	33.9	170	20.7
Potential cut marks	0	0.0	0	0.0	0	0.0	0	0.0	1	0.8	1	1.1	1	3.0	3	1.8	6	0.7
Bone tools	1	1.4	0	0.0	0	0.0	2	0.9	2	1.5	0	0.0	0	0.0	1	0.6	6	0.7
Potential bone tools	0	0.0	0	0.0	1	1.0	3	1.3	0	0.0	0	0.0	0	0.0	2	1.2	6	0.7
Total	72	100.0	15	100.0	96	100.0	226	100.0	133	100.0	90	100.0	33	100.0	168	100.0	833	100.0

Table S9. MP ungulate remains (NISP) from Ghar-e Boof. NISP values, and specimens with cut marks (CMs) and percussion (P) damage (N) by element and body size groups (all MP layers combined). In order to provide a more robust sample, the relative proportions (%) of anthropogenic modifications by element are shown only for all the ungulate remains combined, including specimens assigned to intermediate categories (e.g., small/medium ungulate). Tooth specimens are excluded.

	Small ungulate			**Medium ungulate**			**Large ungulate**			**Very-large ungulates**			**Total**				
Elements	NISP	CMs	P	NISP	CMs	P	NISP	CMs	P	NISP	CMs	P	NISP	CMs	%	P	%
Cranial																	
Horn	1	0	0	0	0	0	0	0	0	0	0	0	4	0	0.0	0	0.0
Cranium	4	0	0	37	1	0	0	0	0	0	0	0	52	3	5.8	0	0.0
Mandible	2	1	1	20	3	0	0	0	0	1	0	0	27	5	18.5	1	3.7
Hyoid	0	0	0	1	0	0	1	0	0	0	0	0	2	0	0.0	0	0.0
Subtotal	7	1	1	58	4	0	1	0	0	1	0	0	85	8	9.4	1	1.2
Axial																	
Atlas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0	0.0
Axis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0	0.0
Cervical vertebra	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0.0	0	0.0
Thoracic vertebra	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0.0	0	0.0
Lumbar vertebra	0	0	0	2	0	0	0	0	0	0	0	0	3	0	0.0	0	0.0
Rib	2	1	0	4	0	0	1	0	0	0	0	0	11	3	27.3	0	0.0
Innominate	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0.0	0	0.0
Subtotal	2	1	0	8	0	0	1	0	0	0	0	0	19	3	15.8	0	0.0
Appendicular																	
Scapula	0	0	0	1	1	0	0	0	0	1	0	1	2	1	50.0	1	50.0
Humerus	3	1	1	29	6	3	0	0	0	0	0	0	33	8	24.2	5	15.6
Radius	4	2	0	32	9	4	1	1	0	0	0	0	38	12	31.6	4	10.5
Ulna	0	0	0	12	1	0	0	0	0	0	0	0	12	1	8.3	0	0.0
Carpals	0	0	0	3	0	0	0	0	0	0	0	0	4	0	0.0	0	0.0
Metacarpal	3	0	0	2	1	0	0	0	0	0	0	0	5	1	20.0	0	0.0
Femur	4	2	1	24	9	3	0	0	0	1	1	1	29	12	41.4	5	17.9
Patella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0	0.0
Tibia	2	1	0	61	16	10	3	1	1	1	0	1	69	18	26.1	13	18.8
Tarsals	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0.0	0	0.0
Astragalus	0	0	0	2	1	0	0	0	0	0	0	0	2	1	50.0	0	0.0
Calcaneus	0	0	0	1	1	0	0	0	0	0	0	0	1	1	100.0	0	0.0
Metatarsal	2	0	1	10	2	3	0	0	0	0	0	0	13	2	15.4	4	30.8
Subtotal	18	6	3	178	47	23	4	2	1	3	1	3	209	57	27.3	32	15.3

Table S9. Continued.

	Small ungulate			**Medium ungulate**			**Large ungulate**			**Very-large ungulates**			**Total**				
Elements	NISP	CMs	P	NISP	CMs	P	NISP	CMs	P	NISP	CMs	P	NISP	CMs	%	P	%
Feet																	
Sesamoid	2	0	0	25	0	0	0	0	0	0	0	0	28	0	0.0	0	0.0
First phalanx	4	0	0	12	1	0	1	0	0	0	0	0	17	1	5.9	0	0.0
Second phalanx	3	1	0	10	4	0	0	0	0	0	0	0	14	5	35.7	0	0.0
Third phalanx	1	0	0	3	0	0	0	0	0	0	0	0	4	0	0.0	0	0.0
Subtotal	10	1	0	50	5	0	1	0	0	0	0	0	63	6	9.5	0	0.0
Others																	
Unknown long bone	17	12	1	139	60	27	15	4	3	1	0	0	185	80	43.2	33	17.8
Flat bone	0	0	0	2	0	0	1	0	0	0	0	0	6	1	16.7	0	0.0
Unknown vertebra	0	0	0	3	0	0	0	0	0	0	0	0	4	0	0.0	0	0.0
Unknown carpal/ tarsal	0	0	0	1	1	0	0	0	0	0	0	0	1	1	100.0	0	0.0
Unknown metapodial	6	2	0	19	4	1	0	0	0	0	0	0	30	7	23.3	1	3.3
Unknown phalanx	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0.0	0	0.0
Subtotal	23	14	1	165	65	28	16	4	3	1	0	0	228	89	39.0	34	14.9
Total	60	23	5	459	121	51	23	6	4	5	1	3	604	163	27.0	67	11.1

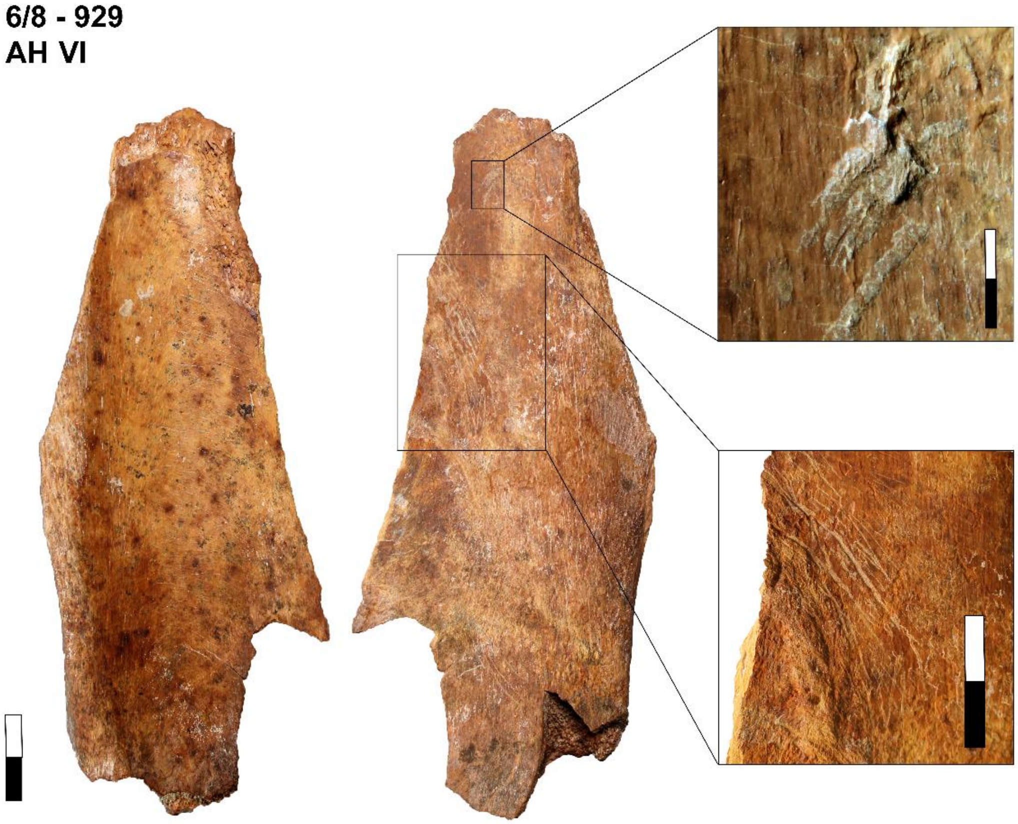


Fig. S5. Scapula of an aurochs recovered from the MP sequence of Ghar-e Boof, which has a percussion impact and longitudinal scraping. Scale: general view = 20 mm; closer-up view = 2 mm.

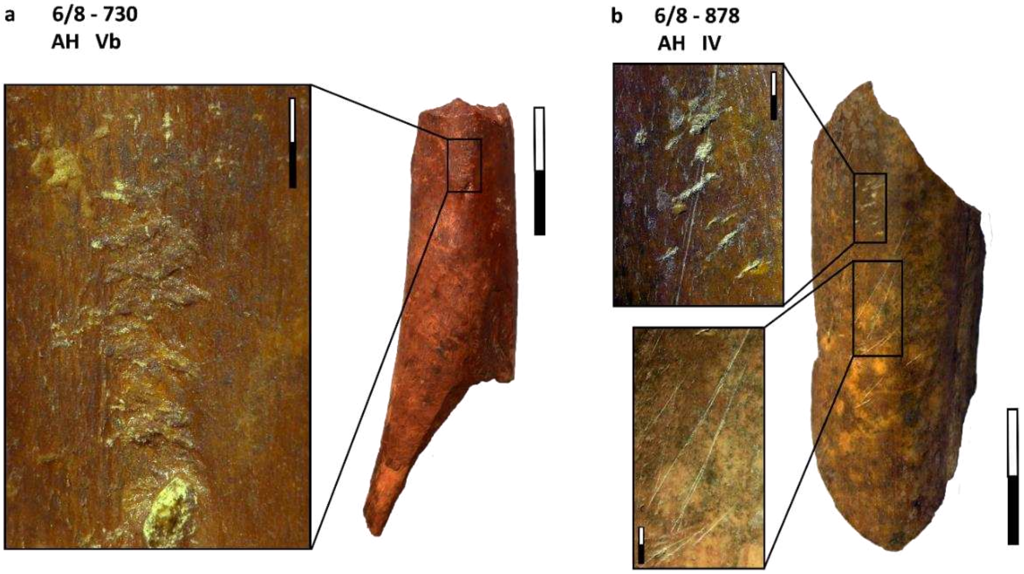


Fig. S6. Bone retouchers from the MP sequence of Ghar-e Boof: a) medium ungulate humerus with retouching marks; and B) medium ungulate femur with cut marks/scraping and retouching marks. Scale: general view = 10 mm; closer-up view = 2 mm.

Table S10. MP carnivore and small game remains from Ghar-e Boof. Skeletal elements (data in NISP) by taxon or body size group (all layers combined)

Elements	**Carnivores**			**Tortoise**	**Birds**			**Total**
	Red fox (Vulpes vulpes)	Large carnivore	Leopard (*Panthera* cf. *pardus*)	Tortoise (*Testudo* sp.)	Medium birds	Partridge (*Alectoris* cf. *chukar*)	Large birds	Total
Cranial								
Cranium	0	0	0	0	3	0	0	3
Indet. canine	0	1	0	NA*	NA*	NA*	NA*	1
Upper molar	1	0	0	NA*	NA*	NA*	NA*	1
Subtotal	1	1	0	0	3	0	0	5
Axial								
Axis	0	0	0	0	1	0	0	1
Cervical vertebra	0	0	0	0	3	0	0	3
Thoracic vertebra	0	0	0	0	1	0	0	1
Pelvic girdle	0	0	0	1	2	0	0	3
Furculum	NA*	NA*	NA*	NA*	2	0	0	2
Subtotal	0	0	0	1	9	0	0	10
Appendicular								
Coracoid	NA*	NA*	NA*	1	1	1	0	3
Scapula	0	0	0	1	1	0	0	2
Humerus	0	0	0	5	1	2	0	8
Radius	0	0	1	0	1	1	0	3
Ulna	0	0	0	0	2	1	0	3
Carpometacarpus	NA*	NA*	NA*	NA*	3	1	0	4
Femur	0	0	0	2	3	1	0	6
Tibia	0	0	0	2	NA*	NA*	NA*	2
Tibiotarsus	NA*	NA*	NA*	NA*	5	4	1	10
Fibula	0	0	0	0	1	0	0	1
Tarsometatarsus	NA*	NA*	NA*	NA*	4	1	0	5
Indet. long bone	0	0	0	1	2	0	0	3
Subtotal	0	0	1	12	433	12	1	50
Phalanges								
1st phalanx	0	0	3	0	11	0	0	14
2nd phalanx	0	0	1	0	0	0	1	2
3rd phalanx	0	0	0	0	1	0	0	1
Subtotal	0	0	4	0	12	0	1	17
Shell fragments								
Carapace & Plastron	NA*	NA*	NA*	148	NA*	NA*	NA*	148
Others								
Unknown	0	0	0	0	1	0	0	1
Total	1	1	5	161	49	12	2	231

NA* (Not Applicable).

References:

1. Blanco-Lapaz, A., Mata-González, M., Starkovich, B. M., Zeidi, M. & Conard, N. J. Late Pleistocene environments in the southern Zagros of Iran and their implications for human evolution. *Archaeol. Anthropol. Sci.* **14,** 161; https://doi.org/10.1007/s12520-022-01615-1 (2022).

2. Emerson, A. M. The role of body part utility in small-scale hunting under two strategies of carcass recovery in *From Bones to Behavior. Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains* (ed. Hudson, J.) 138–155 (Center for Archaeological Investigation. Southern Illinois University, 1993).

3. Metcalfe, D. & Jones, K. T. A reconsideration of animal body-part utility indices. *Am. Antiq.* **53,** 486–504; https://doi.org/10.2307/281213 (1988).

4. Morin, E. Fat composition and Nunamiut decision-making: a new look at the marrow and bone grease indices. *J. Archaeol. Sci.* **34,** 69–82; https://doi.org/10.1016/j.jas.2006.03.015 (2007).

APPENDIX 4

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J. Prey choice and changes in site occupation intensity during the Middle and early Upper Paleolithic at Ghar-e Boof (southern Zagros Mountains, Iran).

(Manuscript ready for submission to Archaeol. Anthropol. Sci.)

Prey choice and changes in site occupation intensity during the Middle and Upper Paleolithic at Ghar-e Boof (southern Zagros Mountains, Iran)

Mario Mata-González[a,*], Britt M. Starkovich[a,b], Mohsen Zeidi[b,c], and Nicholas J. Conard[a,b,c]

[a]Institute for Archaeological Sciences, University of Tübingen, Hölderlinstr. 12, 72074 Tübingen, Germany

[b]Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstr. 12, 72074 Tübingen, Germany

[c]Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Schloss Hohentübingen, D-72070 Tübingen, Germany

*Corresponding author:

E-mail address: mario.mata-gonzalez@student.uni-tuebingen.de

Abstract

Ghar-e Boof represents an exceptional Paleolithic site in the southern Zagros Mountains. Due to its long and undisturbed Late Pleistocene sequence that spans from around 81,000 to 35,000 years ago, the site offers a unique opportunity to investigate long-term hominin behavioral shifts on a local scale. In this paper, we examine diachronic trends in prey choice and site occupation intensity during the Middle Paleolithic (MP) through the early Upper Paleolithic (UP) at Ghar-e Boof as determined from zooarchaeological data, find densities, accumulation rates, and frequencies of retouched tools. To better understand foraging conditions, variations (or the lack thereof) in species representation and relative abundances are analyzed following the prey choice model of optimal foraging theory. Based on energetic return rates and procurement costs, we distinguish between high-ranked (large and small, slow-moving game) and low-ranked (small-bodied or small, fast-moving game) resources. The occupants of Ghar-e Boof preferentially hunted large game during the MP and early UP and relied on caprines as the main source of meat and marrow. However, there is an increase in the exploitation of fast-moving animals, mostly partridges, relative to small, slow-moving tortoises through the sequence. In addition, site occupation intensity also increased with time. A more intense use of Ghar-e Boof during the early UP may reflect larger groups of people living at the site, more frequent visits, longer periods of occupation, or some, if not all, of these possibilities combined. The increased economic importance of lower-ranked prey does not appear to track major environmental or climatic changes, and most likely is tied to higher hunting pressures. Thus, the archaeological record of Ghar-e Boof is currently the only example in the Zagros that illustrates the complex interactions between demography, site use, and socioeconomic decisions during the Late Pleistocene, a crucial time period in human evolution.

Keywords: Middle to early Upper Paleolithic; Zagros Mountains; Zooarchaeology; Prey choice model; Occupation intensity; Paleodemography.

1. Introduction

Occupation intensity refers to the length of stay, frequency of visits, and number of people living at a given site (Munro, 2004; Stiner et al., 2012). All these variables strongly depend on human population size or density, and different proxy measures of site occupation intensity are commonly used in studies of Paleolithic demography (French, 2015). Population size is among the proposed drivers of some of the major evolutionary events that occurred in Eurasia during the Late Pleistocene, such as the Neanderthals' extinction (Vaesen et al., 2021), the appearance of cultural innovations, and increased technological complexity (Shennan, 2001; Powell et al., 2009). Over the last two decades, archaeologists have documented an increase in occupation intensity at numerous Eurasian sites across the MP to UP transition and throughout the early/initial UP (i.e., Grayson and Delpech, 2003; Münzel and Conard, 2004; Kuhn et al., 2009; Marín-Arroyo, 2011; Mellars and French, 2011, Conard et al., 2012; Starkovich, 2017; Yeshurun et al., 2019; Smith et al., 2021; Real and Villaverde, 2022). There are also some deviations from this pattern (e.g., Morin, 2008), and some authors have even questioned the methods and assumptions applied to the analysis of site occupation intensity as a 'paleodemographic barometer' (Dogandžić and McPherron, 2013; French, 2015). Yet the available evidence for changes in occupation intensity between the MP to UP and across the early/initial UP points to either more recurrent visits, longer stays on site and less mobility, larger population densities, or even a combination of some or all of these factors (Grayson and Delpech, 2003; Münzel and Conard, 2004; Kuhn et al., 2009; Marín-Arroyo, 2011; Mellars and French, 2011; Conard et al., 2012; Starkovich, 2017; Smith et al., 2021; Yeshurun et al., 2021; Real and Villaverde, 2022).

