

The 10,000-year biocultural history of fallow deer and its implications for conservation policy

Article

Published Version

Creative Commons: Attribution 4.0 (CC-BY)

Open Access

Baker, K. H. ORCID: <https://orcid.org/0009-0003-7897-9490>,
Miller, H., Doherty, S. ORCID: <https://orcid.org/0000-0002-5503-2734>, Gray, H. W. I., Daujat, J. ORCID:
<https://orcid.org/0009-0000-5470-3500>, Çakırlar, C. ORCID:
<https://orcid.org/0000-0002-7994-0091>, Spassov, N. ORCID:
<https://orcid.org/0000-0002-2891-7457>, Trantalidou, K. ORCID:
<https://orcid.org/0000-0002-3761-0481>, Madgwick, R., Lamb,
A. L. ORCID: <https://orcid.org/0000-0003-1809-4327>, Ameen,
C. ORCID: <https://orcid.org/0000-0002-4580-2125>, Atici, L.
ORCID: <https://orcid.org/0000-0002-4929-173X>, Baker, P.,
Beglane, F., Benkert, H., Bendrey, R. ORCID:
<https://orcid.org/0000-0001-5286-1601>, Binois-Roman, A.
ORCID: <https://orcid.org/0000-0002-7704-3100>, Carden, R. F.
ORCID: <https://orcid.org/0000-0002-2829-4667>, Curci, A.
ORCID: <https://orcid.org/0000-0001-6403-9359>, De Cupere, B.
ORCID: <https://orcid.org/0000-0001-7559-8965>, Detry, C., Gál,
E. ORCID: <https://orcid.org/0000-0002-4226-3218>, Genies, C.
ORCID: <https://orcid.org/0009-0006-3514-0574>, Kunst, G. K.,
Liddiard, R., Nicholson, R., Perdikaris, S. ORCID:
<https://orcid.org/0000-0001-6523-2249>, Peters, J. ORCID:
<https://orcid.org/0000-0003-0894-2628>, Pigièrè, F.,

Pluskowski, A. G. ORCID: <https://orcid.org/0000-0002-4494-7664>, Sadler, P., Sicard, S. ORCID: <https://orcid.org/0009-0002-8081-2035>, Strid, L. ORCID: <https://orcid.org/0000-0003-1375-6811>, Sudds, J., Symmons, R., Tardio, K., Valenzuela, A., van Veen, M. ORCID: <https://orcid.org/0009-0005-6131-0613>, Vuković, S. ORCID: <https://orcid.org/0000-0003-2731-2146>, Weinstock, J., Wilkens, B. ORCID: <https://orcid.org/0000-0002-2217-5288>, Wilson, R. J. A. ORCID: <https://orcid.org/0000-0002-4026-3177>, Evans, J. A., Hoelzel, A. R. ORCID: <https://orcid.org/0000-0002-7265-4180> and Sykes, N. ORCID: <https://orcid.org/0000-0001-6114-7557> (2024) The 10,000-year biocultural history of fallow deer and its implications for conservation policy. *Proceedings of the National Academy of Sciences*, 121 (8). e2310051121. ISSN 1091-6490 doi: 10.1073/pnas.2310051121 Available at <https://centaur.reading.ac.uk/115303/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1073/pnas.2310051121>

Publisher: Proceedings of the National Academy of Sciences

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online



The 10,000-year biocultural history of fallow deer and its implications for conservation policy

Karis H. Baker^a, Holly Miller^b, Sean Doherty^c, Howard W. I. Gray^a, Julie Daujat^b, Canan Çakırlar^d, Nikolai Spassov^e, Katerina Trantalidou^f, Richard Madgwick^g, Angela L. Lamb^h, Carly Ameen^c, Levent Aticiⁱ, Polydora Baker^j, Fiona Beglane^k, Helene Benkert^c, Robin Bendrey^l, Annelise Binois-Roman^m, Ruth F. Cardenⁿ, Antonio Curci^o, Bea De Cupere^p, Cleia Detry^q, Erika Gál^r, Chloé Genies^s, Günther K. Kunst^t, Robert Liddiard^u, Rebecca Nicholson^v, Sophia Perdikaris^w, Joris Peters^{x,y}, Fabienne Pigièrè^z, Aleksander G. Pluskowski^{aa}, Peta Sadler^{bb}, Sandra Sicard^{cc}, Lena Strid^{dd}, Jack Sudds^e, Robert Symmons^{ee}, Katie Tardio^{ff}, Alejandro Valenzuela^{gg}, Monique van Veen^{hh}, Sonja Vukovićⁱⁱ, Jaco Weinstock^{jj}, Barbara Wilkens^{kk}, Roger J. A. Wilson^{ll}, Jane A. Evans^h, A. Rus Hoelzel^{aa}, and Naomi Sykes^{c,1}

Edited by Melinda Zeder, Smithsonian National Museum of Natural History, Washington, DC; received June 15, 2023; accepted December 14, 2023

Over the last 10,000 y, humans have manipulated fallow deer populations with varying outcomes. Persian fallow deer (*Dama mesopotamica*) are now endangered. European fallow deer (*Dama dama*) are globally widespread and are simultaneously considered wild, domestic, endangered, invasive and are even the national animal of Barbuda and Antigua. Despite their close association with people, there is no consensus regarding their natural ranges or the timing and circumstances of their human-mediated translocations and extirpations. Our mitochondrial analyses of modern and archaeological specimens revealed two distinct clades of European fallow deer present in Anatolia and the Balkans. Zooarchaeological evidence suggests these regions were their sole glacial refugia. By combining biomolecular analyses with archaeological and textual evidence, we chart the declining distribution of Persian fallow deer and demonstrate that humans repeatedly translocated European fallow deer, sourced from the most geographically distant populations. Deer taken to Neolithic Chios and Rhodes derived not from nearby Anatolia, but from the Balkans. Though fallow deer were translocated throughout the Mediterranean as part of their association with the Greco-Roman goddesses Artemis and Diana, deer taken to Roman Mallorca were not locally available *Dama dama*, but *Dama mesopotamica*. Romans also initially introduced fallow deer to Northern Europe but the species became extinct and was reintroduced in the medieval period, this time from Anatolia. European colonial powers then transported deer populations across the globe. The biocultural histories of fallow deer challenge preconceptions about the divisions between wild and domestic species and provide information that should underpin modern management strategies.

fallow deer | translocations | extinctions | zooarchaeology | biomolecules

There are two recognized species of fallow deer: the Persian (*Dama mesopotamica*) and the European (*Dama dama*). The Persian fallow deer was once widespread across Southwest Asia and the eastern Mediterranean, but following a severe population decline, the species is currently considered Endangered by the International Union for the Conservation of Nature (IUCN) (1). Conversely, the European fallow deer, native to the eastern Mediterranean, is classified as Least Concern due to their human-mediated translocation and establishment across Eurasia, Africa, America and Oceania (2, 3). Despite their large population size and broad distribution, their genetic diversity is very low, suggesting conservation vulnerability (4). The herd of European fallow deer at Güllük Dağı-Termessos National Park (Turkey) is considered the last native wild population and, as such, has a protected status (5). Conservation measures extend to the *Dama* population on the nearby island of Rhodes, which is protected by Greek law (6).

The Rhodes *Dama* are thought to descend from a population of European fallow deer introduced ~7,000 y ago (6–8). Early farmers of the 6th–5th millennium BCE also established populations of European fallow deer on the islands of Lemnos, Lesbos, Chios, and Crete (9–11), whereas Persian fallow deer were transported to Cyprus ~10,000 y ago (12).

Both species were as heavily influenced by people as other taxa classically associated with the Neolithic Package including cattle, sheep, goats, and pigs. In addition, modern European fallow deer are farmed in their millions (13) and exhibit coat color variations indicative of selective breeding (14). Despite these characteristics, fallow deer are rarely included in large-scale reviews of domestic animals (12, 15). European fallow deer have been equally overlooked by conservation scientists, for whom the species' domestic legacy

Significance

Persian and European fallow deer formed part of the Levantine Neolithic Package were worshiped as Greco-Roman deities and, over millennia, were the subject of repeated human-mediated translocations and extirpations. By integrating biomolecular datasets with archaeological and textual evidence, we reveal these species' biocultural histories—spanning their Glacial refugia to their global spread as symbols of colonial power. The deep histories of fallow deer highlight the problems inherent in dichotomous categorizations of all species as either wild or domestic. In addition, they complicate existing wildlife conservation strategies and offer alternative perspectives on the management of translocated animals.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2024 the Author(s). Published by PNAS. This open access article is distributed under Creative Commons Attribution License 4.0 (CC BY).

¹To whom correspondence may be addressed. Email: N.Sykes@exeter.ac.uk.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2310051121/-DCSupplemental>.

