1 **Main Manuscript for**

2 The 10,000-year biocultural history of fallow deer and its implications for
3 conservation policy
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70   contributed to the writing of the paper.
71

72   **Competing Interest Statement:** NA
73

74   **Classification:** Biological Science and Social Science: Anthropology
75

76   **Keywords:** Fallow deer; Translocations; Extinctions; Zooarchaeology; Biomolecules
77

78   **This PDF file includes:**
79   Main Text
80   Figures 1 to 4
81

Abstract

Over the last 10,000 years, 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 Chios and Rhodes in the Neolithic 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. We argue that these biocultural histories of fallow deer should underpin modern management strategies.

Significance Statement

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 new perspectives on the management of translocated animals.

Main Text

1. Introduction

There are two recognised 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 Daği-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 years ago(6–8). Early farmers of the 6th-5th millennium BCE also established populations of European fallow deer on the islands of Lemnos, Lesvos, Chios and Crete(9–11), whereas Persian fallow deer were transported to Cyprus ~10,000 years ago(12).

130

131 Both species were as heavily influenced by people as other taxa classically associated with the Neolithic
132 Package including cattle, sheep, goats and pigs. In addition, modern European fallow deer are farmed in
133 their millions(13) and exhibit coat colour variations indicative of selective breeding(14). Despite these
134 characteristics, fallow deer are rarely included in large-scale reviews of domestic animals(12, 15).
135 European fallow deer have been equally overlooked by conservation scientists, for whom the species'
136 domestic legacy has meant they are often considered an introduced alien or invasive threat, and thus
137 undeserving of protection(16–18).

138

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

148

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

158

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

166

167 **2. Results and Discussion**

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

170

171 For the European fallow deer, 181 sequences from archaeological samples were combined with those for
172 222 modern individuals. A Bayesian phylogeny constructed from the complete alignment (Fig 1A)
173 revealed a well-supported (0.89 posterior probability) monophyletic clade consisting of modern and
174 ancient European fallow deer from Northern Europe and Anatolia (depicted in yellow on Fig 1A-B).

175

176 A second clade is made up of ancient and modern fallow deer derived from southern and western
177 European sites and Roman England (depicted in red - Fig 1A-B). Both clades are distinct from the
178 mitochondrial lineage derived from a single modern Persian fallow deer at the base of the phylogeny.
179
180 A shorter sequence was available (128bp) that showed 18 fixed differences between European and
181 Persian fallow deer, allowing *D. mesopotamica* to be identified from archaeological remains (depicted in
182 purple in Fig 1B and Fig S1)
183
184 The zooarchaeological representation data (Table S2) and genetic results are summarized in Figure 2A-
185 D, which also incorporates the radiocarbon dating evidence (Fig 3). Multi-element isotope data were
186 generated from 418 specimens (Table S1), with results presented in (Fig 4, SI6 and SI7)
187

2.1 Refugia and Native Range

189 Our genetic analysis demonstrated that 38 specimens originally identified morphologically as *D. dama*
190 were actually *D. mesopotamica* (Fig S1). Their presence at the Bronze Age/early Iron Age sites of Kinet
191 Höyük and Kilise Tepe, Anatolia (Figs 2A-B) pushes the ancient distribution of Persian fallow deer further
192 west than previously proposed(12).
193
194 For the European fallow deer, our data suggest their glacial refugium was restricted entirely to the eastern
195 Mediterranean and there is no zooarchaeological evidence to suggest the existence of autochthonous
196 Holocene fallow deer populations in Iberia or Italy. Within Anatolia, the *D. dama* population demonstrates
197 continuity through time: Neolithic, Roman and medieval deer share haplotypes (H31) and are closely
198 related to the modern population at Güllük Daği-Termessos National Park (H47, H48). The modern deer
199 population on Rhodes are genetically distinct from Anatolian deer (a result that corroborates previous
200 studies(7, 8)) and appear more closely related to populations from the Balkans, Italy and Iberia.
201
202 The phylogenetic split between the two populations of European fallow deer (Fig. 1) is consistent with the
203 frequently observed phylogeographic divide found in numerous species with populations that span the
204 Bosporus(35–37). When combined with the zooarchaeological data (Fig. 2A) this result supports the
205 suggestion of a second glacial refugium in the southern and central Balkans(25, 38). Large quantities of
206 fallow deer remains have been recovered from Neolithic and Bronze Age sites in Bulgaria which
207 demonstrate their early presence in this region. Intriguingly, their remains exhibit morphologies distinct
208 from the Anatolian fallow deer (Fig S3 and S4) which may be the result of underlying genetic, not
209 environmental differences(25, 38, 39). Despite the phenotypic distinction, stable and radiogenic isotope
210 data show no difference in fallow deer diets between these regions (Fig S6 and S7) (40).
211
212