From a zooarchaeological standpoint, occupation intensity and population pressure are key aspects to consider when investigating Paleolithic diets and subsistence patterns, alongside many other variables, both internal and external, such as climatic and environmental constraints, and technological, cultural, and social adaptations. All else held constant, the human pressure on the local food resources would be greater as site occupation intensity increases (Stiner and Munro, 2002; Munro, 2004). In many regions of Eurasia, zooarchaeological data indicate changes in prey choice and resource intensification during the Late Pleistocene (Stiner et al., 1999, 2000; Stiner and Munro, 2002, 2011; Speth and Clark, 2006; Stiner, 2009; Kuhn et al., 2009; Starkovich, 2012, 2014, 2017; Fernández-López de Pablo et al., 2014; Baumann et al., 2020; Romandini et al., 2020; Yeshurun et al., 2021), which has generally been attributed to higher hunting pressures and population growth. Alternatively, some researchers have also found evidence for shifts in prey selection related to climatic fluctuations (Discamps et al., 2011), sites that show either no signs of intensification (Morin, 2012; Yravedra-Sainz de los Terreros et al., 2016) or just marginal changes in the way certain prey were used (e.g., birds, Laroulandie et al., 2020), early exploitation of small, fast-moving game during the MP (Blasco et al., 2022), and intensified processing of ungulate carcasses without any apparent modifications in diet breadth during the UP (Manne et al., 2012; Manne, 2014). Moreover, the increased use of birds and small carnivores since the early/initial UP onwards could also be associated with the adoption of new technological developments, for example, traps, nets, or snares (Baumann et al., 2020; Bertacchi et al., 2021), which might have allowed hunter-gatherers to lower their procurement and pursuit costs (Morin et al., 2020, 2022). These contributions, therefore, highlight the importance of evaluating overarching behavioral and demographic shifts, while taking into account the unique characteristics of each Paleolithic site within its local and regional contexts. Unfortunately, there are still vast regions for which we currently do not have such data, such as the Zagros Mountains.

The river valleys of the Zagros Mountains most likely served as major biogeographical corridors for Pleistocene hominin groups to travel across Eurasia (Vahdati Nasab et al. 2013; Shoaee et al. 2021). Some areas of the region also present high environmental diversity and a very heterogeneous topography (Heydari-Guran, 2014), which might have provided past hunter-gatherers access to different and numerous animal and plant resources. Since the early twentieth century, scholars have demonstrated the archaeological potential of the Zagros Mountains for understanding Paleolithic lifeways and cultural traditions (Garrod, 1930, 1957; Coon, 1951; Field, 1951; Solecki, 1958, 1963; Braidwood and Howe, 1960, Young and Smith, 1966; Hole and

Flannery, 1967; Piperno, 1972, 1974; Ikeda, 1979; Rosenberg, 1979, 1985). However, the Paleolithic record of the region has been historically understudied in comparison to other parts of southwestern Asia, such as the Levant. During the last two decades, Paleolithic research has prospered substantially in the Zagros, and both national and international archaeologists have not only revisited previously excavated sites (i.e., Yafteh Cave, Otte et al., 2007; Gar Arjeneh, Bazgir et al., 2014; Shanidar Cave, Reynolds et al., 2016), but also dug newly discovered ones, for example, Ghar-e Boof (Conard et al., 2007; Conard and Zeidi, 2019; Zeidi and Conard, 2019), Kaldar Cave (Bazgir et al., 2014, 2017), and Gelimgoush Cave (Heydari-Guran et al., 2021a), among others. These recent investigations and ongoing projects are facilitating the incorporation of the Zagros Mountains within the broader body of knowledge and existing debates on the bio-cultural transition that took place during the MP and UP across Eurasia (e.g., Goder-Goldberger and Malinsky-Buller, 2022).

In southern Zagros (Fig. 1), excavations at Ghar-e Boof have revealed what is currently the longest and most important Paleolithic sequence in the region, spanning from ca. 81 to 35 ka (Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017; Heydari et al., 2021). The rich archaeological record of this cave includes MP and early UP Rostamian lithic assemblages (Conard and Ghasidian, 2011; Ghasidian, 2014; Ghasidian et al., 2017; Bretzke and Conard, 2017; Conard and Zeidi, 2019; Zeidi and Conard, 2019), and provides evidence for techno-cultural discontinuity between the two lithic traditions (Bretzke and Conard, 2017). As a result, researchers have proposed that the site was occupied by different hominin groups during the MP and UP (Bretzke and Conard, 2017; Heydari et al., 2021). Moreover, our previous zooarchaeological studies have focused mainly on determining the integrity and anthropogenic origin of the faunal remains from Ghar-e Boof, in order to reconstruct diet breadth, transport decisions, butchery strategies, and carcass processing (Mata-González et al., 2022, 2023), as well as paleoenvironmental conditions (Blanco-Lapaz et al., 2022). In Mata-González et al. (2022), we observed shifts in prey choice and occupation intensity over the early UP, suggesting larger human groups dispersed across the region and resource intensification. Yet, we do not know when these changes started or whether they go further back in time. Considering all lines of evidence together, Ghar-e Boof allows us to investigate the complex interplay of foraging conditions, economic decisions, and site use in the southern Zagros during the Late Pleistocene.

Fig. 1. Location of Ghar-e Boof (1) in the Zagros, alongside other MP and UP sites for which zooarchaeological data have been published: Eshkaft-e Gavi (2), Kunji Cave (3), Yafteh Cave (4), Kaldar Cave (5), Ghar-e Khar (6), Warwasi Rockshelter (7), Kobeh Cave (8), Gelimgoush Cave (9), Darai Rockshelter and Kenacheck Cave (10), Palegawra Cave (11), and Shanidar Cave (12).

In this paper, we evaluate for the first time diachronic trends in prey choice and site occupation intensity across the MP to early UP at Ghar-e Boof in order to better understand long-term hominin behavioral shifts on a local scale. First, we provide new data on fragmentation and burning damage to assess whether there is differential bone fragmentation between archaeological layers. Second, we use our zooarchaeological data and the prey choice model of optimal foraging theory to examine shifts in animal use over time. Third, we analyze chronological changes in site occupation intensity as determined from find densities, accumulation rates, and the frequency of retouched tools. Fourth, we explore overarching patterns in prey choice and occupation intensity through the archaeological sequence to establish how animal exploitation is related to the intensity of site use: do these trends reflect changes in demographic and hunting pressures and resource intensification? Or, instead, do they primarily track environmental and climatic fluctuations? Finally, the results are discussed in the context of demographic, technological, and paleoenvironmental shifts that occurred in the southern Zagros over the Late Pleistocene. Our study thus addresses key issues in human evolution, such as behavioral and demographic differences between MP and UP hominins, resilience to changing environments, and the role of technology in foraging efficiency.

2. Background to Ghar-e Boof

The Dasht-e Rostam region sits on the southern Zagros Mountains, at the northwestern margin of the Fars Province, Iran, and is not far from the Mesopotamian Plain and the Persian Gulf to the west (Fig. 1). It presents a heterogeneous landscape with mountains that range from 700 to 2,500 m.a.s.l., and has flat, broad and interconnected plains and valleys (Heydari-Guran, 2014). The current climate of the Dasht-e Rostam region is characterized by temperate Mediterranean-like conditions where winters are wet and cold, and summers are warm and dry (Bobek, 1968; Ganji, 1968; Heydari-Guran, 2014). The mean annual temperature is 19.4 ºC, while the total annual precipitation is 655 mm (data from the Nourabad-Mamasani weather station, https://en.climate-data.org/asia/iran/fars/nurabad-mamasani-51375/). Despite the strong seasonal variations in rainfall and aridity, the region is drained by a perennial river, known as the Fahliyan, and two other seasonal streams, the Shiv and Solak Rivers (Conard and Ghasidian, 2011; Heydari-Guran, 2014). Today, the natural vegetation of the southern Zagros is mostly steppic, with scattered shrubs and trees, such as oak (*Quercus* spp.), pistachio (*Pistacia* spp.), and almond (*Prunus amygdalus*), among others (Zohary, 1973; Heshmati, 2007). Due to the predominance of rocky and very steep terrains, large game is dominated by wild goat (*Capra aegragrus*; Karami et al., 2016). Persian gazelle (*Gazella subgutturosa*) is also relatively abundant, but it usually prefers flat plains and grasslands (Karami et al., 2016).

Ghar-e Boof (N 30.2839º, E 51.4352º) is one of the multiple caves and rockshelters in which archaeologists have documented evidence of hominin occupations in the Dasht-e Rostam region during the Late Pleistocene and the Holocene (Nowroozi, 1997; Conard et al., 2006; Zeidi et al., 2006; Conard and Ghasidian, 2011). Most sites, however, have only yielded lithic artifact assemblages recovered from the surface. Ghar-e Boof is unique in the region since it preserves well-stratified archaeological deposits due to the presence of large boulders at its entrance that sealed the sediments within the site (Conard and Ghasidian, 2011). Formed in limestone, the cave is relatively small and shallow (inside area: ca. 60 m^2; ceiling height: ca. 8 m), with its entrance oriented towards the north (Fig. 2a, Conard and Ghasidian, 2011). It is situated at an elevation of 905 m.a.s.l., about 190 m from the bottom of the plain and the Solak River, and in the Yagheh Sangar Pass. This natural corridor constitutes the narrowest point in the landscape, divides the plain in half, and most likely represented a strategic spot from where past hunter-gatherers could have a panoramic view of the region (Conard et al., 2006; Conard and Ghasidian, 2011; Heydari-Guran, 2014), access to water (Blanco-Lapaz et al., 2022), plants (Baines et al., 2014; Conard et al., 2023) and animal resources (Mata-González et al., 2022, 2023).

Led by Nicholas J. Conard and Mohsen Zeidi, the Tübingen-Iranian Stone Age Research Project (TISARP) team excavated Ghar-e Boof for the first time in 2006 and 2007 (Conard et al., 2007; Conard and Ghasidian, 2011). During these excavations, archaeologists not only recovered numerous Epipaleolithic and UP artifacts intermixed with other fragments of pottery, glass, and metal objects from Historical periods, but they also reached intact deposits that were rich in lithic artifacts and organic remains dated to the early UP (Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017). Subsequently, the TISARP team conducted two more campaigns of excavations at Ghar-e Boof in 2015 and 2017, expanding the archaeological sequence into the MP (Bretzke and Conard, 2017; Conard and Zeidi, 2019; Zeidi and Conard,

2019) and reaching bedrock at a depth of ~6 m below the modern surface (Heydari et al., 2021). The excavated area is 18 m^2 (2 x 9 m), and it runs across the north-south axis of the cave, from the back wall to its entrance, alongside the dripline (Fig. 2b., Conard and Ghasidian, 2011). In total, the stratigraphic sequence of Ghar-e Boof comprises six main archaeological horizons (AHs), which were divided into 19 sub-layers based on sedimentological characteristics (Fig. 3; Heydari et al., 2021; Blanco-Lapaz et al., 2022). 15 of them (AHs VI to III) contain undisturbed Late Pleistocene deposits that span from ~81 to 35 ka (Heydari et al., 2021).

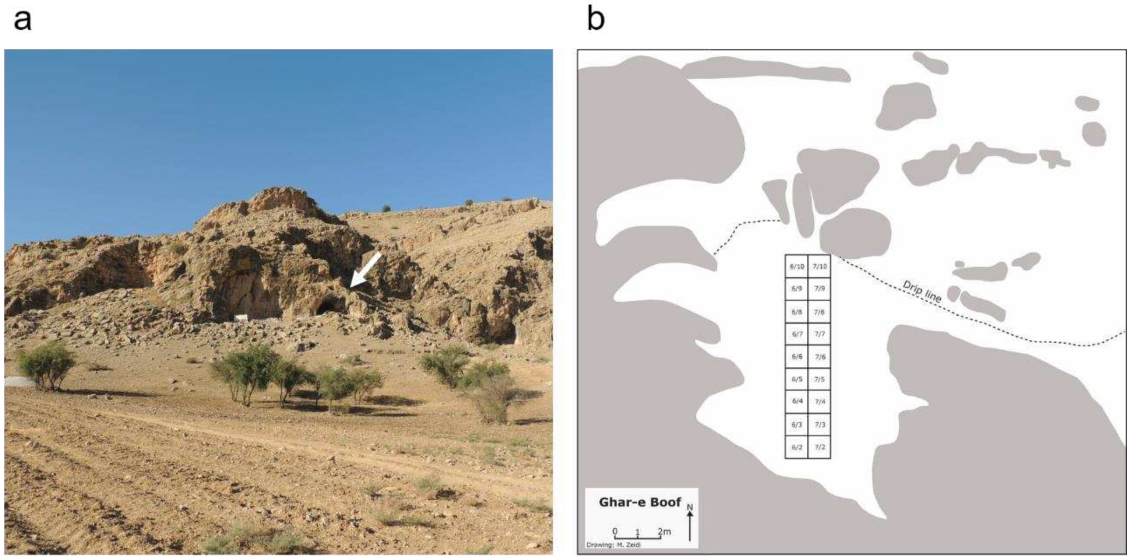


Fig 2. Ghar-e Boof: a) view of the cave's entrance (white arrow; photo by N. J. Conard, 2017); b) plan of the site and excavation area (modified from Conard and Zeidi, 2019).

Excavators have only dug the MP layers in a small area of Ghar-e Boof (quadrants 6/7, 6/8, and 7/7, Fig. 2b) so far. Overlying the bedrock, the earliest evidence of human occupations from the cave came from AH VI, dated by OSL between 81–72 ka or MIS5a/MIS4 (68% credible interval; Heydari et al., 2021). Our team also recovered MP lithic artifacts in AHs Vd to V, whose OSL chronology ranges from 70–63 ka (AH Vd) to 49–46 ka (AH V; Heydari et al., 2021). The tecno-typological analysis of the MP lithic assemblages is ongoing, but the first observations show a technology mainly centered on flake production (Bretzke and Conard, 2017). These assemblages consist of isolated lithic artifacts, which reflect incomplete knapping sequences (Conard and Zeidi, 2019). In general, our study of the small vertebrate remains recovered from

Ghar-e Boof, including rodents, insectivores, amphibians, squamate reptiles, and Passeriformes, indicates that during the MP the Dasht-e Rostam region was characterized by dry, warm conditions, and a rocky, open environment, where the vegetation cover was mostly restricted to grass and shrubs (Blanco-Lapaz et al., 2022). Nevertheless, our data also support the existence of water sources near the cave (Blanco-Lapaz et al., 2022). To date, although archaeologists have found multiple Neanderthal fossils at Late Pleistocene sites located in the central and northern Zagros Mountains, most of them in direct association with MP lithic artifacts (Solecki, 1963, 1975; Pomeroy et al., 2017, 2020; Zanolli et al., 2019; Heydari-Guran et al., 2021b; among others), no hominin remains have been recovered in the MP record of the southern Zagros. Thus, we still lack of compelling evidence to link the MP occupations at Ghat-e Boof with either Neanderthals or Anatomically Modern Humans (AMHs; Bretzke and Conard, 2017; Heydari et al., 2021).

Up next, an OSL age for AH IVd falls in the range of 48–45 ka; however, due to the low densities of artifacts, the techno-cultural attribution of both AHs IVd and IVc remains inconclusive (Heydari et al., 2021). Despite this fact, archaeologists did not record any Arjeneh points (equivalent to Font-Yves/el-Wad points, after Olszewski and Dibble, 1994) or perforated shells, which are characteristic artifacts of the UP techno-cultural assemblages documented across the Zagros region (Heydari et al., 2021). Instead, the following layers (AHs IVb to IV) have yielded both Arjeneh points and shell beads, regardless of comparable low artifact densities (Heydari et al., 2021). Based on the available evidence, Heydari et al. (2021) have suggested that AHs IVd and IVc may correspond to the MP–UP transition. The paleoenvironmental information inferred from the small vertebrate assemblages for these layers should be considered with caution since the sample size is small (Blanco-Lapaz et al., 2022). In comparison to the MP, rodents are rare in AHs IVd and IVc, and the only record of Afghan pika (*Ochotona* cf. *rufescens*) comes from AH IVc, which likely reflects lower temperatures and/or an increase in aridity (Blanco-Lapaz et al., 2022).

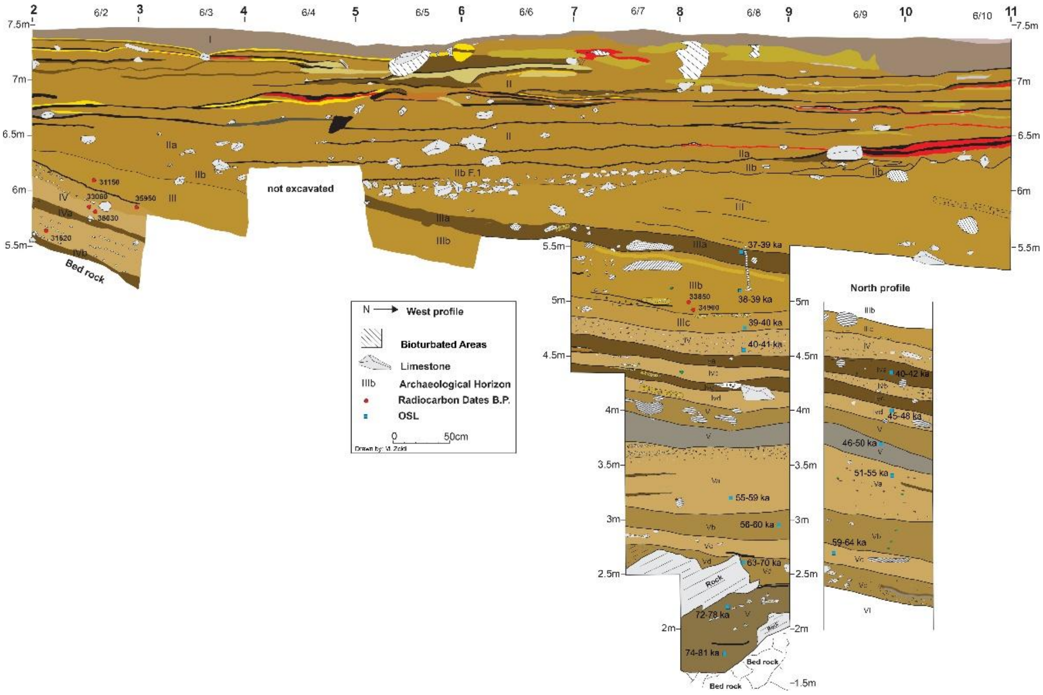


Fig. 3. Ghar-e Boof. Schematic representation of the stratigraphic sequence, based on the west profile, and part of the north (figure from Heydari et al., 2021).

