Spread of domestic animals across Neolithic western Anatolia: New stable isotope evidence fromUGHurlu Höyük, the island of Gökçeada, Turkey

Suzanne E. Pilaar Birch1,2,*, Levent Atici3, Burçin Erdoğan4
1 Department of Anthropology, University of Georgia, Athens, Georgia, United States of America, 2 Department of Geography, University of Georgia, Athens, Georgia, United States of America, 3 Department of Anthropology, University of Nevada, Las Vegas, Las Vegas, Nevada, United States of America, 4 Department of Archaeology, University of Akdeniz, Antalya, Turkey

* sepbirch@uga.edu

Abstract

The origins of agriculture in Southwest Asia over 10,000 years ago and its subsequent spread into Europe during the Neolithic have been the focus of much archaeological research over the past several decades. Increasingly more sophisticated analytical techniques have allowed for better understanding of the complex interactions that occurred amongst humans, animals, and their environments during this transition. The Aegean Islands are critically situated where Anatolia and the mainland Greece meet, making the region pivotal for understanding the movement of the Neolithic into Europe. Located on the largest Turkish Aegean island of Gökçeada, the site of UĞurlu Höyük dates to the early Neolithic and has been the subject of ongoing excavations and research integrating a rigorous dating program with comprehensive zooarchaeological research. This paper focuses on the combination of bone collagen and tooth enamel stable isotope data with existing archaeological data to develop a fine-resolution picture of the spread of the Neolithic, particularly the importation and management of domestic fauna on Gökçeada, with broader relevance for understanding Aegean-Anatolian interactions. The stable isotope values from the fauna at UĞurlu have been used for both diachronic intrasite analyses and intersite comparisons between contemporaneous mainland sites. Integrating stable isotope and zooarchaeological datasets makes UĞurlu one of the first island sites to provide a comprehensive understanding of the geographic origin of Neolithic livestock populations and the timing of their spread from Anatolia into Europe during the process of Neolithization.

Introduction

The current body of research surrounding the Neolithization of Europe and the spread of agricultural lifestyles from the Near East across Anatolia, the Balkans, and beyond has grown exponentially in recent years, with studies that increasingly combine emerging methodologies and
techniques with extant archaeological data. It is critical that secondary types of analysis on faunal remains, such as that of stable isotopes and ancient DNA, are performed at sites and on material that has already been studied by a zooarchaeologist in order to provide a solid foundation for interpretation [1]. This paper builds on over a decade of excavations at the site of Uğurlu Höyük, Gökçeada, Turkey, directed by B. Erdoğan [2–8] and the most recent comprehensive analysis of the faunal assemblage to date, published by the authors (Atici et al.) in 2017 [9]. Here, we first incorporate the stable isotope analysis of terrestrial taxa at Uğurlu into broader anthropological questions about the spread of agriculture from approximately 6500 to 5000 cal. BC. We then situate the site and our results within a wider regional context (Fig 1) and explanatory framework. We do not set out to provide an exhaustive review of the multifaceted and complex process of the spread of domestic livestock throughout Anatolia, but rather consider the unique contribution of stable isotope data from faunal remains to our understanding of their role at Uğurlu, given its setting as both an island “endpoint” as well as a dynamic landmark on the thoroughfare of agricultural spread.

Regional zooarchaeological context

Uğurlu Höyük is a low mound covering an area of approximately 250 × 200 m. Six main cultural phases have so far been identified and designated I–VI from the top down. In this paper, we focus on Phases V–III at Uğurlu, which correspond to the early Neolithic (6500–6000 cal BC, Phase V), late Neolithic (5900–5600 cal BC, Phase IV) and early Chalcolithic (5500–5000 cal BC, Phase III) [3]. In our previous paper [9], we discussed established relationships between Uğurlu and the island of Gökçeada with sites in western and central Anatolia, Marma, Thrace, the Balkans, and other Aegean islands based on ceramics, technological typologies and lithic sources, and added faunal evidence to that corpus. Here, we briefly review some of these as well as other sites relevant to a discussion of faunal assemblages and their isotopic analysis. Despite the continuing growth of stable isotope analysis in archaeology in general, there are still relatively few published faunal-centered studies with large sample sizes in Turkey that date to the Neolithic. Contemporaneous sites in western Anatolia include Çukuriçi and Ulucak. At Çukuriçi, the earliest dates for the Neolithic are 6770–6480 cal BC and there are domestic sheep, goat, cattle, and some young pigs, with substantial marine input in the diet; wild animals are rare [10,11] and there is currently no stable isotope data available for comparison. At Ulucak, we see a similar subsistence economy in terms of domesticates, but very little marine input in the diet, though shells do seem to be used for decoration; wild animals are also rare [12,13]; there is published stable isotope data from caprines from both bone collagen and tooth enamel [1]. The earliest Neolithic at Ulucak dates to c. 7030–6460 cal BC; the middle Neolithic to 6650–6050 cal BC; and the late Neolithic 6030–5710 cal BC (14sea.org). In central Anatolia, there is good evidence for early domestic sheep, goat, and cows, but no pigs [9,14,15]. There, the sites of Asikli Höyük and Çatalhöyük provide two large stable isotope datasets for bone collagen and bone collagen and tooth enamel, respectively. At Asikli Höyük, the first half of the 8th millennium BC (approximately 8,000–7,500 cal BC) was characterized by plant cultivation and had a faunal assemblage dominated by what were considered “proto-domestic” caprines (over 80%) and cows [16]. The early Neolithic at the well-known site of Çatalhöyük dates to the second half of the 8th millennium BC and continues well into the late 7th millennium BC, with up to 80% of the assemblage constituted by domestic sheep and goat in some levels. In the Marmara region, there is evidence for the herding of sheep, goats, and cattle by 6600 BC, and pigs by 6000 BC [13]. Contemporaneous sites include Barçın Höyük, Fikirtepe, Ilıpınar, Menteşe Höyük, and Aktopraklık. There is a faunal bone collagen stable isotope dataset from the late Neolithic Aktopraklık (6400–5600 cal.) [17,18].
Across the Aegean Sea, in the Peloponnese, the site of Franchthi famously spans thousands of years of occupation, with dates of 7028–6648 cal BC for the earliest Neolithic. Like the western Anatolian sites, there is evidence for sheep, goat, cattle, and pig; previously abundant fish and wild taxa become rare, though marine molluscs remain moderately present [19,20]. At Knossos on Crete, which was entirely depauperate of any endemic fauna prior to human settlement in the Neolithic [21–23] there is evidence for the introduction of domestic sheep, goat, cattle, pig, with limited marine input and no wild fauna. This has led to the inference of settlement by “seafaring farmers” rather than “farming seafarers” [24,25]. In contrast, though a better understanding of the chronology is needed, Maroulas on Kythnos and Cyclops on Youra both have evidence for the presence of sheep and goat, but also substantial marine assemblages, at the start of the 7th millennium BC [26–28]. There are currently no large stable isotope from fauna for these sites during these time periods.

