Direct chemical evidence for widespread dairying in prehistoric Britain

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Domesticated animals formed an important element of farming practices in prehistoric Britain, a fact revealed through the quantity and variety of animal bone typically found at archaeological sites. However, it is not known whether the ruminant animals were raised purely for their tissues (e.g., meat) or alternatively were exploited principally for their milk. Absorbed organic residues from pottery from 14 British prehistoric sites were investigated for evidence of the processing of dairy products. Our ability to detect dairy fats rests on the observation that the $\delta^{13}C$ values of the $C_{18:0}$ fatty acids in ruminant dairy fats are ≈2.3‰ lower than in ruminant adipose fats. This difference can be ascribed to (*i*) the inability of the mammary gland to biosynthesize $C_{18:0}$; (*ii*) the biohydrogenation of dietary unsaturated fatty acids in the rumen; and (*iii*) differences (i.e., 8.1‰) in the $\delta^{13}C$ values of the plant dietary fatty acids and carbohydrates. The lipids from a total of 958 archaeological pottery vessels were extracted, and the compound-specific $\delta^{13}C$ values of preserved fatty acids ($C_{16:0}$ and $C_{18:0}$) were determined via gas chromatography-combustion-isotope ratio mass spectrometry. The results provide direct evidence for the exploitation of domesticated ruminant animals for dairy products at all Neolithic, Bronze Age, and Iron Age settlements in Britain. Most significantly, studies of pottery from a range of key early Neolithic sites confirmed that dairying was a widespread activity in this period and therefore probably well developed when farming was introduced into Britain in the fifth millennium B.C.

There is little doubt that domesticated cattle, sheep, goats, and pigs were an integral part of early Neolithic farming in Britain. However, difficulties in establishing whether they were exploited for dairy products, wool, and traction, the so-called "secondary products" (1), has proved to be a major hurdle in our understanding of the evolution of prehistoric economies. The recognition by early farmers that animals could be reared for their milk would have had major impacts on diet, health, and subsistence economy (2). As such, it is of great archaeological and scientific interest to determine how these domesticates were utilized in antiquity: were they valued primarily as a meat source, were they exploited for their "secondary products" such as milk, or were different economic strategies used to maximize the production of both commodities? Evidence for dairying in prehistory is currently limited to certain specialist vessels, e.g., putative cheese strainers (3), and evidence from faunal remains of herds that are suggestive of dairying (4, 5). However, direct chemical evidence for widespread dairying at prehistoric sites anywhere in the world is currently lacking.

Degraded animal fats, recognized by the high abundances of *n*-hexadecanoic ($C_{16:0}$) and *n*-octadecanoic ($C_{18:0}$) acids, are preserved widely within archaeological pottery, particularly those vessels involved in the preparation, consumption, and storage of food (6–8). Our recent research has shown that a range of chemical criteria, namely saturated fatty acid compositions, double-bond positions, triacylglycerol distributions, and $\delta^{13}C$ values, can be used to assign the origins of these ancient fats to the most important domesticated animals namely: sheep/goats, cattle, and pigs (9).

Fresh milk contains high abundances of short-chain fatty acids ($C_{4:0}$ to $C_{12:0}$), which account for up to 20% of all of the fatty acyl moieties present (10). However, over archaeological time scales, these compounds appear not to survive in archaeological pottery. There are two reasons for this. First, short-chain fatty acids are usually located on the *sn*-3 position in the triacylglycerols (11, 12). Due to reduced steric hindrance, these moieties will be more susceptible to hydrolysis during the processing of the milk fats or during burial. Second, the short-chain fatty acids are more water-soluble than their longer-chain counterparts (13). Therefore, following enzymatic or chemical hydrolysis, the short-chain fatty acids are more liable to be lost through leaching in the burial environment. Thus, whereas fresh milk fat contains significant quantities of short-chain fatty acids, they do not persist in archaeological pottery vessels and so cannot be used as diagnostic criteria for the detection of dairy fats. Hence, other means of detection have been sought, leading to the stable isotope approach detailed herein.

The new approach is based on the differential routing of dietary carbon and fatty acids during synthesis of adipose and dairy fats in ruminant animals. This metabolic distinction results in different $\delta^{13}C$ values for saturated fatty acids in the two classes of fat (14). In the present work, isotopic compositions of fatty acids and carbohydrates from modern plants and animals have been used to develop and test a model relating the isotopic compositions of fatty acids in adipose and dairy sources. This model underpins the approach that is then used to provide direct chemical evidence in support of the hypothesis that the exploitation of domesticated animals for milk was a well established component of the animal husbandry practices of the early Neolithic settlers of Britain, i.e., ≈6,000 years before the present. The results have potentially important implications for our wider understanding of the development of agriculture, particularly the secondary products revolution and human nutrition.