Moving upwards in the archaeological sequence, the early UP starts with AH IVb and extends to AH III (Conard and Ghasidian, 2011; Conard and Zeidi, 2019). Here, the oldest dated layer is AH IVa, for which Heydari et al. (2021) provided an OSL age of 42–40 ka. In addition, a series of both OSL and radiocarbon dates place AHs IV to III at around 41–35 ka cal. BP (Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017). AHs IIIc to III were very rich in lithic artifacts, including debris derived from all stages of the reduction sequence, and comprising over 95% of the total lithic artifacts recovered at the site (Conard and Ghasidian, 2011; Conard and Zeidi, 2019). The early UP lithic assemblages from Ghar-e Boof present a high degree of homogeneity from a technological and typological perspective, and they may belong to a single cultural tradition (Ghasidian, 2014; Conard and Zeidi, 2019). Due to the unique set of characteristics of these assemblages and other surface collections from the Dasht-e Rostam region, Conard and Ghasidian (2011) defined the Rostamian cultural group. Unlike the coeval Baradostian or Zagros Aurignacian industries, which contain high proportions of burins, blades and bladelets, but with a clear focus on flake production (Solecki, 1958; Olszewski and Dibble, 1994, 2006; Tsanova, 2013, to name a few), the Rostamian technocomplexes are mainly dominated by small blade and bladelet artifacts, and unidirectional, single planform cores (Conard and Ghasidian, 2011; Ghasidian, 2014; Ghasidian et al., 2017; for a different view, see Olszewski, 2017; Shidrang, 2018). The primary raw materials used for the manufacture of lithic artifacts are radiolarian-chert gravels from local rivers (Conard and Ghasidian, 2011; Conard and Zeidi, 2019). Furthermore, our team also recorded possible combustion features and identified a few bone tools and personal ornaments, such as incised beads made from shells and at least one ungulate incisor (Conard and Ghasidian, 2011; Conard and Zeidi, 2019; Mata-González et al., 2022). During the beginning of the early Upper Paleolithic, paleoenvironmental conditions seem to have remained relatively cold and dry until ca. 40–39 ka (Blanco-Lapaz et al., 2022). In contrast, the subsequent increase in small mammal taxa points to an environmental amelioration, though the overall landscape was still slightly more open and arid during the early UP compared to the MP (Blanco-Lapaz et al., 2022). In the Zagros Mountains, archaeologists thus far have only recovered human remains from the UP deposits of Eshkaft-e Gavi (Scott and Marean, 2009), Warwasi Rockshelter (Tsanova, 2013), and Gar Arjeneh (Trinkaus, 2018), demonstrating the association of early UP laminar lithic technologies in the region with AMHs.

Besides the early UP Rostamian assemblages, at the uppermost part of AH III, our team documented presumably Zarzian (Epipaleolithic) artifacts, such as thumbnail scrapers or a small backed triangle, though their temporal and cultural attribution, as well as their stratigraphic integrity, has not yet been supported by radiocarbon dates (Conard and Zeidi, 2019). Finally, our team has evidenced to a different extent the disturbance of the upper layers of the cave (Conard and Ghasidian, 2011). AHs IIb and IIa contained mostly pieces of flint of Pleistocene age, but excavators have found a small number of pottery sherds, and two grains of barley remains that were radiocarbon dated to ~1,243 and 1,080 cal. BP respectively (Conard and Ghasidian, 2011; Baines et al., 2014; calibrated dates from Ghasidian, 2014). Likewise, flint artifacts are also present in AHs II and I, yet these layers correspond primarily to ashy silts of the surface and sub-surface related to the use of Ghar-e Boof during recent times (Conard and Ghasidian, 2011).

3. Material and methods

Regarding the excavation of the site, our team focused on digging each square meter in 50 x 50 cm sub-squares, and in over two to three cm increments that follow the natural inclination of the deposits (Conard and Zeidi, 2019). When possible, archaeological finds were piece-plotted in three dimensions with a total station, including the orientation for large and elongated artifacts or bone specimens (Conard and Zeidi, 2019). In order to ensure practically the complete recovery of organic remains and lithic artifacts and debitage, archaeologists floated all the removed sediments, and then they water-screened the heavy fractions through the use of superimposed five- and two-mm mesh (Conard and Ghasidian, 2011; Ghasidian, 2014; Conard and Zeidi, 2019; Blanco-Lapaz et al., 2022). An important challenge for the excavators working at the cave was the identification of biogalleries throughout the entire stratigraphy. In AH III, for instance, the biogalleries seem to be recent; they were either hollow voids or filled with grey homogenized silts from the AH II complex, and thus it was relatively easy to differentiate them from the undisturbed sediments (Conard and Zeidi, 2019). Moving downward in the sequence, the biogalleries were occasionally filled with sediments that were difficult to tell apart from the in-situ deposits (Conard and Zeidi, 2019). When possible, archaeologists systematically isolated and removed the content of the biogalleries from the intact sediments, yet small-scale disturbances might exist (Conard and Zeidi, 2019).

Overall, after four seasons of excavations carried out at Ghar-e Boof, the MP and early UP layers (AHs VI to III) of Ghar-e Boof produced ~18,000 liters of sediment, more than 61,000 lithic artifacts (retouched tools, cores, unmodified flakes, small and micro debitage), and 4022 identified macro-faunal specimens, 386 of which are burned (Table 1). As we did in Mata-González et al. (2022), here we exclude any identifiable specimens recovered from near the top of AH III and towards the northern part of the excavation area, since these bone remains seem to be associated with Epipaleolithic artifacts that postdate the main early UP Rostamian assemblages (Conard and Zeidi, 2019). Because of time limitations, we did not count all the unidentifiable bone fragments, though a very rough estimate of which may be over 17,000 specimens.

Table 1. Ghar-e Boof. Volume (liters) of excavated sediment, total count (N) of lithic artifacts, number of identified specimens (NISP), and burned NISP by layer.

Layer	Culture	Sediment volume (liters)	Lithic artefacts (N)	NISP	Burned NISP
AH III	Rostamian (UP)	7220	46874	1320	165
AH IIIa	Rostamian (UP)	1121	4004	287	52
AH IIIb	Rostamian (UP)	1885	5392	685	45
AH IIIc	Rostamian (UP)	770	2653	285	23
AH IV	Rostamian (UP)	743	444	169	12
AH IVa	Rostamian (UP)	709	331	233	23
AH IVb	Rostamian (UP)	506	279	102	10
AH IVc	MP-UP (?)	427	174	81	3
AH IVd	MP-UP (?)	139	21	17	1
AH V	MP	499	133	102	12
AH Va	MP	944	428	241	5
AH Vb	MP	641	175	144	13
AH Vc	MP	440	187	116	2
AH Vd	MP	515	117	41	3
AH VI	MP	1536	192	199	17
Total	-	18095	61404	4022	386

For the analysis of the animal remains from Ghar-e Boof, we followed standard zooarchaeological methods (Grayson, 1984; Stiner, 1994, 2005; Lyman, 2008; among others; for further details, see Mata-González et al., 2022, 2023). We used the comparative zooarchaeological collection from the University of Tübingen, and other zooarchaeological guides and unpublished electronic osteological atlases to identify taxonomically and anatomically the bone fragments (Mata-González et al., 2022, 2023). Our basic counting unit is the number of identified specimens (NISP), and it includes remains identified to genus or species, and those with less diagnostic features that we assigned to body size categories (e.g., small or medium ungulate). In Mata-González et al. (2022, 2023), we estimated the minimum number of individuals (MNI) by layer to facilitate regional comparisons with other Pleistocene faunal assemblages from the Zagros or southwestern Asia for which zooarchaeologists have reported MNI values; nonetheless, here our analyses of species representation and abundances are entirely based on NISP counts and relative proportions (%NISP) between different prey groups.

From a taphonomic perspective, we analyzed bone surface modifications and fracture types in order to evaluate and identify 1) the agent(s) responsible for the accumulation of the bones at the cave, and 2) post-depositional processes that might have affected the integrity and preservation of our faunal assemblages (Mata-González et al., 2022, 2023). For each specimen, we documented the presence of natural modifications (i.e., weathering, root etching, sediment concretions, chemical weathering, carnivore bite marks, or rodent gnawing), and anthropogenic damage related to butchery and bone processing activities, including cut marks, percussion impacts, burning, and green fractures (Behrensmeyer, 1978; Fisher, 1995; Lyman, 1994; Stiner et al., 1995; Fernández-Jalvo and Andrews, 2016). Our previous studies demonstrated that hominins were the primary accumulating agent at Ghar-e Boof, while carnivore remains and bite marks were very uncommon (Mata-González et al., 2022, 2023). We observed anthropogenic modifications on almost all taxa, indicating that the occupants of the site exploited to a different extent small- to very-large ungulates, tortoises, and carnivores during the MP (Mata-González et al., 2023), in addition to birds during the early UP (Mata-González et al., 2022). Although we did not find any anthropogenic modifications on bird and fish remains recovered from the MP and early UP deposits of Ghar-e Boof respectively, the absence of carnivore damage and digestion marks on those specimens means that hominins cannot be ruled out as potential accumulators (Blanco-Lapaz et al., 2022; Mata-González et al., 2023). The general preservation of our faunal assemblages is good, despite the high proportions of bones covered by sediment concretions or altered by chemical weathering, which most certainly obscured and obliterated other taphonomic modifications (Mata-González et al., 2022, 2023). Yet, we feel confident that these alterations did not have a major biasing effect on our analyses. Particularly, when possible, we removed mineral concretions from the occlusal surfaces of tooth specimens and the articular surfaces of bone ends following a systematic cleaning protocol (Mata-González et al., 2022). After removing the sediment concretions, we were able to easily provide precise taxonomic and anatomical identifications for most of the specimens that were partially or completely encased in concretions. We also assessed whether or not attritional processes or bone loss occurred at the site, and our results suggested that density-mediated attrition did not play a significant role in shaping the faunal assemblages (Mata-González et al., 2022, 2023), and thus they mostly reflect human behavioral patterns and socioeconomic decisions. However, before testing for diachronic shifts in prey choice and site occupation intensity from the MP to the early UP, further analyses are still necessary to support that temporal trends did not result from differential bone fragmentation.

3.1. Bone fragmentation

Independently of the behavioral implications of burning, such as cooking or waste disposal practices (i.e., Lyman, 1994; Asmussen, 2009), experimental and archaeological studies have indicated that thermally altered bones are more susceptible to fragmentation (Johnson, 1989; Stiner et al., 1995; Cáceres et al., 2002; Cain, 2005; Stiner, 2005; Pérez et al., 2017). Since the rate of bone identification decreases with the intensity of burning and increased fragmentation (Stiner et al., 1995), we measured the length (cm) of all identified specimens across their longest axis and compared the mean length of burned and unburned bones by layer to examine the effects of burning on fragmentation in our assemblage. Moreover, bone remains of large-bodied animals are also more affected by burning than specimens of small-bodied taxa; in other words, species with different body sizes are subject to differential fragmentation and identification (Morin, 2010). Previously, we observed that the intensity of burning and the proportion of burned specimens remain stable over the MP at Ghar-e Boof (Mata-González et al., 2023). However, even if the proportion of burned specimens scarcely changes over the UP sequence, we documented a slight increase in burning damage in the uppermost layers (AHs IIIa and III; Mata-González et al., 2022). To investigate to which extent our interpretations based on relative taxonomic abundance or prey groups might have been affected by potential changes in the intensity of burning and differential fragmentation across archaeological layers, we combine the MP and UP databases and test statistically whether or not there is a diachronic shift in the relative proportion of burned specimens throughout the stratigraphic sequence.

Besides burning, archaeologists have demonstrated that hunter-gatherers preferentially processed more intensely skeletal elements with higher marrow and grease yields, which greatly influence bone frequencies and fragmentation (e.g., Binford, 1978; Jones and Metcalfe, 1988; Lyman, 1994; Munro and Bar-Oz, 2005; Bar-Oz and Munro, 2007; Morin, 2007). At Ghar-e Boof, we also noticed that anthropogenic damage associated with marrow exploitation of ungulate bones, such as cone fractures and percussion impacts, are more common in elements with high utility values (Mata-González et al., 2022, 2023). Yet the intensity of within-bone nutrient extraction does not necessarily remain constant over time, and it could vary due to fluctuations in prey availability and environmental productivity (Burger et al., 2005; Lupo et al., 2013); for instance, in southern Europe, there is evidence for changes in the processing intensity of bones during the MP and UP (Starkovich, 2014, 2017) or simply differences in the exploitation of bone elements (Boscato and Crezzini, 2012; Romandini et al., 2020), but also very intensive processing of ungulate carcasses for fat rendering during the UP (Manne et al., 2012; Manne, 2014). We assess the possibility that the occupants of the site processed within-bone nutrients at different intensities through the MP and UP, which might have resulted in differential fragmentation and identification of ungulate specimens. As a proxy for processing intensity, we use the bone length of ungulates and compare the median length between layers.

3.2. Measures of site occupation intensity and analytical assumptions

3.2.1. Prey choice and relative abundance. We follow the prey choice or diet breadth model of optimal foraging theory (Stephens and Krebs, 1986, Pianka, 2000), which has been previously applied to similar archaeological contexts and zooarchaeological investigations in southwestern Asia and the Mediterranean Basin (e.g., Stiner et al., 1999, 2000; Stiner and Munro, 2002, 2011; Speth and Clark, 2006; Kuhn et al., 2009; Stiner, 2009; Starkovich, 2012, 2014, 2017; Yeshurun et al., 2021). Within the prey choice model, animals are ranked according to their caloric returns, after subtracting search and processing costs (Stephens and Krebs, 1986; Kelly, 1995; Pianka, 2000). By assuming that foragers choose food resources with the highest nutritional return rates in order to maximize their foraging efforts, reproductive success, and overall fitness within a given environment (Stephens and Krebs, 1986; Pianka, 2000), the prey choice model allows us to predicts the type of prey that past hunter-gatherers would have exploited or ignored whenever they encountered them while foraging (Kelly, 1995). Normally, ungulates or large-bodied mammals are considered high-ranked prey by foragers because they represent a larger nutritional package in comparison to low-ranked, small-bodied taxa (Broughton, 1994; Stiner et al., 1999, 2000; Stiner and Munro, 2002; for a review of this assumption and criticisms, see also Morin et al., 2022). Nonetheless, small animals differ considerably in terms of capture costs and technological investment due to predator avoidance strategies (Madsen and Schmitt, 1998; Stiner et al., 1999, 2000; Stiner and Munro, 2002; Steele and Klein, 2009). For instance, slow-moving tortoises are easier to harvest and higher-ranked than small, quick-moving, or difficult-to-procure taxa, such as partridges or fish (Stiner et al., 1999, 2000; Stiner and Munro, 2002). Humans are expected to hunt high-ranked taxa as long as they are available in the environment (Stephens and Krebs, 1986). As the occupation of a site intensifies, the human influence on local resources will increase and encounter rates of high-ranked prey may decline (Stiner and Munro, 2002; Munro, 2004); consequently, foragers will have to turn to lower-ranked (either small game or fast-moving) taxa (Stephens and Krebs, 1986). Our first zooarchaeological measure of site occupation intensity is thus based on the relative proportion of high- and low-ranked prey.

We use two indices to compare the abundance of prey types: 1) small game relative to large game (small game NISP/[large game NISP + small game NISP]); and 2) small, fast-moving (mostly partridges and other birds, along with a little bit of fish) prey relative to small, slow-moving game (small, fast NISP/[small, slow NISP + small, fast NISP]). We expect therefore high-ranked ungulates or sessile and easy-to-catch tortoises to be more abundant in relation to small-bodied animals or fast-moving taxa with higher procurement costs when site occupation intensity is low, while foraging efforts and the exploitation of low-ranked prey should increase with a more intensive occupation of the site (Munro, 2004; Munro et al., 2016).

3.2.2. Find densities and accumulation rates. Researchers commonly utilize find densities and accumulation rates as proxy measures of occupation intensity in Late Pleistocene sites (e.g., Conard et al., 2012, Stiner and Munro, 2011; Stiner et al., 2012; Tryon and Faith, 2016; Liu et al., 2020). These analyses rely on a very basic premise: the more intensively humans use a site, either by being occupied by more people, during longer periods of time or visited more frequently, the higher the amount of food waste and occupational debris they generate, and vice versa (French, 2015, and references therein). We estimate find densities by standardizing the total number of finds against the approximate volume of excavated sediment by layer (density = find count/sediment volume in liters). Among the different types of archaeological materials recovered at Ghar-e Boof, we focus on NISP values of animal remains, burned NISP, and the number of lithic artifacts (Table 1). Because deposition and sedimentation rates are not always constant (Ferring, 1986; Jerardino, 1995), we also have to take into account the duration over which finds and sediment accumulated at each archaeological layer, and calculate find accumulation rates as follows: (find count/sediment volume in liters)/duration. Following Stiner et al. (2012), we multiplied the accumulation rate values by 10^3 to make them more readable. Here duration is estimated as the difference between the average ages of any two archaeological layers or samples (after Stein et al., 2003). Table 2 presents the age estimates, which are mostly based on OSL dates from Heydari et al. (2021). There are two exceptions: 1) for AH III, we have only radiocarbon dates available (Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017); and 2), since AH IVc and IVb have not been dated so far, we used the difference between the closest available OSL ages at the bottom (AH IVd) and top (AH IVa) of these layers, and we divided then the estimated interval equally between AH IVc and IVb. Even if duration estimates represent course-grained values of time lapses, they can still be very informative, especially when layer accumulation times fluctuate by more than an order of magnitude through a stratigraphic sequence (Stiner and Munro, 2011; Stiner et al., 2012), as occurs at Ghar-e Boof.

3.2.3. Relative frequency of retouched tools. Finally, we use the relative frequency of retouched tools as an indicator of site occupation intensity. The relative frequency of retouched tools is the ratio between the count of retouched or modified “pieces” and the total amount of lithic debris in an assemblage (Riel-Salvatore and Barton, 2004), which, in our study, includes cores, flakes, and small- and micro-debitage. Based on ethnoarchaeological studies (e.g., Binford, 1977, 1979), it is assumed that mobile hunter-gatherers constantly need to supply themselves with tools and carry them as they move from one place to another. Researchers predict that, in contexts of high mobility and low site occupation intensity, people would rely on curating and resharpening tools that have been transported from previous sites, with little or no on-site production of new artifacts (Riel-Salvatore and Barton, 2004; Kuhn and Clark, 2015; Liu et al., 2020). This leads to high proportions of discarded retouched tools relative to waste flakes and other debris. As occupation intensity increases, more lithic artifacts are manufactured at the site, and the knappers generate even more debris (Riel-Salvatore and Barton, 2004; Kuhn and Clark, 2015; Liu et al., 2020); in line with this logic, relatively low frequencies of retouched tools in archaeological assemblages may reflect episodes of high occupation intensity.

Table 2. Ghar-e Boof. Available OSL dates from Heydari et al. (2021), along with date and duration estimates by layer. The approximate age provided for AH III is based on radiocarbon dating analyses (after Conard and Ghasidian, 2011; Baines et al., 2014; Becerra-Valdivia et al., 2017).

Layer	Culture	Dates (ka)	Dates (estimates, ka)	Duration (years)
AH III	Rostamian (UP)	~35	35.0	3000
AH IIIa	Rostamian (UP)	37 – 39	38.0	500
AH IIIb	Rostamian (UP)	38 – 39	38.5	1000
AH IIIc	Rostamian (UP)	39 – 40	39.5	1000
AH IV	Rostamian (UP)	40 – 41	40.5	500
AH IVa	Rostamian (UP)	40 – 42	41.0	2000
AH IVb	Rostamian (UP)	NA*	43.0	1000
AH IVc	MP-UP (?)	NA	44.0	1500
AH IVd	MP-UP (?)	45 – 48	46.5	1000
AH V	MP	46 – 49	47.5	7300
AH Va	MP	51 – 55 55 – 58	54.8	3200
AH Vb	MP	56 – 60	58.0	2500
AH Vc	MP	58 – 63	60.5	6000
AH Vd	MP	63 – 70	66.5	10000
AH VI	MP	72 – 78 75 – 81	76.5	9000

*NA (Not available).