In the broader Neolithic context in Anatolia and the Aegean, then, there are certainly diverse subsistence practices. The relationship of the extant zooarchaeological data at Uğurlu in the broader context of archaeological evidence of Neolithization processes is reviewed in depth in Atici et al. 2017 [9]. Generally, while the diffusion of domesticates likely followed multiple routes, two main ‘streams’—overland and coastal—have gained favor in the literature and supported differences between distinct ‘zones’ as defined by other archaeological material, such as lithics and pottery [29, 30]; see Fig 1 in [31]. A recent review by Orton et al. (2016) reinforces the concept of two ‘streams’ of movement (one inland, one coastal) into the Balkans for sheep, goat, cattle, and pig [32]. However, as evidenced by the presence of Melian obsidian...
on a number of Aegean islands, movement was not unidirectional, and inter-island and inter-
mainland exchange networks were nuanced. Atici et al. (2017) demonstrated that the faunal 
assemblages on Uğurlu represent this nuanced picture through the use of domestic and wild 
resources through time in the Neolithic [9]. Here we will consider the site’s relationship to 
contemporary Anatolian sites for which stable isotope data already exist (Uluçak, Aşıklı 
Höyük, and Çatalhöyük), though future comparisons with other sites may be possible pending 
generation and publication of more stable isotope datasets from both bone collagen and 

tooth enamel.

Given this background and regional context, we investigate how stable isotope evidence 
may illuminate animal management practices throughout the early Neolithic at Uğurlu, the 
earliest Neolithic site in the eastern Aegean. In order to address this question and to aide in 
interpretation regarding paleoenvironmental data and regional archaeology, we first sought to 
directly date bone from each stratum and compare it with the established chronologies. The 
earliest domestic fauna must have been imported to the island. Considering the diversity of 
possible pathways over land and across the sea, we seek to evaluate the stable isotope data of 
fauna from Gökçeada in the context of other known early Neolithic sites along the route of 
spread of agriculture for which stable isotope data are currently available in order to shed light 
on the possible relationships between these regional zones. We aim to identify potential 
“source” populations for domesticates while recognizing that these data represent a portion of 
a growing body of evidence in support of a nuanced approach to the application of stable iso-
tope techniques in reconstructing the movements of livestock in the past.

Environmental setting and its relationship to stable isotope expectations

Currently there is a lack of detailed paleoenvironmental proxy data for the island of Gökçeada. 
Though Gökçeada was connected to mainland Anatolia during the Last Glacial Maximum, it 
became an island by the early Holocene and certainly by the Neolithic [8,33,34]. Due to its 
proximity to the coast (22km), there was likely always some relationship to the mainland 
throughout the Holocene. It is the largest (289 km²) and westernmost Turkish island and has a 
maximum elevation of 673 m, at the peak of the extinct volcano İlyas Dağ. As a result, the geol-
ogy of the island is constituted primarily of late Oligocene volcanic and metamorphic rock as 
well as limestone and Eocene deltaic sediments [35]. There are four saltwater lagoons on the 
island that are used for irrigation in the modern period, along with multiple reservoirs that 
provide drinking water. A large river, İmroz-Büyükdere, spans 3 km and would likely have 
been a primary source of freshwater in the early Holocene, as well as local springs and rainwa-
ter. The vegetation is typical Mediterranean, with forests comprised of black larch, oak, and 
Calabrian pine at higher elevations; olive trees are ubiquitous and low lying scrub covers a 
majority of the landscape [36]. The site of Uğurlu is located on the southwest of the island.