Published February 12, 2024.

has meant they are often considered an introduced alien or invasive threat and thus undeserving of protection (16–18).

As neither an accepted domesticated nor a “pristine” wild species, both Persian and European fallow deer have been under-researched relative to other cervids such as reindeer (*Rangifer tarandus*) and red deer (*Cervus elaphus*) which have been the subject of numerous studies concerning their ancient range and management (19–23). By contrast, there is no consensus regarding the European fallow deer’s glacial refugia or natural post-glacial distribution. While some have suggested a single refugium in Anatolia (2), others have claimed multiple refugia across Anatolia, the southern Balkans, Italy, Sicily, and Iberia (4, 24, 25). The timing and circumstances of the fallow deer’s anthropogenic translocations are equally obscure, although numerous human cultures have been held responsible including early Neolithic farmers, Phoenicians, Romans, Normans, and early modern imperialists (26).

Attempts to answer questions about the fallow deer’s history have relied largely on genetic studies of modern animals (4, 7, 8, 27). However, modern DNA has limited retrodictive power, especially when applied to species whose distributions have been heavily modified by humans (15, 28). Recent aDNA studies of fallow deer have demonstrated the necessity of a joined-up ancient-modern genetics approach (29–33), exemplified by Baker et al.’s (34) time-calibrated genetic analyses of fallow deer evolution in Europe from the last glacial period. There is also a need to integrate genetic analyses with other sources of biomolecular data, such as isotope studies, and rich empirical records from across the Humanities and Social Sciences, which together can be used to evidence the long-term management and cultural value of fallow deer.

Here, in order to characterize the glacial range of Persian and European fallow deer, we combined zooarchaeological and biomolecular analysis of ancient and modern *Dama* remains. To increase the power of our results, we integrated them with evidence from archaeology, historical sources, and iconography and show how ancient humans have shaped the modern-day distributions and management strategies of these two species. As such, they represent cultural heritage and arguably deserve protection by the United Nations Educational Scientific and Cultural Organization (UNESCO) as much as from wildlife conservation bodies such as the IUCN.

Results and Discussion

We analyzed 635 osteological samples purported to derive from fallow deer using at least one method (Dataset S1) and generated genetic sequences from 228 ancient samples.

For the European fallow deer, 181 sequences from archaeological samples (35) were combined with those for 222 modern individuals (4, 36). A Bayesian phylogeny constructed from the complete alignment (Fig. 1A) revealed a well-supported (0.89 posterior probability) monophyletic clade consisting of modern and ancient European fallow deer from Northern Europe and Anatolia (depicted in yellow on Fig. 1A and B).

A second clade is made up of ancient and modern fallow deer derived from southern and western European sites and Roman England (depicted in red—Fig. 1A and B). Both clades are distinct from the mitochondrial lineage derived from a single modern Persian fallow deer at the base of the phylogeny.

A shorter sequence was available (128 bp) that showed 18 fixed differences between European and Persian fallow deer, allowing *D. mesopotamica* to be identified from archaeological remains (depicted in purple in Fig. 1B and SI Appendix, Fig. S1).

The zooarchaeological representation data (Dataset S2) and genetic results are summarized in Fig. 2A–D, which also

incorporates the radiocarbon dating evidence (Fig. 3). Multi-element isotope data were generated from 418 specimens (Dataset S1), with results presented in Fig. 4 and SI Appendix, Figs. S6 and S7.

Refugia and Native Range. Our genetic analysis demonstrated that 38 specimens originally identified morphologically as *D. dama* were actually *D. mesopotamica* (SI Appendix, Fig. S1). Their presence at the Bronze Age/early Iron Age sites of Kinet Höyük and Kilise Tepe, Anatolia (Fig. 2A and B) pushes the ancient distribution of Persian fallow deer further west than previously proposed (12).

For the European fallow deer, our data suggest their glacial refugium was restricted entirely to the eastern Mediterranean and there is no zooarchaeological evidence to suggest the existence of autochthonous Holocene fallow deer populations in Iberia or Italy. Within Anatolia, the *D. dama* population demonstrates continuity through time: Neolithic, Roman, and medieval deer share haplotypes (H31) and are closely related to the modern population at Güllük Dağı-Termessos National Park (H47, H48). The modern deer population on Rhodes is genetically distinct from Anatolian deer [a result that corroborates previous studies (7, 8)] and appears more closely related to populations from the Balkans, Italy, and Iberia.

The phylogenetic split between the two populations of European fallow deer (Fig. 1) is consistent with the frequently observed phylogeographic divide found in numerous species with populations that span the Bosphorus (38–40). When combined with the zooarchaeological data (Fig. 2A), this result supports the suggestion of a second glacial refugium in the southern and central Balkans (25, 41). Large quantities of fallow deer remains have been recovered from Neolithic and Bronze Age sites in Bulgaria which demonstrate their early presence in this region. Intriguingly, their remains exhibit morphologies distinct from the Anatolian fallow deer (SI Appendix, Figs. S3 and S4) which may be the result of underlying genetic, not environmental differences (25, 41, 42). Despite the phenotypic distinction, stable and radiogenic isotope data show no difference in fallow deer diets between these regions (SI Appendix, Fig. S6 and S7) (43).

Translocations as Proxies for the Movement of People and Ideologies. Both species of fallow deer were translocated during the Neolithic/Bronze Age (Fig. 2A). We partially sequenced one Persian fallow deer specimen (PT608) from the Bronze Age site of Politiko-Troullia, Cyprus, and two Late Neolithic/Early Bronze Age European fallow deer samples from Ayio Galas Cave, Chios (CH680 and CH681). The Chios samples possessed unique haplotypes (H45 and H46) that are most closely related to individuals from modern Rhodes (H64 and H65). This result supports Masseti et al.’s (7, 8) proposal that the modern Rhodes deer population descends from a Neolithic introduction.

The Neolithic Chios and modern Rhodes deer are more closely related to (and likely descend from) the Balkan rather than Anatolia population. This may seem counter-intuitive, especially given that Rhodes is only 11 miles from mainland Turkey and Chios is <3 miles. However, animal translocations frequently result from factors other than geographic proximity, including attitudes to the natural world, religious ideologies and culture-contacts, issues to which we now turn.

Early domestication. The transfer of animals beyond their natural range has been equated with a closing of human–animal relationships and associated with the process of domestication (44).

According to Masseti (45) and Vigne et al. (12), island *Dama* populations were established specifically for hunting but textual and iconographic evidence from the Bronze Age indicate a more