Materials and Methods

More than 950 well stratified potsherds were selected from 14 archaeological sites spanning the entire prehistoric period in Britain, i.e., early Neolithic to the late Iron Age. A greater proportion of these were selected from the Neolithic to increase the sensitivity of the study during this key period. Upper-body or rim sherds were sampled from vessels likely to have been used during "cooking."

Lipid analyses were performed using protocols described in detail in earlier publications (15, 16). Briefly, ≈2 g of potsherds were taken and their surfaces cleaned by using a modeling drill to remove any exogenous lipids. The sherds were then ground to a powder, an internal standard added, and solvent-extracted by sonication (chloroform/methanol, 2:1 vol/vol, 10 ml). The solvent was evaporated under a gentle stream of nitrogen to obtain the total lipid extract (TLE). Aliquots of the TLEs were then

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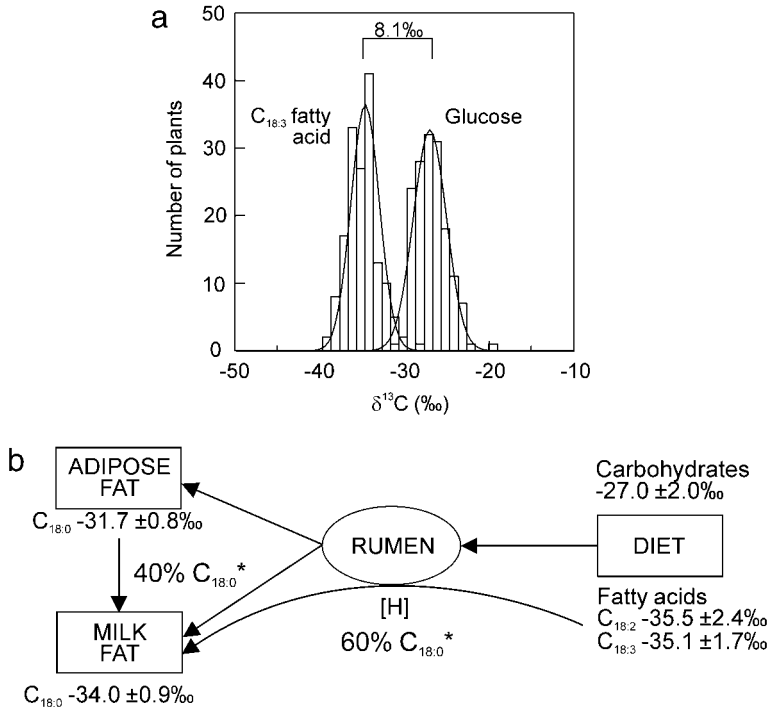


Fig. 1. (*a*) Histogram of the $\delta^{13}C$ values of $C_{18:3}$ fatty acid and glucose extracted from plants. The histogram demonstrates that there is an 8.1‰ mean difference in the $\delta^{13}C$ values of $C_{18:3}$ fatty acid (mean = −36.3‰) and glucose (mean = −28.2‰), and these isotopic differences are known to result from fractionation during the formation of acetylCoA (21). (*b*) Diagram showing the routing of dietary fatty acids and carbohydrates in the rumen, adipose tissue, and mammary gland of the ruminant animal. Approximately 60% of the $C_{18:0}$ in ruminant milk appears to be directly incorporated from the diet, after biohydrogenation of unsaturated fatty acids (e.g., $C_{18:3}$) in the rumen (*) and reflects the inability of the mammary gland to biosynthesize $C_{18:0}$ (19, 20). The difference in the $\delta^{13}C$ values of $C_{18:0}$ in ruminant adipose tissues and dairy fats can also be seen graphically in Fig. 2.

trimethylsilylated [*N*,*O*-bis(trimethylsilyl)trifluoroacetamide 20 μl, 70°C, 60 min] and submitted to analysis by GC and GC/MS.

Further aliquots of the TLEs were treated with methanolic sodium hydroxide (5% vol/vol, 70°C, 1 h). After neutralization, lipids were extracted into hexane and the excess solvent evaporated under a gentle stream of nitrogen. Fatty acid methyl esters (FAMEs) were prepared by reaction with BF_3-methanol (14% wt/vol, 70°C, 1 h). The methyl ester derivatives were extracted with chloroform and the solvent removed under nitrogen. The FAMEs were redissolved into hexane for analysis by GC and GC–combustion–isotope ratio MS.