According to data derived from the nearest weather station in Limnos, Greece, the weather 
on Gökçeada is warm and dry in the summer months of July and August (average maximum 
temperature 30˚C, average precipitation 10mm) and cooler and wetter in the winter months of 
December and January (average minimum temperature 5˚C, average precipitation 80mm). 
The average annual rainfall is approximately 500mm and the mean temperature is 15˚C. In 
comparison, the western Anatolian coast is slightly warmer and wetter (for Izmir, an average 
of 17˚C and 700mm/year), while the Konya Plain in Central Anatolia receives just 300mm/ 
year and has an average mean temperature of 11˚C. Given the lack of more comprehensive 
paleo reconstructions of temperature, rainfall, and groundcover, these data will be useful when 
considering the stable isotope results from fauna on Gökçeada as compared to potential 
“source” populations at sites located in Western and Central Anatolia, below.
Generally, increased precipitation, warmer temperatures, and higher humidity suggest more productive ecosystems and C3 vegetation, for which more negative values for both $\delta^{13}C$ and $\delta^{15}N$ are expected [37–39]. In contrast, more positive $\delta^{15}N$ values would be expected in hot, arid environments, in individuals experiencing water stress, consuming brackish water, and consuming plants growing in manured or more saline soil [40–42]. In environments that are drier and have less precipitation, C4 plants are generally more abundant (and C3 plants may behave more like C4 plants in terms of $13C$ discrimination during photosynthetic uptake), leading to more positive $\delta^{13}C$ values and more positive $\delta^{15}N$ [39,43,44]. In turn, animal diets reflect this natural pattern; herbivores consuming local vegetation will possess a local stable isotope “signature” in their soft tissues, long since decayed, and their hard tissues, available to the archaeologist [45–49]. In particular, the protein portion of bone (collagen) can be analyzed for $\delta^{13}C$ and $\delta^{15}N$, while the inorganic component of tooth enamel, hydroxyapatite (carbonate) can be analyzed for $\delta^{13}C$ and $\delta^{18}O$. In temperate environments, the $\delta^{18}O_{\text{water}}$ values are higher in warm temperatures and lower in cooler temperatures and are likewise related to seasonal fluctuations in rainfall amount [50,51]. The $\delta^{18}O$ signature recorded in tooth enamel carbonate in mammals is related to ingested $\delta^{18}O$ such that tooth enamel $\delta^{18}O_{\text{carbonate}}$ can be used as a proxy for temperature and rainfall [48,52,53]. Tooth enamel carbonate $\delta^{13}C$ values are reflective of carbon isotopic values of the whole diet with herbivore bioapatite $\delta^{13}C$ values higher than the diet by 12–14‰ in ruminants [54,55]. The length of time over which a tissue forms also influences what its stable isotope signature will be; for example, in ungulates, teeth form incrementally over the first 1–2 years of life. Bones, in contrast, generally reflect the last several years of life, depending on which element is sampled. Based on the relationships between climate and environmental factors such as precipitation, humidity, aridity, temperature, and vegetation type (C3 or C4), with the isotopic values recorded in bone collagen and tooth enamel carbonate, we can distinguish relative expected ranges of values related to individuals’ zone of origin: i.e., central mainland Anatolia, the western Anatolian coast or Marmara region, and the island of Gökçeada. For example, an animal living in a relatively more arid climate such as central Anatolia may exhibit elevated $\delta^{15}N$ values in comparison to an animal living in a more humid setting such as the Aegean Coast. Likewise, animals living on the island of Gökçeada and the Aegean coastal areas, which experience higher average annual rainfall than the interior, are likely to record, on average, more negative $\delta^{18}O$ values in their teeth than individuals derived from central Anatolia. It is also important to keep in mind temporal scale differences in local and regional climate and environmental change; for example, evidence for increased mid-Holocene aridity in southwestern Turkey [56]. The fluctuations of regional precipitation and temperature manifest in isotope ratios, and therefore specifics of isotopic composition of local vegetation [57], with implications for the interpretation of these faunal isotope data from archaeological sites.

Materials and methods

Field recording of faunal remains was carried out by Levent Atici (2011, 2013, and 2014) and by Levent Atici and Suzanne E. Pilaar Birch (2015) on site at the Uğurlu Höyük Excavations, directed by Burçin Erdoğlu. Samples were exported to the U.S. under the permit granted by the Ministry of Culture and Tourism, Turkey, number 77366169–160.01.01, dated 13 August 2015. Pretreatment of samples was carried out in the Quaternary Isotope Paleocology Laboratory, directed by Pilaar Birch and based at the Center for Applied Isotope Studies (CAIS), University of Georgia, USA, where all stable isotope and radiocarbon analyses were conducted.
Radiocarbon dates

Five specimens (one canid and four sheep/goat) provided radiocarbon dates from Phases V-III. These were selected in order to strengthen the existing radiocarbon chronology and provide direct dates on bones analyzed for stable isotopes in this study. At CAIS, the samples were demineralized with cold (4°C) 1 N HCl for 24 hours, filtered, and washed with deionized water. The samples were then rinsed with 0.1M NaOH to remove humic acids, washed, and rinsed with 1N HCl to remove atmospheric CO₂. The samples were rinsed in deionized water to pH 4 (slightly acidic) and heated at 80°C for 8 hours. The solutions were filtered through glass fiber filters to isolate the total acid insoluble fraction (“collagen”) and freeze-dried. Collagen was combusted at 575°C in evacuated and sealed Pyrex tubes in the presence of CuO to produce CO₂. The resulting CO₂ samples were cryogenically purified from the other reaction products and catalytically converted to graphite using the method of Vogel et al. (1984)[58]. Graphite ¹⁴C/¹³C ratios were measured using the 0.5 MeV accelerator mass spectrometer (AMS). The sample ratios were compared to the ratio measured from the Oxalic Acid I standard (NBS SRM 4990). The sample ¹³C/¹²C ratios were measured separately using an isotope ratio mass spectrometer (IRMS) and expressed as δ¹³C with respect to PDB, with an error of less than 0.1‰. The quoted uncalibrated date is given in radiocarbon years before 1950 (years BP), using the ¹⁴C half-life of 5568 years. The error is quoted as one standard deviation and reflects both statistical and experimental errors. The dates have been corrected for isotope fractionation. Dates were calibrated using OxCal v.4.3.2 and the IntCal13 calibration curve; dates are reported to 1σ.