2.2 Translocations as proxies for the movement of people and ideologies

214 Both species of fallow deer were translocated during the Neolithic/Bronze Age (Fig. 2A). We partially
215 sequenced one Persian fallow deer specimen (PT608) from the Bronze Age site of Politiko-Troullia,
216 Cyprus and two Late Neolithic/Early Bronze Age European fallow deer samples from Ayio Galas Cave,
217 Chios (CH680 and CH681). The Chios samples possessed unique haplotypes (H45 and H46) that are
218 most closely related to individuals from modern Rhodes (H64 and H65). This result supports Masseti et
219 al.'s(7, 8) proposal that the modern Rhodes deer population descends from a Neolithic introduction.
220
221 The Neolithic Chios and modern Rhodes deer are more closely related to (and likely descend from) the
222 Balkan rather than Anatolia population. This may seem counter-intuitive, especially given that Rhodes is
223 only 11 miles from mainland Turkey, and Chios is <3 miles. However, animal translocations frequently

224 result from factors other than geographic proximity, including attitudes to the natural world, religious
225 ideologies and culture-contacts, issues to which we now turn.
226
227 ### 2.2i Early domestication
228 The transfer of animals beyond their natural range has been equated with a closening of human-animal
229 relationships and associated with the process of domestication (41).
230
231 According to Masseti(42) and Vigne et al.(12) island *Dama* populations were established specifically for
232 hunting but textual and iconographic evidence from the Bronze Age indicate a more complex relationship
233 between people and fallow deer. For instance, Linear B texts (the earliest form of Greek) list different
234 kinds of fallow deer: those that are wild, those that are tame, and those used in games or for sacrifices,
235 while fresco fragments from Aghia Triadha, Crete, depict a woman leading two fallow deer to a sacrificial
236 altar(11). Similar evidence exists across Anatolia and Egypt(43) and given that the Latin name *Dama*
237 derives from the Persian word for tame or pet(44) there is a compelling case that fallow deer were initially
238 no different in their relationships with humans than other animals that make up the canonical suite of
239 domesticates.
240
241 ### 2.2ii Religion
242 Many cultures equate geographical distance with supernatural distance perceiving that the further
243 something has traveled, the greater its prestige and power(45). In this way, introduced animals have
244 frequently been viewed as gods(46, 47).
245
246 Fallow deer were certainly associated with both the goddess Artemis and her Roman incarnation,
247 Diana(11, 43, 44, 48). There is debate about the geographical genesis of the Artemis myth but the
248 possibility she originated in the Balkans is given credence by the density of both fallow deer remains (Fig.
249 2A) and Artemis-related paraphernalia, such as fallow deer-shaped religious drinking vessels that have
250 been recovered from the region(49). In Late Minoan Crete (c.1550-1100 BCE) Linear B texts mention not
251 only fallow deer but also provide the earliest reference to Artemis(10, 50).
252
253 Historical studies suggest that the Artemis cult was taken to Sicily by early Greek settlers(51) and
254 statuettes of the goddess have been recovered from the Bronze Age site of Morgantina, together with a
255 shed fallow deer antler(52). This skeletal element could have been transported as an object in its own
256 right (as was the case for other *Dama* body parts recovered from a Phoenician ship-wreck off the coast of
257 Sicily (40, 53)) rather than deriving from an animal that lived on the island. At Morgantina, a small number
258 of post-cranial bones have been tentatively identified as *Dama(52)*. Our metrical analysis shows that their
259 size is more consistent with red deer from the island (Fig S5) though we were unable to confirm their
260 identification genetically.
261
262 ### 2.2iii Roman Empire
263 The Roman period witnessed a major expansion in fallow deer distribution (Fig. 2B). This was in part due
264 to their connection with the goddess Diana and also linked to the parks and menageries that became
265 increasingly fashionable throughout the Roman Empire.
266
267 The earliest evidence for the presence of fallow deer beyond the Mediterranean comes from the highly
268 'Romanised' palatial site of Fishbourne (southern England) that was constructed shortly after the Roman
269 invasion of Britain in 43 CE. Here, *Dama* remains have been directly dated to the 1st century CE (Fig. 3).
270 Multi-element isotope analysis revealed a first-generation import that likely traveled from the
271 Mediterranean in the first few months of its life (Fig. 4). Our evidence also shows that other fallow deer
272 were born and raised at Fishbourne(54) and managed in diverse ways (55).