Alditol acetates of the carbohydrates obtained from the plant reference materials were prepared by using established methods (17). Briefly, 10 mg of lipid extracted plant material was dissolved in 0.1 ml of 72% sulfuric acid in a Young's tube and held at room temperature for 1 h. The acid was diluted with 0.9 ml of water and then heated to 100°C for 6 h. After cooling, the solution was made slightly alkaline (pH 8–9) by the addition of 0.3 ml of 18 M ammonia solution, and a portion of the hydrosylate was transferred to screw-top test tubes. Reduction of the monosaccharides to their alditols was completed by reaction with 2 ml of sodium borohydride solution (2 mg of $NaBH_4$ in 100 ml of dimethyl sulfoxide, 40°C, 1.5 h). Excess sodium borohydride was destroyed by the addition of 0.2 ml of glacial acetic acid.

The alditols were acetylated by reaction with 0.2 ml of *N*-methylimidazole and 1 ml of acetic anhydride. Excess acetic anhydride was destroyed by the addition of 5 ml of H_2O, and then the alditol acetates were extracted in diethyl ether. The diethyl ether was dried over magnesium sulfate and then evaporated under a stream of nitrogen. Alditol acetates were dissolved in dichloromethane for analysis by GC–combustion–isotope ratio MS (18).

Results and Discussion

Modeling Synthesis and Routing of Dairy and Adipose Fatty Acids in Ruminants. A significant advance has been the development of a stable carbon isotope approach that allows ruminant adipose and dairy fats to be distinguished (14). This separation rests on differences in the $\delta^{13}C$ values of the principal fatty acids ($C_{16:0}$ and $C_{18:0}$) that are present in all animal fats. Importantly, the mammary gland is able to biosynthesize $C_{16:0}$ but is unable to biosynthesize $C_{18:0}$ (19, 20) and therefore obtains the $C_{18:0}$ from other sources. The principal unsaturated fatty acids from dietary plants ($C_{18:1}$, $C_{18:2}$, and $C_{18:3}$) can be biohydrogenated in the rumen (10). The products represent the major source of $C_{18:0}$ in milk fats. In contrast, the $C_{18:0}$ in adipose fats derives to a significant extent from *de novo* biosynthesis from acetate. It is thus likely to include carbon originating predominantly from the carbohydrate component of the animals diet, which has a significantly higher $\delta^{13}C$ value than the fatty acids from the same plants.

To demonstrate this, 166 modern plant specimens representative of the diets of grazing and browsing animals were collected from locations in Southern Britain in May, July, and October 2000, and the $\delta^{13}C$ values of the major fatty acids ($C_{16:0}$, $C_{18:0}$, $C_{18:1}$, $C_{18:2}$, and $C_{18:3}$) and the carbohydrates (glucose, arabinose, xylose, mannose, galactose, rhamnose, inositiol, and fucose) determined. The histograms shown in Fig. 1*a* demonstrate that there is an 8.1‰ mean difference in the $\delta^{13}C$ values of $C_{18:3}$ fatty acid (mean = −36.3‰) and glucose (mean = −28.2‰), which can be accounted for through fractionation during the decarboxylation of pyruvate in forming acetylCoA (21). The $\delta^{13}C$ values for glucose are not significantly different to the weighted mean values for the other carbohydrates, and similarly the $\delta^{13}C$ values for $C_{18:3}$ fatty acid is not different to those obtained from the other unsaturated C_{18} fatty acids. By taking plant samples at

