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Development of synanthropic beetle faunas over the last 9000 years in the British Isles

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ABSTRACT

The timing and mechanisms for the develpment of synanthropy for insects is under-explored worldwide; however, substantial archaeoentomological datasets are required to explore this issue in detail. In the British Isles, 50 years of research has generated such a dataset, which we have compiled for this paper. It consists of beetle (Coleoptera) faunas from 55 archaeological sites, comprising 85,829 individuals; out of which 22,670 individuals, representing 128 taxa, were classed as semi- or fully-synanthropic (human-dependent). The data were analysed in terms of presence/absence of different synanthropic taxa; as well as the relative proportions of a range of synanthropic 'groupings' for each archaeological period, type of deposit and type of archaeological site. We argue that there are distinct waves of the development or introduction of synanthropes in the British Isles. This initially consisted of a limited group of taxa, derived from the natural environment during the Mesolithic and Neolithic. A second wave of taxa associated with intensive stock raising, pasture and fodder production occurs in the Late Bronze Age/Iron Age. Finally, a range of strongly synanthropic species, including grain pests, were introduced into the British Isles by the Romans as a result of large-scale trade and the development of urban life. Further areas of research, particularly internationally, are outlined.

1. Introduction

In most entomological literature, synanthropy is regarded as an essentially modern phenomenon, which must have been more localised and limited in the past (Sousa, 1984; Steffen et al., 2007; Ellis et al., 2013; Guetté et al., 2017); a point of view with which we disagree and will argue is not supported by archaeoentomological data. This paper presents the analysis of a large dataset of archaeological insect faunas which establishes that synanthropy in the British Isles has a long history, spreading back over at least 6000 years and considers both the timing and mechanisms for the appearance of synanthropes over time in the British Isles.

2. Past archaeological investigations of insect synanthropy

Initial archaeoentomological studies in the 1970s from Roman (AD 46–420) and early Medieval (c. AD 900–1066) York (UK) commonly encountered a range of synanthropic beetles which occur in modern housing and a wider range of species, mainly associated with farm waste and muddy watersides, that appear to be essentially synanthropic in the past (Buckland et al., 1974; Hall et al., 1980, 1983; Hall and Kenward, 1990; Kenward and Hall, 1995). Kenward and Allison (1995, 70) suggested that our present day synanthropic fauna is 'a restricted and poor shadow of the past' and has declined as a result of changes/improvements in living conditions, building materials and waste disposal (Kenward, 1982; Hall and Kenward, 1990; Kenward and Allison, 1994, 1995; Kenward and Hall, 1995; Smith, 2012a; Forbes et al., 2016).

Two mechanisms have been suggested for the origins of this archaeological synanthropic fauna:

- gradual accretion from natural environments into settlement where conditions allow these species to breed up to a level of superabundance (Kenward, 1978, 1982; Kenward and Allison, 1995).
- arrival in imported food, fodder, and building materials which can be the result of local and international trade (e.g. Kenward and Allison, 1995; Kenward, 1997; Smith and Kenward, 2011; Panagiotakopulu and Buckland, 2017).

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3. Synanthropy, urbanisation and the need for a longer time dimension

Urbanisation is one of the most extreme forms of anthropogenic landscape modification (e.g. Sanderson et al., 2002; Ellis et al., 2013). Purely entomological studies of synanthropes usually concentrate on the ecological criteria that determine their success and modern changes in distribution rather than the original timing of their introduction in the past (McKinney, 2006).

Synanthropy classically concerns *synurbic* taxa that are from urban environments (Luniak, 2004; Francis and Chadwick, 2012). Strongly synanthropic species actively exploit the spatially limited and 'homogenised' ecology of the urban environment (e.g. Hansen et al., 2005; McKinney, 2006; Guetté et al., 2017). However, a broader definition of synanthropy can encompass a diverse range of species that benefit from more open and ecologically diverse human landscapes; such as, suburbs and farmland (Sousa, 1984; Francis and Chadwick, 2012; Guetté et al., 2017). These 'quasi-synanthropes' often are endemic and associated with the first stages of ecological successions, often classified as 'intermediate disturbance environments' (Sousa, 1984; Blair, 1999; McKinney, 2006). Synanthropy is a gradient with 'strong synanthropes' at one extreme and 'weak synanthropes' at the other (Chace and Walsh, 2006; Battisti and Fanelli, 2016; Guetté et al., 2017).

The criteria that allow synanthropes to exploit the urban landscape includes a tolerance for high levels of disturbance and/or an ability to exploit specific aspects of the human landscape (e.g. underground service spaces or concentrations of human waste – Lim and Sodhi, 2004; Chace and Walsh, 2006; Battisti and Fanelli, 2016; Guetté et al., 2017). 'New' synanthropes often are regarded as 'exotic importations' that result from globalised trade (Hansen et al., 2005; Battisti and Fanelli, 2016).

This paper considers a number of specific questions over a longer timescale:

- When do different synanthropic beetles first appear in the British Isles?
- Was the introduction of synanthropes gradual? or is it associated with distinct periods?
- Are specific synanthropic species endemic? or were they 'exotic' introductions?
- What are the potential origins of these synanthropic species?

4. Methods and Analysis

4.1. Archaeological background to the sites and site selection

The location, archaeology and dating of the 55 archaeological sites included in this survey are outlined in Table 1 and Fig. 1. We include sites which are published and our own unpublished data. The sites selected also had to have clear dating, reliable archaeology and the full Minimum Numbers of Individuals (MNI) recorded for each taxon rather than 'estimated counts'. The data surveyed here spans the Mesolithic to the end of the Early Medieval period and have been subdivided into 64 discrete 'chronological entities', based on the Historic England chronological framework (see Table 2). As a result, multiperiod sites will be listed more than once in Table 1 and Fig. 1.

The sites are grouped on their archaeological interpretation, rather than the nature of their beetle faunas, into the following site types:

1) Rural and Isolated Settlements. This group consist of 202 samples from 10 sites. One site is Mesolithic (c. 9500–4000 cal. BC), one Bronze Age (2200–800 cal. BC), six Iron Age (800 cal. BC – AD 43) and two date between AD 1–500. This group includes all prehistoric settlement sites for which faunas are available, but numbers are limited due to the comparative rarity of prehistoric settlement sites. These rural/isolated sites are included to provide a comparison with the later, Roman urban settlements.