273

274   By the fourth-century CE, fallow deer were established in Britain more broadly, and specimens from
275   Belgium(56) and Portugal(57) have been direct-dated to this period (Figs 2B and 3). The earliest secure
276   evidence for fallow deer on Sicily dates to the 5th century CE (Fig. 3 and S3) and isotope analysis
277   indicates these animals were born and raised on the island (Fig. 4). Genetically, Sicilian deer are
278   consistent with the western Mediterranean (Balkan) clade. They share a haplotype (H36) with animals
279   from Sardinia, where populations were established in the medieval period(58, 59). The Sardinian deer
280   also share haplotypes (H23) with deer from Roman France.

281

282   The European fallow deer established in Iberia and Italy both appear to be the progenitors of the modern
283   populations in those regions. For instance, one haplotype (H29) is observed in both medieval and modern
284   Portugal, and is closely related to Roman haplotypes (H43 and H44). Similarly, haplotypes found in
285   ancient Italy (H36) are closely related to those of modern deer (H69). These modern populations are
286   therefore legacies of the Roman Empire and should be treated as living cultural heritage (Figs 2B and
287   2D).

288

289   Large numbers of *Dama* remains have been recovered on Mallorca in contexts dating from the third to the
290   fifth century AD (31). Surprisingly, they were genetically determined to be Persian and not European
291   fallow deer (Fig S1), which has implications for understanding Roman and early medieval trade routes.
292   For instance, it is possible they arrived via north Africa where there are iconographic representations of
293   fallow deer. Recently, zooarchaeological evidence for fallow deer has been discovered in Roman North
294   Africa, but their remains are scarce and have not yet been subject to dating or biomolecular analysis
295   which means their species assignment is unconfirmed(60, 61).

296

297   *2.2iii Extinctions and population replacements*
298   The native *D. mesopotamica* distribution contracted substantially through time and by the medieval period
299   was replaced in eastern Turkey by *D. dama* (Fig 2). The Balkan population of *D. dama* was likely extinct
300   by the end of the medieval period (Fig. 2C). Of the translocated populations, the Persian fallow deer of
301   Mallorca went extinct around the seventh century CE(31) and the population on Cyprus disappeared by
302   the late medieval/early modern period(62). The *D. dama* population established in northern Europe during
303   the Roman period vanished rapidly following the Empire's withdrawal, and new populations were re-
304   established centuries later (Fig 2B-C).

305

306   For Britain, our study overturns the received wisdom that fallow deer were brought from the Norman
307   kingdom of Sicily following the Norman Conquest of 1066(63, 64). Our skyline plot (S1 Fig. 2) suggests
308   an introduction ~1000 CE and this model is supported by the evidence from the site of Goltho,
309   Lincolnshire. Isotope analyses of the Goltho deer indicate they were born and raised locally ((33); Fig. 4)
310   and direct dating suggests that a population was established before the Norman Conquest, by at least
311   1000 CE (Fig. 3). The possibility that these deer were derived from Sicily can be discounted from the
312   genetic evidence which demonstrates that the North European medieval deer are unrelated to either the
313   Roman or Western Mediterranean populations (Figs 1 and 2C). Instead, they are more closely related to
314   Anatolian deer, both of which lack a 21 bp mtDNA insertion present in 88% of modern Italian and Spanish
315   individuals(4).

316

317   *2.2iv Elite exchange and colonial expansion*
318   Following the second introduction to Britain, the maintenance of fallow deer within parks became a
319   statement of elite identity(33) and by the early 13th century, parks and fallow deer had been established
320   in Ireland by Anglo-Norman colonial powers(32, 65, 66). About this time fallow deer were exported to
321   France, sent by King Henry II to stock King Philip II's park at Vincennes(67).