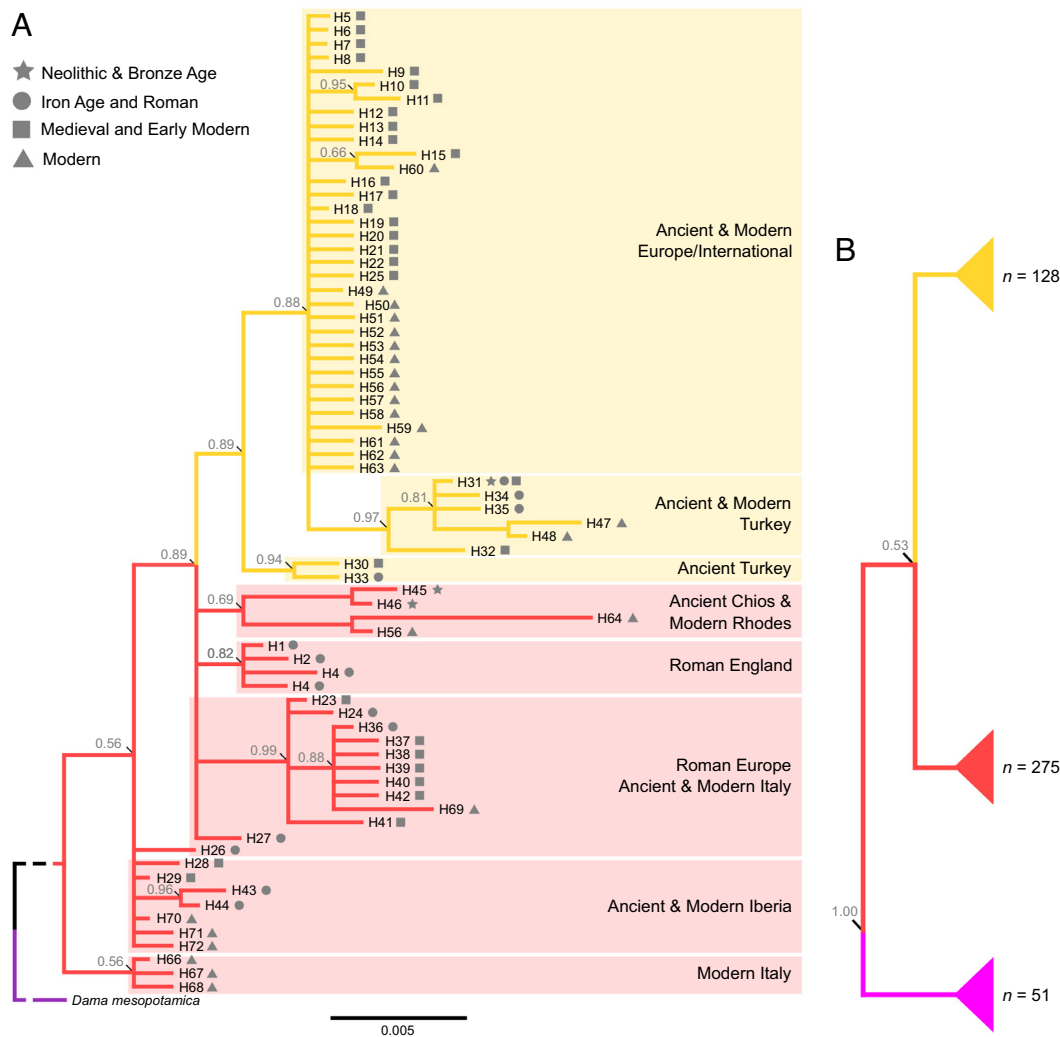


Fig. 1. Phylogenetic trees depicting the relationships between mitochondrial haplotypes derived from ancient and modern European and Persian fallow deer. The tree in Panel (A), rooted with Persian fallow deer and based upon 532 basepairs, shows a distinctive well-supported (0.89 posterior probability) monophyletic clade of European fallow deer (depicted in yellow) and separate lineages of fallow deer associated with a population originally present in the Balkans (depicted in red). Individuals from both these populations (as well as Persian fallow deer) have been transported beyond their native ranges by people at different times (Fig. 2). The collapsed tree in Panel (B) is rooted to *Cervus elaphus* and based upon 128 basepairs (see *SI Appendix, Fig. S1* for detailed tree). It shows how European fallow deer (yellow and red) can be differentiated from the well supported (1.0 posterior probability) clade of Persian fallow deer (purple).

complex relationship between people and fallow deer. For instance, Linear B texts (the earliest form of Greek) list different kinds of fallow deer: those that are wild, those that are tame, and those used in games or for sacrifices, while fresco fragments from Aghia Triadha, Crete, depict a woman leading two fallow deer to a sacrificial altar (11). Similar evidence exists across Anatolia and Egypt (46) and given that the Latin name *Dama* derives from the Persian word for tame or pet (47), there is a compelling case that fallow deer were initially no different in their relationships with humans than other animals that make up the canonical suite of domesticates.

Religion. Many cultures equate geographical distance with supernatural distance perceiving that the further something has traveled, the greater its prestige and power (48). In this way, introduced animals have frequently been viewed as gods (49, 50).

Fallow deer were certainly associated with both the goddess Artemis and her Roman incarnation, Diana (11, 46, 47, 51). There is debate about the geographical genesis of the Artemis myth but the possibility she originated in the Balkans is given credence by the density of both fallow deer remains (Fig. 2A) and Artemis-related paraphernalia, such as fallow deer-shaped religious drinking vessels that have been recovered from the region (52). In Late Minoan

Crete (c.1550–1100 BCE), Linear B texts mention not only fallow deer but also provide the earliest reference to Artemis (10, 53).

Historical studies suggest that the Artemis cult was taken to Sicily by early Greek settlers (54) and statuettes of the goddess have been recovered from the Bronze Age site of Morgantina, together with a shed fallow deer antler (55). This skeletal element could have been transported as an object in its own right [as was the case for other *Dama* body parts recovered from a Phoenician ship-wreck off the coast of Sicily (43, 56)] rather than deriving from an animal that lived on the island. At Morgantina, a small number of post-cranial bones have been tentatively identified as *Dama* (55). Our metrical analysis shows that their size is more consistent with red deer from the island (*SI Appendix, Fig. S5*) though we were unable to confirm their identification genetically.

Roman Empire. The Roman period witnessed a major expansion in fallow deer distribution (Fig. 2B). This was in part due to their connection with the goddess Diana and also linked to the parks and menageries that became increasingly fashionable throughout the Roman Empire.

The earliest evidence for the presence of fallow deer beyond the Mediterranean comes from the highly “Romanised” palatial site

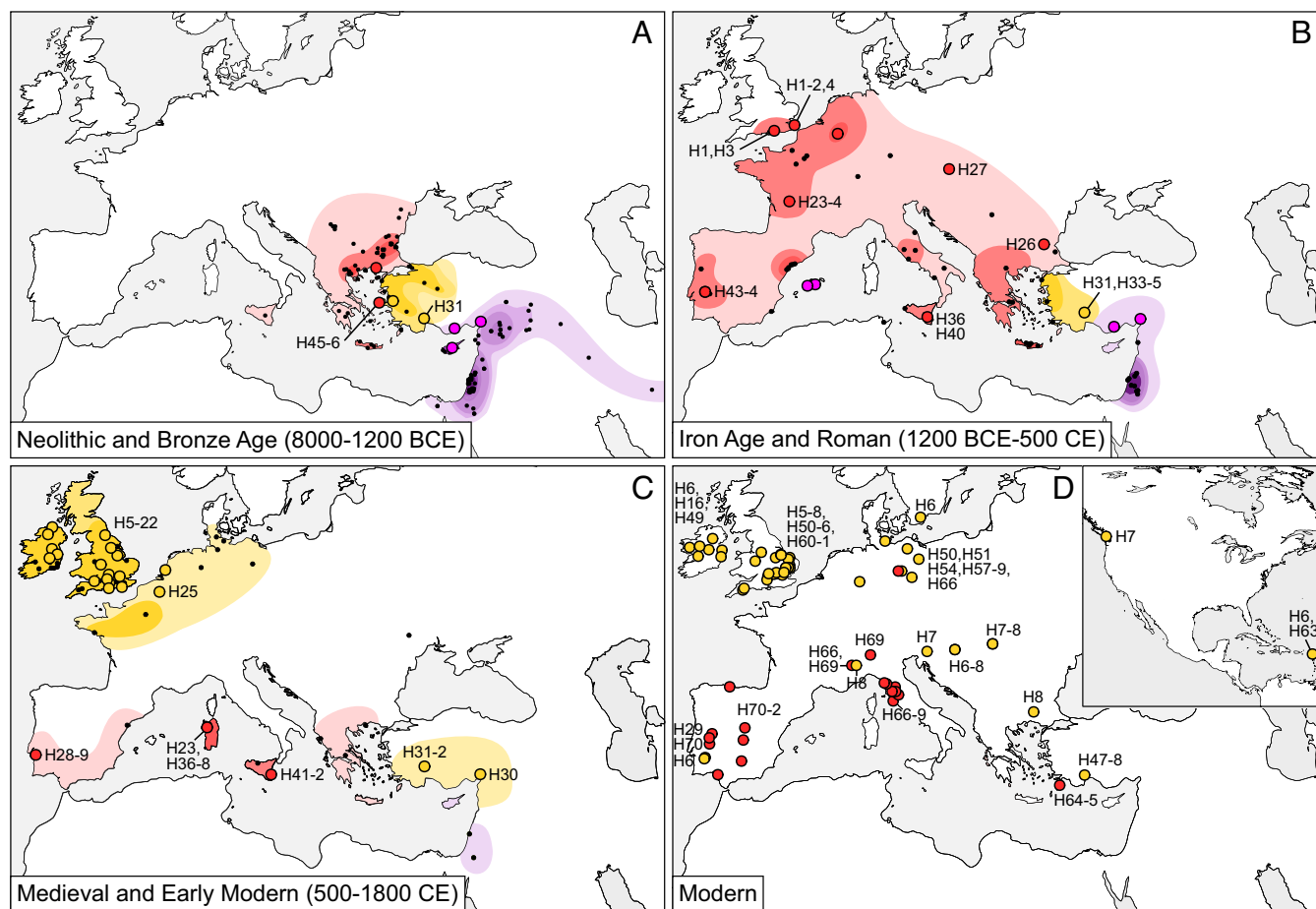


Fig. 2. Maps showing the location and density of European and Persian fallow deer remains in zooarchaeological assemblages (A–C, data from Dataset S2) and modern samples (D, data from Datasets S3 and S4) colored according to genetic results (Fig. 1 and Dataset S1).

of Fishbourne (southern England) that was constructed shortly after the Roman invasion of Britain in 43 CE. Here, *Dama* remains have been directly dated to the 1st century CE (Fig. 3). Multi-element isotope analysis revealed a first-generation import that likely traveled from the Mediterranean in the first few months of its life (Fig. 4). Our evidence also shows that other fallow deer were born and raised at Fishbourne (57) and managed in diverse ways (58).