2) Urban Settlements and Towns. These sites date from the start of Roman occupation (AD 43) to the end of the Roman occupation (c. AD 410) and represent urban occupation. In total, 205 faunas from ten sites are included but are subdivided into eight 'chronological entities'. Several urban Roman sites have been excluded from this survey, notably those from York, because the faunas were recorded as 'estimate counts' and not as MNI (see Kenward et al., 1985 for the explanation for this recording method). Saxon and Medieval urban sites have not been included in this study, because we wished to concentrate on the initial phases in the development of urban synanthropy.

3) Rural Farmed Landscapes. These sites usually consist of large field systems and associated wells, ditches and waterholes from farmed rural landscapes. This group consists of 29 sites which subdivide into 37 discrete archaeoentomological datasets spanning the main chronological entities as follows: Two are Neolithic (c. 4000–2200 cal. BC), seven are Bronze Age, nine are Iron Age and 19 are Romano-British. This dataset includes the majority of the published insect faunas associated with this type of archaeology and also was used by Smith et al. (2019) to define the 'farmland' fauna, which dominates rural landscapes at this time. These sites are a rural comparison for the faunas from the other groups.

4) ***'Urwaldrelikt' forest sites.*** Ten sites represent 'natural' deposits with no, or limited, human disturbance in order to assess which 'synanthropic' taxa can occur in natural environment of the British Isles. The 122 samples consist mainly of 'wood peats' from Early and Middle Holocene woodlands. Four of these sites are Mesolithic, five Neolithic and one Bronze Age in date. Many of these sites were included in Whitehouse and Smith (2010) discussion of the insect faunas from woodland landscapes. We chose to limit this survey of natural deposits to woodlands (rather than wetlands, moors, floodplains and coastal sites).

4.2. Sampling, processing, identification and quantification and taphonomic issues

The insect faunas used in this survey were produced by several different archaeoentomologists; nevertheless, the sampling and analytical methods used are comparable. Typically, samples weighed 5–10 kg and were 3–10 L in volume. Insects were extracted using paraffin flotation (e.g. Coope and Osborne, 1968; Kenward et al., 1980). Insect remains were sorted and identified using low-power binocular microscopy at magnifications between ×15 – x45. Where achievable, the insect remains were identified to species level by direct comparison to reference collections. The nomenclature used in this paper is based on Duff (2012) for the beetles and Stace (2010) for any plants mentioned. The extent of a species' degree of synanthropy is based on the lists in Kenward and Hall (1995) and Kenward (1997) and are presented in Table 3. A total of 22,670 individuals were defined as synanthropic, from the complete dataset of 85,829 individual beetle identifications.

One criticism which can be made of this work is that it often is comparing 'apples with oranges', since insect remains become incorporated in wood peats, field ditches and settlement deposits, etc … through very different sets of taphonomic processes (Kenward, 1976; Smith, 2013a). We deal with this issue by effectively 'smoothing the data' using the techniques outlined by Kenward (Kenward, 1978; Hall and Kenward, 1990). For example, the primarily data is combined at the site level, rather than by sample or context, and then combined further by date ranges and site type. Data were recorded as both presence/absence and as fully quantified scores based on minimum number of individuals (i.e. if 3 heads and 4 right wing cases were recovered for a beetle taxon, the minimum number of individuals would be 4); this approach allows for a variety of statistical analyses to be carried out in order to explore patterns in the dataset (see §3.4 below).

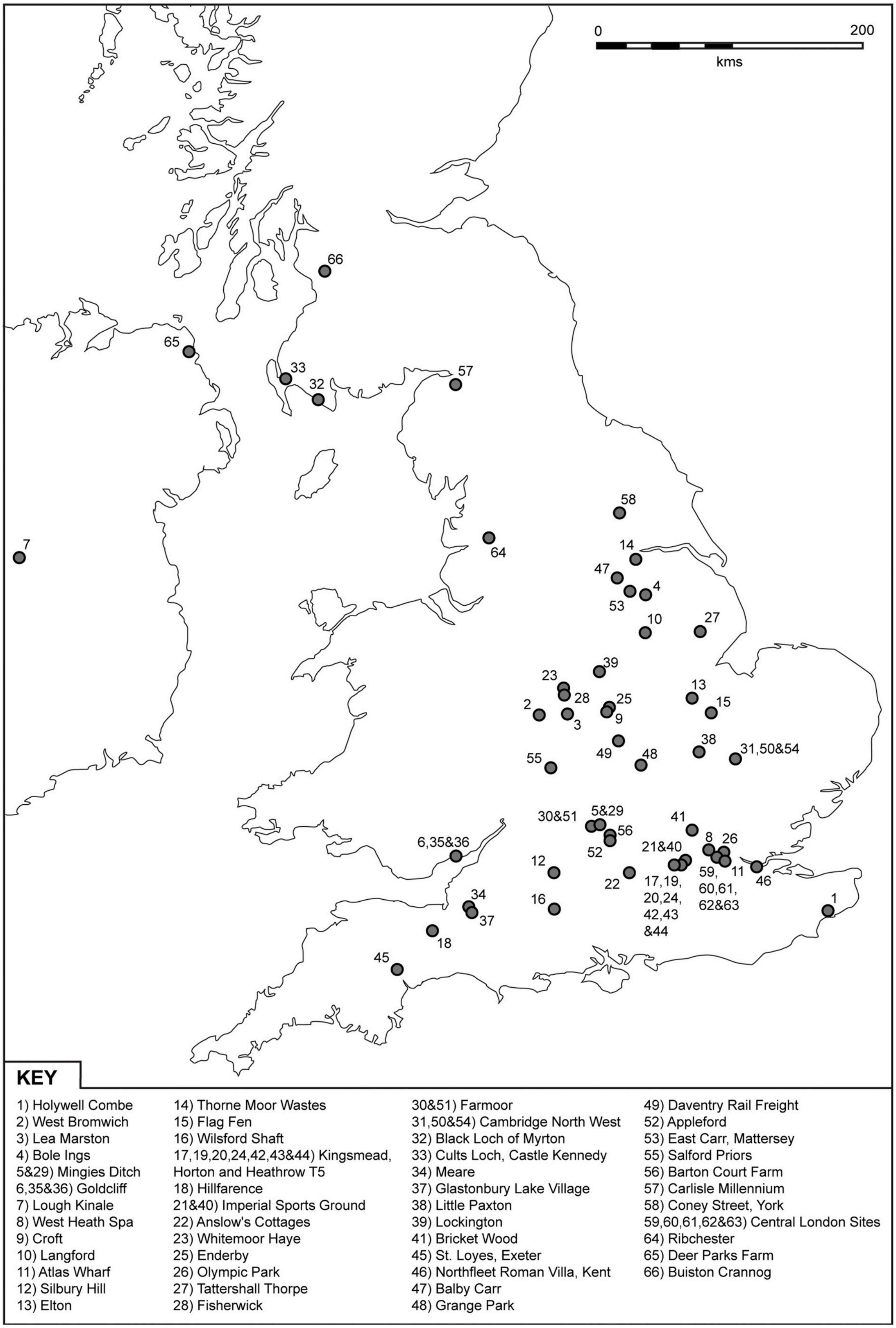
Table 1
Site details, dating and site publication references.