322

323 In fact, England was likely the source of the deer reintroduced to other countries of northern Europe. A

324 16th/17th-century specimen from the Boussu castle, Belgium(68) was found to have a unique haplotype

325 (H25) closely related to the most common English haplotype (Fig. 2C). The 16th/17th-century specimen

326 from Bierstraat-The Hague (Netherlands) yielded insufficient aDNA to understand its relationship to the

327 broader dataset. Nevertheless, the oxygen isotope results suggest it may have been a first-generation

328 import from England (Fig. 4) and historical evidence supports this possibility. For example, the 17th

329 century Dutch hunting manuscript, Jacht-Bedryff, notes that Maurice of Nassau (later Prince of Orange)

330 acquired 100 fallow deer from England to stock The Hague forest(69).

331

332 The combination of historical research and genetic results indicates that England was the source of the

333 fallow deer exported across the British Empire. The *Dama* of the Caribbean island of Barbuda (H63) are

334 closely related to English deer, which is consistent with documentary evidence that fallow deer were

335 transported to the island, along with many African slaves, by the Codrington family of

336 Gloucestershire(70). The meaning attached to these Barbudan deer changed through time. Initially they

337 were a symbol of colonial authority and dominance, but after the slave emancipation of 1834, fallow deer

338 became a symbol of freedom, adopted as Barbuda's national animal. Today, fallow deer are an important

339 part of Barbuda's economy and cultural heritage but, as an introduced 'alien' species, they fall outside

340 legal protection. This is despite clear threats from over-hunting and natural disasters, such as hurricane

341 Irma that devastated the island in 2017, which have put the culturally important population at risk(70, 71).

342

343 **2.3. Implications for Fallow Deer Management and Conservation**

344 The Barbudan fallow deer are just one of many global populations that possess cultural importance. Yet it

345 is precisely the close association with humans, and particularly their human-assisted translocation, that

346 excludes them from IUCN protection. We argue that the cultural heritage represented by a species should

347 be taken into consideration when conservation decisions are being made.

348

349 The results presented here serve as a warning about the vulnerability of island fallow deer. Ancient

350 introductions to Crete, Chios, Cyprus, Sicily, Sardinia, Mallorca and Roman Britain all went extinct (Fig.

351 2D). The modern Barbudan population could follow a similar trajectory without a conservation plan akin to

352 that which allowed the Rhodes fallow deer to endure from their Neolithic introduction. It is the deer from

353 Rhodes, along with those from Italy and Portugal, that preserve traces of the now extinct refugial

354 population that once inhabited the Balkans.

355

356 There are several active campaigns to re-establish fallow deer in the Balkans and preserve the last

357 remaining wild herd at Daği-Termessos National Park, Turkey. Without knowledge of the species' deep-

358 time biomolecular and phylogeographic history, deer are being sourced from the least appropriate

359 populations. For instance, those being reintroduced to the Balkans possess Anatolian ancestry (Fig. 2D).

360 Furthermore, these Anatolian deer are being introduced to regions that have, for thousands of years,

361 preserved deer with Balkan ancestry (Fig. 2D). Whilst Anatolia-derived deer are increasing in number

362 around the world, the Daği-Termessos herd is still under threat. Our contention is that North European

363 deer of Anatolian ancestry could be introduced to the Daği-Termessos park, whilst Iberian/Italian/Rhodes

364 deer populations would be a better source for Balkan rewilding projects.

365

366 **3. Conclusion**

367 This study combined zooarchaeology and ancient and modern biomolecular datasets with evidence from

368 Humanities disciplines to reveal new insights into the history of both fallow deer and the people who

369 transported them. We argue that after the Last Glacial Maximum, Persian fallow deer were more

370 widespread than has previously been proposed, whilst European fallow deer were likely restricted to