3.3. Statistics

We carried out all statistical tests in R Studio (R core Team, 2023). To analyze diachronic trends, we fitted generalized linear models to our data. Rather than arranging the data by archaeological layer from the oldest to the most recent, we considered time estimates (from Table 2) as one of the variables in the generalized linear models, since they better represent chronologically the occupational sequence of Ghar-e Boof. We used a quasi-binomial family generalized linear model to analyze changes in relative proportions through time because 1) the data are under-dispersed, 2) take continuous values, and 3) only encompass values between 0 and 1. When the data can theoretically range from 0 to positive infinity (i.e., find densities and accumulation rates), we applied a log-normal family generalized linear model. After Weitzel (2023), we assessed statistical significance and good of fit for all generalized linear models reported in this study with a likelihood ratio test in the *lmtest* package (Hothorn et al., 2022) and the calculation of D^2 values (or the proportion of variation accounted for by the models) in the *modEva* package (Barbosa et al., 2023). For quasi-likelihood models, we calculated D^2 values by hand as one minus the quotient of the residual and null deviance and conducted likelihood ratio tests as X^2 tests using the base anova function. We also plotted the model fit and the 95% confidence intervals. Besides generalized linear models, we conducted a Kruskal-Wallis rank sum test to evaluate whether fragmentation and the identifiability of ungulate bones vary over the stratigraphic sequence by comparing the median bone length of ungulate specimens between layers. Results are considered to be statistically significant when p values are < 0.05.

4. Results and preliminary discussion

4.1. Bone preservation and fragmentation

In Table 3, we report the mean length values for burned and unburned specimens to examine the impact of burning on fragmentation. On average, burned bone remains are smaller than unburned bones. The proportion of burned bones, however, is relatively low in our assemblage; only 10.4% of the total identified bone remains are burned, of which 7.3% are carbonized, and 3.1% are calcined (SOM Fig. S1). Despite the fact that the uppermost AHs IIIa and III yielded higher frequencies of burned bones (19.1% and 13.8% respectively) in comparison to the rest of the layers, there is no statistically significant increase in the proportion of burned bones over time ($X^2 = 1.130$, df = 1, $p = 0.307$; $D^2 = 0.075$). The results of a Kruskal-Wallis test reveal that there are statistically significant differences in the length (cm) of ungulate bone fragments between layers ($X^2 = 32.69$, df = 14, $p = 0.003$; SOM Table S1 and Fig. S2). We performed a pairwise comparison between groups, and among all the 15 layers included in our study, we only found a statistically significant difference between AH VI and AH IVa ($p = 0.002$).

It appears that any temporal patterns in species representation and prey types at Ghar-e Boof are not due to differential bone fragmentation, and therefore reflect primarily hominin subsistence practices and socioeconomic decisions.

Table 3. Mean length (mm) of burned and unburned bone fragments by layer. Teeth are excluded from this analysis. The sample size may vary slightly in comparison to the datasets published in Mata-González et al. (2022, 2023) because a small portion of bone specimens were attached to each other in a matter that it was not possible for us to measure them.

Layer	**Burned**			**Unburned**		
	n	**Mean (cm)**	**Standard deviation**	***n***	**Mean (cm)**	**Standard deviation**
III	147	2.7	1.9	971	3.4	2.2
IIIa	51	2.6	1.1	210	3.1	1.9
IIIb	43	3.0	1.9	563	3.2	2.1
IIIc	20	2.5	2.1	238	3.4	2.2
IV	12	1.4	0.9	149	2.9	1.9
IVa	23	2.9	2.6	198	3.1	1.9
IVb	10	2.4	1.4	86	3.5	2.1
IVc	3	2.7	1.3	69	3.7	2.8
IVd	1	28.0	0.0	14	4.0	2.7
V	12	2.4	1.4	83	3.5	1.8
Va	5	2.1	1.2	220	3.2	2.1
Vb	13	2.6	0.7	119	2.9	1.8
Vc	2	1.4	0.3	88	3.1	1.8
Vd	3	2.6	2.5	30	2.9	2.2
VI	17	3.8	2.2	148	4.3	2.5

4.2. Species representation and relative abundance

NISP and MNI counts for all taxa are provided in SOM Table S2, and Fig. 4 depicts NISP values for prey body-size groups by layer. At Ghar-e Boof, ungulates are the most abundant prey throughout the MP and UP sequence. The ungulate fraction of the assemblage is dominated by medium-bodied ungulates, namely caprines (*Ovis*/*Capra*). Based on species-specific identifications, wild goat is considerably more common than sheep. Small ungulates or gazelle (*Gazella* sp.) are also frequent, but large and very-large ungulates, such as red deer (*Cervus elaphus*), wild pig (*Sus scrofa*), equid (*Equus* sp.), and wild cattle (*Bos primigenius*), are rare in our assemblage. Along with ungulates, the MP and UP occupants of the site consistently preyed on small game animals. Tortoise (*Testudo* sp.) is the only taxon assigned to the small, slow-moving game category. Within the small, fast-moving game component, most remains are from chukar partridges (*Alectoris chukar*) and other medium birds. This latter group seems to consist predominantly of Galliformes, though it may include some Columbiformes since we recorded a few specimens as cf. dove (cf. *Streptopelia*/*Columba*). Large and huge birds (raptors) and fish (indeterminate Leuciscinae and nase, *Chondrostoma* sp.) are also considered small, fast-moving game, but they are uncommon. Finally, the hominin exploitation of carnivores at Ghar-e Boof was very sporadic; we documented small quantities of large carnivores – a felid, most likely leopard (*Panthera* cf. *pardus*) – and small carnivores – red fox (*Vulpes vulpes*) and wild cat (*Felis* sp.).

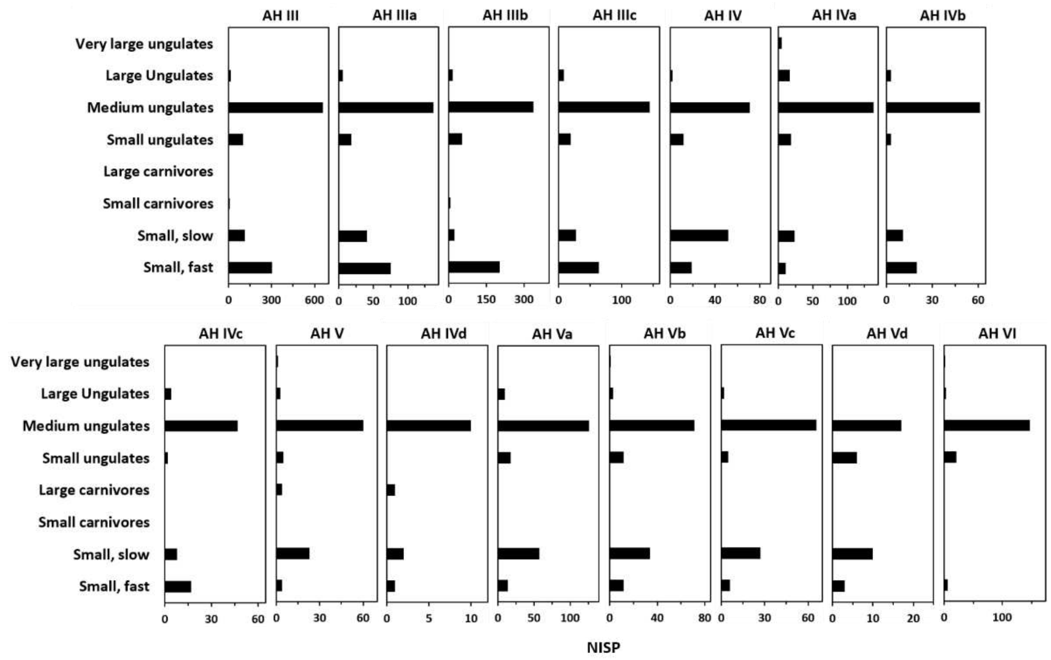


Fig. 4. Ghar-e Boof. NISP counts for prey body groups by layer. Data from SOM Table S3, and Mata-González et al. (2022, 2023).

Table 4 presents NISP values and relative proportions for large and small game, as well as for small, slow- and small, fast-moving game. From a diachronic perspective, there is a positive relationship between time and the proportion of small game relative to large game (Small Game Index, Fig. 5a), yet the trend is neither strong nor statistically significant ($X^2 = 4.654$, df = 1, $p = 0.050$; $D^2 = 0.240$). Despite being close to the threshold of significance, the results show that the occupants of Ghar-e Boof preferentially hunted large game prey during the MP and early UP. As for the proportion of small, fast-moving game relative to small, slow-moving game as a function of time (Fast Game Index, Fig. 5b), the relationship is positive and statistically significant (X^2 = 12.079, df = 1, p = 0.005; D^2 = 0.508), which indicates an increased use of small, fast-moving or less cost-effective animals over time at the site.

Table 4. Ghar-e Boof. NISP counts and proportions of large (ungulates) game and small game by layer. Small game is also split into NISP and relative proportion of small, slow- and small, fast-moving animals.

Layer	Total NISP	Ungulates NISP	Proportion of NISP		Small game NISP	Slow, moving	Fast, moving	Proportion of NISP	
			Large game	Small game				Slow, moving	Fast, moving
AH III	1312	893	0.68	0.32	419	115	304	0.28	0.73
AH IIIa	287	171	0.60	0.40	116	41	75	0.35	0.65
AH IIIb	679	453	0.67	0.33	226	22	204	0.10	0.90
AH IIIc	284	192	0.68	0.32	92	28	64	0.30	0.70
AH IV	169	98	0.58	0.42	71	52	19	0.73	0.27
AH IVa	233	199	0.85	0.15	34	23	11	0.68	0.32
AH IVb	102	71	0.70	0.30	31	11	20	0.36	0.65
AH IVc	81	56	0.69	0.31	25	8	17	0.32	0.68
AH IVd	16	13	0.81	0.19	3*	2	1	0.67	0.33
AH V	98	71	0.72	0.28	27	23	4	0.85	0.15
AH Va	239	168	0.70	0.30	71	57	14	0.80	0.20
AH Vb	144	98	0.68	0.32	46	34	12	0.74	0.26
AH Vc	116	83	0.72	0.28	33	27	6	0.82	0.18
AH Vd	41	28	0.68	0.32	13	10	3	0.77	0.23
AH VI	199	193	0.97	0.03	6*	0	6	0.00	1.00
Total	4000	2787	0.70	0.30	1213	453	760	0.37	0.63

*Asterisk indicates sample with small sample size.

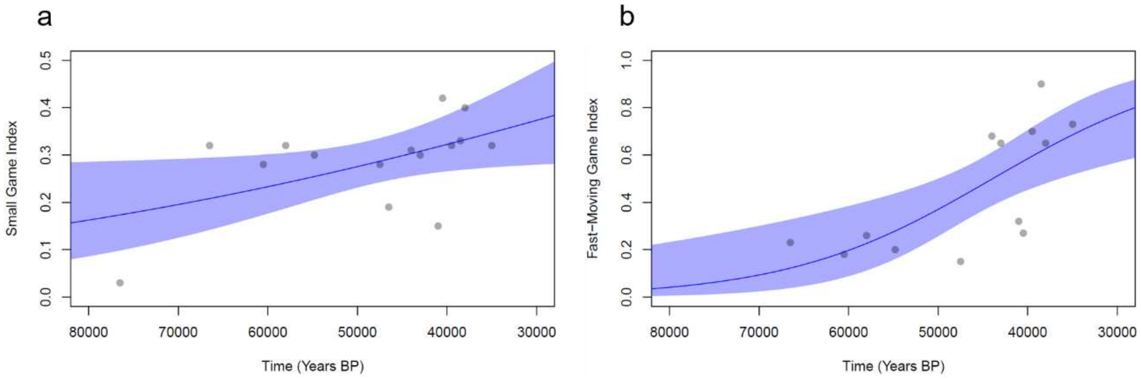


Fig. 5. Ghar-e Boof: a) Small Game Index (proportion of small game relative to large game), and b) Fast-Moving Game Index (proportion of small, fast-moving game relative to small, slow-moving game), as a function of time.

4.3. Find densities and accumulation rates

All temporal trends in find densities are positive and statistically significant (Fig. 6a,c,e, and Table 5). When we use accumulation rates to correct for differences in the duration of deposition and sedimentation between archaeological layers, the trends are also positive and statistically significant (Fig. 6b,d,f, and Table 5). Both density values and accumulation rates of faunal remains, burned bones, and lithic artifacts show that occupation intensity at Ghar-e Boof was consistently low during the MP. Instead, the site became more intensively used during the UP.

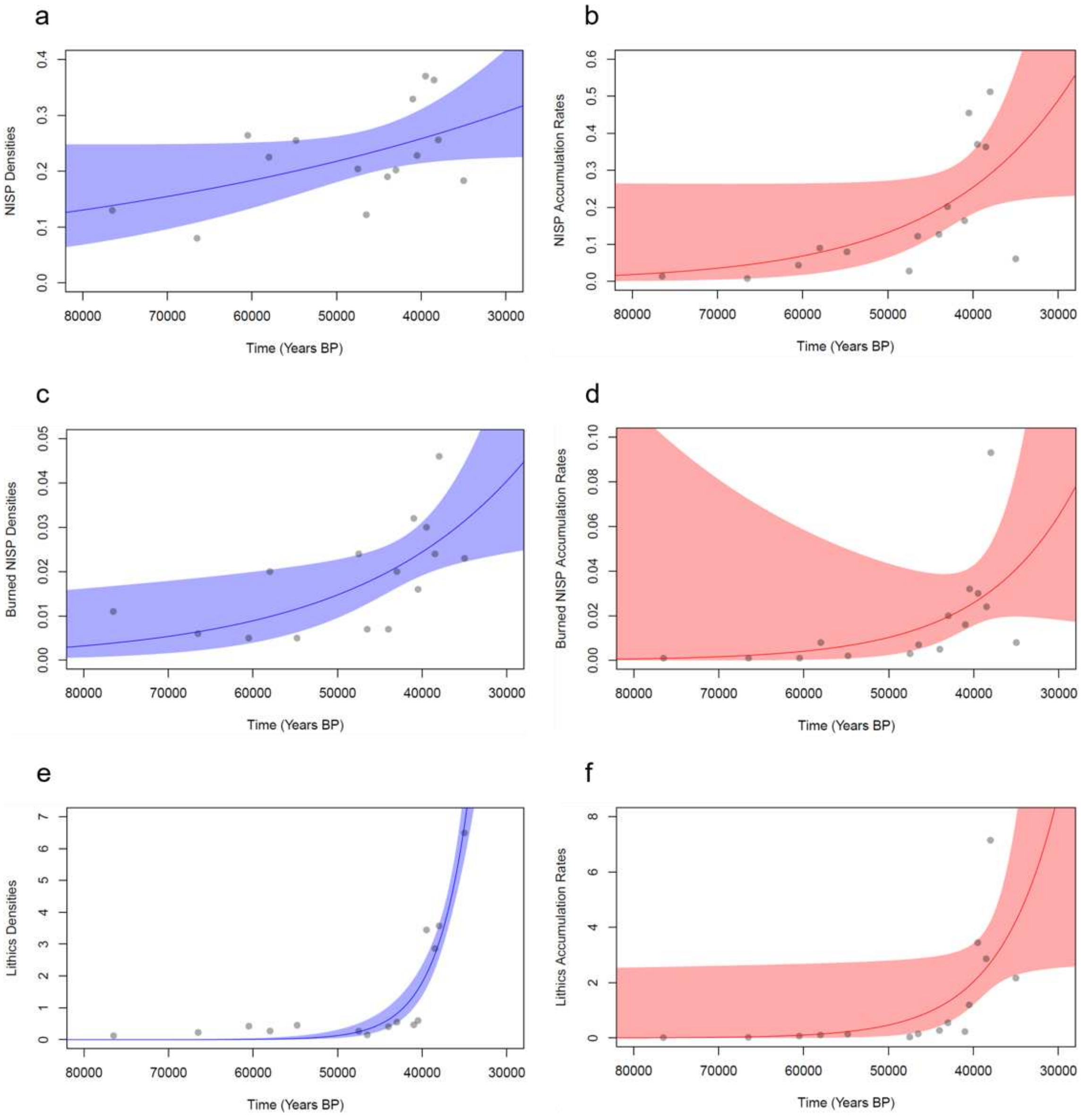


Fig. 6. Ghar-e Boof: find densities (in blue), and accumulation rates (in red), as a function of time.

Table 5. Ghar-e Boof. Results of log-normal family generalized linear models for find densities and accumulation rates, as a function of time.

	X^2	df	p	D^2
Find densities				
NISP	4.575	1	0.032	0.263
Burned NISP	8.400	1	0.004	0.429
Lithics	35.110	1	< 0.001	0.904
Accumulation rates				
NISP	8.218	1	0.004	0.422
Burned NISP	5.474	1	0.019	0.306
Lithics	8.910	1	0.003	0.448

4.4. Relative frequency of retouched tools

Raw counts of different classes of lithic artifacts by layer are found in SOM Table S4. Overall, MP and UP deposits yielded low proportions of retouched tools relative to other types of lithic artifacts and debris. Despite that, there is a negative and statistically significant relationship between time and the relative frequencies of retouched tools (Fig. 7; $X^2 = 11.768$, df = 1, $p = 0.005$; $D^2 = 0.489$). In other words, the lithic data point to a general decrease in retouched tools throughout the sequence at Ghar-e Boof, reflecting not only more knapping activities and on-site production of lithic waste during the UP, but also an increase in site occupation intensity.

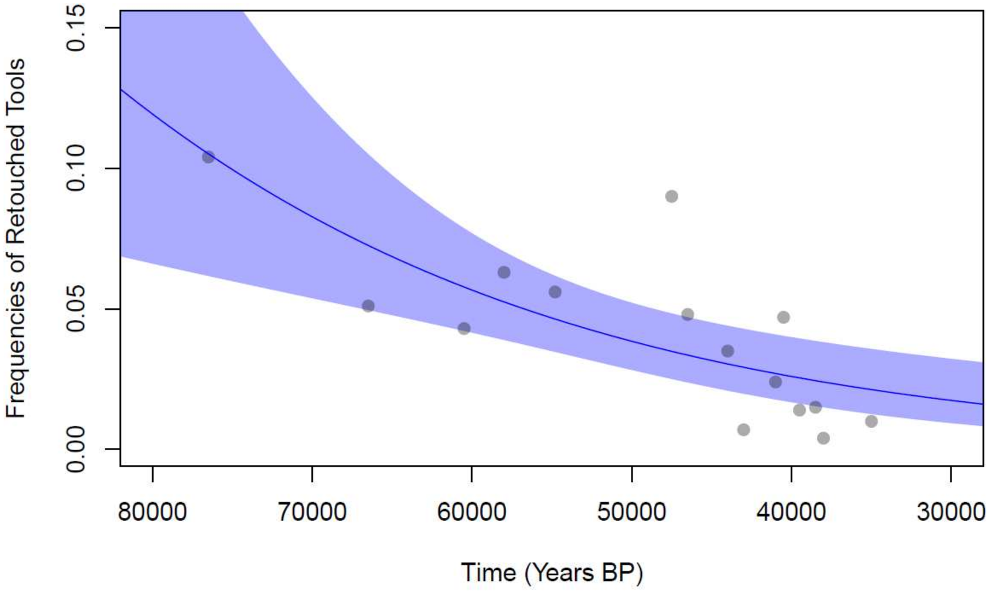


Fig. 7. Ghar-e Boof: frequencies of retouched tools, as a function of time.