By the fourth-century CE, fallow deer were established in Britain more broadly, and specimens from Belgium (59) and Portugal (60) have been direct-dated to this period (Figs. 2B and 3). The earliest secure evidence for fallow deer on Sicily dates to the 5th century CE (Fig. 3 and SI Appendix, Fig. S3) and isotope analysis indicates these animals were born and raised on the island (Fig. 4). Genetically, Sicilian deer are consistent with the western Mediterranean (Balkan) clade. They share a haplotype (H36) with animals from Sardinia, where populations were established in the medieval period (61, 62). The Sardinian deer also share haplotypes (H23) with deer from Roman France.

The European fallow deer established in Iberia and Italy both appear to be the progenitors of the modern populations in those regions. For instance, one haplotype (H29) is observed in both medieval and modern Portugal, and is closely related to Roman haplotypes (H43 and H44). Similarly, haplotypes found in ancient Italy (H36) are closely related to those of modern deer (H69). These modern populations are therefore legacies of the Roman Empire and should be treated as living cultural heritage (Fig. 2B and D).

Large numbers of *Dama* remains have been recovered on Mallorca in contexts dating from the third to the fifth century AD (31). Surprisingly, they were genetically determined to be Persian and not European fallow deer (SI Appendix, Fig. S1), which has implications for understanding Roman and early medieval trade routes. For instance, it is possible they arrived via north Africa where there are iconographic representations of fallow deer. Recently, zooarchaeological evidence for fallow deer has been discovered in Roman North Africa, but their remains are scarce and have not yet been subject to dating or biomolecular analysis which means their species assignment is unconfirmed (63, 64).

Extinctions and population replacements. The native *D. mesopotamica* distribution contracted substantially through time and by the medieval period was replaced in eastern Turkey by *D. dama* (Fig. 2). The Balkan population of *D. dama* was likely extinct by the end of the medieval period (Fig. 2C). Of the translocated populations, the Persian fallow deer of Mallorca went extinct around the seventh century CE (31) and the population on Cyprus disappeared by the late medieval/early modern period (65). The *D. dama* population established in northern Europe during the Roman period vanished rapidly following the Empire's withdrawal, and new populations were re-established centuries later (Fig. 2B and C).

For Britain, our study overturns the received wisdom that fallow deer were brought from the Norman kingdom of Sicily following the Norman Conquest of 1066 (66, 67). Our skyline plot (S1 Fig. 2) suggests an introduction ~1000 CE and this model is supported by the evidence from the site of Goltho, Lincolnshire. Isotope analyses of the Goltho deer indicate they were born and

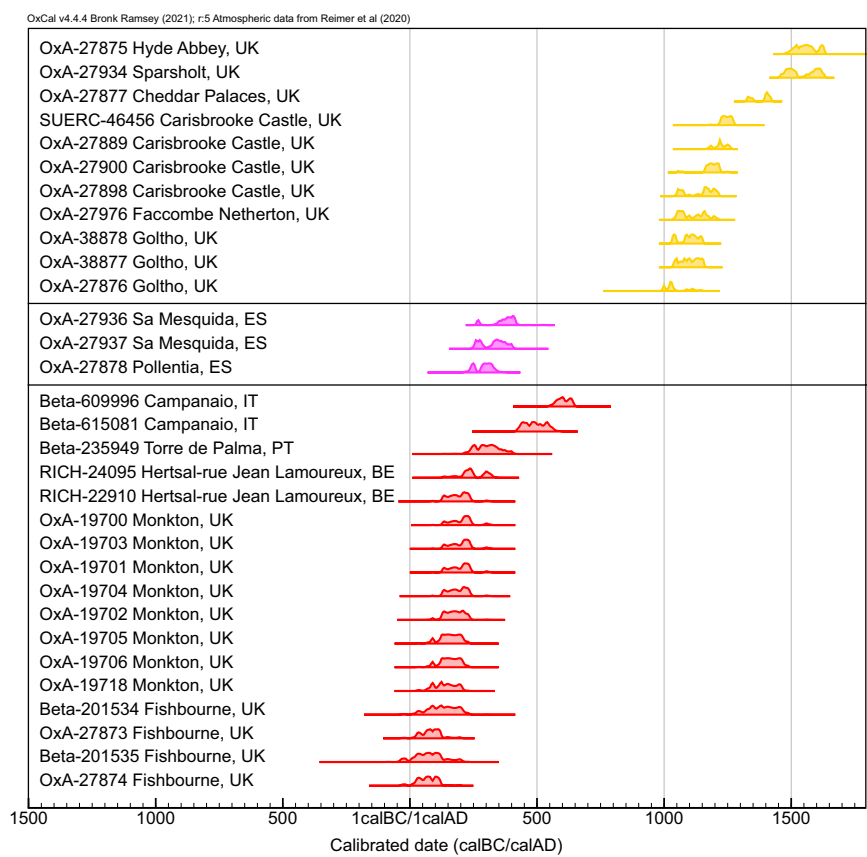


Fig. 3. Calibrated radiocarbon dates of fallow deer, color-coded by genetic results (Fig. 1).

raised locally (ref. 33 and Fig. 4) and direct dating suggests that a population was established before the Norman Conquest, by at least 1000 CE (Fig. 3). The possibility that these deer were derived from Sicily can be discounted from the genetic evidence which demonstrates that the North European medieval deer are unrelated to either the Roman or Western Mediterranean populations (Figs. 1 and 2C). Instead, they are more closely related to Anatolian deer,

both of which lack a 21 bp mtDNA insertion present in 88% of modern Italian and Spanish individuals (4). **Elite exchange and colonial expansion.** Following the second introduction to Britain, the maintenance of fallow deer within parks became a statement of elite identity (33) and by the early 13th century, parks and fallow deer had been established in Ireland by Anglo-Norman colonial powers (32, 68, 69). About this time

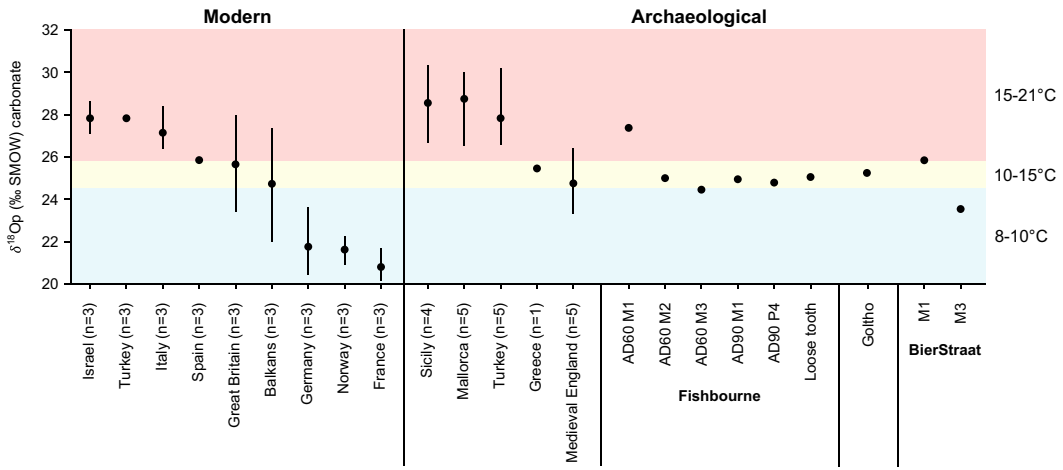


Fig. 4. Range and mean of oxygen isotope data for modern fallow deer (37) compared with ancient specimens. The graph is colored by average temperatures for the regions from which the modern specimens derive. Those from ancient Turkey, Greece, Sicily, Mallorca, and medieval England are consistent with animals that lived and died in those regions. By contrast, the AD60 mandible from Fishbourne Roman Palace has a value for its first molar (M1, which develops <4 mo) that is more in line with those from Turkey, Israel, the Balkans, and Italy. The values for the same deer's second molar (M2, develops 8 to 9 mo) and third molar (M3, develops <18 mo), along with those for the other Fishbourne fallow deer, align with those from modern and medieval England. The specimen from Goltho is consistent with UK values. The specimen from post-medieval Bierstraat-The Hague, the Netherlands, has an M1 value consistent with England but its M3 value is more suggestive of continental northern Europe.

fallow deer were exported to France, sent by King Henry II to stock King Philip II's park at Vincennes (70).