Archaeological Period	Site Type	Site name	Dates (radio carbon dated unless indicated)	References	Site number (maintained in Figures)
MESOLITHIC	‘undisturbed’ wood peats often in alluvial sequences	Holywell Combe, Kent	9667 -7482 cal BC	Coope (1998)	1
		West Bromwich, Staffordshire	9277-8764 and 9756-7177 cal BC	Osborne (1980)	2
		Lea Marston B, Warwickshire	9400-8307 cal BC	Osborne (1974)	3
		Bole Ings (C), Nottinghamshire	7455- 7081 to 5466-5059 cal BC	Dinnin (1997)	4
		Mingies Ditch O, Oxfordshire	5981-5657 cal BC	Robinson (1993)	5
		Goldcliff, Gwent, Wales	4791-4546 cal BC	Smith et al. (2000)	6
	settlement: fluvial deposits associated with possible settlement	Lough Kinale, County Longford, Ireland		Hill (2015)	7
NEOLITHIC	‘undisturbed’ wood peats often in alluvial sequences	West Heath Spa, London	< *c.* 3900 BC (dated by presence of elm decline boundary in pollen data)	Girling (1989)	8
		Croft, Leicestershire	3800-2900 cal BC to 2020-1530 cal BC	Smith et al. (2005)	9
		Langford, Nottinghamshire	*2350*-2030 BC *(*dendrochronological *date)*	Howard et al. (1999)	10
		Atlas Wharf, Isle of Dogs, London	3938-3543 cal BC	Smith (2001)	11
	‘farmland’: old ground surface and peat stack below mound	Silbury Hill, Wiltshire	3521-2918 cal BC	Robinson (1997)	12
	‘farmland’ base of enclosure ditch of Causeway Camp	Etton causewayed enclosure, Cambridgeshire	*c.* 3964-3538 – 2194-1954 cal BC	Robinson (1998)	13
BRONZE AGE	‘undisturbed’ wood peats associated with trackway	Thorne Moor	1451-914 cal BC	Buckland (1979)	14
	wood peats underlying and associated with timber structure	Flag Fen	1365 to 967 BC (dendrochronological date)	Robinson (1992a)	15
	‘farmland’ ditches and waterholes	Wilsford Shaft, Wiltshire	1470–1290 cal BC	Osborne (1969)	16
		Perry Oaks Heathrow Terminal 5, Greater London	1450–1210 cal BC and 1380–1040 Cal BC	Robinson (2006)	17
		Hillfarence, Somerset	1450-1130 cal BC	Smith and Tetlow (2007)	18
		Horton Quarry 71,808 Berkshire	1200–700 BC (based on archaeology)	Smith (2014a)	19
		Kingsmead Horton Quarry, Berkshire	1200–700 BC (based on archaeology)	Smith (2009)	20
		Imperial Sports Ground, Greater London (Bronze Age)	1210-910 cal. BC	Smith (2015a)a	21
		Anslow’s Cottages, Burghfield, Berkshire	91–431 cal. BC	Robinson (1992b)	22
IRON AGE	‘farmland’ ditches and waterholes	Whitemoor Haye, Staffordshire	ca. 500–200 BC (based on archaeology)	Smith (2002)	23
		Kingsmead Horton Quarry, Berkshire (LBA - IA)	ca. 1000–0 BC (based on archaeology)	Smith (2009)	24
		Enderby, Leicestershire	200–00 BC (based on archaeology)	Hill (2016)	25
		Olympic Park, Greater London.	750-260 cal. BC (based on archaeology)	Smith (2012b)	26
		Tattershall Thorpe, Lincolnshire	770–200 BC(based on archaeology)	Chowne et al. (1986)	27
		Fisherwick, Staffordshire	380 BC – 70 cal AD	Osborne (1979)	28
		Minges Ditches, Oxfordshire	390-40 cal. BC	Robinson (1993)	29
		Farmoor, Oxfordshire (Iron Age)	382 BC-76 cal. AD	Robinson (1979)	30
		Cambridge North West	100 BC – 250 AD (based on archaeology)	Smith (2014b)	31
	settlement deposits from Crannog	Black Loch of Myrton, Dumfries and Galloway, Scotland	435 BC – c. 405 BC (based on a combination of dendrochronology and radiocarbon dates from Structures 1 and 2)	Allison (2015)	32
	settlement deposits from Crannog	Cults Loch, Castle Kennedy, Galloway, Ireland	800–200 BC (based on a range of radiocarbon dates)	Allison (2017)	33
	range of settlement deposits	Meare Lake Village, Somerset	400–0 BC (based on range of radiocarbon dates)	Girling (1979)	34
	Internal floor deposits	Building 1 Goldcliff, Gwent, Wales	382–342 BC (dendrochronological dates)	Smith et al. (2000)	35
	floor material from surrounding paleochannel	Building 6 Goldcliff, Gwent. Wales	273 BC (dendrochronological dates)	Smith et al. (2000)	36
	floor materials and dumps of settlement waste	Glastonbury Lake Village, Somerset	400–200 BC (based on range of radiocarbon dates)	Hill and Smith (2015)	37
ROMAN	‘farmland’ wells, ditches and waterholes	Little Paxton, Cambridgeshire	80–250 AD (dated by pottery)	Smith (2011a)	38
		Lockington, Derbyshire, waterholes,	Roman (estimated period dates from archaeology)	Smith (2012b)	39
			240–510 cal. AD	(2015a)	40

(*continued on next page*)

Table 1 (*continued*)