5. Discussion and conclusions

The zooarchaeological assemblages recovered from Ghar-e Boof show that both MP and UP hominins hunted predominantly large game species. Among them, caprines were the most common prey, which constituted the main sources of meat and marrow for the occupants of the site (Mata-González et al., 2022, 2023). Despite the environmental and topographic heterogeneity that characterizes the southern Zagros (Heydari-Guran, 2014), the landscape in the Dasht-e Rostam region is dominated by rocky terrains and steep slopes, which is the preferred habitat of wild goats (Karami et al., 2016). Consequently, the hunting behaviors and prey selection of the hunter-gatherer groups that lived in the area during the Late Pleistocene most likely reflect the constraints posed by the local landscape (e.g., Hodgkins and Marean, 2017). Alternatively, following the assumptions of the prey choice model (Stephens and Krebs, 1986; Pianka, 2000), and as we suggested recently in Mata-González et al. (2023), these groups appear to have optimized their foraging efforts by targeting the highest-ranked prey available in their environment. If we consider just the animal component of the diet, the zooarchaeological record of Ghar-e Boof may evidence that during the Late Pleistocene people managed to obtain most of their daily nutritional needs with high-ranked resources (Mata-González et al., 2023), which might have been only possible under circumstances of ephemeral occupations of sites or relatively low population densities in the region (Stiner et al., 1999, 2000; Stiner and Munro, 2002).

Because of the differences in maturation rates, predator escape behaviors, capture costs, and overall energetic return rates, most changes in the dietary spectrum of paleolithic hunter-gathers in relation to hunting pressure and resource availability are expected to occur within the small game fraction (Stiner et al., 1999, 2000; Stiner and Munro, 2002). Returning to one of the premises of the prey choice model, since tortoises are slow-moving and easy-to-collect animals, they would have constituted higher-ranked packages of food for Pleistocene foragers in comparison to quick-moving prey (Stiner et al., 1999, 2000; Stiner and Munro, 2002). Ghar-e Boof is the first Pleistocene site in the Zagros where the zooarchaeological data indicate increased exploitation of small, fast-moving game, namely partridges, relative to tortoises between the MP and early UP. Several zooarchaeological assemblages from Late Pleistocene sites located in the eastern Mediterranean region, including the Balkan Peninsula (Starkovich, 2012, 2014, 2017) and the Levant (Stiner et al., 1999; Kuhn et al., 2009; Stiner, 2009; Yeshurun et al., 2021) show similar shifts in prey choice across the MP to UP transition or through the early UP. Even though the exact timing and mechanics that affected these trends most probably varied from site to site (Starkovich, 2017), researchers have usually interpreted these changes as indicators of resource intensification (Stiner et al., 1999; Kuhn et al., 2009; Stiner, 2009; Starkovich, 2012, 2014, 2017; Yeshurun et al., 2021). But at Ghar-e Boof, do the increased use of partridges can be attributed to fluctuations in the local environmental conditions, and prey availability? Did the adoption of a new techno-cultural repertoire allowed early UP hunter-gatherers to expand their diets and diversify their hunting practices? Or do the observed trends reflect, instead, higher hunting pressure due to an increase in site occupation intensity or demographic growth over time?

Jones (2012) argued that broadening diets during the terminal Pleistocene and some shifts in species abundances in France are associated with changes in vegetation cover or landscape patchiness. Likewise, Blasco et al. (2013, 2022) have explained some of the early evidence of small game exploitation in Iberia as local adaptations related to environmental diversity and prey availability. Studies of sediment cores from lakes Zeribar and Urmia (situated in central and norther Zagros, respectively) have revealed that during the Late Pleistocene the paleoclimate and paleoenvironment of the region fluctuated between relatively cold/warm and dry/wet conditions (Wasylikowa, 2005; Djamali et al., 2008). However, these lakes are located hundreds of kms further north in the Zagros, and the analyses of their sediment cores were based on a few radiocarbon dates (Wasilikowa et al., 2005; Djamali et al., 2008), which prevents us from correlating these paleoenvironmental reconstructions with the archaeological sequence of Ghar-e Boof. As we mentioned above, we used small vertebrate remains to infer the local environmental conditions, but the results are tentative and must be taken with caution because of small sample sizes (Blanco-Lapaz et al., 2022). During the Late Pleistocene, the surrounding environment of the cave was dominated by warm, dry conditions, shrublands and rocky terrain (Blanco-Lapaz et al., 2022). Changes in species representation within the small mammal assemblages point to a period with slightly colder and/or drier conditions between ca. 45–39 kya (Blanco-Lapaz et al., 2022). After ~40–39 kya, the site's occupants faced a relatively better and more stable environment in the Dasht-e Rostam region, but the general conditions of the landscape appear to have remained slightly drier and more open in comparison to those present throughout most of the MP sequence of the site (Blanco-Lapaz et al., 2022). We have hypothesized that climatic and environmental fluctuations likely affected Late Pleistocene hominin groups that lived across the region (Blanco-Lapaz et al., 2022). Yet, we claim that the temporal trends in the small game fraction of the hominin diets documented at Ghar-e Boof were not primarily driven by changes in the local climate and environment. Both partridges and tortoises are flexible in their ecological requirements (Kaboli et al., 2016; Mozaffari et al., 2016), and shifts in the relative abundances of small game taxa can be used effectively to monitor changes in hominin prey choice and hunting behavior (Munro, 2004; Starkovich, 2012).

Based on ethnographic and actualistic research of small game hunting, Morin et al. (2020, 2022) have demonstrated that hunting technology and procurement methods influence how foragers perceive the profitability of a prey type. Mass collecting and the use of nets can lower pursuit costs and increase return rates of small game species (Morin et al., 2020, 2022). For instance, at some sites with UP deposits located in central Europe, archaeologists have suggested among other hypotheses that the introduction of new harvesting methods and technological innovations (e.g., traps, nets and snares) may have facilitated the exploitation of birds and small carnivores (Baumann, et al., 2020; Bertacchi et al., 2021). The same argument can be made for the increased use of partridges during the early UP at Ghar-e Boof. Nevertheless, Ugan (2005) argued that overall return rates for mass-collected birds tend to remain low because they have to be processed individually, which still requires high handling costs. It is likely that the changes in technology and harvesting practices that took place between the MP and early UP might have raised the efficiency of hunting small, fast-moving animals. But at Ghar-e Boof, we see the increased economic importance of these animals over the early UP as an indication of resource intensification caused by shifts in hunting pressures, mobility, and population density in the southern Zagros. Indeed, as the prey choice model predicts, the increasing reliance on lower yield resources would have allowed foragers to raise the carrying capacity of their environment (Stephens and Krebs, 1986), particularly if moving into new foraging areas was no longer an option due to increased demographic packing and territorial circumscription (e.g., Flannery, 1969; Stiner et al., 2000; Stiner, 2001, 2009).

Our study shows that density values for NISP, burned NISP, and lithic artifacts increased with time at Ghar-e Boof. Yet, as pointed out by some scholars (Ferring, 1986; Jerardino, 1995), rates of sedimentation and deposition often fluctuate through time at a given site, which can bias intra-site comparisons between densities values calculated for different archaeological layers. Our duration estimates reveal that the sedimentation rates were not constant at the cave, varying by more than an order of magnitude between some layers. Despite that, there is also an increase in find accumulation rates throughout the sequence. At the same time, frequencies of retouched tools relative to other types of lithic artifacts and debris decline, which is expected to happen when foragers manufactured lithic tools more often on-site and, as a consequence, they produced even more lithic waste (Riel-Salvatore and Barton, 2004; Kuhn and Clark, 2015; Liu et al., 2020). Therefore, all these proxies indicate that the occupation of Ghar-e Boof intensified through the early UP.

A common concern that may raise when working with estimates that rely on raw counts of archaeological materials is that they are largely affected by methods of excavation, recovery and sorting, and the quality of available data (Conard et al., 2012), which could even differ between seasons of excavation carried out at the same site (Jerardino, 1995). This potential problem does not apply to our case, since the TISARP team excavated Ghar-e Boof during four seasons of excavation using systematically the same methods and techniques. Additionally, it is important to consider whether the differences in the extension of the excavated areas between layers may have an effect on the observed diachronic patterns, and for instance, we might be capturing changes in activity areas (e.g., Clark and Plug, 2008). While archaeologists exposed larger horizontal areas for AHs IV to III at the site (Fig. 3), we have not found any signs of well-defined activity areas, except for the presence of some combustion features (Conard and Zeidi, 2019). Even if we must be cautious due to the limited spatial extent of the excavated areas, the current archaeological record of Ghar-e Boof shows a broad range of hominin activities that took place in the cave during the formation of each single layer, and most probably is representative of how intensively the site was used as a whole. Finally, although all the temporal trends for find densities and accumulation rates are positive and statistically significant, the results are more robust when we used counts of lithic artifacts. There are three reasons that could explain the differences between the density values and accumulation rates for lithics and faunal remains: 1) lithic artifacts are more resistant and preserve better than bones; 2) many skeletal elements were heavily processed for marrow extraction (Mata-González et al., 2022, 2023), yielding large amounts of fragments that are unidentifiable; and 3) as we mentioned above, we have only been able to quantify NISP so far, while for lithics we took into account even the smallest pieces of debitage. Based on the lithic artifacts, the hominins used the site ephemerally during the MP, but also at the onset of the early UP. Then, the occupation intensity drastically increased over the course of just a few millennia. Schilt (2011) analyzed micromorphological samples from AHs IV and III. Her study shows that AH IV is dominated by sediments of a geogenic origin, and instead, AH III consists mostly of anthropogenic input and is rich in ash and other organic materials (Schilt, 2011), which supports that the major shifts in the occupation intensity of Ghar-e Boof only occurred after ~40 kya.

Previously, we have also analyzed skeletal element patterns and bone processing damage for caprines and medium ungulates from the MP and UP deposits (Mata-González et al., 2022, 2023), and comparisons between the two datasets can offer further insights on changes in subsistence strategies and mobility related to local resource intensification and site occupation intensity. According to the central place foraging model, when foragers travel longer distances, which increases transport costs, they become more selective in terms of the skeletal portions they transport (Cannon, 2003). Both ethnographic and archaeological observations have shown the preferential transport of body portions with higher utility values to a camp site as the distance to the kill increases (i.e., Binford, 1978; Cannon, 2003; Nagaoka, 2005). An alternative and complementary model to assess changes in foraging efficiency or resource intensification is the patch choice model, derived from the marginal value theorem. The model is concerned with the costs and time that foragers invest in a given patch before moving to the next one (Charnov, 1976). The concept of a "patch" refers to resources that cluster in space, such as a river, forest, or a single tree, but Burger et al. (2005) proposed that it can be applied to an individual carcass and its different tissues and skeletal elements. As foragers exploit a patch, the available resources within it are depleted. The model predicts that patches are not exploited till exhaustion, but foragers would leave a patch once its return rates drop below the average return rates of other potential patches, with travel time and moving costs included (Charnov, 1976). By extension, if resource stress occurs, and there is a decline in the average return rates for the patches that can be exploited, then we can expect a more intensive exploitation of each patch (Nagaoka, 2002).

At Ghar-e Boof, we found that during the MP hominins transported to the cave more frequently elements with high marrow or unsaturated fatty acid content (Mata-González et al., 2023), whereas early UP foragers seem to have been less selective, transporting whole ungulate carcasses (Mata-González et al., 2022). In other words, the early UP foragers that occupied Ghar-e Boof traveled shorter distances to hunt than their MP counterparts, since the transport of whole carcasses to a site is most cost-effective when hunting nearby (Cannon, 2003). The observed differences in transport decisions between the MP and UP suggest that during the later period hunting further away from the campsite might have not been possible anymore because of increased territorial circumscriptions and larger populations spread across the region (Starkovich, 2017; Mata-González et al., 2022). Furthermore, in the MP faunal assemblages, phalanges are relatively rare, and they do not exhibit any percussion damage (Mata-González et al., 2023). In contrast, foot elements are well represented in all early UP layers, and even if percussion impacts are more common on long-bone elements with higher marrow quantities, we also recorded them on phalanges (Mata-González et al., 2022), which are bones with very low marrow and fat utility values (Binford, 1978; Morin, 2007). Despite small sample sizes and the fact that some specimens were partly or completely covered by sediment concretions (Mata-González et al., 2022, 2023), it seems that carcass and bone processing were more intensive during the early UP, which could evidence local resource depression and decreased foraging efficiency (Burger et al., 2005). Therefore, the synchronic shifts in species abundances, transport strategies, carcass processing, and site occupation intensity documented at Ghar-e Boof support a scenario of resource intensification over the early UP in the southern Zagros Mountains due to higher hunting pressures and population growth.

5.1. Ghar-e Boof in the context of animal exploitation by Late Pleistocene hominins and changing population densities in the Zagros Mountains

Across the entire geographic range of the Zagros, a growing number of MP and UP sites have yielded zooarchaeological assemblages, though the available published information varies considerably, from just mentioning the most common taxa or species lists to rather detailed taphonomic studies (Fig. 1; Solecki, 1963; Perkins, 1964; Hole and Flannery, 1967; Turnbull, 1975; Evins, 1982; Hesse, 1989; Marean, 1998; Marean and Kim, 1998; Otte et al., 2007, Mashkour et al., 2009; Bazgir et al., 2017; Hodgkins and Marean, 2017; Biglari and Shidrang, 2019; Campana and Crabtree, 2019; Heydari-Guran et al., 2021a). The study of these assemblages not only improves our understanding of human adaptations to local environments but also allows us to elucidate regional patterns concerning foraging conditions, site use, and demographic pulses. From Shanidar Cave, located in northern Zagros, to Eshkaft-e Gavi in the southernmost part of the mountain range, the animal subsistence economies of MP and UP foragers focused on large game, mostly caprines, alongside gazelles and equids, and to a lesser extent, cervids, wild cattle and wild pig (Solecki, 1963; Perkins, 1964; Hole and Flannery, 1967; Turnbull, 1975; Evins, 1982; Hesse, 1989; Marean, 1998; Marean and Kim, 1998; Otte et al., 2007, Mashkour et al., 2009; Bazgir et al., 2017; Hodgkins and Marean, 2017; Biglari and Shidrang, 2019; Campana and Crabtree, 2019; Heydari-Guran et al., 2021a).

Establishing a regional comparison of small game use in the Zagros Mountains during the Late Pleistocene is more difficult since, aside from Ghar-e Boof, we have scant evidence. Evins (1982) suggested that MP hominins might have collected land tortoises for dietary purposes at Shanidar Cave based on their high relative abundances and the recovery of burned shell specimens. Researchers have also identified Testudines in the UP deposits of Yafteh and Kaldar caves (Otte et al., 2007; Mashkour et al., 2009; Bazgir et al., 2017), though they did not discuss the main agent of accumulation of these remains, and thus far the only reported specimen exhibiting anthropogenic modifications is a burned epiplastron from Kaldar. As for the Epipaleolithic, tortoises are relatively abundant at Palegawra Cave, and they appear to have been accumulated and consumed by the site's inhabitants (Asouti et al., 2020). The situation is not much different in the Zagros when it comes to fish, birds, and hares. Currently, we do not have direct evidence for the human use of small, fast-moving species during the MP in the region (but see Mata-González et al., 2023). At the early UP Baradostian layers of Shanidar Cave, archaeologists have reported the presence of fish scales, which they have interpreted tentatively as the result of fishing activities (Reynolds et al., 2018), though no taphonomic data have been reported. Otte et al. (2007) proposed that during the UP at Yafteh Cave, carnivores or raptors were the main agents responsible for the accumulation of fish because some fish remains show digestion marks. Yet, Otte et al. (2007) do not rule out an anthropogenic origin of, at least, part of the fish assemblage. Although bird specimens have been recovered at a few Pleistocene cave sites (e.g., Hesse,1989; Otte et al., 2007; Mashkour et al., 2009; Bazgir et al., 2017; Asouti et al., 2020), Gelimgoush Cave is the only locality where UP foragers seem to have exploited birds due to the presence of a presumably cut-marked raven bone (Heydari-Guran et al., 2021a). Finally, Mashkour et al. (2009) claimed that hares played a relatively important role in the UP subsistence economies because of their ubiquity across all the excavated spits at Yafteh Cave, but once again, further taphonomic information is needed to support this hypothesis.

There are a few alternative explanations as to why small game taxa and anthropogenic modifications on them are so rare in the zooarchaeological record of the Zagros. First, according to Evins (1982), the presence or absence of tortoises in Pleistocene sites might track their availability in the local environment. Nonetheless, a common trait of tortoises and partridges is their ecological flexibility and, in fact, nowadays they can live in diverse habitats across the Zagros (Kaboli et al., 2016; Mozaffari et al., 2016), which made us consider that these taxa most likely were available resources for MP and UP foragers (Mata-González et al., 2023). Second, if high-ranked prey were abundant or the occupation intensity of most sites was low, hominins could have ignored less profitable or lower-ranked resources (Stiner et al., 1999, 2000; Stiner and Munro, 2002). Third, regarding anthropogenic modifications, actualistic experiments have shown that humans usually dismember and deflesh medium-bodied birds (e.g., pidgeons and doves) with just their teeth and hands, and without using stone tools (Val et al., 2016). The lack of cut marks on small game specimens hence does not allow zooarchaeologists to exclude hominins as the agent of bone accumulation. Fourth, the general picture of small game use during the Late Pleistocene in the Zagros may just reveal research biases: archaeologists not always kept or recovered all the faunal remains, especially at some excavations of key sites conducted during the 1950s and 1960s (Coon, 1951; Hodgkins and Marean, 2017; Campana and Crabtree, 2019); and partly as a consequence, they have paid disproportionate attention to the taphonomic study of ungulate bones (Mata-González et al., 2023). Fortunately, recent archaeological projects that include the water-screened of excavated sediments, and the analysis of complete zooarchaeological assemblages (e.g., Bazgir et al., 2017; Reynolds et al., 2018; Asouti et al., 2020; Heydari-Guran et al., 2021a; Mata-González et al., 2022, 2023), most certainly will clarify the socioeconomic importance of small game exploitation for hunter-gatherer groups over the MP and UP.

Besides our work on hominin prey choice and occupation intensity at Ghar-e Boof, another demographic proxy that has been applied to the Paleolithic record of the Zagros Mountains is site counts or density of lithic artifacts based on surface finds collected during surveys (Conard and Ghasidian, 2011; Heydari-Guran and Ghasidian, 2020). Despite the methodological difficulties and problems associated with this approach (Dogandžić and

McPherron, 2013; French, 2015), archaeologists usually assume that the number of sites or density of surface finds in a given region can reflect population size. The Kermanshah region (west-central Zagros) contains a relatively high concentration of MP sites (Heydari-Guran and Ghasidian; 2020), while in the Dasht-e Rostam region (southern Zagros), the presence of MP sites is very scarce, and the density of lithic artifacts is low (Conard and Ghasidian, 2011). However, even if the preservation and distribution of MP sites might have been affected by geological processes, the number of UP sites is higher in both regions (Conard and Ghasidian, 2011; Heydari-Guran, 2020). The increase in sites could, indeed, reflect generalized population growth or larger population/occupation densities over the UP, and across the central and southern Zagros and neighboring regions (Conard and Ghasidian, 2011; Heydari-Guran and Ghasidian, 2020; Mata-González et al., 2022).