Collagen

Out of sixty-five samples initially selected for stable isotope analysis, fifty-nine bones produced viable collagen, including five specimens that were selected for radiocarbon dating (Table 1 and S3 Table). We chose unarticulated same-sided elements within species to avoid sampling the same individual; when multiple skeletal elements from the same context and taxon were used, determinations were made based on qualitative characteristics in which we have a high confidence. Bones sampled for isotopic analysis were derived from stratigraphically secure contexts, and these contexts are reflected in the faunal specimen number. Collagen samples were prepared using a modified Longin method [59] by demineralizing fragmented 0.5 g bone chunks in 0.5 M HCl for several days. The acid was changed every two days until the sample floated and was soft. The collagen was gelatinized by heating it in pH 3.0 water at 75°C for 48 hours. Each sample was filtered using an EZEE filter and the supernatant liquor was freeze-dried. Subsamples of freeze dried collagen powders were weighed into tin capsules and analyzed on a Costech Elemental Analyzer coupled to a Finnigan Delta IV Plus IRMS. Stable carbon is reported relative to VPDB and stable nitrogen is reported relative to AIR. Standards (n = 36) were supplied from the National Institute of Standards & Technology (NIST); for carbon, polyethylene foil (δ¹³C = −32.15 ‰) and sucrose (δ¹³C = −10.45 ‰) were used and for nitrogen, ammonium sulfate (δ¹⁵N = +20.41 ‰) and potassium nitrate (δ¹⁵N = +4.7 ‰) were used. Two internal standards (spinach, δ¹⁵N = −0.54 ‰; δ¹³C = −27.44 ‰ and protein, δ¹⁵N = +8.19 ‰; δ¹³C = −17.43 ‰) were also used. Precision was better than ±0.15 ‰.

Enamel

Thirty-eight teeth from twenty-nine individuals (9 M2-M3 pairs) were subsampled for analysis of δ¹⁸O and δ¹³C in tooth enamel carbonate (Table 2). The subsamples were drilled in approximately 1mm increments, <1mm deep and 3-5mm wide, perpendicular to the vertical axis of a single cusp using a Dremel Micro and 0.5mm diameter diamond-tipped drill bit and weighed
Table 1. Specimen metadata for samples analyzed for bone collagen.