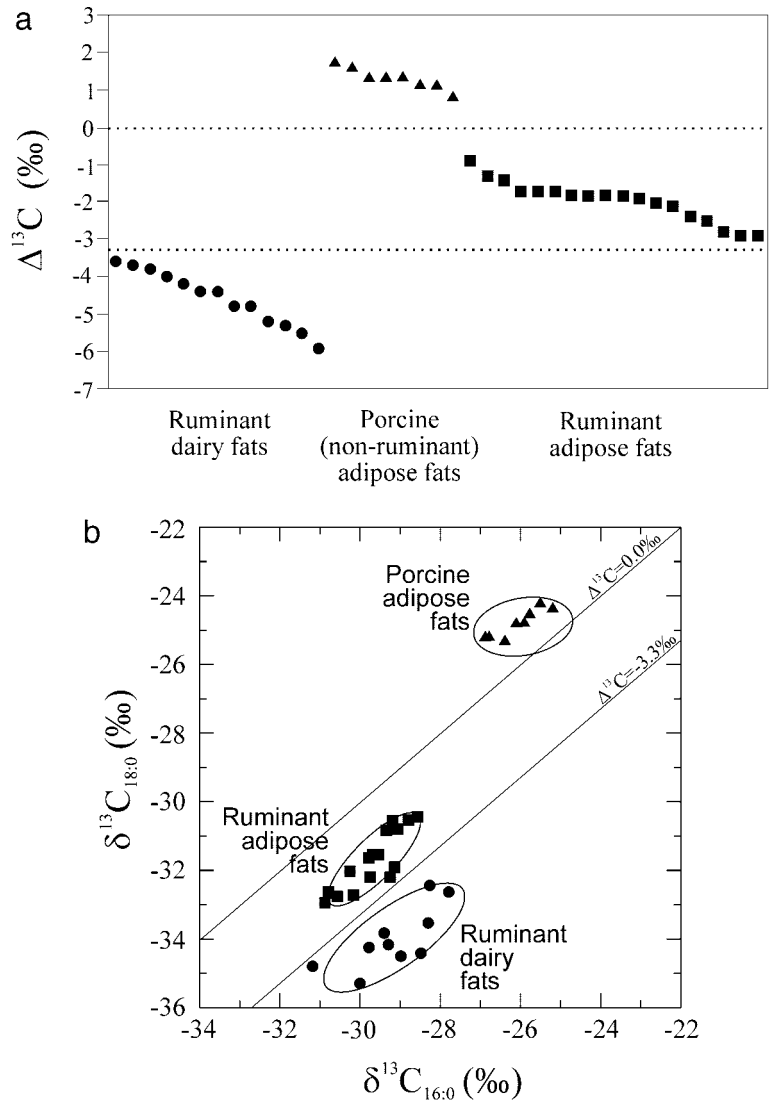


Fig. 2. (*a*) Plot of the difference in the $\delta^{13}C$ values of the $C_{18:0}$ and $C_{16:0}$ fatty acids (= $\Delta^{13}C$ value) obtained from the modern reference fats. The mean and 2 SD are depicted and demonstrate that the animal fats are also distinguished by using this criterion. (*b*) Plot of the $\delta^{13}C$ values of the major fatty acid components ($C_{16:0}$ and $C_{18:0}$) of modern reference fats. The three fields correspond to $P = 0.684$ confidence ellipses calculated for the $\delta^{13}C$ values of the domesticates known to comprise the major component of prehistoric economies in Britain. All of the animals were raised on C_3 diets. The $\delta^{13}C$ values obtained from the modern reference materials have been adjusted for post-Industrial Revolution effects of fossil fuel burning by the addition of 1.2‰ (31). Analytical precision is ±0.3‰.

various times of the year, any seasonal changes in the $\delta^{13}C$ values of the plant biochemical components are accounted for (22). Other possible influences on the overall $\delta^{13}C$ values of plants include altitude (23), latitude (24), and atmospheric CO_2 concentrations (24); however, these factors are unlikely to have been sources of major variation in $\delta^{13}C$ values of prehistoric animal fats from these Southern British sites.

The $\delta^{13}C$ values of the $C_{16:0}$ and $C_{18:0}$ fatty acids from 16 modern ruminant adipose fats, 10 modern ruminant dairy fats, and eight porcine (nonruminant) adipose fats were determined. All of the animals were raised on strict C_3 diets on organic farms, thus closely reflecting the diets of analogous domesticated animals in British prehistory. A difference of ≈2.3‰ between the mean $\delta^{13}C_{18:0}$ values of the ruminant adipose fats and dairy fats was observed (Figs. 1*b* and 2*b*). This is principally due to the routing of biohydrogenated $C_{18:0}$ fatty acids to the mammary gland and the differences that exist in the $\delta^{13}C$ values of carbohydrates and fatty acids in plant tissues (Fig. 1*b*), as explained above.

Fig. 2*b* shows the $\delta^{13}C$ values for the 34 modern reference animal fats referred to above. The species have been grouped together by using $P = 0.684$ confidence ellipses [SYSTAT 7.0, SPSS (Chicago)]. The $\Delta^{13}C$ values (defined as $\delta^{13}C_{18:0}$–$\delta^{13}C_{16:0}$) were calculated for the three fat types (Fig. 2*a*). Ruminant dairy fats are distinguished from adipose fats by displaying $\Delta^{13}C$ values of less than –3.3‰ (shown in Fig. 2). Classification of the sherds was accomplished through comparison of the isotopic composition of the fatty acids from the pottery vessels with (*i*) the reference animal fat ellipses, and (*ii*) the $\Delta^{13}C$ values of the reference animal fats. The $\delta^{13}C$ values also allow the extent of any mixing of fats in archaeological pottery to be recognized, because when this occurs, the extracts plot in between the reference ellipses. Furthermore, any isotopic variances in dietary carbon can also be detected by using both Fig. 2 *a* and *b*. For example, milk obtained from a cow whose diet included a marine component would have $\delta^{13}C$ values that plot to the right of (and along the axis of) the dairy fat ellipse. Crucially however, the $\Delta^{13}C$ values would be lower than –3.3‰.