Archaeological Period	Site Type	Site name	Dates (radio carbon dated unless indicated)	References	Site number (maintained in Figures)
		Imperial Sports Ground, Greater London (Roman)			
		Brickets Wood Bund, Hertfordshire	Roman (estimated period dates from archaeology)	Smith (2013b)	41
		Perry Oaks (Terminal 5) Heathrow, Greater London (Roman)	*c* 100–250 AD and *c* 200–300 AD (based on archaeology)	Robinson (2006)	42
		Kingsmead Horton Quarry (Roman)	Roman (estimated period dates from archaeology)	Smith (2009)	43
		Terminal 5 Heathrow (Roman)	One radiocarbon date of 170 cal BC to 220 AD. (Other features estimated from archaeology)	Tetlow (2010)	44
		St. Loyes College, Exeter	60–100 AD (estimated dates from archaeology)	Smith (2011b)	45
		Northfleet Roman Villa, Kent,	80–120 AD (estimated dates from archaeology)	Smith (2011c)	46
		Balby Carr, Catesby Business Park, South Yorkshire,	100–130 AD (estimated dates from archaeology)	Smith and Tetlow (1997)	47
		Grange Park, Well. Courteenhall, Northamptonshire	50–450 AD (estimated dates from pottery in fill deposit)	Smith (2006)	48
		Daventry Rail Freight Terminal (Covert Farm),	c. 150–225 AD (based on pottery assemblage)	Smith (2015b)	49
		Cambridge north West 13, Cambridgeshire,	100 BC – 250 AD? (Estimated dates from archaeology)	Smith (2014b)	50
		Farmoor, Oxfordshire (Roman)	ca. 150–350 AD (based on archaeology)	Robinson (1979)	51
		Appleford, Oxfordshire	200–400 AD (Estimated dates from archaeology and pottery)	Robinson (1981)	52
		East Carr, Mattersey, Nottinghamshire,	Radiocarbon date of 361 cal. BC to 252 cal. AD but 200–300 AD (estimated dates from archaeology)	Smith (1997)	53
		Cambridge North West 12, Cambridgeshire,	200–450 AD (estimated dates from archaeology and pottery)	Smith (2014b)	54
		Salford Priors, Warwickshire	300–450 AD (estimated dates from archaeology)	Smith and Langham (2000)	55
		Barton Court Farm, Oxfordshire	c. 350–500 AD (estimated dates from archaeology)	Robinson et al. (1984)	56
	series of deposits from Roman fort	Carlisle millennium, Carlisle	c. 72–150 AD (range of dates from archaeology)	Smith and Tetlow (2010)	57
	deposits associated with urban grain store	Coney Street, York	c. late first century AD (based on archaeology)	Kenward and Williams (1979)	58
	range of urban deposits	Copthall Avenue, London	c. Late first and second century AD (based on archaeology)	Allison and Kenward (1987), de Moulins (1990)	59
	range of urban deposits	One Poultry, London	c. pre 70, late first century and second century AD deposits (based on archaeology)	Smith (2011d)	60
	range of urban deposits	Guildhall, London	Late first to second century AD (based on archaeology)	Smith and Morris (2008)	61
	Range of urban deposits	Blackfriars Road, Southwark, London	Late first century AD (based on archaeology)	Smith (2015c)	62
	Range of Urban deposits	Bloomberg, London	Late first century and second AD (based on archaeology)	Smith and Goddard (2015)	63
	Roman fort	Ribchester, Lancashire,	71–74 AD (based on archaeology)	Carrott et al. (2000)	64
EARLY MEDIEVAL	house floor and settlement deposits from rural settlements	Deer Park Farms, County Antrim, Northern Ireland	7th to 10th Century AD (based on archaeology)	Kenward et al. (2011)	65
		Buiston Crannog, Ayrshire, Scotland	C. 500–680 AD (based on archaeology)	Kenward et al., (1994) 2000	66



1) Holywell Combe
2) West Bromwich
3) Lea Marston
4) Bole Ings
5&29) Mingies Ditch
6,35&36) Goldcliff
7) Lough Kinale
8) West Heath Spa
9) Croft
10) Langford
11) Atlas Wharf
12) Silbury Hill
13) Elton
14) Thorne Moor Wastes
15) Flag Fen
16) Wilsford Shaft
17,19,20,24,42,43&44) Kingsmead, Horton and Heathrow T5
18) Hillfarence
21&40) Imperial Sports Ground
22) Anslow's Cottages
23) Whitemoor Haye
25) Enderby
26) Olympic Park
27) Tattershall Thorpe
28) Fisherwick
30&51) Farmoor
31,50&54) Cambridge North West
32) Black Loch of Myrton
33) Cults Loch, Castle Kennedy
34) Meare
37) Glastonbury Lake Village
38) Little Paxton
39) Lockington
41) Bricket Wood
45) St. Loyes, Exeter
46) Northfleet Roman Villa, Kent
47) Balby Carr
48) Grange Park
49) Daventry Rail Freight
52) Appleford
53) East Carr, Mattersey
55) Salford Priors
56) Barton Court Farm
57) Carlisle Millennium
58) Coney Street, York
59,60,61,62&63) Central London Sites
64) Ribchester
65) Deer Parks Farm
66) Buiston Crannog

Fig. 1. Location of sites discussed.

Table 2
The Chronological Entities used in this paper (based on Historic England's definitions which are listed at http://heritage-standards.org.uk/wp-content/uploads/2015/08/Periods-List-HE-FISH-WP.pdf).

Chronological Entity	Description	Maximum Date	Minimum Date
MESOLITHIC	The Middle Stone Age, falling between the Palaeolithic and the Neolithic; marks the beginning of a move from a hunter-gatherer society towards food producing society	4000 BC	7000 BC
NEOLITHIC	The New Stone Age, this period follows on from the Palaeolithic and the Mesolithic and is itself succeeded by the Bronze Age. This period is characterized by the practice of a farming economy and extensive monumental constructions.	2200 BC	4000 BC
BRONZE AGE	This period follows on from the Neolithic and is characterized by the increasing use of bronze work. It is subdivided in the Early, Middle and Late Bronze Age.	700 BC	2600 BC
IRON AGE	This period follows on from the Bronze Age and is characterized by the use of iron for making tools and monuments such as hillforts and oppida. The Iron Age is taken to end with the Roman invasion.	43 BC	800 AD
ROMANO-BRITISH	Traditionally begins with the Roman invasion in 43AD and ends with the emperor Honorius directing Britain to see to its own defence in 410AD	410 AD	43 AD
EARLY MEDIEVAL	This dates from the breakdown of Roman rule in Britain to the Norman invasion in 1066 and is to be used for monuments of post Roman, Saxon and Viking date.		