| Site and Year | Faunal Specimen Number | Taxon     | Phase | Lab ID | Sampled Element |
|---------------|-------------------------|-----------|-------|--------|-----------------|
| UZH11         | P5-B.50-11              | Cervid    | III   | UZ 83  | mandible        |
| UZH11         | P5-B.50-8               | OC        | III   | UZ 84  | mandible        |
| UZH11         | P5-B.50-10              | OC        | III   | UZ 85  | mandible        |
| UZH11         | P5-B.55-8               | OC        | III   | UZ 86  | mandible        |
| UZH11         | P5-B.55-4               | OC        | III   | UZ 87  | mandible        |
| UZH11         | P5-B.50-261             | OC        | III   | UZ 88  | scapula         |
| UZH11         | P5-B.55-2               | OC        | III   | UZ 89  | scapula         |
| UZH11         | P5-B.50-25              | Sus       | III   | UZ 90  | mandible        |
| UZH11         | P5-B.51-6               | Cervid    | III   | UZ 91  | scapula         |
| UZH11         | P5-B.52-3               | OC        | III   | UZ 92  | scapula         |
| UZH11         | P5-B.51-3               | Sus       | III   | UZ 94  | metapodial      |
| UZH11         | P5-B.55-1               | OC        | III   | UZ 95  | scapula         |
| UZH11         | P5-B.51-2               | OC        | III   | UZ 96  | scapula         |
| UZH14         | P5-B.128-1              | OC        | III   | UZ 97  | scapula         |
| UZH11         | P5-B.51-5               | Bos       | III   | UZ 98  | metacarpal      |
| UZH11         | P5-B.50-263             | OC        | III   | UZ 99  | scapula         |
| UZH11         | P5-B.50-1               | Bos       | III   | UZ 101 | metacarpal      |
| UZH11         | P5-B.50-257             | Cervid    | III   | UZ 102 | scapula         |
| UZH11         | P5-B.55-5               | Sus       | III   | UZ 103 | mandible        |
| UZH11         | P5-B.52-6               | Sus       | III   | UZ 104 | maxilla         |
| UZH11         | P5-B.52-10              | Bos       | III   | UZ 105 | metatarsal      |
| UZH14         | P5-B.128-4              | Cervid    | III   | UZ 106 | antler          |
| UZH11         | P5-B.55-6               | Lepus     | III   | UZ 107 | humerus         |
| UZH11         | P5-B.52-7               | Lepus     | III   | UZ 108 | ulna            |
| UZH11         | P5-B.50-252             | Canid     | III   | UZ 109 | maxilla         |
| UZH11         | P5-B.50-9               | OC        | III   | UZ 204 | mandible        |
| UZH14         | P5-B.128-3              | OC        | III   | UZ 205 | mandible        |
| UZH11         | P5-B.106.6              | OC        | IV    | UZ 203 | mandible        |
| UZH13         | P5-B.106-32             | Lepus     | IV    | UZ 60  | pelvis          |
| UZH13         | P5-B.107-2              | Lepus     | IV    | UZ 61  | scapula         |
| UZH14         | P6-B.37-1               | Bos       | IV    | UZ 62  | pelvis          |
| UZH14         | P6-B.33-9               | Bos       | IV    | UZ 63  | ulna            |
| UZH14         | P6-B.33-4               | Bos       | IV    | UZ 64  | metacarpal      |
| UZH14         | P6-B.34-40              | Bos       | IV    | UZ 65  | metapodial      |
| UZH13         | P5-B.106-9              | Cervid    | IV    | UZ 66  | mandible        |
| UZH13         | P5-B.106-10             | Cervid    | IV    | UZ 67  | mandible        |
| UZH14         | P5-B.126-1              | Cervid    | IV    | UZ 69  | pelvis          |
| UZH15         | P6-B.44-1               | Dama      | IV    | UZ 70  | calcaneus       |
| UZH14         | P6-B.34-28              | OC        | IV    | UZ 71  | pelvis          |
| UZH14         | P6-B.34-27              | OC        | IV    | UZ 72  | pelvis          |
| UZH14         | P6-B.34-17              | OC        | IV    | UZ 74  | humerus         |
| UZH14         | P5-B.107-3              | Bos       | IV    | UZ 75  | ulna            |
| UZH14         | P6-B.34-26              | OC        | IV    | UZ 76  | pelvis          |
| UZH13         | P5-B.106-15             | OC        | IV    | UZ 77  | scapula         |
| UZH14         | P6-B.33-3               | OC        | IV    | UZ 78  | scapula         |
| UZH15         | P5-B135-1               | OC        | IV    | UZ 79  | scapula         |
| UZH14         | P6-B.37-6               | OC        | IV    | UZ 81  | humerus         |
between 1-5mg each. Preparation included treatment with 2% NaOCl for 24 hours at room temperature to remove any potential organic contaminants, followed by rinsing with Millipore water. Samples were then treated with 0.1M acetic acid for four hours to remove secondary carbonates before being rinsed using Millipore water (after [60]) and placed in a desiccator. Once dry, samples were weighed into exetainers, which were then flooded with helium gas under a vacuum. The sample was then reacted with 100% phosphoric acid and the resulting CO₂ inducted to the IRMS via gas bench. All values are reported per mil (‰) with reference to the standard Vienna Pee-Dee Belemnite (VPDB) calibrated through the standards of NIST: NBS19 (δ¹³C = +1.95 ‰ and δ¹⁸O = –2.20 ‰) and RM-8545 (δ¹³C = –46.6 ‰ and δ¹⁸O = –26.41 ‰) and two internal, pure calcite standards, Fisher (δ¹³C = –0.64 ‰ and δ¹⁸O = –14.90 ‰) and A1296 (δ¹³C = +2.56 ‰ and δ¹⁸O = –0.60 ‰), with precision better than ±0.15 ‰ for both ¹⁸O/¹⁶O and ¹²C/¹³C.

Results and discussion

Radiocarbon dates

These dates fit well within the existing understanding of site chronology, spanning from c. 6500 cal BC to 5200 cal BC (Phases V-III) (Table 3). They contribute to the existing understanding of the duration of site occupation, provide an early date for the presence of canids at the site, and allow us to anchor our stable isotope interpretation firmly within the cultural context of the period as well as compare our results to other sites in mainland Anatolia.

Collagen summary

In order to analyze the collagen results, the quality of the data was first evaluated. The accepted C/N ratio is 2.9 to 3.6 [61]. Most samples had a value of 3.4 with an overall success rate of 91% (59 out of 65 samples; see S1 Table for values). Samples that failed did not have either enough carbon or nitrogen left to be measured. Three of these were from Phase V (two Ovis/Capra and one Sus), two were from Phase IV (a cervid and Ovis/Capra) and one from Phase III (Sus). Data were found to be normally distributed using a Shapiro-Wilk test.
In Fig 2, shapes indicate taxa, while colors indicate the respective archaeological contexts. Though coarse, a few observations can account for the degree of variability and patterning within taxa. On average and in all contexts, deer (n = 9) and hare (n = 5) have the most negative values for both δ^{13}C (-20.8‰ and -20.3‰, respectively) and δ^{15}N (5.8‰ and 5.3‰).

Given our expectations for these species based on their preferred forage (woodland and woodland edge) and "baseline" values for the island of Gökçeada based on physiogeographic