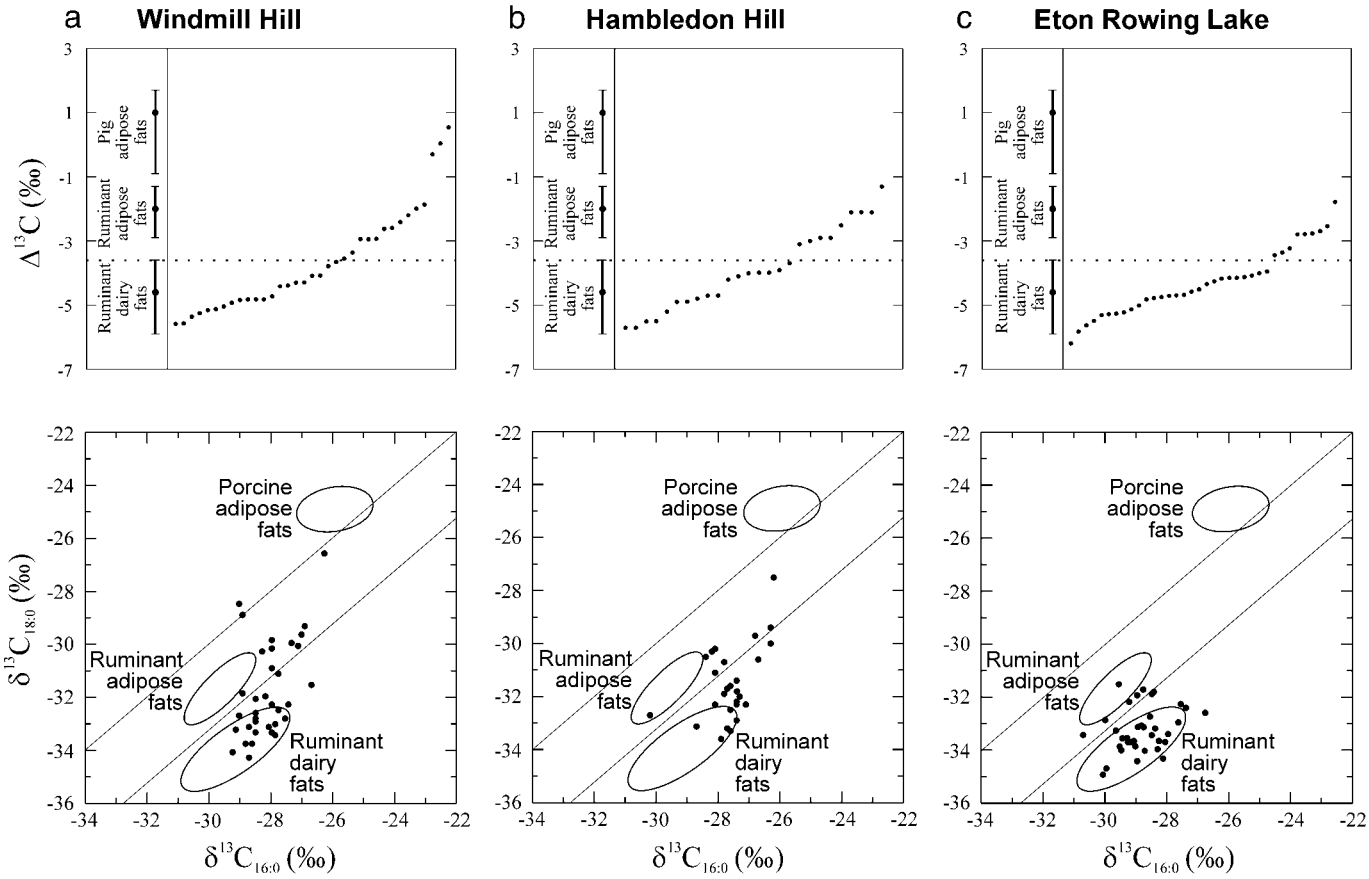


Fig. 3. Plots of the $\delta^{13}C$ values of the major fatty acid components ($C_{16:0}$ and $C_{18:0}$) and the $\Delta^{13}C$ values of lipid extracts from potsherds from the Neolithic sites of Windmill Hill (*a*), Hambledon Hill (*b*), and Eton Rowing Lake (*c*). The fields and ranges corresponding to the modern reference fats (see Fig. 2) serve to classify the lipid extracts. Extracts that plot between the reference ellipses are indicative of the mixing of commodities in antiquity.

Application of the Model to Fats Preserved in Archaeological Pottery. In accordance with results for more recent Romano–British and post-Roman sites (8), pottery from all periods shows stable isotope evidence of dairy fats (Fig. 3; Tables 1 and 2). Three of the early sites warrant particular consideration, because these provide clear evidence for dairying being a significant economic activity among the peoples of early Neolithic Britain. Two of these are enclosure sites (Windmill Hill and Hambledon Hill), for which there exists strong evidence for a ritual function (25, 26), and the third (Eton Rowing Lake) is typical of a domestic site (26). Table 2 shows the relative proportions of the main domesticates, based on relative numbers of identified bones and teeth, and the results of the organic residue analyses.