In fact, England was likely the source of the deer reintroduced to other countries of northern Europe. A 16th/17th-century specimen from the Boussu castle, Belgium (71) was found to have a unique haplotype (H25) closely related to the most common English haplotype (Fig. 2C). The 16th/17th-century specimen from Bierstraat-The Hague (Netherlands) yielded insufficient aDNA to understand its relationship to the broader dataset. Nevertheless, the oxygen isotope results suggest that it may have been a first-generation import from England (Fig. 4) and historical evidence supports this possibility. For example, the 17th century Dutch hunting manuscript, *Jacht-Bedryff*, notes that Maurice of Nassau (later Prince of Orange) acquired 100 fallow deer from England to stock The Hague forest (72).

The combination of historical research and genetic results indicates that England was the source of the fallow deer exported across the British Empire. The *Dama* of the Caribbean island of Barbuda (H63) is closely related to English deer, which is consistent with documentary evidence that fallow deer were transported to the island, along with many African slaves, by the Codrington family of Gloucestershire (73). The meaning attached to these Barbudan deer changed through time. Initially, they were a symbol of colonial authority and dominance, but after the slave emancipation of 1834, fallow deer became a symbol of freedom, adopted as Barbuda's national animal. Today, fallow deer are an important part of Barbuda's economy and cultural heritage but, as an introduced "alien" species, they fall outside legal protection. This is despite clear threats from over-hunting and natural disasters, such as hurricane Irma that devastated the island in 2017, which have put the culturally important population at risk (73, 74).

Implications for Fallow Deer Management and Conservation.

The Barbudan fallow deer are just one of many global populations that possess cultural importance. Yet, it is precisely the close association with humans, and particularly their human-assisted translocation, that excludes them from IUCN protection. We argue that the cultural heritage represented by a species should be taken into consideration when conservation decisions are being made.

The results presented here serve as a warning about the vulnerability of island fallow deer. Ancient introductions to Crete, Chios, Cyprus, Sicily, Sardinia, Mallorca, and Roman Britain all went extinct (Fig. 2D). The modern Barbudan population could follow a similar trajectory without a conservation plan akin to that which allowed the Rhodes fallow deer to endure from their Neolithic introduction. It is the deer from Rhodes, along with those from Italy and Portugal, that preserve traces of the now extinct refugial population that once inhabited the Balkans.

There are several active campaigns to re-establish fallow deer in the Balkans and preserve the last remaining wild herd at Dağı-Termessos National Park, Turkey. Without knowledge of the species' deep-time biomolecular and phylogeographic history, deer are being sourced from the least appropriate populations. For instance, those being reintroduced to the Balkans possess Anatolian ancestry (Fig. 2D). Furthermore, these Anatolian deer are being introduced to regions that have, for thousands of years, preserved deer with Balkan ancestry (Fig. 2D). Whilst Anatolia-derived deer are increasing in number around the world, the Dağı-Termessos herd is still under threat. Our contention is that North European deer of Anatolian ancestry could be introduced to the Dağı-Termessos park, whilst Iberian/Italian/Rhodes deer populations would be a better source for Balkan rewilding projects.

Conclusion

This study combined zooarchaeology and ancient and modern biomolecular datasets with evidence from Humanities disciplines to reveal new insights into the history of both fallow deer and the people who transported them. We argue that after the Last Glacial Maximum, Persian fallow deer were more widespread than has previously been proposed, whilst European fallow deer were likely restricted to Anatolia and the Balkans, and two distinct populations existed on either side of the Bosphorus. Our integrated study suggests early translocations of deer as a viable alternative to fallow deer surviving anywhere else outside these regions.

Tracing their spread from these refugia reveals that fallow deer were repeatedly sourced from the furthest available populations: The deer on Neolithic Chios (and likely Rhodes) derived from the Balkans, rather than nearby Anatolia; those on Roman Mallorca were *Dama mesopotamica* rather than the *Dama dama* which could have been acquired from the Iberian peninsula; and the deer reintroduced to medieval Britain were brought from Anatolia instead of Iberia or Italy. This reflects the human desire to possess the exotic which, across cultures, is linked to concepts of power and other-worldliness. Not surprisingly then, the earliest translocations of fallow deer are linked to the religious cults of Artemis and Diana.

Ancient dispersals of people, ideas, and animals are widely celebrated as cultural heritage. However, the more recent the migrations, the more negative the attitudes toward them. Such perceptions can translate into animal management and policy making. For instance, the fallow deer of Rhodes were introduced during the Neolithic and are viewed as a cultural asset, protected by Greek law and featured on the IUCN Red List. The fallow deer of Barbuda are equally culturally significant as the island's national animal, yet they have no legal protection and are labeled as "invasive" within the conservation literature. In truth, they are dismissed only because their introduction occurred too recently to have acquired a patina of age-based authenticity.

Given the planet's biodiversity crisis, it is time to rethink our attitudes to animals. Whilst many species may legitimately be labeled as invasive, this is not true of all translocated populations and some do deserve protection. Preoccupation with native and wild species can come at the expense of (often equally endangered) translocated animals that are not only critically entangled with human history but also offer a conservation resource for replenishing diminished autochthonous populations.

Materials and Methods

Spatiotemporal shifts in European and Persian fallow deer distribution were initially reconstructed through synthesis of the zooarchaeological literature. Reports referencing the presence of fallow deer were collated ($n = 336$) and the frequency of fallow deer (relative to main mammals) within each assemblage was calculated (Dataset S2). The location and frequency data were mapped for three key chronological periods—Neolithic and Bronze Age (8000 to 1200 BCE), Iron Age and Roman (1200 BCE to 500 CE), and medieval and early modern (500 to 1800 century CE)—to create Fig. 2 A–C.

To add resolution to the zooarchaeological survey, 635 osteological samples (archaeological, historical, and modern) were acquired from sites across the fallow deer's ancient and modern range (Dataset S1). Samples were subject to full-suite analysis using the following techniques (SI Appendix for full details):

Zooarchaeological Analysis. Contextual information (site type, date, and associated archival data) was recorded for each specimen, which was identified to skeletal element and examined for evidence of taphonomic process and pathology. Metrical analysis (75) and age determinations (76) were undertaken to assist with species assignment and demographic profiling. Osteometric data were compared

against those published on the Deer Bone Database https://www.nottingham.ac.uk/zooarchaeology/deer_bone/search.php.

Isotope Analysis. A total of 418 specimens were submitted for multi-element isotope analyses, including carbon and nitrogen ($n = 418$), oxygen ($n = 31$), strontium ($n = 18$), and sulfur ($n = 22$). Collagen extractions were undertaken at the University of Nottingham. Other preparation methods and analyses were undertaken at the National Environmental Isotope Facility (formerly NERC Isotope Geosciences Laboratory) at the British Geological Survey, Keyworth, UK. Oxygen data were compared against Miller et al.'s modern baseline (37).

Chronologies and Radiocarbon Dating. Dating of the archaeological specimens was based largely on contextual association. To check issues of stratigraphic migration [which have been noted in smaller animals (50)] and refine the chronology of fallow deer translocations, published radiocarbon dates were collated ($n = 9$) and key specimens ($n = 23$) were directly dated: 21 at the University of Oxford's Radiocarbon Accelerator Unit (ORAU) UK and two at Beta Analytic (USA).

Genetic Analysis. The genetic data generation and analysis was carried out at the Molecular Ecology Group at the Department of Biosciences, Durham University, UK. In order to maximize both the number of variable positions and to be able to compare to data generated from modern specimens, we targeted a 532 bp fragment of the 5' end of the control region of the mitochondrial genome using a combination of overlapping primer pairs. PCR products were sequenced using the Sanger method on an ABI 3100 automated sequencer at DBS Genomics, Durham University.

Out of 561 ancient specimens, we generated the entire fragment from 190 European fallow deer and generated a sequence alignment alongside 219 modern samples (Datasets S3 and S4), published in Baker et al. (4). For discrimination between *D. dama* and *D. mesopotamica*, we used a 128 bp sub-fragment from the same control region sequence. This allowed us to identify 38 ancient specimens as Persian fallow deer (SI Appendix, Fig. S1).

All sequences were aligned using the MUSCLE algorithm (77) as implemented in Geneious v. R6 (www.geneious.com, ref. 78). The relationship amongst haplotypes was examined by constructing both median-joining networks (79) in NETWORK v. 3.1.1.1 (www.fluxus-engineering.com) and a Bayesian phylogeny within MrBayes v. 3.2.6 (80). The demonstrated phylogenetic distinctiveness of the two subspecies *D. dama* and *D. mesopotamica* (31) allowed us to confirm species identifications when zooarch assessments were equivocal. This was based on 18 fixed differences out of the 128bp sequence. Additional details pertaining to the data generation, analyses, and GenBank accession details (Dataset S5) are found in SI Appendix.