Our synthesis highlights that we are still far from having a comprehensive view of the economic developments in animal exploitation and changes in subsistence strategies that occurred at local and regional scales in the Zagros during the Late Pleistocene. A more challenging task is to articulate zooarchaeological data with evidence for techno-cultural innovations, environmental fluctuations, and demographic pulses due to the limited number of available and comparable datasets for the region. This would certainly become easier in the coming years as more and more long and well-dated Paleolithic sequences are studied in the Zagros. Meanwhile, our study can serve as a baseline for future comparisons with other sites located across the Zagros Mountains and Southwest Asia. In summary, the analysis of the faunal remains recovered from Ghar-e Boof shows that there is a shift in the proportion of small, fast-moving taxa relative to small, slow-moving game over the MP to early UP. The increased use of small, fast-moving taxa, mostly partridges, with lower energetic return rates than tortoises, may be due to local resource intensification or higher hunting pressures, particularly since the early UP. Other variables, such as the adoption of a new and more efficient technology, might have lowered the energetic costs and pursuing time involved in hunting partridges or other more difficult-to-catch prey. Moreover, site occupation intensity increases through time as determined from find densities, accumulation rates and frequencies of retouched tools. A more intense occupation of Ghar-e Boof over the early UP could have been the result of larger groups of people living at the site, more frequent visits, longer periods of occupation, or some, if not all, of these factors combined. Taking everything together, the observed diachronic trends in prey choice and site occupation intensity are consistent with population growth and rising pressures on animal resources across the MP to early UP in the Dasht-e Rostam valley of the southern Zagros.

Author contributions

M.M.-G. and B.M.S. designed the research. M.M.-G. studied the zooarchaeological material and performed all the analyses included in this paper under the supervision of B.M.S. Excavations at Ghar-e Boof were led by M.Z. and N.J.C., who also contributed with contextual information. M.Z. collected and provided the lithic data. Finally, M.M.-G. wrote the first manuscript, while all the authors took part in the review and editing process of the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The Deutsche Forschungsgemeinschaft (grant CO 226/30–1), and the project “Role of Culture in Early Expansions of Humans” (ROCEEH) of the Heidelberg Academy of Science and Humanities funded the excavations conducted at Ghar-e Boof, which were also supported by the university of Tübingen and Senckenberg Centre for Human Evolution and Palaeoenvironment. M.M.-G. was the beneficiary of a research grant awarded to N.J.C. from the Ministerium für Wissenschaft, Forschung und Kunst Baden-Württemberg as part of the Evolution of Cultural

Modernity Project at the University of Tübingen. We are very grateful to the Iranian Center for Archaeological Research (ICAR) and the Research Institute of Cultural Heritage and Tourism (RICHT) for granting us permission to carry out our research in the Fars Province of Iran. Many thanks to the members of the TISARP team, especially Saman Hamzavi and Ángel Blanco-Lapaz, for their valuable contributions during fieldwork and for recovering, sorting, and cleaning the faunal material included in this study. Thanks must also be given to Elic Weitzel for helping us with the statistics; Christian Tryon for his methodological recommendations concerning alternative ways to examine site occupation intensity; and Nicholas A. Gonzalez and Elisa Luzi for their thoughtful comments and suggestions that greatly improved our paper. Last but not least, we are thankful to M. Gema Chacón for organizing the session "S8-7: Characterizing changing technology, subsistence and settlement dynamics of the Middle Stone Age and Middle Paleolithic" at the XX Congress of the International Union for Prehistoric and Protohistoric Sciences (UISPP), celebrated in Timișoara (Romania), in which we presented a preliminary version of this work.

References

Asmussen, B., 2009. Intentional or incidental thermal modification? Analysing site occupation via burned bone. J. Archaeol. Sci. 36. 528–536.

Asouti, E., Baird, D., Kabukcu, C., Swinson, K., Martin, L., García-Suárez, A., Jenkins, E., Rasheed, K., 2020. The Zagros Epipalaeolithic revisited: new excavations and ^{14}C dates from Palegawra cave in Iraqi Kurdistan. PLoS One 15 (9), e0239564.

Baines, J.A., Riehl, S., Conard, N.J., Zeidi, M., 2014. Upper Palaeolithic archaeobotany of Ghar-e Boof cave, Iran: a case study in site disturbance and methodology. Archaeol. Anthropol. Sci. 7, 245–256.

Barbosa, A.M., Brown, J.A., Jimenez-Valverde, A., Real, R., 2023. modEvA: Model Evaluation and Analysis. R package version 3.9.3.

Bar-Oz, G., Munro, N.D., 2007. Gazelle bone marrow yields and Epipalaeolithic carcass exploitation strategies in the southern Levant. J. Archaeol. Sci. 34, 946–956.

Baumann, C., Wong, G.L., Starkovich, B.M., Münzel, S.C., Nicholas J. Conard, N.J., 2020. The role of foxes in the Palaeolithic economies of the Swabian Jura (Germany). Archaeol. Anthropol. Sci. 12, 208.

Bazgir, B., Otte, M., Tumung, L., Ollé, A., Deo, S.G., Joglekar, P., López-García, J.M., Picin, A., Davoudi, D., van der Made, J., 2014. Test excavations and initial results at the Middle and Upper Paleolithic sites of Gilvaran, Kaldar, Ghamari caves and Gar Arjene rockshelter, Khorramabad Valley, western Iran. C. R. Palevol 13, 511–525.

Bazgir, B., Ollé, A., Tumung, L., Becerra-Valdivia, L., Douka, K., Higham, T., van der Made, J., Picin, A., Saladié, P., López-García, J.M., Blain, H.A., Allué, E., Fernández-García, M., Rey-Rodríguez, I., Arceredillo, D., Bahrololoumi, F., Azimi, M., Otte, M., Carbonell, E., 2017. Understanding the emergence of modern humans and the disappearance of Neanderthals: insights from Kaldar Cave (Khorramabad Valley, western Iran). Sci. Rep. 7, 43460.

Becerra-Valdivia, L., Douka, K., Comeskey, D., Bazgir, B., Conard, N.J., Marean, C.W., Ollé, A., Otte, M., Tumung, L., Zeidi, M., Higham, T.F.G., 2017. Chronometric investigations of the Middle to Upper Paleolithic transition in the Zagros Mountains using AMS radiocarbon dating and Bayesian age modelling. J. Hum. Evol. 109, 57–69.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–160.

Bertacchi, A., Starkovich, B.M., Conard, N.J., 2021. The zooarchaeology of Sirgenstein Cave: a Middle and Upper Paleolithic site in the Swabian Jura, SW Germany. J. Paleolit. Archaeol. 4, 7.

Biglari, F., Shidrang, S., 2019. Rescuing the Paleolithic Heritage of Hawraman, Kurdistan, Iranian Zagros. Near East. Archaeol. 82, 4.

Binford, L.R., 1977. Forty-seven trips: a case study in the character of archaeological formation processes. In: Wright, R.V.S. (Ed.), Stone Tools as Cultural Markers. Australian Institute of Aboriginal Studies, Canberra, pp. 24–36.

Binford, L.R., 1978. Nunamiut Ethnoarchaeology. Academic Press, New York.

Binford, L.R., 1979. Organization and formation processes: looking at curated technologies. J. Anthropol. Res. 35(3), 255–273.

Blanco-Lapaz, A., Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. Late Pleistocene environments in the Southern Zagros of Iran and their implications for human evolution. Archaeol. Anthropol. Sci. 14, 161.

Blasco, R., Rosell, J., Fernández Peri, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). Quat. Sci. Rev. 70, 124–144.

Blasco, R., Cochard, D., Colonese, A.C., Laroulandie, V., Meier, J., Morin, E., Rufà, A., Tassoni, L., Thompson, J.C., 2022. Small animal use by Neanderthals. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals: Understanding Behavioral Complexity in the Late Middle Palaeolithic. Elsevier Academic Press, London, pp. 123-143.

Bobek, H., 1968. Vegetation. In: Fisher, W.B. (Ed.), The Cambridge History of Iran, vol. 1. The Land of Iran. Cambridge University Press, Cambridge, pp. 280–293.

Boscato, P., Crezzini, J., 2012. Middle-Upper Palaeolithic transition in southern Italy: Uluzzian macromammals from Grotta del Cavallo (Apulia). Quat. Int. 252, 90–98.

Braidwood, R.J., Howe, B., 1960. Prehistoric Investigations in Iraqi Kurdistan. University of Chicago Press, Chicago.

Bretzke, K., Conard, N.J., 2017. Not just a crossroad: population dynamics and changing material culture in southwestern Asia during the Late Pleistocene. Curr. Anthropol. 58 (S17), S449–S462.

Broughton, J.M., 1994. Declines in mammalian foraging efficiency during the Late Holocene, San Francisco Bay, California. J. Anthropol. Archaeol. 13, 37–401.

Burger, O., Hamilton, M.J., Walker, R., 2005. The prey as patch model: optimal handling of resources with diminishing returns. J. Archaeol. Sci. 32, 1147–1158.

Cáceres, I., Bravo, P., Esteban, M., Expósito, I., Saladié, P., 2002. Fresh and heated bones breakage. An experimental approach. In: De Renzi, M., Pardo, M., Belinchón, M., Peñalver, E., Montoya, P., Márquez-Aliaga, A. (Eds.), Current Topics on Taphonomy and Fossilization. Ayuntamiento de Valencia, Valencia, pp. 471–479.

Cain, C.R., 2005. Using burned animal bone to look at Middle Stone Age occupation and behavior. J. Archaeol. Sci. 32, 873–884.

Cannon, M.D., 2003. A model of central place forager prey choice and an application to faunal remains from the Mimbres Valley, New Mexico. J. Anthropol. Archaeol. 22, 1–25.

Campana, D.V., Crabtree, P., 2019. Evidence for skinning and craft activities from the Middle Paleolithic of Shanidar Cave, Iraq. J. Archaeol. Sci. Rep. 25, 7–14.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

Clark, J.L., Plug, I., 2008. Animal exploitation strategies during the South African Middle Stone Age: Howiesons Poort and post-Howiesons Poort fauna from Sibudu Cave. J. Hum. Evol. 54, 886–898.

Conard, N.J., Ghasidian, E., 2011. The Rostamian cultural group and the taxonomy of the Iranian Upper Palaeolithic. In: Conard, N.J., Drechsler, P., Morales, A. (Eds.), Between Sand and Sea, the Archaeology and Human Ecology of South-Western Asia. Kerns Verlag, Tübingen, pp. 33–52.

Conard, N.J., Zeidi, M., 2019. New research on the Paleolithic occupation of Ghar-e Boof, Fars Province. J. Iranian Center Archaeol. Res. 2, 7–16.

Conard, N.J., Ghasidian, E., Heydari, S., Zeidi, M., 2006. Report on the 2005 Survey of the Tübingen Iranian Stone Age Research Project in the Provinces of Esfahan, Fars and Kohgiluyeh-Boyerahmad. In: Azarnoush, M. (Ed.), Archaeological Reports 5. ICAR, Tehran, pp. 9–34.

Conard, N.J., Ghasidian, E., Heydari, S., Naderi, R., Zeidi, M., 2007. The 2006 season of the Tübingen-Iranian Stone Age Research Project in the Provinces of Fars and Markazi. In: Fazeli, H. (Ed.), 9th Annual Report of Archaeological Organisation. ICAR, Tehran, pp. 43–67.

Conard, N.J., Bolus, M., Münzel, S.C., 2012. Middle Paleolithic land use, spatial organization and settlement intensity in the Swabian Jura, southwestern Germany. Quat. Int. 247, 236–245.

Conard, N.J., Miller, C.E., Riehl, S., Zeidi, M., 2023. Testing the Palaeolithic harvesting hypothesis at Ghar-e Boof with improved botanical recovery. In: Richter, T., Darabi, H. (Eds.), The Epipalaeolithic and Neolithic in the Eastern Fertile Crescent. Revisiting the Hilly Flanks. Routledge, London, pp. 350–370.

Coon, C.S., 1951. Cave Explorations in Iran, 1949. University Museum, University of Pennsylvania, Philadelphia.

Discamps, E., Jaubert, J., Bachellerie, F., 2011. Human choices and environmental constraints: deciphering the variability of large game procurement from Mousterian to Aurignacian times (MIS 5-3) in southwestern France. Quat. Sci. Rev. 30, 2755–2775.

Djamali, M., de Beaulieu, J.L., Shah-Hosseini, M., Andrieu-Ponel, V., Ponel, P., Amini, A., Akhani, H., Leroy, S.A.G., Stevens, L., Lahijani, H., Brewer, S., 2008. A Late Pleistocene long pollen record from Lake Urmia, NW Iran. Quat. Res. 69, 413–420.

Dogandžić, T., McPherron, S.P., 2013. Demography and the demise of Neandertals: A comment on 'Tenfold population increase in Western Europe at the Neandertal-to-modern human transition'. J. Hum. Evol. 64, 311–313.

Evins, M.A., 1982. The fauna from Shanidar Cave: Mousterian wild goat exploitation in northeastern Iraq. Paléorient 8, 37–58.

Fernández-Jalvo, Y., Andrews, P., 2016. Atlas of Taphonomic Identifications: 1001+ Images of Fossil and Recent Mammal Bone Modification. Springer, New York.

Fernández-López de Pablo, J., Badal, E., Ferrer García, C., Martínez-Ortí, A., Sanchis Serra, A., 2014. Land snails as a diet diversification proxy during the early Upper Palaeolithic in Europe. PLoS ONE 9(8), e104898.

Ferring, C.R., 1986. Rates of fluvial sedimentation: implications for archaeological variability. Geoarchaeology 1(3), 259–274.

Field, H., 1951. Reconnaissance in Southwestern Asia. Southwest. J. Anthropol. 7(1), 86-102.

Fisher, J.W.J., 1995. Bone surface modifications in zooarchaeology. J. Archaeol. Method Theory 2, 7–68.

Flannery, K.V., 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko, P.J., Dimbleby, G.W. (Eds.), The Domestication and Exploitation of Plants and Animals. Duckworth, London, pp. 73–100.

French, J.C., 2015. Demography and the Palaeolithic Archaeological Record. J. Archaeol. Method Theory 23, 150–199.

Ganji, M.H., 1968. Climate. In: Fisher, W.B. (Ed.), The Cambridge History of Iran, vol. 1. The Land of Iran. Cambridge University Press, Cambridge, pp. 212–249.

Garrod, D.A.E., 1930. The Paleolithic of southern Kurdistan: excavations in the caves of Zarzi and Hazar Merd. Bull. Am. Sch. Prehist. Res. 6, 9–43.

Garrod, D.A.E., 1957. Notes sur le Paléolithique Supérieur du Moyen Orient. Bull. Soc. Prehist. Fr. 54, 439–445.

Ghasidian, E., 2014. Early Upper Palaeolithic Occupation at Ghar-E Boof Cave: a Reconstruction of Cultural Traditions in Southern Zagros Mountains of Iran. Kerns Verlag, Tübingen.

Ghasidian, E., Bretzke, K., Conard, N.J., 2017. Excavations at Ghar-e Boof in the Fars Province and its bearing on models for the evolution of the Upper Paleolithic in the Zagros. J. Anthropol. Archaeol. 47, 33–49.

Goder-Goldberger, M., Malinsky-Buller, A., 2022. The Initial Upper Paleolithic and its place within the Middle-to-Upper Paleolithic transition of Southwest Asia: what hides behind the curtain of taxonomies? J. Paleolit. Archaeol. 5, 2.

Grayson, D.K., 1984. Quantitative Zooarchaeology. Academic Press, Orlando.

Grayson, D.K., Delpech, F., 2003. Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France). J. Archaeol. Sci. 30, 1633–1648.

Heshmati, G.A., 2007. Vegetation characteristics of four ecological zones of Iran. Int. J. Plant Prod. 1 (2), 215–224.

Hesse, B., 1989. Paleolithic faunal remains from Ghar-i Khar, western Iran. In: Crabtree, P.J., Campana, D., Ryan, K. (Eds.), Early Animal Domestication and its Cultural Context. MASCA, the

University Museum of Archaeology and Anthropology. University of Pennsylvania, Philadelphia, pp. 37e45.

Heydari, M., Guérin, G., Zeidi, M., Conard, N.J., 2021. Bayesian luminescence dating at Ghar-e Boof, Iran, provides new chronology for Middle and Upper Paleolithic in the southern Zagros. J. Hum. Evol. 151, 102926.

Heydari-Guran, S., 2014. Paleolithic Landscapes of Iran. BAR international series, Oxford.

Heydari-Guran, S., Ghasidian, E., 2020. Late Pleistocene hominin settlement patterns and population dynamics in the Zagros Mountains: Kermanshah region. Archaeol. Res. Asia 21, 100161.

Heydari-Guran, S., Douka, K., Higham, T., Münzel, S.C., Deckers, K., Hourshid, S., Nadari, R., Asiabani, S., Ghasidian, E., 2021a. Early Upper Palaeolithic occupation at Gelimgoush Cave, Kermanshah; West-Central Zagros mountains of Iran. J. Archaeol. Sci. Rep. 38, 103050.

Heydari-Guran, S., Benazzi, S., Talamo, S., Ghasidian, E., Hariri, N., Oxilia, G., Asiabani, S., Azizi, F., Naderi, R., Safaierad, R., Hublin, J.J., Foley, R.A., Mirazón-Lahr, M., 2021b. The discovery of an *in situ* Neanderthal remain in the Bawa Yawan Rockshelter, West-Central Zagros Mountains, Kermanshah. PLoS ONE 16(8), e0253708.

Hodgkins, J.M., Marean, C.W., 2017. New information from old excavations: a comparative analysis of Paleolithic zooarchaeological assemblages from the Zagros Mountains. In: Biglari, F., Mashkour, M., Shidrang, S. (Eds.), The Pleistocene Archaeology of the Iran and Neighboring Regions. National Museum of Iran Paleolithic Studies Series, No. 1. National Museum of Iran, Tehran.

Hole, F., Flannery, K.V., 1967. The Prehistory of southwestern Iran: a preliminary report. Proc. Prehist. Soc. 33, 147–206.

Hothorn, T., Zeileis, A., Farebrother, R.W., Cummins, C., Millo, G., Mitchell, D., 2022. lmtest: Testing Linear Regression Models. R package version 0.9-40.

Ikeda, J., 1979. Preliminary Report of an Archaeological Survey in Arsanjan Area, Fars Province, Iran, 1977. Kyoto University, Kyoto.