*NB the Historic England chronology includes some overlap between main chronological entities (e.g. it is not always possible to distinguish the Late Neolithic site from the Early Bronze Age site).

4.3. *Analysis*

The taxa lists used in this survey are from published site reports, most of which are included in the BUGS-CEP database (Buckland and Buckland, 2006), and from the authors' unpublished data. The individual faunas from each site (or 'chronological entity') were combined to give a 'site level' MNI for each taxon. The following analyses were then carried out:

1) The presence or absence of individual synanthropic taxa for each chronological period was recorded.
2) The percentage of synanthropic groupings for each 'chronological entity' was calculated from the number of terrestrial species recovered (tMNI); this acts to remove the aquatic species, which can occur in very variable amounts from the calculations. The synanthropic groupings are based on the coding devised by Kenward (Kenward and Hall, 1995; Kenward, 1997), which include facultative (**sf**), typical (**st**) and strong (**ss**) groupings (and are further defined at the base of Table 3). Kenward's 'house fauna' (**h**) (Kenward and Hall, 1995) and a coding for grain pests (**g**) also have been calculated. The codes assigned to individual taxa are shown in Table 3.
3) A single summary 'synanthropic value' (**SV**) for each chronological entity was calculated. This new statistic was developed by Hill (2015). It assesses the relative strength of synanthropy at a site without assuming that all taxa have equal value. The SV formula assigns three times more value to strong synanthropes, and two times more to typical synanthropes, than to facultative synanthropes (valued at x1). The formula used to calculate **SV** is presented at the base of Table 3. Some strong synanthropes also can 'breed up' in suitable settlement materials to become 'superabundant' and the SV value can indicate this abundance or dominance within datasets.

5. Results

Table 3 presents the results of the presence/absence analysis by archaeological period. The taxa recovered are arranged by the degree of synanthropy (**sf** - light grey, **st** – dark grey and **ss** – black) and then by taxonomic order within these groupings.

Fig. 2 presents the relative proportion of synanthropic groupings arranged by chronological period as 'box and whisker plots'. The box indicates the proportion of a synanthropic grouping for the second and third quartiles of the range of synanthropic grouping proportions (accounting for 50% of the variation) and the 'whiskers' represent the full extent of variation in the first and fourth quartile. Sites and 'chronological entities' which are substantial outliers are represented by dots. Fig. 3 presents the 'box and whisker plots' by type of archaeological site examined ('Urwaldrelikt', farmed landscape, rural settlement and urban settlement). Fig. 4 presents the plots for the farmed landscape sites and for rural and urban settlement sites arranged by chronological period.

The Synanthropic Values for each chronological period are presented in Fig. 5, for each type of archaeological site examined in Fig. 6 and for the farmed landscape sites and for the rural and urban settlement arranged by chronological period in Fig. 7.

A full set of data for this project is available as an excel spreadsheet which can be downloaded from the *Journal of Archaeological Science* website.

6. Discussion

6.1. *Presence or absence of taxa across the various archaeological periods*

Table 3 establishes that the range of synanthropes present increases over time. The Mesolithic (c. 9500–4000 BC) faunas from the 'Urwaldrelikt' wood peats, and the possible settlement at Loch Kinale, produced a range of only 24 synanthropic taxa. Only one of the 'Urwaldrelikt' sites has a strong synanthrope ('**ss**' - *Dermestes* spp. from Lee Marston), but this beetle also can occur in natural habitats; such as, rot holes and bird's nests in woodland. 'Typical' synanthropes (*Cryptophagus* spp., *Lathridius minutus* (group), *Corticaria* spp. and *Atomaria* spp.) are quite common, particularly at Lock Kinale. These taxa often occur in dry settlement materials like hay (Smith, 2000; Forbes et al., 2016) but also can found in natural habitats, including dry leaf litter and grass tussocks (e.g. Hinton and Corbet, 1989; Coombs and Woodroffe, 1955; Smith, 2000). The woodworm (*Anobium punctatum*) is considered a ubiquitous household pest but also naturally occurs in dry, dead timber in woodland (e.g. Smith and Whitehouse, 2005; Whitehouse and Smith, 2010). Many of the 'facultative' species recovered (i.e. *Megasternum 'concinnum'* (now split into two species), *Micropeplus* spp. and several other small staphylinids) can be associated with animal dung and decaying plant matter in nature. The *Carpelimus bilineatus* aggregate (*'C. bilineatus'* may be *C. erichsoni* at many sites) is often found in puddled mud and wet vegetation by water. The Mesolithic 'synanthropic' taxa probably represent a natural fauna rather than a strictly synanthropic one. We have adopted this Mesolithic data as the baseline for comparison against settlement faunas from later periods.

A similar pattern is seen in the Neolithic and Bronze Age sites (c. 4000–1600 BC). A wider range of synanthropic taxa has been recovered (54 – a percentage increase of 125% over the Mesolithic) but these are mainly facultative synanthropes (**sf**) that can occur in the natural landscape (e.g. *Margarinotus* spp., *Atholus* spp., *Omalium rivulare* and *Tachinus rufipes,* as well as *Oxytelus* and *Anotylus* species). 'Typical'