### Table 2. Specimen metadata for samples analyzed for tooth enamel.

| Site and Year | Faunal Specimen Number | Taxon | Phase | Lab ID | Tooth | n Subsamples |
|---------------|-------------------------|-------|-------|--------|-------|--------------|
| UZH11         | P5-B.50-8               | OC    | OC    | UZ 1   | LRM2  | 6            |
|               |                         |       |       | UZ 2   | LRM3  |              |
| UZH11         | P5-B.55-4               | OC    | OC    | UZ 3   | LRM2  | 13           |
|               |                         |       |       | UZ 4   | LRM3  |              |
| UZH11         | P5-B.55-10              | OC    | OC    | UZ 5   | LRM2  | 16           |
|               |                         |       |       | UZ 6   | LRM3  |              |
| UZH11         | P5-B.50-9               | OC    | OC    | UZ 7   | LLM2  | 11           |
| UZH11         | P5-B.50-10              | OC    | OC    | UZ 8   | LLM2  | 16           |
| UZH11         | P5-B.51-24              | OC    | OC    | UZ 9   | LRM2  | 11           |
| UZH11         | P5-B.55-8               | OC    | OC    | UZ 10  | LRM2  | 13           |
| UZH11         | P5-B.55-25              | OC    | OC    | UZ 11  | LRM2  | 14           |
| UZH11         | P5-B128-3               | OC    | OC    | UZ 12  | LRM2  | 17           |
| UZH11         | P5-B.50-253             | OC    | OC    | UZ 13  | LLM3  | 11           |
| UZH11         | P5-B.55-9               | OC    | OC    | UZ 14  | LRM3  | 11           |
| UZH11         | P5-B.52-9               | OC    | OC    | UZ 15  | LLM3  | 14           |
| UZH11         | P5-B.50-11              | Cervid| Cervid| UZ 35  | LLM3  | 7            |
| UZH13         | P5-B.106-6              | OC    | OC    | UZ 16  | LRM2  | 13           |
|               |                         |       |       | UZ 17  | LRM3  |              |
| UZH13         | P5-B.106-7              | OC    | OC    | UZ 18  | LLM2  | 17           |
|               |                         |       |       | UZ 19  | LLM3  |              |
| UZH13         | P5-B.106-11             | OC    | OC    | UZ 20  | LRM2  | 16           |
|               |                         |       |       | UZ 21  | LRM3  |              |
| UZH14         | P5-B.106-8              | OC    | OC    | UZ 22  | LRM2  | 12           |
| UZH13         | P5-B.106-12             | OC    | OC    | UZ 23  | LLM2  | 14           |
| UZH14         | P6-B.33-1               | Cervid| Cervid| UZ 36  | LRM2  | 7            |
|               |                         |       |       | UZ 37  | LRM3  | 10           |
| UZH13         | P5-B.106-9              | Cervid| Cervid| UZ 38  | LLM2  | 6            |
| UZH13         | P5-B.106-10             | Cervid| Cervid| UZ 39  | LLM3  | 6            |
| UZH14         | BB120-21-B.57-1         | OC    | OC    | UZ 25  | LLM2  | 15           |
|               |                         |       |       | UZ 26  | LLM3  |              |
| UZH14         | BB120-21-B.58-4         | OC    | OC    | UZ 27  | LRM2  | 13           |
|               |                         |       |       | UZ 28  | LRM3  |              |
| UZH14         | BB120-21-B.57-7         | OC    | OC    | UZ 29  | LLM3  | 18           |
| UZH14         | BB120-21-B.57-8         | OC    | OC    | UZ 30  | LRM3  | 13           |
| UZH14         | BB120-21-B.58-3         | OC    | OC    | UZ 31  | LRM3  | 8             |
| UZH10         | BB22-B.11-293           | OC    | OC    | UZ 32  | LLM3  | 18           |
| UZH10         | BB120-21-B.57-2         | Cervid| Cervid| UZ 40  | LLM2  | 5             |

Values for each subsample can be found in S2 Table.

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properties, these lower values suggest that these species are likely wild and endemic rather than brought to the island from elsewhere. *Ovis/Capra* (n = 27) and *Bos* (n = 9) are indistinguishable (δ^{13}C -20.2±0.8 ‰ and -20.1±0.6‰; δ^{15}N 7.1±1.0‰ and 7.1±0.9‰, respectively).

There is, however, more time-dependent variability in these taxa, as discussed below. Likewise, specimens of *Sus* spp. (n = 7) fall within the expected range for C3 omnivores with an average δ^{13}C of -20.2‰ and δ^{15}N of 8.1‰, but (in spite of small sample size) there is a shift to more negative values for both C and N in individuals through time, suggesting that these individuals may have initially arrived on the island from elsewhere and reflect “domestic” stock rather

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**Table 3. New radiocarbon dates on bone sampled for isotopic analysis.**

| Site and Year | Faunal Specimen Number | Lab ID | Taxon | Phase | Context | ¹⁴C age years BP | Age cal BC | Age cal BP |
|---------------|-------------------------|--------|-------|-------|---------|-----------------|------------|------------|
| UZH11         | P5-B.50-9               | UGAMS 25381 | OC    | III   | courtyard | 6260±30       | 5297–5220  | 7246–7169  |
| UZH14         | P5-B128-3               | UGAMS 25382 | OC    | III   | plastered pit | 6360±30       | 5367–5311  | 7316–7260  |
| UZH13         | P5-B.106-6              | UGAMS 25380 | OC    | IV    | floor of Building 5 | 6570±30       | 5537–5485  | 7486–7434  |
| UZH14         | BB120-21-B.58-4         | UGAMS 25379 | OC    | V     | floor of Building 10 | 7100±30       | 6014–5927  | 7963–7876  |
| UZH10         | BB22-B.10-25            | UGAMS 25377 | CANID | V     | oldest sounding | 7490±30       | 6424–6272  | 8373–8221  |

Dates have been calibrated using OxCal v4.3.2 and IntCal13 and are shown in BC/AD and BP, reported to 1σ.

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Fig 2. Stable isotope results of faunal collagen from Üghuru (n = 59).

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than endemic wild boar and support our earlier conclusions based on biometrically inferred size (c.f. [9]). The canid specimens (n = 2) exhibit relatively more positive $\delta^{13}C$ values than the herbivores (-19.6‰) and higher $\delta^{15}N$ (9.7‰) as expected for carnivores.