371   Anatolia and the Balkans, and two distinct populations existed on either side of the Bosporus. Our
372   integrated study suggests early translocations of deer as a viable alternative to fallow deer surviving
373   anywhere else outside these regions.
374
375   Tracing their spread from these refugia reveals that fallow deer were repeatedly sourced from the furthest
376   available populations: the deer on Neolithic Chios (and likely Rhodes) derived from the Balkans, rather
377   than nearby Anatolia; those on Roman Mallorca were *Dama mesopotamica* rather than the *Dama dama*
378   which could have been acquired from the Iberian peninsula; and the deer reintroduced to medieval Britain
379   were brought from Anatolia instead of Iberia or Italy. This reflects the human desire to possess the exotic
380   which, across cultures, is linked to concepts of power and otherwoldliness. Not surprisingly then, the
381   earliest translocations of fallow deer are linked to the religious cults of Artemis and Diana.
382
383   Ancient dispersals of people, ideas and animals are widely celebrated as cultural heritage. However, the
384   more recent the migrations, the more negative the attitudes towards them. Such perceptions can translate
385   into animal management and policy making. For instance, the fallow deer of Rhodes were introduced
386   during the Neolithic and are viewed as a cultural asset, protected by Greek law and featured on the IUCN
387   Red List. The fallow deer of Barbuda are equally culturally significant as the island's national animal, yet
388   they have no legal protection and are labeled as 'invasive' within the conservation literature. In truth, they
389   are dismissed only because their introduction occurred too recently to have acquired a patina of age-
390   based authenticity.
391
392   Given the planet's biodiversity crisis, it is time to rethink our attitudes to animals. Whilst many species
393   may legitimately be labeled as invasive, this is not true of all translocated populations and some do
394   deserve protection. Preoccupation with native and wild species can come at the expense of (often equally
395   endangered) translocated animals that are not only critically entangled with human history but also offer a
396   conservation resource for replenishing diminished autochthonous populations.
397

398   **4. Materials and Methods**
399   Spatiotemporal shifts in European and Persian fallow deer distribution were initially reconstructed through
400   synthesis of the zooarchaeological literature. Reports referencing the presence of fallow deer were
401   collated (n = 336) and the frequency of fallow deer (relative to main mammals) within each assemblage
402   was calculated (SI Table 2). The location and frequency data were mapped for three key chronological
403   periods - Neolithic and Bronze Age (8000-1200 BCE), Iron Age and Roman (1200 BCE-500 CE),
404   medieval and early modern (500-1800 century CE) – to create Figures 2A-C.

405   To add resolution to the zooarchaeological survey, 635 osteological samples were acquired from sites
406   across the fallow deer's ancient and modern range (SI Table 1). Samples were subject to full-suite
407   analysis using the following techniques (SI for full details):

409   **4.1 Zooarchaeological analysis**
410   Contextual information (site type, date and associated archival data) was recorded for each specimen,
411   which was identified to skeletal element and examined for evidence of taphonomic process and
412   pathology. Metrical analysis(72) and age determinations(73) were undertaken to assist with species
413   assignment and demographic profiling. Osteometric data were compared against those published on the
414   Deer Bone Database https://www.nottingham.ac.uk/zooarchaeology/deer_bone/search.php.

416   **4.2 Isotope analysis**
417   A total of 418 specimens were submitted for multi-element isotope analyses, including carbon and
418   nitrogen (n= 418), oxygen (n=31), strontium (n=18) and sulphur (n=22). Collagen extractions were

419 undertaken at the University of Nottingham. Other preparation methods and analyses were undertaken at
420 the National Environmental Isotope Facility (formerly NERC Isotope Geosciences Laboratory) at the
421 British Geological Survey, Keyworth, UK. Oxygen data were compared against Miller et al.'s modern
422 baseline(74).

4.3 Chronologies and radiocarbon dating
425 Dating of the archaeological specimens was based largely on contextual association. To check issues of
426 stratigraphic migration (which have been noted in smaller animals (47)) and refine the chronology of
427 fallow deer translocations, published radiocarbon dates were collated (n=9) and key specimens (n=23)
428 were directly dated: 21 at the University of Oxford's Radiocarbon Accelerator Unit (ORAU) UK and two at
429 Beta Analytic (USA).

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

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

445 All sequences were aligned using the MUSCLE algorithm(75) as implemented in Geneious v. R6
446 (www.geneious.com, (76)). The relationship amongst haplotypes was examined by constructing both
447 median-joining networks(77) in NETWORK v. 3.1.1.1 (www.fluxus-engineering.com) and a Bayesian
448 phylogeny within MrBayes v. 3.2.6(78). The demonstrated phylogenetic distinctiveness of the two
449 subspecies *D. dama* and *D. mesopotamica(31)* allowed us to confirm species identifications when
450 zooarch assessments were equivocal. This was based on 18 fixed differences out of the 128bp
451 sequence. Additional details pertaining to the data generation, analyses and GenBank accession details
452 (SI Table 5) are found in the Supplement.