Jerardino, A., 1995. The problem with density values in archaeological analysis: a case study from Tortoise Cave, Western Cape, South Africa. S. Afr. Archaeol. Bull. 50(161), 21–27.

Johnson, E. 1989. Human modified bones from early southern Plains Sites. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification, University of Maine Center for the Study of the First Americans, Orono, pp. 431-471.

Jones, E.L., 2012. Upper Paleolithic rabbit exploitation and landscape patchiness: the Dordogne vs. Mediterranean Spain. Quat. Int. 264, 52–60.

Jones, K.T., Metcalfe, D., 1988. Bare bones archaeology: bone marrow indices and efficiency. J. Archaeol. Sci. 15, 415–423.

Kaboli, M., Aliabadian, M., Tohidifar, M., Hashemi, A., Musavi, S.B., Roselaar, C.C., 2016. Atlas of Birds of Iran. Department of Environment of Iran, Tehran.

Karami, M., Ghadirian, T., Faizolahi, K., 2016. The Atlas of Mammals of Iran. Department of Environment of Iran, Tehran.

Kelly, R.L., 1995. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. Smithsonian Institution Press, Washington.

Kuhn, S.L., Clark, A.E., 2015. Artifact densities and assemblage formation: evidence from Tabun Cave. J. Anthropol. Archaeol. 38, 8–16.

Kuhn, S.L., Stiner, M.C., Güleç, E., Özer, I., Yılmaz, H., Baykara, I., Açıkkol, A., Goldberg, P., Martínez Molina, K., Ünay, E., Suata-Alpaslan, F., 2009. The early Upper Paleolithic occupations at Üçağızlı Cave (Hatay, Turkey). J. Hum. Evol. 56, 87–113.

Laroulandie, V., Morin, E., Soulier, M-C., Castel, J.-C., 2020. Bird procurement by humans during the Middle and early Upper Paleolithic of Europe: new data for the Aurignacian of southwestern France. Quat. Int. 543, 16–24.

Liu, C., Shimelmitz, R., Friesem, D.E., Yeshurun, R., Nadel, D., 2020. Diachronic trends in occupation intensity of the Epipaleolithic site of Neve David (Mount Carmel, Israel): A lithic perspective. J. Anthropol. Archaeol. 60, 101223.

Lupo, K.D., Fancher, J.M., Schmitt, D.N., 2013. The taphonomy of resource intensification: zooarchaeological implications of resource scarcity among Bofi and Aka Forest foragers. J. Archaeol. Method Theory 20, 420–447.

Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge.

Lyman, R.L., 2008. Quantitative Paleozoology. Cambridge Manuals in Archaeology. Cambridge University Press, New York.

Madsen, D.B., Schmitt, D.N., 1998. Mass collecting and the diet breadth model: a Great Basin Example. J. Archaeol. Sci. 25, 445–455.

Manne, T.H., 2014. Early Upper Paleolithic bone processing and insights into small-scale storage of fats at Vale Boi, southern Iberia. J. Archaeol. Sci. 43, 111–123.

Manne, T., Bicho, N., Marreiros, J., Cascalheira, J., Évora, M., 2012. Intensive subsistence practices at Vale Boi, an Upper Paleolithic site in southwestern Portugal. Quat. Int. 264, 83–99.

Marean, C.W., 1998. A critique of the evidence for scavenging by Neandertals and early modern humans: new data from Kobeh Cave (Zagros Mountains, Iran) and Die Kelders Cave 1 Layer 10 (South Africa). J. Hum. Evol. 35, 111–136.

Marean, C.W., Kim, S.Y., 1998. Mousterian large-mammal remains from Kobeh Cave. Behavioral implications for Neanderthals and early modern humans. Curr. Anthropol. 9(S1), S79–S113.

Marín-Arroyo, A.B., 2011. Palaeolithic human subsistence in Mount Carmel (Israel). A taphonomic assessment of Middle and Early Upper Palaeolithic faunal remains from Tabun, Skhul and el-Wad. Int. J. Ostearchaeol. 23(3), 254–273.

Mashkour, M., Radu, V., Mohaseb, A., Hashemi, N., Otte, M., Shidrang, S., 2009. The Upper Paleolithic faunal remains from Yafteh cave (central Zagros) 2005 campaign. A preliminary study. In: Otte, M., Biglari, F., Jaubert, J. (Eds.), Le Paleolithique D'Iran. Archaeopress, Oxford, pp. 73–85.

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran). Quat. Sci. Rev. 279, 107350.

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2023. Evidence of diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros). Sci. Rep. 13, 19006.

Mellars, P., French, J.C., 2011. Tenfold Population Increase in Western Europe at the Neandertal–to–modern human transition. Science 333, 623–627.

Morin, E., 2007. Fat composition and Nunamiut decision-making: a new look at the marrow and bone grease indices. J. Archaeol. Sci. 34, 69–82.

Morin, E., 2008. Evidence for declines in human population densities during the early Upper Paleolithic in western Europe. Proc. Natl. Acad. Sci. USA 105, 48–53.

Morin, E., 2010. Taphonomic implications of the use of bone as fuel. Palethnologie 2, 209–217.

Morin, E., 2012. Reassessing Paleolithic Subsistence. Cambridge University Press, Cambridge.

Morin, E., Bliege Bird, R., Bird, D., 2020. Mass procurement and prey rankings: insights from the European rabbit. Archaeol. Anthropol. Sci. 12, 262.

Morin, E., Bird, D., Winterhalder, B., Bliege Bird, R., 2022. Deconstructing hunting returns: can we reconstruct and predict payoffs from pursuing prey? J. Archaeol. Method Theory 29, 561–623.

Mozaffari, O., Kamali, K., Fahimi, H., 2016. The Atlas of Reptiles of Iran. Department of Environment of Iran, Tehran.

Munro, N.D., 2004. Zooarchaeological measures of hunting pressure and occupation intensity in the Natufian. Curr. Anthropol. 45, S5–S33.

Munro, N.D., Bar-Oz, G., 2005. Gazelle bone fat processing in the Levantine Epipaleolithic. J. Archaeol. Sci. 32, 223–239.

Munro, N.D., Kennerty, M., Meier, J.S., Samei, S., al-Nahar, M., Olszewski, D.I., 2016. Human hunting and site occupation intensity in the Early Epipaleolithic of the Jordanian western highlands. Quat. Int. 396, 31–39.

Münzel, S.C., Conard, N.J., 2004. Change and continuity in subsistence during the Middle and Upper Palaeolithic in the Ach Valley of Swabia (South-west Germany). Int. J. Ostearchaeol. 4 (3–4), 225–243.

Nagaoka, L., 2002. The effects of resource depression on foraging efficiency, diet breadth, and patch use in southern New Zealand. J. Anthropol. Archaeol. 21, 419–442.

Nagaoka, L., 2005. Declining foraging efficiency and moa carcass exploitation in southern New Zealand. J. Archaeol. Sci. 32, 1328–1338.

Nowroozi, R. 1997. Archaeological survey of prehistoric localities in Nourabad Mmasani plain. Unpublished Master thesis. University of Tehran (in Farsi).

Olszewski, D.I., 2017. Assessing patterning in the Upper Paleolithic and Epipaleolithic at Warwasi, Iran. Int. J. Soc. Iranian Archaeol. 3, 1–12.

Olszewski, D.I., Dibble, H.L., 1994. The Zagros Aurignacian. Curr. Anthropol. 35, 68–75.

Olszewski, D.I., Dibble, H.L., 2006. To be or not to be Aurignacian: the Zagros Upper Paleolithic. In: Bar-Yosef, O., Zilhão, J. (Eds.), Towards a Definition of the Aurignacian. Trabalhos de Arqueologia, vol. 45. Instituto Português de Arqueologia, Lisboa, pp. 355–373.

Otte, M., Biglari, F., Flas, D., Shidrang, S., Zwyns, H., Mashkour, M., Naderi, R., Mohased, A., Hashemi, N., Darvish, J., Radu, V., 2007. The Aurignacian in the Zagros region: new research at Yafteh cave, Lorestan, Iran. Antiquity 81, 82–96.

Pérez, L., Sanchis, A., Hernández, C.M., Galván, B., Sala, R., Mallol, C., 2017. Hearths and bones: An experimental study to explore temporality in archaeological contexts based on taphonomical changes in burnt bones. J. Archaeol. Sci. Rep. 11, 287–309.

Perkins, D.J., 1964. Prehistoric fauna from Shanidar, Iraq. Science 144, 1565–1566.

Pianka, E.R., 2000. Evolutionary Ecology, sixth ed. Addison Wesley Education Publishers, Inc., Benjamin/Cummings, San Francisco.

Piperno, M., 1972. Jahrom, a Middle Palaeolithic site in Fars, Iran. East and West 22, 183–197.

Piperno, M., 1974. Upper Paleolithic caves in southern Iran, preliminary report. East and West 24, 9–13.

Pomeroy., E., Mirazón-Lahr, M., Crivellaro, F., Farr, L., Reynolds, T., Hunt, C.O., Barker, G., 2017. Newly discovered Neanderthal remains from Shanidar Cave, Iraqi Kurdistan, and their attribution to Shanidar 5. J. Hum. Evol. 111, 102–118.

Pomeroy, E., Bennett, P., Hunt, C.O., Reynolds, T., Farr, L., Frouin, M., Holman, J., Lane, R., French, C., Barker, G., 2020. New Neanderthal remains associated with the 'flower burial' at Shanidar Cave. Antiquity 94(373), 11–26.

Powell, A., Shennan, S., Thomas, M.G., 2009. Late Pleistocene demography and the appearance of modern human behavior. Science 324, 1298–1301.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Real, C., Villaverde, V., 2022. Subsistence activities and settlement dynamics of the first anatomically modern humans in the central–eastern Mediterranean Iberia: New insights from Cova de les Cendres (Alicante, Spain). Quat. Sci. Rev. 285, 107533.

Reynolds, T., Boismier, W., Farr, L., Hunt, C., Abdulmutalb, D., Barker, G., 2016. New investigations at Shanidar Cave, Iraqi Kurdistan. In: Kopanias, K., MacGinnis, J. (Eds.), The Archaeology of the Kurdistan Region of Iraq and Adjacent Regions. Archaeopress, Oxford, pp. 29–48.

Reynolds, T., Farr, L., Hill, E., Hunt, C., Jones, S., Gratuze, B., Nymark, A., Abdulmutalb, D., Barker, G., 2018. Shanidar Cave and the Baradostian, a Zagros Aurignacian industry. L'Anthropologie 122, 737–748.

Riel-Salvatore, R., Barton, C.M., 2004. Late Pleistocene technology, economic behavior, and land-use dynamics in southern Italy. Am. Antiq. 69(2), 257–274.

Romandini, M., Crezzini, J., Bortolini, E., Boscato, P., Boschin, F., Carrera, L., Nannini, N., Antonio Tagliacozzo, A., Terlato, G., Arrighi, S., Badino, F., Figus, C., Lugli, F., Marciani, G., Oxilia, G., Moroni, A., Negrino, F., Peresani, M., Riel-Salvatore, J., Ronchitelli, A., Spinapolice, E.E., Benazzi, S., 2020. Macromammal and bird assemblages across the late Middle to Upper Palaeolithic transition in Italy: an extended zooarchaeological review. Quat. Int. 551, 188–223.

Rosenberg, M.S., 1979. Eshkaft-e Gavi (The Malyan Project), Iran. J. British Institute of Persian Studies 17, 148–149.

Rosenberg, M.S., 1985. Report on the 1978 sondage at Eshkaft-e Gavi, Iran. J. British Institute for Persian Studies 23, 51–62.

Schilt, F.C., 2011. Micromorphology of Upper Paleolithic and Historic Sediments from Boof Cave, Iran. Unpublished Master’s Thesis. Eberhard-Karls Universität Tübingen, Germany.

Scott, J.E., Marean, C.W., 2009. Paleolithic hominin remains from Eshkaft-e Gavi (southern Zagros Mountains, Iran): description, affinities, and evidence for butchery. J. Hum. Evol. 57, 248–259.

Shennan, S., 2001. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. Camb. Archaeol. J. 11(1), 5–16.

Shidrang, S., 2018. The Middle to Upper Paleolithic transition in the Zagros: the appearance and evolution of the Baradostian. In: Nishiaki, Y., Akazawa, T. (Eds.), The Middle and Upper Paleolithic Archeology of the Levant and beyond. Springer International Publishing, Singapore, pp. 133–156.

Shoaee, M.J., Vahdati Nasab, H., Petraglia, M.D., 2021. The Paleolithic of the Iranian Plateau: Hominin occupation history and implications for human dispersals across southern Asia. J. Anthropol. Archaeol. 62, 101292.

Smith, G.M., Spasov, R., Martisius, N.L., Sinet-Mathiot, V., Aldeias, V., Rezek, Z., Ruebens, K., Pederzani, S., McPherron, S.P., Sirakova, S., Sirakov, N., Tsanova, T., Hublin, J.-J., 2021. Subsistence behavior during the Initial Upper Paleolithic in Europe: site use, dietary practice, and carnivore exploitation at Bacho Kiro Cave (Bulgaria). J. Hum. Evol. 161, 103074.

Solecki, R.S., 1958. The Baradostian Industry and the Upper Palaeolithic in the Near East. Unpublished Ph.D. dissertation. Colombia University, USA.

Solecki, R.S., 1963. Prehistory in Shanidar Valley Northern Iraq. Science 139(3551), 179–193.

Solecki, R.S., 1975. Shanidar IV, a Neanderthal flower burial in Northern Iraq. Science 190(4217), 880–881.

Speth, J.D., Clark, J.L., 2006. Hunting and overhunting in the Levantine Late Middle Palaeolithic. Before Farming 3, 1–42.

Starkovich, B.M., 2012. Intensification of small game resources at Klissoura Cave 1 (Peloponnese, Greece) from Middle Paleolithic to Mesolithic. Quat. Int. 264, 17–31.

Starkovich, B.M., 2014. Optimal foraging, dietary change, and site use during the Paleolithic at Klissoura Cave 1 (southern Greece). J. Archaeol. Sci. 52, 39–55.

Starkovich, B.M., 2017. Paleolithic subsistence strategies and changes in site use at Klissoura Cave 1 (Peloponnese, Greece). J. Hum. Evol. 111, 63–84.

Steele, T.E., Klein, R.G., 2009. Late Pleistocene subsistence strategies and resource intensification in Africa. In: Hublin, J.J., Richards, M.P. (Eds.), The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence. Springer Science + Business Media B. V., New York, pp. 113–126.

Stein, J.K., Deo, J.N., Phillips, L.S., 2003. Big sites–short time: accumulation rates in archaeological sites. J. Archaeol. Sci. 30, 297–316.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Monographs in Behavior and Ecology. Princeton University Press, Princeton.

Stiner, M.C., 1994. Honor Among Thieves: a Zooarchaeological Study of Neandertal Ecology. Princeton University Press, Princeton.

Stiner, M.C., 2001. Thirty years on the “Broad Spectrum Revolution” and Paleolithic demography. Proc. Natl. Acad. Sci. U.S.A. 98, 6993–6996.

Stiner, M.C., 2005. The Faunas of Hayonim Cave, Israel: a 200,000 Year Record of Paleolithic Diet, Demography, and Society. In: Peabody Museum of Archaeology and Ethnology, vol. 48. American School of Prehistoric Research Bulletin, Cambridge, Massachusetts. Harvard University.

Stiner, M.C., 2009. Prey choice, site occupation intensity & economic diversity in the Middle e early Upper Palaeolithic at the Üçağızlı Caves, Turkey. Before Farming 3, 1–20.

Stiner, M.C., Munro, N.D., 2002. Approaches to Prehistoric Diet Breadth, Demography, and Prey Ranking Systems in Time and Space. J. Archaeol. Method Theory 9, 181–214.

Stiner, M.C., Munro, N.D., 2011. On the evolution of diet and landscape during the Upper Paleolithic through Mesolithic at Franchti Cave (Peloponnese, Greece). J. Hum. Evol. 60, 618–636.

Stiner, M.C., Weiner, S., Bar-Yosef, O., Kuhn, S.L., 1995. Differential burning, fragmentation and preservation of archaeological bone. J. Archaeol. Sci. 22, 223–237.

Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E., Bar-Yosef, O., 1999. Paleolithic population growth pulses evidenced by small animal exploitation. Science 283, 190–194.

Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small-game use, the Broad-Spectrum Revolution, and Paleolithic demography. Curr. Anthropol. 41, 39–73.

Stiner, M.C., Munro, N.D., Starkovich, B.M., 2012. Material input rates and dietary breadth during the Upper Paleolithic through Mesolithic at Franchthi and Klissoura 1 Caves (Peloponnese, Greece). Quat. Int. 275, 30–42.

Trinkaus, E., 2018. Pleistocene human remains from Iran. In: Biglari, F., Shidrang, S., Mashkour, M. (Eds.), The Pleistocene Archaeology of the Iranian Plateau, Iraq and the Caucasus. National Museum of Iran, Tehran, pp. 53–63.

Tryon, C.A., Faith, J.T., 2016. A demographic perspective on the Middle to Later Stone Age transition from Nasera rockshelter, Tanzania. Phil. Trans. R. Soc. B 371, 20150238.

Tsanova, T., 2013. The beginning of the Upper Paleolithic in the Iranian Zagros. A taphonomic approach and techno-economic comparison of early Baradostian assemblages from Warwasi and Yafteh (Iran). J. Hum. Evol. 65, 39–64.

Turnbull, P., 1975. The mammalian fauna of Warwasi Rock Shelter, West-Central Iran. Fieldiana Geol. 33, 141–155.

Ugan, A., 2005. Does size matter? Body size, mass collecting, and their implications for understanding prehistoric foraging behavior. Am. Antiq. 70, 75–89.

Vaesen, K., Dusseldorp, G.L., Brandt, M.J., 2021. An emerging consensus in palaeoanthropology: demography was the main factor responsible for the disappearance of Neanderthals. Sci. Rep. 11, 4925.

Vahdati Nasab, H., Clark, G.A., Torkamandi, S., 2013. Late Pleistocene dispersal corridors across the Iranian Plateau: a case study from Mirak, a Middle Paleolithic site on the northern edge of the Iranian Central desert (Dasht-e Kavir). Quat. Int. 300, 267–281.

Val, A., de la Peña, P., Wadley, L., 2016. Direct evidence for human exploitation of birds in the Middle Stone Age of South Africa: the example of Sibudu Cave, KwaZulu-Natal. J. Hum. Evol. 99, 107–123.

Wasylikowa, K., 2005. Palaeocology of Lake Zeribar, Iran, in the Pleniglacial, Lateglacial and Holocene, reconstructed from plant macrofossils. Holocene 15(5), 720–735.

Weitzel, E.M., 2023. Resilience of white-tailed deer (*Odocoileus virginianus*) to human hunting in precolonial New England: The faunal remains from the Morgan Site (6HT120), Rocky Hill, Connecticut. J. Archaeol. Sci. Rep. 48, 103913.

Yeshurun, R., Schneller-Pels, N., Barzilai, O., Marder, O., 2021. Early Upper Paleolithic subsistence in the Levant: zooarchaeology of the Ahmarian-Aurignacian sequence at Manot Cave, Israel. J. Hum. Evol. 160, 102619.