Data, Materials, and Software Availability. Genetics data have been deposited in GenBank (<https://www.ncbi.nlm.nih.gov/nucleotide> (35, 36): H1 OR220344 H2 OR220345 H3 OR220346 H4 OR220347 H5 OR220348 H6 OR220349 H7 OR220350 H8 OR220351 H9 OR220352 H10 OR220353 H11 OR220354 H12 OR220355 H13 OR220356 H14 OR220357 H15 OR220358 H16 OR220359 H17 OR220360 H18 OR220361 H19 OR220362 H20 OR220363 H21 OR220364 H22 OR220365 H23 OR220366 H24 OR220367 H25 OR220368 H26 OR220369 H27 OR220370 H28 OR220371 H29 OR220372 H30 OR220373 H31 OR220374 H32 OR220375 H33 OR220376 H34 OR220377 H35 OR220378 H36 OR220379 H37 OR220380 H38 OR220381 H39 OR220382 H40 OR220383 H41 OR220384 H42 OR220385 H43 OR220386 H44 OR220387 H45 OR220388 H46 OR220389 H47 KY564399.1 1 H48 KY564400.1 2 H49 KY564402.1 4 H50 KY564415.1 17 H51 KY564405.1 7 H52 KY564406.1 8 H53 KY564408.1 10 H54 KY564409.1 11 H55 KY564410.1 12 H56 KY564411.1 13 H57 KY564416.1 18 H58 KY564418.1 20 H59 KY564417.1 19 H60 KY564413.1 15 H61 KY564414.1 16 H62 KY564420.1 22 H63 OR531442 n/a H64 OR531443 n/a H65 KY564422.1 24 H66 KY564421.1 23,25,26 H67 KY564426.1 28 H68 KY564427.1 29 H69 KY564425.1 27 H70 KY564428.1 30,32 H71 KY564432.1 34 H72 KY564431.1 33 *Dama mesopotamica* XIV AF291896 n/a XV JN632630 n/a XVI OR531435 n/a XVII OR531436 n/a XVIII OR531437 n/a XIX OR531438 n/a XX OR531439 n/a XXI OR531440 n/a XXII OR531441 n/a). All other data are included in the manuscript and/or supporting information.

ACKNOWLEDGMENTS. This research was funded by the Arts and Humanities Research Council (AH/I026456/1) with support for radiocarbon dating provided by the National Environmental Isotope Facility (NF/2012/2/3 and NF/2018/2/16).

J.D. was supported by a Leverhulme Early Career Fellowship (ECF-2015-139). E.G. and G.K.K. were employed in the project FWF 22903 at the Austrian Academy of Sciences (2011-2014) when identifying the Roman specimen from Carnuntum-Mühlacker. A. Alen and F. Pigière were employed at the Royal Belgian Institute of Natural Sciences when identifying and sampling the specimens from Boussu (Belgium). We are grateful to Cécile Ansieau (SPW-TLPE-AWaP-DZO) and Didier Willems (SPW-TLPE-AWaP-DZC), who excavated the site of Boussu and provided chronological data on the fallow deer remains. Our thanks also go to the non-profit Gy Seray Boussu A.S.B.L. in charge of the archaeological site. The contribution of Sonja Vuković was supported by the Science Fund of the Republic of Serbia, # GRANT no 7750265, The Holocene History of Human-Wildlife Conflict and Coexistence: Archaeozoological, Archaeobotanical, Isotopic, Ancient DNA, Iconographic and Written Evidence from the Central Balkans – ARCHAEOIWILD. We are grateful to the Ephorates of Antiquities of the Greek Ministry of Culture and the Sports, Dr. E. Psathi who has worked both on Chios and Antiparos material and the excavators of Greek sites for the permit to use the relevant samples, Dr. J. T. Zeiler for information on the Dutch medieval fallow deer bones, and Dr. C. Rainsford and York Archaeological Trust for fallow deer bones from Hungate, York. We are indebted to Simon Davis, Michael McKinnon, Greger Larson, and Rory Putman who read, and significantly improved, the draft manuscript, as did the two anonymous referees. Thanks also go to the members of *Dama* International's steering committee, in particular Hella Eckardt and Marco Masseti, for all their guidance.

Author affiliations: ^aDepartment of Biosciences, Durham University, Durham DH1 3LE, United Kingdom; ^bDepartment of Classics and Archaeology, University of Nottingham, Nottingham NG7 2RD, United Kingdom; ^cDepartment of Archaeology and History, University of Exeter, Exeter EX4 4QE, United Kingdom; ^dGroningen Institute of Archaeology, University of Groningen, Groningen 9712 ER, The Netherlands; ^eDepartment of Paleontology, National Museum of Natural History, Bulgarian Academy of Sciences, Sofia 1000, Bulgaria; ^fEphorate for Palaeoanthropology-Speleology, Hellenic Ministry of Culture, Athens 106 82, Greece; ^gSchool of History, Archaeology and Religion, Cardiff University, Cardiff CF10 3EU, United Kingdom; ^hNational Environmental Isotope Facility, British Geological Survey, Nottingham NG12 5GG, United Kingdom; ⁱDepartment of Anthropology, University of Nevada, Las Vegas, NV 89154; ^jHistoric England, Portsmouth PO4 9LD, United Kingdom; ^kCentre for Environmental Research Innovation and Sustainability, Atlantic Technological University, Sligo F91 YW50, Ireland; ^lSchool of History, Classics and Archaeology, University of Edinburgh, Edinburgh EH8 9AG, United Kingdom; ^mSchool of Art History and Archaeology, University of Paris 1 Panthéon-Sorbonne, Paris 75006, France; ⁿSchool of Archaeology, University College Dublin, Dublin D04 V1W8, Ireland; ^oDepartment of History and Cultures, University of Bologna, Bologna 40124, Italy; ^pOperational Directorate Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels 1000, Belgium; ^qCenter of Archaeology of the University of Lisbon, Department of History, School of Arts and Humanities of the University of Lisbon, Alameda da Universidade, Lisboa 1600-214, Portugal; ^rInstitute of Archaeology, HUN-REN Research Centre for the Humanities, Budapest 1097, Hungary; ^sBureau d'études, Éveha, Saint-Avertin, Tour 37550, France; ^tVienna Institute for Archaeological Science, Research Network Human Evolution and Archaeological Sciences, University of Vienna, Vienna 1090, Austria; ^uSchool of History, University of East Anglia, Norwich Research Park, Norwich NR4 7TJX, United Kingdom; ^vOxford Archaeology Ltd., Osney Mead, Oxford OX2 0ES, United Kingdom; ^wSchool of Global Integrative Studies, University of Nebraska-Lincoln, Lincoln, NE 68588; ^xInstitute of Palaeoanatomy, Domestication Research and the History of Veterinary Medicine, Department of Veterinary Sciences, Ludwig Maximilian University of Munich, Munich 80539, Germany; ^yBavarian Natural History Collections, State Collection of Palaeoanatomy Munich, Munich 80333, Germany; ^zDepartment of Geography, Royal Holloway, University of London, Egham TW20 0EX, United Kingdom; ^{aa}Department of Archaeology, University of Reading, Reading RG6 6AX, United Kingdom; ^{ab}Independent Researcher, Buckinghamshire, Greater Missenden HP16 0LF, United Kingdom; ^{ac}Département de la Charente, Angoulême Cedex 9 1616917, France; ^{ad}Department of Archaeology and Ancient History, Lund University, Lund 223 62, Sweden; ^{ae}Fishbourne Roman Palace, Chichester PO19 3QR, United Kingdom; ^{af}Department of Classics and Ancient Mediterranean Studies, Bucknell University, Lewisburg, PA 17837; ^{ag}Mediterranean Institute for Advanced Studies, Ecology and Evolution, Miquel Marqués Street, Esporles, Illes Balears 2107190, Spain; ^{ah}Department of Archaeology, Municipality of The Hague, Den Haag 2500 DP, The Netherlands; ^{ai}Laboratory for Bioarchaeology, Archaeology Department, University of Belgrade, Belgrade 11000, Serbia; ^{aj}Department of Archaeology, University of Southampton, School of Humanities, Southampton SO171BF, United Kingdom; ^{ak}Independent Researcher, Alghero, Vancouver 07041, Italy; and ^{al}Department of Ancient Mediterranean and Near Eastern Studies, V6T 1Z1, Canada

Author contributions: H.M., S.D., H.W.I.G., J.D., C.C., N. Spassov, K. Trantalidou, R.M., A.L.L., C.A., L.A., P.B., F.B., H.B., R.B., R.F.C., B.D.C., E.G., C.G., G.K.K., S.P., P.S., L.S., J.S., A.V., J.A.E., A.R.H., and N. Sykes analyzed data; C.C., N. Spassov, K. Trantalidou, L.A., P.B., F.B., R.B., R.F.C., A.C., B.D.C., C.D., E.G., C.G., G.K.K., R.N., S.P., F.P., P.S., S.S., L.S., R.S., A.V., M.V.V., J.W., B.W., and R.J.A.W. provided samples and data; A.B.-R., J.P., K. Tardio, and S.V. provided data; R.L., A.G.P., and M.V.V. provided historical input; and K.H.B., H.M., S.D., H.W.I.G., J.D., C.C., N. Spassov, K. Trantalidou, R.M., A.L.L., C.A., L.A., P.B., F.B., R.B., A.B.-R., R.F.C., A.C., B.D.C., C.D., E.G., C.G., G.K.K., R.L., R.N., S.P., J.P., F.P., A.G.P., P.S., S.S., L.S., R.S., K. Tardio, A.V., M.V.V., S.V., J.W., B.W., R.J.A.W., J.A.E., A.R.H., and N. Sykes wrote the paper.