Windmill Hill, Wiltshire, U.K., comprised three concentric causewayed enclosures, and a high abundance of animal bone was excavated from the site (26). Although there is some intrasite variability in the faunal evidence (e.g., in different ditches), the overall indication is that adult cattle predominate, and that where the sex of the animal can be determined, there are more female than male cattle (27). This age and sex herd structure is consistent with models (4, 5), suggesting milking of these domesticates was undertaken at Windmill Hill. Smaller quantities of sheep/goat and young pigs were evident and were most likely reared for their meat (27).

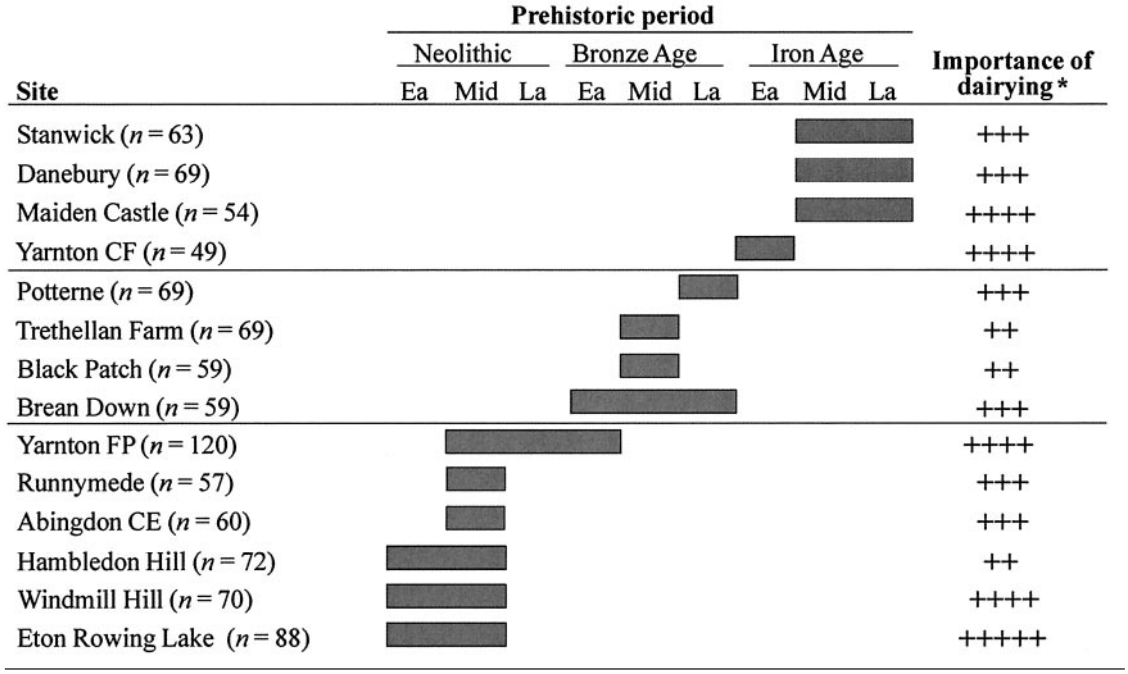
Seventy potsherds were analyzed from Windmill Hill, of which 37 yielded appreciable concentrations of lipid (up to 0.85 $mg{\cdot}g^{-1}$, mean 0.13 $mg{\cdot}g^{-1}$). These sherds originated from contexts radiocarbon dated between 3700 and 3100 cal B.C. The $\delta^{13}C_{16:0}$ and $\delta^{13}C_{18:0}$ values show distinctly that the majority (54%) of the sherds contained predominantly dairy fats (Fig. 3*a*). Mixing of ruminant and porcine adipose fats in individual vessels, due to the processing of a range of commodities over time, was indicated by the large numbers of sherds plotting between the respective reference ellipses.

Hambledon Hill, Dorset, U.K., consists of the Main Causewayed Enclosure, with associated cross-dykes and the Stepleton Enclosure (25). As with Windmill Hill, large quantities of animal bone were recovered during excavations, and the age and sex structure of the herd is also suggestive an economy with an emphasis on dairying, but also including the rearing of some species of domesticates for meat. Although pig bones were found in lower abundances than cattle bones, in some contexts pig and cattle bones were present in equal quantities, whereas in all contexts, sheep/goat bones appear in much lower abundances.

Organic residue analyses of 72 sherds from Hambledon Hill recovered from contexts dating from 3700 to 3300 cal B.C. showed 42 (58%) yielded appreciable lipid residues (up to 0.89 $mg{\cdot}g^{-1}$, mean 0.11 $mg{\cdot}g^{-1}$). The $\delta^{13}C$ values for the principal fatty acids of the 27 sherds containing sufficient fatty acid showed the majority to plot (Fig. 3*b*) between the ruminant and porcine reference ellipses, consistent with the fats having a mixed ruminant/porcine origin. Although a few sherds (7%) plot within the reference ruminant adipose field, a significantly greater proportion (26%) exhibited $\delta^{13}C$ values indicative of dairy fats.