If the data are parsed by stratum rather than by species (Fig 3), we can see that there is a notable shift in mean $\delta^{13}C$ values between phases V (n = 10), IV (n = 22), and III (n = 27) using a student’s T test, with the mean $\delta^{13}C$ of -19.6‰ for Phase V being significantly higher than that of IV (-20.6‰; p < 0.005). The mean $\delta^{13}C$ of Phase V and III (-20.2‰; p = 0.06) were not found to be significantly different; nor are Phase IV and III (p = 0.07). An Epps-Singleton test of equal distributions found that the spread of values was not significantly different between any phase. In $\delta^{15}N$, the Phase V mean (8.5‰) is significantly higher than Phase IV (6.2‰; p < 0.001) and Phase III (7.0‰; p < 0.01), and IV and III also differ significantly from one another (p = 0.03). In contrast to $\delta^{13}C$, the $\delta^{15}N$ values become more variable through time. The distribution of values in Phase V was significantly different from both Phase IV and III, but not between Phase IV and III. We argue that the differences in means and overall distributions of values seen here are not due to the different proportions of taxa (e.g., herbivores vs. carnivores or grazers vs. browsers) within each phase. Instead, these differences more likely reflect factors related to the environmental setting in which individual animals were raised; for example, individuals in Phase V derive from a more arid environment. Fig 3 helps to visualize differences between phases in Fig 2: in Phase V, which shows more positive $\delta^{15}N$ values overall, the highest value (from a pig, an omnivore) is expressed as an outlier in the figure, while the canid (a carnivore) has an $\delta^{15}N$ of 9.1‰, only marginally higher than herbivore values, from two sheep/goat individuals (8.7‰, 9.0‰) and a hare (8.7‰). These individuals also vary in their $\delta^{13}C$ values, with the pig and canid notably falling between the values for the caprines and hare, supporting values influenced by individual dietary and environmental inputs independent of taxonomic status.

If domesticates were imported to Ugurulu in the early Neolithic, as suggested by their high degree of inter-individual variability and significantly different mean value, where might they have been derived from? Were these island populations or were they brought in from further afield? Though the average values for sheep and goat from Ugurulu through time are fairly typical for C3 herbivores, with an overall average (n = 27) of -20.2‰ $\delta^{13}C$, 7.1‰ $\delta^{15}N$, there is a significant discrepancy in values—just within sheep/goat—between Phase V and phases IV and III (Fig 4). The average values for individuals in Phase V (n = 5) fall within the ranges of variation and closer to the mean values for contemporaneous sheep and goat individuals from Asikli Hoyuk (-18.9‰ $\delta^{13}C$, 8.1‰ $\delta^{15}N$, n = 49) and Catalhoyuk (-18.0‰ $\delta^{13}C$, 9.4 ‰ $\delta^{15}N$, n = 60) (16). In contrast, average values from Ulucak in Western Anatolia (-20.3‰ $\delta^{13}C$, 6.0‰...
Δ15N, n = 11; c.f. 1) and Aktopraklık in the Marmara (-20.2‰ Δ13C, 6.1‰ Δ15N, n = 13) are closer to those from later phases at Uğurlu. While not asserting that these are indeed from a Central Anatolian stock brought over to Uğurlu, it does suggest 1) an origin point that is more arid than that of Gökçeada and the Western Anatolian coast and 2) that the stock did not live longer than a few years after being brought to Gökçeada. Alternatively, regional climate may have been significantly different during the time the earliest Neolithic contexts formed such that these individuals may be reflecting temporally influenced variability rather spatial; in other words, they could derive from Gökçeada Island if it was significantly more arid overall during this time, or if there was a patchy and highly variable range of microhabitats present on the island. While we do not view these latter examples as parsimonious scenarios, it cannot be ruled out without the existence of more refined paleoenvironmental reconstructions based on local proxy data.

**Enamel summary**

Stable isotope data (δ18O and δ13C) from teeth of sheep, goat, and deer were analyzed from all strata (Fig 5). The average δ13C for deer (n = 6 teeth) is -12.6‰, reflecting a C3 diet, whereas
δ¹⁸O values average -5.0‰. Though the sample size is small, the values are congruent with the data derived from bone collagen in terms of suggesting habitation in a wooded setting, and the more negative δ¹⁸O values support the interpretation of an island/coastal location based on expectations from rainfall and temperature. There is no significant difference in the overall average δ¹³C values for sheep and goat (n = 32 teeth) (-12.6‰) nor in δ¹⁸O (-5.0‰), suggesting that these animals lived in a similar environment. Like bone collagen, the scenario becomes interesting when we consider variation between phases V (n = 108 values), IV (n = 135 values), and III (n = 200 values) for the sheep and goat samples (Fig 6). There is a significant trend towards more negative average δ¹³C values through time (Student’s t test; p < 0.001) and, as with the collagen results, the most variation within Phase V. In particular, there are “real” outliers with more positive δ¹³C values, suggesting that these may be part of an outgroup who are derived from a different environment than those clustering with the endemic deer. However, the δ¹⁸O values lack this trend through time, with the average δ¹⁸O for Phase V at -5.4‰, Phase IV at -4.3‰, and Phase III at -5.2‰, well within the average standard deviation (1.5‰) in δ¹⁸O in each phase; therefore, there is no significant change in mean δ¹⁸O through time in sheep and goat.