1. N. Y. Werner, A. Rabiei, D. Saltz, J. Daujat, K. Baker, Dama mesopotamica (errata version published in 2016). The IUCN Red List of Threatened Species 2015: e.T6232A97672550. <https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T6232A2164332.en>. Accessed 4 January 2024.
2. D. Chapman, *Fallow Deer: Their History, Distribution, and Biology* (Coch-y-bonddu Books, Machynlleth, United Kingdom, 1997).
3. N. G. Chapman, D. I. Chapman, The distribution of fallow deer: A worldwide review. *Mamm. Rev.* **10**, 61–138 (1980).
4. K. H. Baker *et al.*, Strong population structure in a species manipulated by humans since the Neolithic: The European fallow deer (Dama dama dama). *Heredity* **119**, 16–26 (2017).
5. Z. Arslangundođdu *et al.*, Development of the population of the European Fallow Deer, Dama dama (Linnaeus, 1758), Turkey. *Zool. Middle East* **49**, 3–12 (2010).
6. M. Masseti, D. Mertzani, Dama dama. The IUCN Red List of Threatened Species 2008: e.T42188A10656554. <https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T42188A10656554.en>. Accessed 4 January 2024.
7. M. Masseti, A. Cavallaro, E. Pecchioli, C. Vernesi, Artificial occurrence of the Fallow Deer, Dama dama (L., 1758), on the island of Rhodes (Greece): Insight from mtDNA analysis. *Hum. Evol.* **21**, 167–175 (2006).
8. M. Masseti, E. Pecchioli, C. Vernesi, Phylogeography of the last surviving populations of Rhodian and Anatolian fallow deer (Dama dama L., 1758). *Biol. J. Linn. Soc. Lond.* **93**, 835–844 (2008).
9. V. Isaakidou *et al.*, Changing land use and political economy at Neolithic and Bronze Age Knossos, Crete: Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis of charred crop grains and faunal bone collagen. *Proc. Prehist. Soc.* **88**, 155–191 (2022).
10. K. M. Harris, *The Social Role of Hunting and Wild Animals in Late Bronze Age Crete: A Social Zooarchaeological Analysis* (University of Southampton, 2014).
11. E. Yannouli, K. Trantalidou, "The fallow deer (Dama dama Linnaeus, 1758): Archaeological presence and representation in Greece" in *The Holocene History of the European Vertebrate Fauna: Modern Aspects of Research*, N. Benecke, Ed. (Verlag Marie Leidorf GmbH, 1999), pp. 247–281.
12. J.-D. Vigne, J. Daujat, H. Monchot, First introduction and early exploitation of the Persian fallow deer on Cyprus (8000–6000 cal. BC). *Int. J. Osteoarchaeol.* **26**, 853–866 (2016).
13. T. Daszkiewicz *et al.*, A comparison of the quality of the Longissimus lumborum muscle from wild and farm-raised fallow deer (Dama dama L.). *Small Rumin. Res.* **129**, 77–83 (2015).
14. A. Linderholm, G. Larson, The role of humans in facilitating and sustaining coat colour variation in domestic animals. *Semin. Cell Dev. Biol.* **24**, 587–593 (2013).
15. G. Larson *et al.*, Current perspectives and the future of domestication studies. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6139–6146 (2014).
16. T. G. Martin, P. Arcese, N. Scheerder, Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago. *Biol. Conserv.* **144**, 459–469 (2011).
17. F. Ferretti, S. Lovari, "Introducing aliens: Problems associated with invasive exotics" in *Behaviour and Management of European Ungulates*, R. Putman, M. Apollonio, Eds. (Whittles Publishing, Dunbeath, United Kingdom, 2014), pp. 78–109.
18. C. Chakanya, A.-E.-M. Dokora, V. Muchenje, L. C. Hoffman, The fallow deer (Dama spp.); endangered or not? *Zool. Gard.* **85**, 160–172 (2016).
19. F. E. Zachos, G. B. Hartl, Phylogeography, population genetics and conservation of the European red deer Cervus elaphus. *Mamm. Rev.* **41**, 138–150 (2011).
20. R. F. Carden *et al.*, Phylogeographic, ancient DNA, fossil and morphometric analyses reveal ancient and modern introductions of a large mammal: The complex case of red deer (Cervus elaphus) in Ireland. *Quat. Sci. Rev.* **42**, 74–84 (2012).
21. R. S. Sommer, J. Kalbe, J. Ekström, N. Benecke, R. Liljegen, Range dynamics of the reindeer in Europe during the last 25,000 years. *J. Biogeogr.* **41**, 298–306 (2014).
22. D. W. G. Stanton, J. A. Mulville, M. W. Bruford, Colonization of the Scottish islands via long-distance Neolithic transport of red deer (Cervus elaphus). *Proc. Biol. Sci.* **283**, 20160095 (2016).
23. A.-K. Salmi, "Introduction: Perspectives on the history and ethnoarchaeology of Reindeer domestication and herding" in *Domestication in Action: Past and Present Human-Reindeer Interaction in Northern Fennoscandia*, A.-K. Salmi Ed. (Springer, 2022), pp. 3–33.
24. M. Masseti, M. Rustioni, Considerazioni preliminari sulla diffusione di Dama dama (Linnaeus, 1758) durante le epoche tardiglaciale e postglaciale nell'Italia mediterranea. *Studi per l'Ecolgia del Quaternario* **10**, 93–119 (1988).
25. N. Karastoyanova, J. Gorczyk, N. Spassov, The natural history of the fallow deer, Dama dama (Linnaeus, 1758) in Bulgaria in prehistory and new evidence for the existence of an autochthonous Holocene population in the Balkans. *Int. J. Osteoarchaeol.* **30**, 616–628 (2020).
26. T. O'Connor, N. Sykes, *Extinctions and Invasions: A Social History of British Fauna*, T. O'Connor, N. J. Sykes, Eds. (Windgather Press, Oxford, United Kingdom, 2010).
27. S. Kusza, M. R. Ashrafzadeh, B. Tóth, A. Javor, Maternal genetic variation in the northeastern Hungarian fallow deer (Dama dama) population. *Mamm. Biol.* **93**, 21–28 (2018).
28. L. A. F. Frantz, D. G. Bradley, G. Larson, L. Orlando, Animal domestication in the era of ancient genomics. *Nat. Rev. Genet.* **21**, 449–460 (2020).
29. M. Masseti, C. Vernesi, "Historic zoology of the European fallow deer, Dama dama: Evidence from biogeography, archaeology and genetics", K. Baker, R. Carden, R. Madgwick, Eds. (Windgather Press, Oxford, United Kingdom, 2014).
30. N. J. Sykes *et al.*, New evidence for the establishment and management of the European fallow deer (Dama dama) in Roman Britain. *J. Archaeol. Sci.* **38**, 156–165 (2011).
31. A. Valenzuela *et al.*, Both introduced and extinct: The fallow deer of Roman Mallorca. *J. Archaeol. Sci. Rep.* **9**, 168–177 (2016).
32. F. Beglane *et al.*, "Ireland's fallow deer: Their historical, archaeological and biomolecular records" in *Proceedings of the Royal Irish Academy: Archaeology, Culture, History, Literature* (2018), vol. 118C, pp. 141–165.
33. N. Sykes *et al.*, Wild to domestic and back again: The dynamics of fallow deer management in medieval England (c. 11th–16th century AD). *Sci. Technol. Archaeol. Res.* **2**, 113–126 (2016).
34. K. H. Baker *et al.*, Ancient and modern DNA tracks temporal and spatial population dynamics in the European fallow deer since the Eemian interglacial. *Sci. Rep.*, in press.
35. K. H. Baker *et al.*, OR220344-OR220389. Genbank. <https://www.ncbi.nlm.nih.gov/nuccore>. Deposited 30 June 2023.
36. K. H. Baker *et al.*, OR531435-OR531443. Genbank. <https://www.ncbi.nlm.nih.gov/nuccore>. Deposited 8 September 2023.
37. H. Miller *et al.*, The relationship between the phosphate and structural carbonate fractionation of fallow deer bioapatite in tooth enamel. *Rapid Commun. Mass Spectrom.* **33**, 151–164 (2019).