Eton Rowing Lake, Buckinghamshire, U.K., is situated on the north bank of the River Thames (28). Unlike Hambledon Hill and Windmill Hill, Eton is primarily a domestic site and there-

Table 1. Summary of sites from which pottery was analyzed showing the importance of dairying in prehistoric Britain



CF, Cresswell Fields; FP, floodplain; CE, causewayed enclosure; Ea, early; Mid, middle; La, late.
*Based on relative abundance of sherds containing dairy fat residues ranging from + low to +++++ very high.

fore provides an important contrast with the two enclosure sites. Although the total number of identified bones is smaller than at the other two sites, again cattle predominate over pig and sheep/goat.

Fifty of the 88 sherds (57%) investigated from contexts radiocarbon dated between 4100 and 3500 cal B.C. yielded appreciable lipid residues (up to 1.10 $mg \cdot g^{-1}$, mean 0.11 $mg \cdot g^{-1}$). The $\delta^{13}C$ values of the principal fatty acids from the 23 extracts containing sufficient fatty acids are plotted in Fig. 3*c*. All of the sherds contained either ruminant adipose fats or dairy fats; interestingly, no porcine or significant mixtures of fats were detected in any of the vessels. Most importantly, a high abundance of sherds (78%) contained predominantly dairy fats. Furthermore, 14 of the sherds yielded triacylglycerol distributions containing low (C_{40} to C_{44} acyl carbon atoms) molecular weight components characteristic of degraded dairy fats (18), and all these sherds plotted within the reference dairy fat field, thereby corroborating the origin of the fatty acids based on their $\delta^{13}C$ values.

On the basis of the above findings and faunal evidence (summarized in Table 2), we are now in a position where we can compare the frequency of occurrence of dairy fats with herd structures. At both Windmill Hill and Hambledon Hill, the cattle age and sex structure sites are thought to be indicative of a dairy herd. The sherds from Windmill Hill have provided unequivocal stable isotope evidence that dairy products were consumed/processed at the site, with 54% of the sherds containing predominantly dairy fats. Similar results were also obtained from the sherds from Hambledon Hill, where 26% of the sherds contained predominantly dairy fats. There was also overwhelming evidence for the mixing of porcine and ruminant adipose fats in the vessels at both sites, and this may have occurred contemporaneously or through vessel reuse. The highest number of sherds containing fatty acids with $\delta^{13}C$ values indicative of dairy fats came from the domestic site of Eton. In contrast to Windmill Hill and Hambledon Hill, no mixing of ruminant and nonruminant fats was evident in sherds from this site, even though from the animal bones, it is clear that pig was present. An obvious conclusion is that at this site porcine products were processed in a manner not involving pottery vessels, e.g., spit roasted. The

Table 2. Comparison of the results of organic residue analyses of prehistoric pottery and frequency of faunal remains

	Faunal evidence*			Organic residue evidence†			
Site	Cattle, %	Sheep/goat, %	Pig, %	No. of sherds containing lipids	Dairy fats, %	Ruminant adipose fats, %	Mixed ruminant/nonruminant adipose fats, %
Eton Rowing Lake	70	19	11	50/88	78	22	ND‡
Windmill Hill	62	14	24	37/70	54	3	43
Hambledon Hill	58	17	25	42/69	26	7	67

*Based on number of identified bones and teeth.
†Based on compound-specific $\delta^{13}C$ analyses of $C_{16:0}$ and $C_{18:0}$ fatty acids.
‡ND, not detected.

high abundance (78%) of dairy fats in the sherds from Eton Rowing Lake is significantly higher than at any other prehistoric site, we have studied to date. Interestingly, the faunal evidence at Eton is too sparse to determine whether the domesticates were reared principally for their meat or their secondary products, e.g., dairy products, thereby emphasizing the importance of this stable isotope approach in evaluating the importance of dairying in prehistory.

Table 1 summarizes the relative importance of dairying at all 14 sites based on the stable isotope analyses of fatty acids. The results show clearly that dairying was evident at all sites spanning the 4,500 years of British prehistory. Not unexpectedly there was site-to-site variation, although generally the intensity of dairying was high. Although the domestication of sheep and goat is believed to have occurred before that of cattle in southwest Asia by the eighth millennium B.C. (29), the exploitation of secondary products, e.g., dairy products, is believed to have occurred between one and two millennia later (30). The results presented above fit with the current hypothesis, that the exploitation of animals for milk was already an established practice at the time farming arrived in Britain in the late fifth millennium B.C.