Young, T.C., Smith, P.E.L., 1966. Research in the Prehistory of Central Western Iran. Science 153, 386–391.

Yravedra-Sainz de los Terreros, J., Gómez-Castanedo, A., Aramendi-Picado, J., Montes-Barquín, R., Sanguino-González, J., 2016. Neanderthal and *Homo sapiens* subsistence strategies in the Cantabrian region of northern Spain. Archaeol. Anthropol. Sci. 8, 779–803.

Zanolli, C., Biglari, F., Mashkour, M., Abdi, K., Monchot, H., Debue, K., Mazurier, A., Bayle, P., Le-Luyer, M., Rougier, H., Trinkaus, E., Macchiarelli, R., 2019, A Neanderthal from the Central Western Zagros, Iran. Structural reassessment of the Wezmeh 1 maxillary premolar. J. Hum. Evol. 135, 102643.

Zeidi, M., Conard, N.J., 2019. The fourth season of excavation at Ghar-e Boof, Rostam County, Fars Province. In: Shirazi, R.A. (Ed.), 16th Annual Symposium of the Iranian Archaeology. Iranian Center for Archaeological Research, Tehran, pp. 234–238 (in Farsi).

Zeidi, M., McCall, B., Khosrowzadeh, A. 2006. Survey of Dasht-e Rostam-e Yek and Dasht-e Rostam-e Do. In: Potts, D.T., Roustaei, K. (Eds.), The Mamasani Archaeological Project Stage One: a report on the first two seasons of the ICAR – University of Sydney Expedition to the Mamasani District, Fars Province, Iran. Iranian Center for Archaeological Research, Tehran, pp. 147–168.

Zohary, M., 1973. Geobotanical foundations of the Middle East, vol. 1–2. Gustav Fischer Verlag, Stuttgart.

SUPPLEMENTARY ONLINE MATERIAL

Prey choice and changes in site occupation intensity during the Middle and Upper Paleolithic at Ghar-e Boof (southern Zagros Mountains, Iran)

Mario Mata-González[1*], Britt M. Starkovich[1,2], Mohsen Zeidi[2,3], and Nicholas J. Conard[1,2,3]

[1]Institute for Archaeological Sciences, University of Tübingen, Hölderlinstr. 12, 72074 Tübingen, Germany

[2]Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstr. 12, 72074 Tübingen, Germany

[3]Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Schloss Hohentübingen, D-72070 Tübingen, Germany

*Corresponding author:

E-mail address: mario.mata-gonzalez@student.uni-tuebingen.de

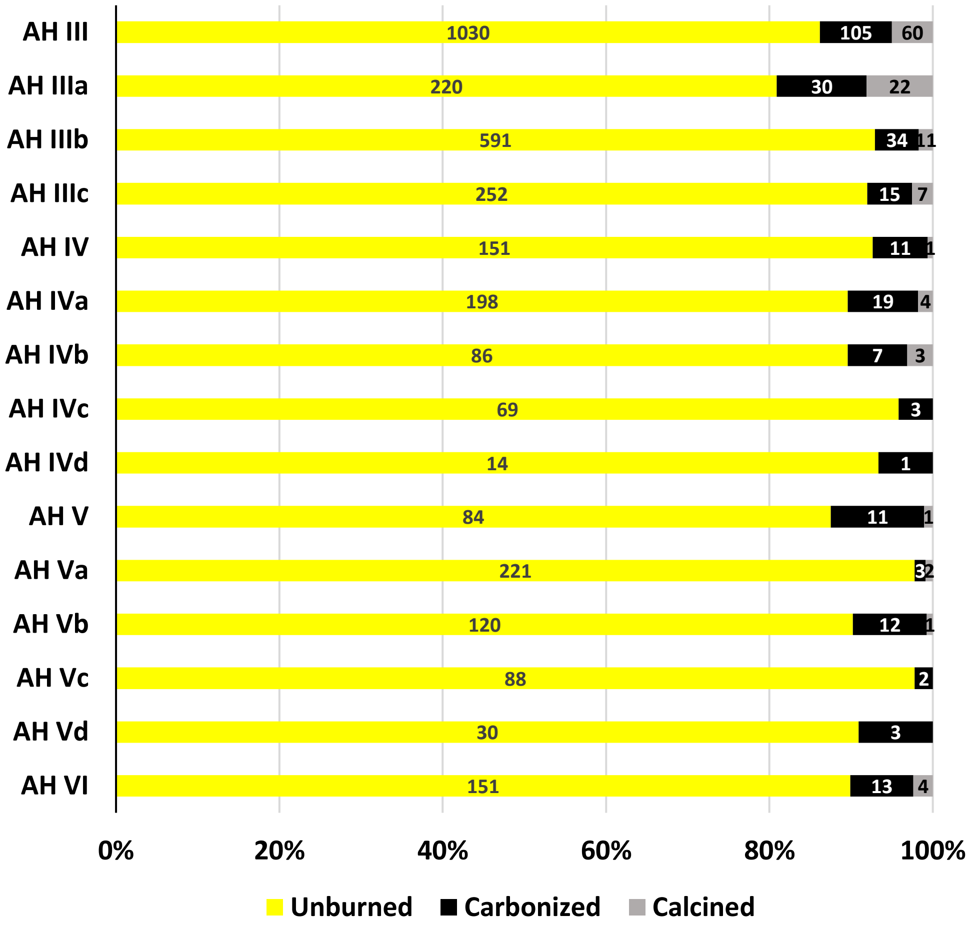


Fig S1. Ghar-e Boof. NISP count and relative proportion of unburned and burned (carbonized/ calcined) bones by layer. Data from Mata-González et al. (2022, 2023). Although in Mata-González et al. (2022) we included small bird and hedgehog specimens in the burning analysis, these taxa are not considered here because they were not accumulated by humans (see Blanco-Lapaz et al., 2022).

Table S1. Ghar-e Boof. Summary statistics for ungulate bone length (cm) by layer. Tooth remains are not included.

Layers	*n*	Mean (cm)	Standard deviation	Median	Interquartile range
III	694	3.9	2.4	3.3	2.8
IIIa	145	3.6	2.0	3.2	2.7
IIIb	375	3.8	2.4	3.4	3.0
IIIc	165	4.0	2.4	3.5	3.1
IV	90	3.4	2.1	3.3	2.7
IVa	187	3.3	2.0	2.8	2.6
IVb	65	4.1	2.1	4.0	3.5
IVc	47	4.5	2.9	3.7	3.6
IVd	11	4.6	2.6	4.2	3.7
V	64	3.8	1.9	3.7	2.6
Va	154	3.8	2.2	3.3	3.1
Vb	86	3.3	1.9	3.0	2.5
Vc	58	3.6	1.9	3.4	2.6
Vd	20	3.7	2.2	4.0	3.4
VI	159	4.3	2.5	3.9	3.1

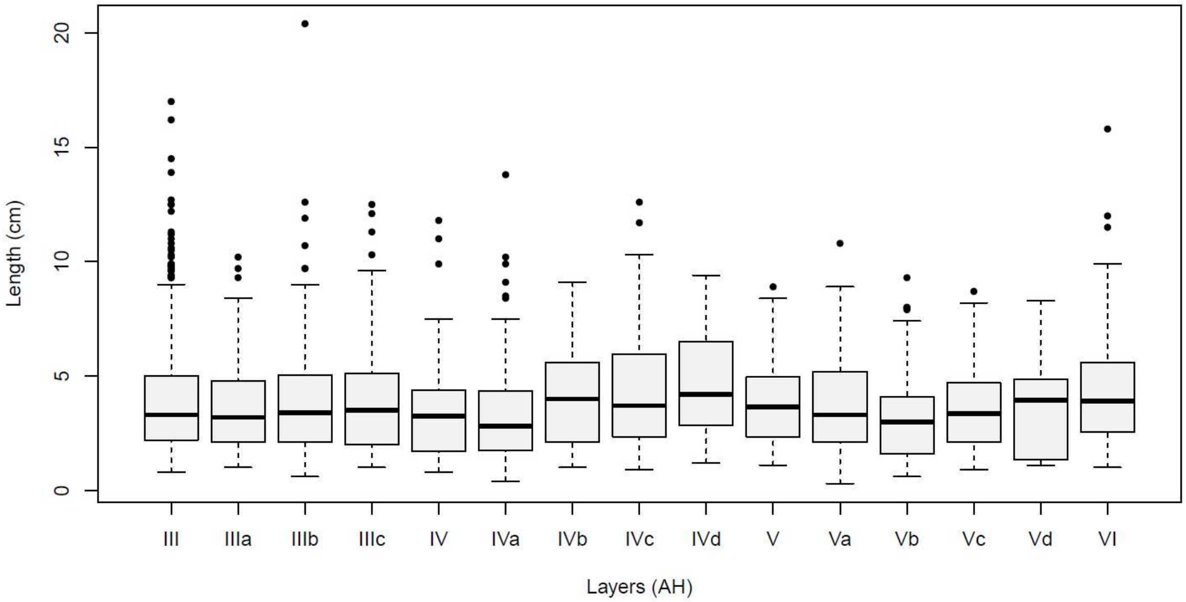


Fig. S2. Ghar-e Boof. Box plots of the length (cm) of ungulate bone fragments by layer. Black lines indicate median, the boxes represent the interquartile range, and the black dots are outliers.

Table S2

Ghar-e Boof. Number of identified species (NISP) and Minimum Number of Individuals (MNI) by layer for each taxon or prey body size. Data from Mata-González et al. (2022, 2023).

	III		*IIIa*		*IIIb*		*IIIc*		*IV*		*IVa*		*IVb*		*IVc*		*IVd*		*V*		*Va*		*Vb*		*Vc*		*Vd*		*VI*		*Total*	
Taxon	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Ungulate																																
Small ungulate	68	NA*	9	NA	34	NA	14	NA	6	NA	12	NA	2	NA	0	NA	0	NA	4	NA	17	NA	11	NA	5	NA	0	NA	15	NA	197	NA
Gazelle (*Gazella* sp.)	34	2	9	1	18	1	5	1	6	1	6	1	1	1	2	1	0	0	1	1	1	1	1	1	0	0	6	1	6	1	96	14
Small/medium ungulate	100	NA	8	NA	40	NA	21	NA	11	NA	15	NA	2	NA	2	NA	1	NA	2	NA	9	NA	11	NA	9	NA	4	NA	16	NA	251	NA
Gazelle/goat (*Gazella/Capra*)	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Medium ungulate	439	NA	89	NA	216	NA	113	NA	54	NA	95	NA	51	NA	35	NA	7	NA	52	NA	111	NA	57	NA	36	NA	16	NA	112	NA	1483	NA
Sheep (*Ovis* sp.)	19	2	3	1	7	1	2	1	3	1	6	1	1	1	0	0	0	0	0	0	2	1	4	1	0	0	0	0	0	0	47	10
Wild goat (*Capra aegagrus*)	95	5	23	1	50	3	6	1	8	1	10	1	7	1	10	1	0	0	4	1	2	1	1	1	7	1	0	0	9	2	232	20
Sheep/goat (*Ovis/Capra*)	105	3	22	1	63	2	23	1	6	1	27	1	2	1	2	1	3	1	4	1	11	1	9	1	23	2	1	1	26	1	327	19
Medium/large ungulate	11	NA	2	NA	5	NA	0	NA	1	NA	4	NA	0	NA	0	NA	2	NA	0	NA	4	NA	0	NA	0	NA	1	NA	3	NA	33	NA
Large ungulate	11	NA	6	NA	11	NA	5	NA	2	NA	15	NA	2	NA	3	NA	0	NA	3	NA	10	NA	2	NA	2	NA	0	NA	2	NA	74	NA
Red deer (*Cervus elaphus*)	0	0	0	0	4	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	3
Wild pig (*Sus scrofa*)	3	1	0	0	2	1	2	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	10	6
Equid (*Equus* sp.)	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	3	3
Large/very large ungulate	3	NA	0	NA	1	NA	0	NA	1	NA	2	NA	2	NA	1	NA	0	NA	0	NA	0	NA	0	NA	1	NA	0	NA	1	NA	12	NA
Very large ungulate	2	NA	0	NA	1	NA	0	NA	0	NA	4	NA	0	NA	0	NA	0	NA	1	NA	1	NA	1	NA	0	NA	0	NA	0	NA	10	NA
Wild cattle (*Bos primigenius*)	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	3
Carnivore																																
Small carnivore	0	NA	0	NA	3	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	3	NA
Wild Cat (*Felis* sp.)	2	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2
Red fox (*Vulpes vulpes*)	4	1	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	8	4
Large carnivore	2	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	1	NA	0	NA	0	NA	0	NA	0	NA	3	NA
Leopard (*Panthera* cf. *pardus*)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	1	0	0	0	0	0	0	0	0	0	0	5	2(1)**
Reptile																																
Tortoises (*Testudo* sp.)	115	2	41	1	22	1	28	1	52	1	23	1	11	1	8	1	2	1	23	1	57	2	34	1	27	1	10	1	0	0	453	16
Fish																																
Indet. Leuciscinae	1	NA	1	NA	8	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	10	NA
Nase (*Chondrostoma* sp.)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Birds																																
Medium birds	199	NA	55	NA	160	NA	50	NA	17	NA	8	NA	17	NA	11	NA	0	NA	3	NA	12	NA	9	NA	6	NA	3	NA	5	NA	555	NA
Partridge (*Alectoris* cf. *chukar*)	92	11	16	2	31	4	8	2	2	1	3	2	3	1	5	2	1	1	1	1	1	1	3	1	0	0	0	0	1	1	167	30
Dove (Cf. *Streptopelia/Columba*)	2	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
Large birds	9	NA	2	NA	4	NA	4	NA	0	NA	0	NA	0	NA	1	NA	0	NA	0	NA	1	NA	0	NA	0	NA	0	NA	0	NA	21	NA
Huge birds	0	NA	1	NA	0	NA	2	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	0	NA	3	NA
Total	1320	34	287	7	685	18	285	10	169	6	233	10	102	7	81	7	17	4	102	6	241	8	144	7	116	4	41	3	199	7	4022	138(7)**

*NA (Not Applicable).

**We recovered all the Leopard's remains just at the transition between AH IVd and V, and within an interval of 7 cm in depth. Despite being recorded in two different layers, these specimens may belong to a single individual on the basis of similar size and age (see Mata-González et al., 2023).

Table S3. Ghar-e Boof. Prey body-size groups (NISP) and their relative proportions by layer. Data from Mata-González et al. (2022, 2023). Prey body-size groups are as follows: very large ungulates (wild cattle), large ungulates (red deer, wild pig and equids), medium ungulates (sheep/goat), small ungulates (gazelle), small carnivores (fox/cat sized), large carnivores (large felids), small, slow-moving game (tortoises), small, fast-moving game (medium -Galliformes/Columbiformes-, large -small raptors-, and huge -large raptors- birds, and fish; after Mata-González et al., 2022).

	III		*IIIa*		*IIIb*		*IIIc*		*IV*		*IVa*		*IVb*		*IVc*		*IVd*		*V*		*Va*		*Vb*		*Vc*		*Vd*		*VI*		*Total*	
Taxon	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Very large ungulate	3	0.3	0	0.0	1	0.2	0	0.0	0	0.0	5	2.4	0	0.0	0	0.0	0	0.0	1	1.0	1	0.4	1	0.8	0	0.0	0	0.0	2	1.1	14	0.4
Large ungulate	15	1.2	6	2.2	17	2.7	8	3.0	2	1.3	17	8.0	3	3.1	4	5.1	0	0.0	3	3.0	10	4.4	3	2.3	2	1.9	0	0.0	3	1.7	93	2.5
Medium ungulate	658	54.6	137	49.5	336	52.6	144	54.6	71	45.5	138	65.1	61	62.2	47	60.3	10	71.4	60	60.0	126	55.3	71	53.4	66	62.3	17	47.2	147	82.1	2089	56.1
Small ungulate	102	8.5	18	6.5	52	8.2	19	7.2	12	7.7	18	8.5	3	3.1	2	2.6	0	0.0	5	5.0	18	7.9	12	9.0	5	4.7	6	16.7	21	11.7	293	7.9
Large carnivore	2	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	7.1	4	4.0	1	0.4	0	0.0	0	0.0	0	0.0	0	0.0	8	0.2
Small carnivore	6	0.5	0	0.0	6	0.9	1	0.4	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.4	0	0.0	0	0.0	0	0.0	0	0.0	14	0.4
Small, slow-moving	115	9.5	41	14.8	22	3.4	28	10.6	52	33.3	23	10.9	11	11.2	8	10.3	2	14.3	23	23.0	57	25.0	34	25.6	27	25.5	10	27.8	0	0.0	453	12.2
Small, fast-moving	304	25.2	75	27.2	204	32.0	64	24.2	19	12.2	11	5.2	20	20.4	17	21.8	1	7.1	4	4.0	14	6.1	12	9.0	6	5.7	3	8.3	6	3.4	760	20.4
Total	1205	100.0	277	100.0	638	100.0	264	100.0	156	100.0	212	100.0	98	100.0	78	100.0	14	100.0	100	100.0	228	100.0	133	100.0	106	100.0	36	100.0	179	100.0	3724	100.0

Table S4. Ghar-e Boof. Counts of different classes of lithic artifacts by layer.

Layer	Culture (period)	Cores	Tools (modified)	Flakes (unmodified)	Small debitage	Micro-debitage	Total
AH III	Rostamian (UP)	563	462	17574	22293	5982	46874
AH IIIa	Rostamian (UP)	38	16	1379	1774	797	4004
AH IIIb	Rostamian (UP)	51	80	2013	2323	925	5392
AH IIIc	Rostamian (UP)	17	38	958	1165	475	2653
AH IV	Rostamian (UP)	4	21	209	167	43	444
AH IVa	Rostamian (UP)	1	8	163	128	31	331
AH IVb	Rostamian (UP)	2	2	113	121	41	279
AH IVc	MP-UP (?)	2	6	84	69	13	174
AH IVd	MP-UP (?)	0	1	11	8	1	21
AH V	MP	1	12	56	61	3	133
AH Va	MP	3	24	172	176	53	428
AH Vb	MP	1	11	72	82	9	175
AH Vc	MP	0	8	90	75	14	187
AH Vd	MP	0	6	46	56	9	117
AH VI	MP	2	20	101	56	13	192
Total	-	685	715	23041	28554	8409	61404

References:

Blanco-Lapaz, A., Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. Late Pleistocene environments in the southern Zagros of Iran and their implications for human evolution. Archaeol. Anthropol. Sci. 14, 161.

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2022. New zooarchaeological perspectives on the early Upper Paleolithic Rostamian sequence of Ghar-e Boof (southern Zagros Mountains, Iran). Quat. Sci. Rev. 279, 107350.

Mata-González, M., Starkovich, B.M., Zeidi, M., Conard, N.J., 2023. Evidence of diverse animal exploitation during the Middle Paleolithic at Ghar-e Boof (southern Zagros). Sci. Rep. 13, 19006.