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Figures

Figure 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 (Figure 2). The collapsed tree in Panel B is rooted to *Cervus elaphus* and based upon 128 basepairs (see 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).
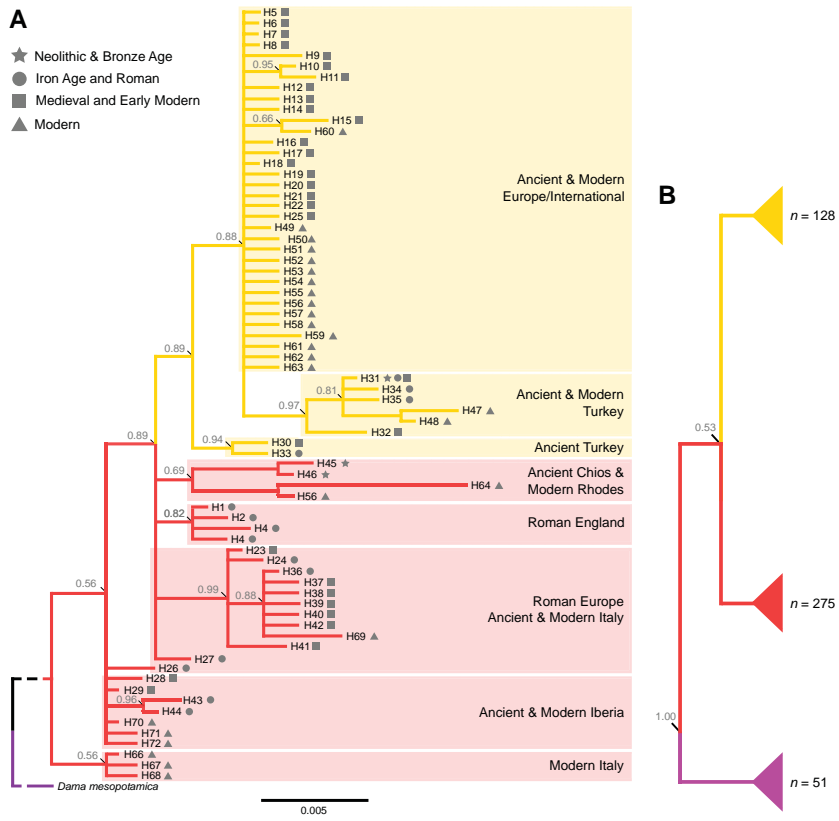
15

674

675   **Figure 2.** Maps showing the location and density of European and Persian fallow deer remains in
676   zooarchaeological assemblages (A-C, data from SI Table 2) coloured according to genetic results (Figure
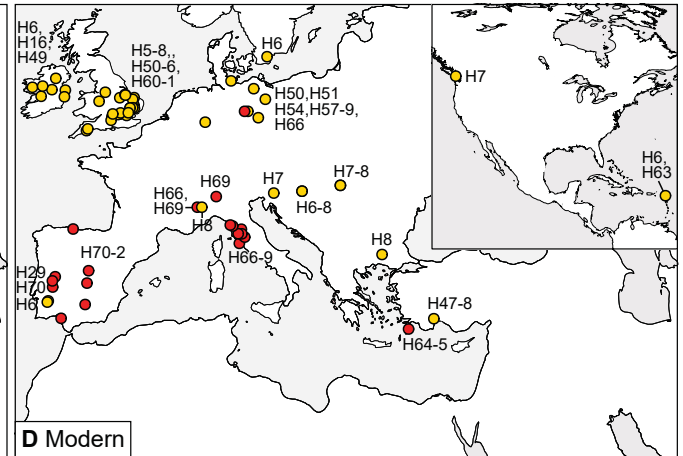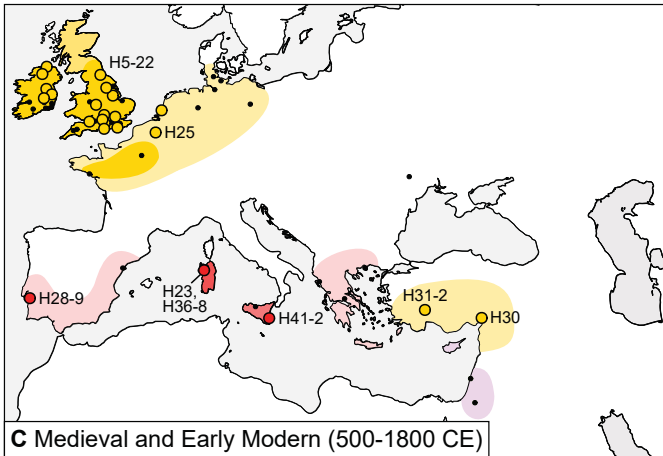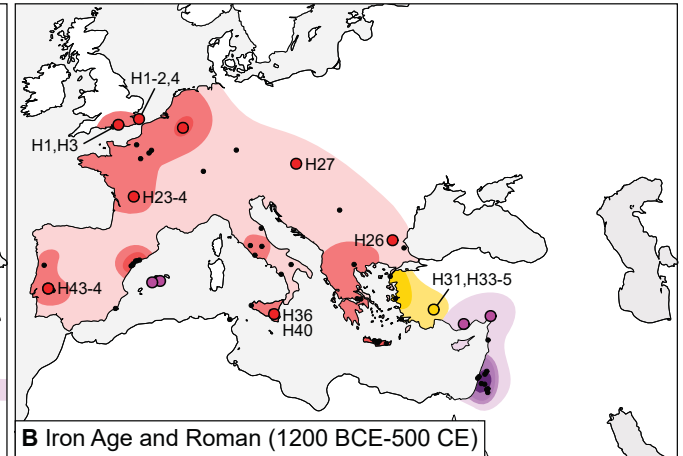677   1, SI Table 1).