Table 3

Occurrence of quasi-synanthropic and synanthropic species by presence or absence displayed by period. The taxa are organised by degree of synanthropy and then ordered by nomenclature following Duff (2012). The taxa above have been assigned to existing codes (i.e. Allison et al., 1997; Kenward 2005a, Kenward et al., 2011) were possible. a)**'sf' - facultative synanthropes (light grey in** Table 3**)**. Clearly favoured by conditions in settlement and often abundant in them but at least equally common in natural habits. Many of these occur in deposits such as stabling or garden waste but are also common in dung pats and organic matter in the countryside. Which taxa are included in this group can be difficult to define. Many of these species are also encountered in varying proportions in undisturbed woodland and in rural farmland (Smith et al., 2019). It could be argued that many 'farmland' species perhaps fall into this category. However, we have decided to stay with the narrower range of species suggested by Kenward, 1997, Allison et al., 1997, Kenward 2005a, 2005b, Kenward et al., 2011) to come mainly from human settlement. b) **'st' – typically synanthropes (Dark grey in** Table 3**)**. Particularly favoured by artificial habitats but believed to be able to survive in nature in the long term in the region considered here. *c)***'ss' – Strong synanthropes (Black in** Table 3**)**. Essentially dependant on human activity and settlement for survival in the region considered here.d) **'h' - the 'house fauna'** This is a notional suite of beetles with a particular affinity to human habitation and settlement that was defined by Kenward (Carrott and Kenward, 2001, Hall and Kenward, 1990; Kenward and Hall, 1995) which is often associated with dry timbers or roofing, bedding materials, floor deposits, the fill of waste pits and floor deposits of buildings (Hall and Kenward, 1990; Smith, 2012a). e) **'g' – grain and storage pests –** his is a range of taxa that are associated with whole or decaying grain often in storage or with other stored products. **'SV' - Synanthropic Value (SV).** This is a statistic which was developed by Hill (2015). It is an attempt to indicate the relative 'strength' of synanthropy at each site taking into account that the taxa have different levels of dependence on human settlement. The percentage for each synanthropic category are calculated as a proportion of the tMNI, which are then weighted according to their level of synanthropy, and finally summed to give the SV for each assemblage:**SV = F + (2 x T) + (3 x S) w**here F = %facultative synanthropes, T = %typical synanthropes and S = % strong synanthropes.

	Mesolithic	Neolithic	Bronze Age	Iron Age	Romano-British	Rural sites from 0- 500 AD	Synanthropic coding	House fauna	Grain pest
Trechus quadristriatus (Schrank)		▨	▨	▨	▨	▨	**sf**		
Megasternum concinnus (Group)	▨	▨	▨	▨	▨	▨	sf		
Acritus nigricornis (Hoff.)			▨	▨	▨	▨	sf		
Acritus sp.		▨			▨		sf		
Gnathoncus rotundatus (Kug.)		▨					sf		
Gnathoncus sp.			▨		▨	▨	sf		
Dendrophilus punctatus (Hbst.)					▨		sf		
Onthophilus striatus (Forst.)		▨		▨	▨	▨	sf		
Margarinotus brunneus (F.)				▨	▨		sf		
Margarinotus striola (Sahl.)					▨		sf		
Margarinotus purpurascens (Hbst.)	▨	▨	▨	▨	▨		sf		
Atholus bimaculatus (L.)				▨	▨		sf		
Atholus duodecimstriatus (Schrank)				▨	▨		sf		
Ptenidium pusillum (Gyll.)						▨	sf		
Aclypea opaca (L.)			▨	▨			sf		
Omalium excavatum Steph.					▨	▨	sf		
Omalium caesum/italicum Grav./Bernh.					▨	▨	sf		
Omalium rivulare (Payk.)			▨	▨	▨	▨	sf		
Phyllodrepa floralis (Payk.)			▨	▨	▨	▨	sf		
Megarthrus bellevoyei Saulcy				▨			sf		
Megarthrus depressus (Payk.)	▨	▨		▨			sf		
Micropeplus fulvus Er.	▨	▨	▨	▨	▨	▨	sf		
Micropeplus staphylinoides (Marsham)	▨	▨	▨	▨	▨	▨	sf		
Cilea silphoides (L.)		▨			▨		sf		
Tachinus rufipes (L.)			▨	▨	▨	▨	sf		
Falagria caesa Er.				▨	▨	▨	sf		
Cordalia obscura (Grav.)				▨	▨	▨	sf		
Anotylus complanatus (Er.)	▨				▨	▨	sf		
Anotylus nitidulus (Grav.)	▨	▨	▨	▨	▨	▨	sf		
Anotylus rugosus (F.)	▨	▨	▨	▨	▨	▨	sf		
Anotylus sculpturatus (Grav.)	▨	▨	▨	▨	▨	▨	sf		
Anotylus tetracarinatus Block				▨	▨	▨	sf		
Carpelimus bilineatus group	▨	▨	▨	▨	▨	▨	sf		
Carpelimus fuliginosus (Grav.)		▨		▨	▨	▨	sf		
Carpelimus pusillus (Grav.)				▨	▨		sf		
Carpelimus pusillus (grp) (Grav.)					▨	▨	sf		
Scydmaenus tarsatus Mull. & Kunze				▨	▨	▨	sf		
Rugilus orbiculatus (Payk.)		▨	▨	▨	▨	▨	sf		
Quedius cinctus (Payk.)				▨		▨	sf		
Neobisnius lathrobioides (Baudi)				▨			sf		
Quedius mesomelinus (Marsham)						▨	sf		
Leptacinus batychrus (Gyll.)					▨		sf		
Leptacinus intermedius Donis.						▨	sf		
Leptacinus spp.				▨	▨	▨	sf		
Megalinus glabratus (Grav.)		▨	▨	▨	▨	▨	sf		
Clambus spp.				▨		▨	sf?		
Attagenus pellio (L.)					▨		sf	h	
Ptinus fur (L.)	▨	▨	▨	▨	▨		sf	h	
Grynobius planus (F.)	▨	▨	▨	▨	▨	▨	sf?		
Xestobium rufovillosum (Deg.)			▨		▨		sf	h	
Anobium punctatum (Deg.)	▨	▨	▨	▨	▨	▨	sf	h	
Ptilinus pectinicornis (L.)		▨		▨	▨		sf	h	
Omosita colon (L.)				▨	▨		sf		
Omosita discoidea (F.)					▨		sf		
Omosita sp.					▨		sf		
Glischrochilus hortensis (Fourc.)	▨						sf?		
Rhizophagus parallelocollis Gyll.			▨		▨		sf		
Sericoderus lateralis (Gyll.)					▨		sf		