38. F. Santucci, B. C. Emerson, G. M. Hewitt, Mitochondrial DNA phylogeography of European hedgehogs. *Mol. Ecol.* **7**, 1163–1172 (1998).
39. R. Bilgin, Back to the suture: The distribution of intraspecific genetic diversity in and around anatolia. *Int. J. Mol. Sci.* **12**, 4080–4103 (2011).
40. P. Alexandri *et al.*, The Balkans and the colonization of Europe: The post-glacial range expansion of the wild boar, Sus scrofa. *J. Biogeogr.* **39**, 713–723 (2012).
41. N. Spassov, N. Iliev, "Animal remains from the submerged late Eneolithic – early Bronze Age settlement near Sozopol (south Bulgarian Black Sea coast)" in *Proceedings of the International Symposium Thracia Pontica VI* (Centre of Underwater Archaeology, Bulgaria, 1994), pp. 287–314.
42. M. Fabis, "Troia and fallow deer" in *Troia and the Troad*, G. A. Wagner, E. Pernicka, H.-P. Uerpmann, Eds. (Springer, 2003), pp. 263–275.
43. H. Miller *et al.*, Dead or alive? Investigating long-distance transport of live fallow deer and their body parts in antiquity. *Environ. Archaeol.* **21**, 246–259 (2016).
44. R. H. Meadow, "Osteological evidence for the process of animal domestication" in *The Walking Larder*, J. Clutton-Brock, Eds. (Routledge, 1989).
45. M. Masseti, M. Island of Deer: Natural History of the Fallow deer of Rhodes and the vertevrates of the Dodecanese (Greece). (Environmental Organisation, Rhodes, 2002).
46. J. Larson, "Venison for Artemis? The problem of deer sacrifice" in *Animal Sacrifice in the Ancient Greek World*, S. Hitch, Ed. (Cambridge University Press, 2017), pp. 48–62.
47. G. Reinken, Wieder-Verbreitung, Verwendung und Namensgebung des Damhirsches Cervus dama L. Europa. *Zeitschrift für Jagdwissenschaft* **43**, 197–206 (1997).
48. M. W. Helms, *Craft and the Kingly Ideal: Art, Trade, and Power* (University of Texas Press, Austin, TX, 2013).
49. N. Sykes, *Beastly Questions: Animal Answers to Archaeological Issues* (Bloomsbury Publishing, London, UK, 2014).
50. J. Best *et al.*, Redefining the timing and circumstances of the chicken's introduction to Europe and north-west Africa. *Antiquity* **96**, 868–882 (2022).
51. S. Klinger, A Terracotta Statuette of Artemis with a Deer at the Israel Museum. *Israel Exploration J.* **51**, 208–224 (2001).
52. H. Miller, N. Sykes, C. Ward, "Diana and her deer: the movement of mythology and medicine" in *The Role of Zooarchaeology in the study of the Western Roman Empire*, Allen M. G., Ed. (2019), vol. 107, pp. 101–112.
53. M. L. Nosch, "Approaches to Artemis in Bronze Age Greece" in *From Artemis to Diana: The Goddess of Man and Beast*, T. Fischer-Hansen, B. Poulsen, Eds. (Danish Studies in Classical Archaeology Museum Tusulanum Press, Copenhagen, 2009), pp. 21–40.
54. T. Fischer-Hansen, "Artemis in Sicily and south Italy: a picture of diversity" in *From Artemis to Diana: The Goddess of Man and Beast*, T. Fischer-Hansen, B. Poulsen, Eds. (Danish Studies in Classical Archaeology Museum Tusulanum Press, Copenhagen, 2009), pp. 207–260.
55. L. Bartosiewicz, "Faunal remains" in *The Archaeology of Houses at Morgantina, Sicily: Excavations of Later Prehistoric Contexts on the Cittadella* (1989–2004), R. Leighton, Ed. (Accordia Research Institute, University of London, 2012), pp. 153–171.
56. M. L. Ryder, "Some Phoenician animal remains from Sicily" in *Archaeozoological Studies*, A. T. Clason, Ed. (North-Holland Publishing, New York, 1975).
57. N. J. Sykes, J. White, T. E. Hayes, M. R. Palmer, Tracking animals using strontium isotopes in teeth: The role of fallow deer (Dama dama) in Roman Britain. *Antiquity* **80**, 948–959 (2006).
58. R. Madgwick *et al.*, Fallow deer (Dama dama) management in Roman South-East Britain. *Archaeol. Anthropol. Sci.* **5**, 111–122 (2013).
59. F. Pigière, D. Henrard, N. Sykes, N. Suarez-Gonzalez, G. Sonet, The introduction of the European fallow deer to the northern provinces of the Roman Empire: A multi-proxy approach to the Herstal skeleton (Belgium). *Antiquity* **94**, 1501–1519 (2020).
60. S. Davis, M. MacKinnon, Did the Romans bring fallow deer to Portugal? *Environ. Archaeol.* **14**, 15–26 (2009).
61. B. Wilkens, *Archeozoologia: il Mediterraneo, la storia, la Sardegna* (Editrice Democratica Sarda, 2012).
62. B. Baldino *et al.*, L'economia animale dal Medioevo all'età moderna nella Sardegna nord-occidentale. *Sardinia, Corsica et Baleares Antiquae: Int. J. Archaeol.* **6**, 109–161 (2008).
63. T. Oueslati, M. Ennaifer, "La maison des deux Chasses (Kélibia, Tunisie). Approche croisée de l'étude des tableaux de vénérie vandalo-byzantins et des ossements animaux (v–vi siècles)" in *L'homme et l'animal au Maghreb, de la Préhistoire au Moyen Âge*, V. Blanc-Bijon *et al.*, Eds. (Presses universitaires de Provence, Aix-en-Provence, 2014), pp. 307–315.
64. M. Azaza, L. Colominas, The Roman introduction and exportation of animals into Tunisia: Linking archaeozoology with textual and iconographic evidence. *J. Archaeol. Sci. Rep.* **29**, 102076 (2020).
65. J. Daujat, *Ungulate Invasion on a Mediterranean Island: The Cypriot Mesopotamian Fallow Deer over the Past 10000 Years* (Muséum National d'histoire Naturelle Paris, 2013).
66. N. J. Sykes, *The Norman Conquest: A Zooarchaeological Perspective* (Archaeopress, Oxford, United Kingdom, 2007).
67. N. Sykes, R. F. Carden, Were Fallow Deer Spotted (OE *pohla/*pocca) in Anglo-Saxon England? Reviewing the Evidence for Dama dama in Early Medieval Europe. *Mediev. Archaeol.* **55**, 139–162 (2011).
68. F. Beglane, *Anglo-Norman Parks in Medieval Ireland* (Four Courts Press, Dublin, Ireland, 2015).
69. F. Beglane, The social significance of game in the diet of later medieval Ireland. *Proc. Royal Irish Acad. Archaeol. Culture History Literature* **115**, 167–196 (2015).
70. B. Clavel, Chasse aux daims à Vincennes à la Renaissance. *Archéopages* **28**, 45 (2010).
71. A. Alen, F. Pigière, W. Wouters, W. Van Neer, Boussu-Boussu: la faune du château de Boussu. *Chronique de l'Archéologie Wallonne* **20**, 108–110 (2013).
72. A. E. H. Swaen, *Jacht-Bedryff, naar het handschrift in de Koninklijke Bibliotheek te's-Gravenhage* (E.J. Brill, Leiden, 1948).
73. S. Perdikaris *et al.*, From Icon of Empire to National Emblem: New Evidence for the Fallow Deer of Barbuda. *Environ. Archaeol.* **23**, 47–55 (2018).
74. N. Sykes, "Fallow deer: The unprotected biocultural heritage of Barbuda" in *Barbuda: Changing Times, Changing Tides*, S. Perdikaris, R. Boger, Eds. (Routledge, 2022).
75. A. Von den Driesch, *A Guide to the Measurement of Animal Bones from Archaeological Sites* (Peabody Museum Press, Cambridge, MA, 1976), vol. 1.
76. F. Bowen *et al.*, Dama Dentition: A new tooth eruption and wear method for assessing the age of fallow deer (Dama dama). *Int. J. Osteoarchaeol.* **26**, 1089–1098 (2016).
77. R. C. Edgar, MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* **32**, 1792–1797 (2004).
78. S. Buxton, M. Cheung, A. Cooper, J. Heled, M. Kearse, Geneious version R6. <https://www.geneious.com>. Accessed 4 March 2022.
79. H. J. Bandelt, P. Forster, A. Röhl, Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* **16**, 37–48 (1999).
80. J. P. Huelssenbeck, F. Ronquist, MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755 (2001).