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1. Sherratt, A. (1981) in *Pattern of the Past: Studies in Honour of David Clark*, eds. Hodder, I., Isaac, G. & Hammond, N. (Cambridge Univ. Press, Cambridge, U.K.), pp. 261–305.
2. Barker, G. (1985) *Prehistoric Farming in Europe* (Cambridge Univ. Press, Cambridge, U.K.).
3. Bogucki, P. I. (1984) *Oxford J. Archaeol.* **3,** 15–30.
4. Payne, S. (1973) *J. Anatol. Studies* **23,** 281–303.
5. Legge, A. J. (1981) in *Farming Practice in British Prehistory*, ed. Mercer, R. (Edinburgh Univ. Press, Edinburgh), pp. 169–181.
6. Evershed, R. P., Heron, C., Charters, S. & Goad, L. J. (1992) in *New Developments in Archaeological Science*, ed. Pollard, A. M. (Oxford Univ. Press, Oxford), pp. 187–208.
7. Evershed, R. P., Mottram, H. R., Dudd, S. N., Charters, S., Stott, A. W., Lawrence, G. J., Gibson, A. M., Conner, A., Blinkhorn, P. W. & Reeves, V. (1997) *Naturwissenschaften* **84,** 402–406.
8. Evershed, R. P., Dudd, S. N., Charters, S., Mottram, H., Stott, A. W., Raven, A., van Bergen, P. F. & Bland, H. A. (1999) *Philos. Trans. R. Soc. London Ser. B* **354,** 19–31.
9. Mottram, H. R., Dudd, S. N., Lawrence, G. J., Stott, A. W. & Evershed, R. P. (1999) *J. Chromatogr. A* **833,** 209–221.
10. McDonald, P., Edwards, R. D. & Greenhalgh, J. F. D. (1988) *Anim. Nutr.* (Pergamon, Essex, U.K.).
11. Parodi, P. W. (1979) *J. Dairy Res.* **46,** 75–81.
12. Parodi, P. W. (1982) *J. Dairy Res.* **49,** 73–80.
13. Bell, G. H. (1973) *Chem. Phys. Lipids* **10,** 1–10.
14. Dudd, S. N. & Evershed, R. P. (1998) *Science* **282,** 1478–1481.
15. Evershed, R. P., Heron, C. & Goad, L. J. (1990) *Analyst* **115,** 1339–1342.
16. Evershed, R. P., Arnot, K. I., Collister, J., Eglinton, G. & Charters, S. (1994) *Analyst* **119,** 909–914.
17. Blakney, A. B., Harris, P. J. & Stone, B. A. (1983) *Carbohydr. Res.* **113,** 291–299.
18. Docherty, G., Jones, V. & Evershed, R. P. (2991) *Rapid Commun. Mass Spectrom.* **18,** 730–738.
19. Moore, J. H. & Christie, W. W. (1981) in *Progress in Lipid Research*, ed. Christie, W. W. (Pergamon, Oxford), pp. 227–277.
20. Byers, F. M. & Schelling, G. T. (1988) in *The Ruminant Animal: Digestive Physiology and Nutrition*, ed. Church, D. C. (Prentice–Hall, Englewood Cliffs, NJ), pp. 298–312.
21. De Niro, M. J. & Epstein, S. (1977) *Science*, 261–263.
22. Lowdon, J. A. & Dyck, W. (1973) *Can. J. Earth Sci.* **11,** 79–88.
23. Vitousek, P. M., Field, C. B. & Matson, P. A. (1990) *Oecologia* **84,** 362–370.
24. Beerling, D. J., Mattey, D. P. & Chaloner, W. G. (1993) *Proc. R. Soc. London Ser. B* **253,** 53–60.
25. Mercer, R. & Healey, F. (1995) *Hambledon Hill–Post-Excavation Assessment* (Edinburgh Archaeological Services, Edinburgh).
26. Whittle, A., Pollard, J. & Grigson, C. (1999) *The Harmony of Symbols: The Windmill Hill Causewayed Enclosure* (Oxbow, Oxford).
27. Grigson, C. (1999) in *The Harmony of Symbols: The Windmill Hill Causewayed Enclosure*, eds. Whittle, A., Pollard, J. & Grigson, C. (Oxbow, Oxford), pp. 164–252.
28. Allen, T. & Walsh, K. (1997) *S. Midlands Archaeol.* **27,** 25–35.
29. Uerpmann, H.-P. (1989) in *The Walking Larder: Patterns of Domestication, Pastoralism and Predation*, ed. Clutton-Brock, J. (Unwin Hyman, London), pp. 91–96.
30. Sherratt, A. (1983) *World Archaeol.* **15,** 90–104.
31. Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U. & Stauffer, B. (1986) *Nature* **324,** 237–238.