Orthoperus spp.	░	░	░	░	░	░	sf		
Stephostethus lardarius (Deg.)					░	░	sf		
Enicmus transversus (Ol.)	░	░	░	░	░		sf		
Dienerella spp.				░	░	░	sf		
Mycetophagus quadriguttatus Müll.		░		░	░		sf		
Corticaria punctulata Marsham			░	░	░	░	sf		
Corticaria spp.	░	░	░	░	░	░	sf		
Cortinicara gibbosa (Hbst.)	░				░	░	sf		
Gracilia minuta (F.)	░						sf		
Leiopus nebulosus (L.)		░	░	░			sf		
Bruchus rufimanus Bohe.				░			sf		
Laemostenus terricola (Hbst.)					▓		st		
Cercyon nigriceps (Marsh.)				▓	▓	▓	st		
Cercyon unipunctatus (L.)				▓	▓	▓	st		
Cercyon analis (Payk.)		▓	▓	▓	▓	▓	st		
Omalium caesum Grav.				▓	▓	▓	st		
Xylodromus concinnus (Marsham)			▓	▓	▓	▓	st	h	
Xylodromus depressus (Grav.)		▓	▓				st		
Crataraea suturalis (Mann.)				▓	▓	▓	st		
Coprophilus striatulus (F.)					▓	▓	st		
Oxytelus sculptus Grav.			▓	▓	▓	▓	st		
Lithocharis ochracea (Grav.)					▓	▓	st		
Lithocharis spp.				▓	▓	▓	st		
Gyrohypnus fracticornis (Mull.)			▓	▓	▓	▓	st		
Leptacinus pusillus (Steph.)				▓	▓	▓	st		
Phacophallus parumpunctatus (Gyll.)						▓	st		
Lyctus linearis (Goeze)			▓	▓	▓		st	h	
Tipnus unicolor (Pill. & Mitt.)		▓	▓		▓	▓	st	h	
Monotoma bicolor (Villa)					▓	▓	st		
Monotoma brevicollis (Aubé)				▓	▓		st		
Monotoma longicollis (Gyll.)				▓	▓	▓	st		
Monotoma picipes (Hbst.)				▓	▓	▓	st		
Monotoma spinicollis (Aube)				▓	▓		st		
Monotoma spp.			▓	▓	▓	▓	st		
Cryptophagus dentatus Group.)					▓		st	h	
Cryptophagus distinguendus (Sturm)					▓		st	h	
Cryptophagus scanicus (L.)		▓		▓	▓		st	h	
Cryptophagus scutellatus Newman				▓	▓	▓	st	h	
Cryptophagus spp.	▓	▓	▓	▓	▓	▓	st	h	
Atomaria nigripennis (Kug.)					▓	▓	st	h	
Atomaria spp.	▓	▓	▓	▓	▓	▓	st	h	
Ephistemus globulus (Payk.)					▓	▓	st		
Latridius minutus (grp) (L.)	▓	▓	▓	▓	▓	▓	st	h	
Latridius spp.	▓			▓	▓		st		
Dienerella ruficollis (Marsham)					▓		st		
Blaps spp.					▓		st		
Omonadus bifasciatus (Rossi)					▓		st		
Omonadus floralis (L.)				▓		▓	st		
Omonadus formicarius (Goeze)					▓		st		
Omonadus floralis/formicarius (L.)/(Goeze)					▓	▓	st		
Dermestes lardarius (L.)			█		█		ss	h	
Dermestes spp.	█		█		█		ss	h	
Anthrenus spp.					█		ss	h	
Stegobium paniceum (L.)			█	█	█		ss		g
Tenebroides mauritanicus (L.)					█		ss		g
Oryzaephilus surinamensis (L.)					█		ss		g
Cryptolestes ferrugineus (Steph.)					█		ss		g
Mycetaea subterranea (Marsham)					█	█	ss	h	
Typhaea stercorea (L.)				█	█	█	ss	h	
Tenebrio molitor (L.)					█		ss	h	
Tenebrio obscurus (F.)		█			█		ss	h	
Tenebrio spp.					█		ss		
Alphitobius diaperinus (Panz.)					█		ss		g
Tribolium castaneum (Hbst.)					█		ss		g
Tribolium spp.					█		ss		g
Palorus ratzeburgii (Wiss.)					█		ss		g
Blaps mucronata (Lat.)					█		ss	h	
Aglenus brunneus (Gyll.)				█	█	█	ss	h	
Sitophilus granarius (L.)					█		ss		g

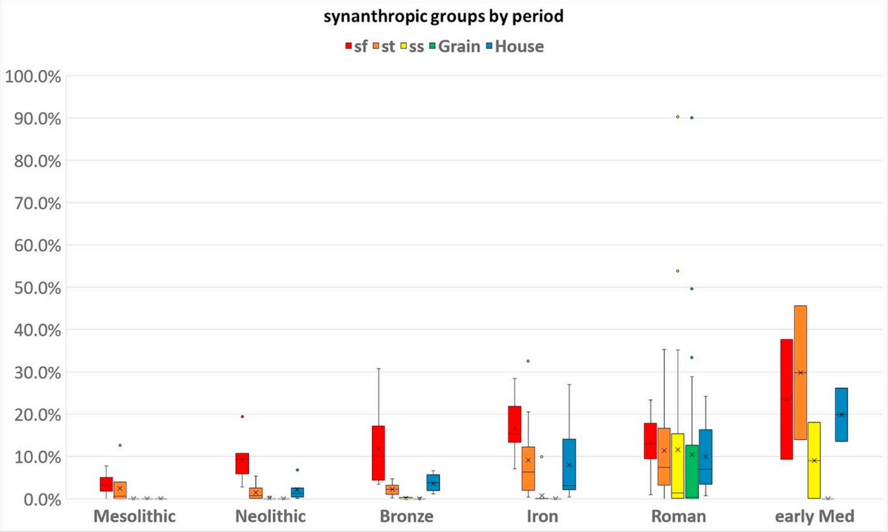


Fig. 2. Relative proportions of synanthropic groupings and statistics arranged by archaeological period.

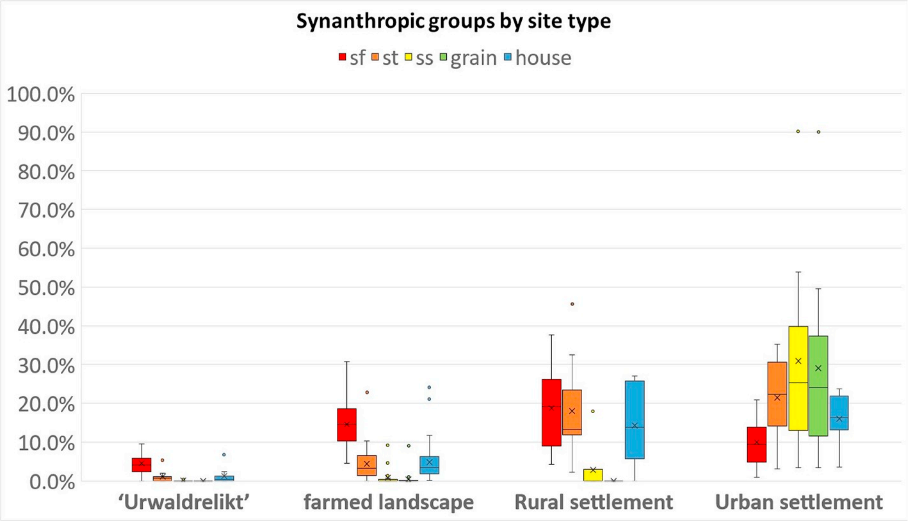


Fig. 3. The relative proportions of synathropic groupings arranged by type of archaeological site.