678

679   **Figure 3.** Calibrated radiocarbon dates of fallow deer, colour-coded by genetic results (see Figure 1).

680

681   **Figure 4.** Range and mean of oxygen isotope data for modern fallow deer (Miller et al. 2019) compared
682   with ancient specimens. The graph is coloured by average temperatures for the regions from which the
683   modern specimens derive. Those from ancient Turkey, Greece, Sicily, Mallorca and medieval England
684   are consistent with animals that lived and died in those regions. By contrast, the AD60 mandible from
685   Fishbourne Roman Palace has a value for its first molar (M1, which develops <4 months) that is more in
686   line with those from Turkey, Israel, the Balkans and Italy. The values for the same deer's second molar
687   (M2, develops 8-9 months) and third molar (M3, develops <18 months), along with those for the other
688   Fishbourne fallow deer, align with those from modern and medieval England. The specimen from Goltho
689   is consistent with UK values. The specimen from post-medieval Bierstraat-The Hague, the Netherlands,
690   has an M1 value consistent with England but its M3 value is more suggestive of continental northern
691   Europe.

A

★ Neolithic & Bronze Age
● Iron Age and Roman
■ Medieval and Early Modern
▲ Modern

B

Ancient & Modern
Europe/International

Ancient & Modern
Turkey

Ancient Turkey

Ancient Chios &
Modern Rhodes

Roman England

Roman Europe
Ancient & Modern Italy

Ancient & Modern Iberia

Modern Italy

Dama mesopotamica

0.005

n = 128

n = 275

n = 51

A Neolithic and Bronze Age (8000-1200 BCE)

B Iron Age and Roman (1200 BCE-500 CE)

C Medieval and Early Modern (500-1800 CE)

D Modern

OxCal v4.4.4 Bronk Ramsey (2021); r:5 Atmospheric data from Reimer et al (2020)

OxA-27875 Hyde Abbey, UK
OxA-27934 Sparsholt, UK
OxA-27877 Cheddar Palaces, UK
SUERC-46456 Carisbrooke Castle, UK
OxA-27889 Carisbrooke Castle, UK
OxA-27900 Carisbrooke Castle, UK
OxA-27898 Carisbrooke Castle, UK
OxA-27976 Faccombe Netherton, UK
OxA-38878 Goltho, UK
OxA-38877 Goltho, UK
OxA-27876 Goltho, UK

OxA-27936 Sa Mesquida, ES
OxA-27937 Sa Mesquida, ES
OxA-27878 Pollentia, ES

Beta-609996 Campanaio, IT
Beta-615081 Campanaio, IT
Beta-235949 Torre de Palma, PT
RICH-24095 Hertsal-rue Jean Lamoureux, BE
RICH-22910 Hertsal-rue Jean Lamoureux, BE
OxA-19700 Monkton, UK
OxA-19703 Monkton, UK
OxA-19701 Monkton, UK
OxA-19704 Monkton, UK
OxA-19702 Monkton, UK
OxA-19705 Monkton, UK
OxA-19706 Monkton, UK
OxA-19718 Monkton, UK
Beta-201534 Fishbourne, UK
OxA-27873 Fishbourne, UK
Beta-201535 Fishbourne, UK
OxA-27874 Fishbourne, UK

1500   1000   500   1calBC/1calAD   500   1000   1500

Calibrated date (calBC/calAD)