As with the bone collagen, it is also possible to consider the tooth enamel data in regional context (Fig 7). The average values for sheep and goat from Uğurlu in the Neolithic are more negative in both δ¹⁸O and δ¹³C than comparable populations at the sites of Ulucak (n = 19) (1)
and Çatalhöyük (n = 80) [62] and pers. comm. Henton 2018, Pearson 2018). The caprine “population” at Üğurlu has an overall standard deviation of 0.8‰ in both $\delta^{13}$C and $\delta^{18}$O values, as does Ulucak. The sample from Çatalhöyük has a standard deviation of 1‰ in $\delta^{13}$C and 1.9‰ in $\delta^{18}$O. Ulucak sheep and goat have an average $\delta^{13}$C of -11.8‰, within the standard deviation of Üğurlu, and suggesting, as at Üğurlu, a C3 diet in a temperate environment. In contrast, the sheep and goat values from teeth $\delta^{13}$C from Çatalhöyük have an average of -8.2‰, significantly more positive than Üğurlu and Ulucak, and likely reflective of the mixed C3/C4 diet suggested from the collagen data, and the arid interior environment of central Anatolia. The average $\delta^{18}$O at Ulucak is -1.1‰, whereas it is -3.6‰ at Çatalhöyük. This falls contrary to expectations given modern rainfall amounts, but since $\delta^{18}$O can be influenced by a combination of climate conditions (e.g. temperature, rainfall) and physiogeographic ones (e.g., source moisture) as well as biological factors, it is difficult to address this question without more detailed local paleoclimatic and paleoenvironmental information. As with the individual remains analyzed for $\delta^{13}$C and $\delta^{15}$N in collagen, some specimens from Üğurlu are relatively more similar to specimens from Çatalhöyük (Phase V) or Ulucak (Phase IV) in their $\delta^{13}$C and $\delta^{18}$O values than they are to overall average for Üğurlu, suggesting that these individuals may have been born in mainland environments and brought to the island later. They may also have been born on the island in years with anomalous rainfall, or derive from a more arid microregion on the island, but this cannot be more rigorously investigated without local, high resolution paleoclimate records. While comparison between teeth and mandibular bone from the same individual might shed further light on this interpretation, the current sample size of individuals with samples from multiple tissue types (n = 11) needs to be expanded before further analysis can be implemented.

Conclusions

When zooarchaeological and stable isotope ecology datasets are combined, a more comprehensive and cohesive picture of Neolithic animal management on the island of Gökçeada and in western Anatolia emerges. The results of zooarchaeological analysis at Üğurlu Höyük previously published by the authors [9] corroborate the results of stable isotope ecology analysis data presented here. More specifically, osteometric data and mean sheep and goat Logarithmic Size Index (LSI) values for the Marmara and western Anatolian Neolithic sites are similar to that of Gökçeada, particularly of the earliest Neolithic or Phase V. If we turn back to our initial
considerations of animal management in the earliest Neolithic and stable isotope ecology differences between phases, there is greater variation in values within the earliest Neolithic (Phase V) fauna than subsequent phases, and a significant difference in $\delta^{15}N$ values. It appears likely that caprines at least are more similar to coastal ‘populations’ than central Anatolian stock, though specimens from the earliest Neolithic phase are slightly different than later periods, suggesting a founder population from the mainland and later, a local island population. Even without more detailed paleoenvironmental data zooarchaeological and stable isotope evidence independently converge to indicate that the first Neolithic inhabitants of Gökçeada may have selected their animals from the same colonizing stock, a mainland population source, that was dispersing across western Anatolia and into mainland Greece as evidenced by similar LSI values documented at Franchthi Cave (Munro and Stiner 2015), and as compared to fauna in phases IV and III at Üğurlu Höyük.

Zooarchaeological and stable isotope ecology data each manifest a different trajectory, however, during the phases IV and III—late Neolithic and early Chalcolithic—at Üğurlu Höyük. Smaller caprine body size and increasingly young male dominated caprine kill-off patterns coupled with a more caprine-dominant species trend at Chalcolithic Üğurlu Höyük hint at a specialized animal husbandry in which sheep and goats were more intensively managed through time. The decreased body size and changes in stable isotope values suggest a selective process focusing on local animal populations on the island. Fauna such as deer and hare are likely endemic, living in a more wooded area of the island, and are not consuming the same diet as domestic sheep, goat, cattle, and pig. Overall, this compliments the case for a nuanced evolution of animal resource use through time during the process of Neolithization in the region.

Supporting information

S1 Table. Stable isotope data from bone collagen samples in this study.
(XLSX)

S2 Table. Stable isotope data from tooth enamel subsamples in this study.
(XLSX)

S3 Table. Metadata for specimens sampled for multiple analyses (stable isotopes from bone collagen and tooth enamel and radiocarbon dating).
(XLSX)

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Author Contributions

Conceptualization: Suzanne E. Pilaar Birch, Levent Atici, Burçin Erdoğuç.

Data curation: Suzanne E. Pilaar Birch, Levent Atici.
Formal analysis: Suzanne E. Pilaar Birch.

Funding acquisition: Suzanne E. Pilaar Birch, Burçin Erdoğan.

Investigation: Suzanne E. Pilaar Birch, Levent Atici, Burçin Erdoğan.

Methodology: Levent Atici.

Project administration: Levent Atici.

Resources: Burçin Erdoğan.

Writing – original draft: Suzanne E. Pilaar Birch.

Writing – review & editing: Suzanne E. Pilaar Birch, Levent Atici, Burçin Erdoğan.

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