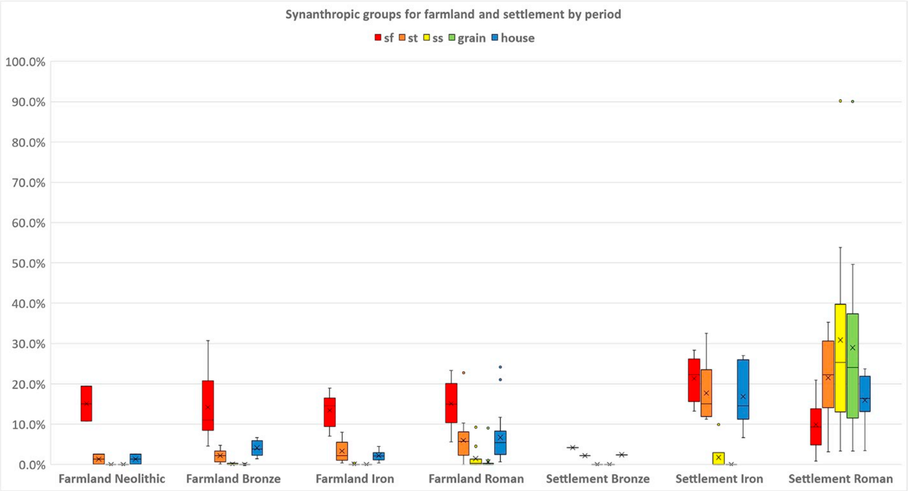


Fig. 4. Relative proportions of synanthropic groupings arranged by site type and them by archaeological period.

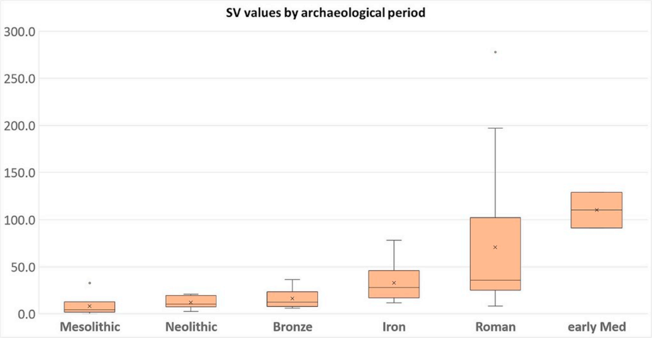


Fig. 5. Values of Synanthropic Values arranged by archaeological period.

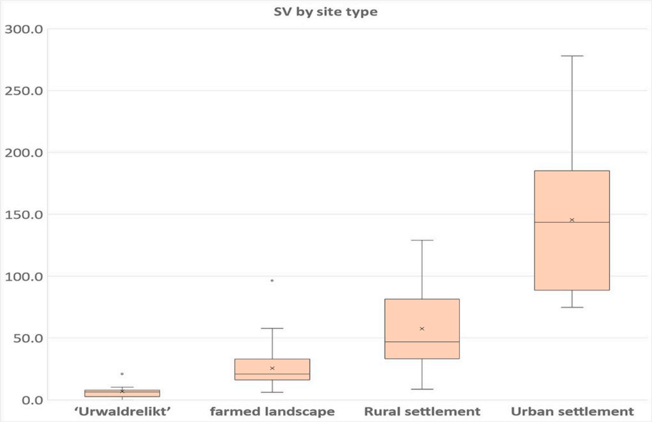


Fig. 6. Synanthropic Values arranged by type of archaeological site.

synanthropes (cryptophagids and lathridiids mainly) only occur in small numbers at most Neolithic – Bronze Age sites. However, these taxa were more numerous at Wilsford Shaft, Kingsmead and Perry Oaks. Some 'typical' synanthropes now occur more frequently (e.g. *Xylodromus concinnus*, *Lyctus linearis,* and *Dermestes* spp.).

The occurrence of the biscuit beetle *Stegobium paniceum* in the Wilsford Shaft assemblage and from several Iron Age sites may be significant. It is a pest of stored, starchy products, including grain (Koch, 1989), and is the only 'pest of stored products' which has been recovered from archaeological deposits in the British Isles prior to the Roman invasion (Buckland, 1981; Smith and Kenward, 2011). *S. paniceum* may represent an indigenous species that is able to exploit stored grain, or it may have been imported within grain at some point from the Early Neolithic onwards. The spider beetle (*Tipnus unicolor*) and the darkling beetle (*Tenebrio obscurus*), are both considered part of the 'house fauna' by Kenward (Kenward and Hall, 1995) and do occur regularly in Roman and later settlement sites. However, in earlier periods they seem to be associated mainly with tree boles and rot holes in trunks (e.g. at Thorne Moor, Lee Marston and Langford).

By the Iron Age, 79 synanthropic species are recorded (a percentage increase of 46.3% from the Neolithic/Bronze Age data) and synanthropes account for a significantly larger proportion of the faunas recovered. Facultative synanthropes (many Oxytelinae, other staphylinids and the *Cercyon* hydrophilids) have been recovered in large proportions at several Iron Age sites. A number of typical synanthropes are recorded for the first time, e.g. *Cercyon unipunctatus, C. atricapillus, Omalium caesum, Lithocharis* spp., *Leptacinus* spp., *Crataraea suturalis*, *Omonadus (Anthicus)* species and a number of *Monotoma* species. These taxa often are associated with stabling waste in the archaeological record (Kenward and Hall, 1997; Carrott and Kenward, 2001; Smith, 2012a). This probably indicates an increased collection and use of fodder as part of the intensification of stock raising and arable farming that occurred at this time and which is reflected in the development of large field systems in the British Isles after the middle Bronze Age (Robinson, 2000a; Dark, 2006; Taylor, 2007; Yates, 2007; Fyfe et al., 2008, 2015; Chadwick, 2013). The Iron Age also sees the development of a distinct 'farmland' beetle fauna, frequently dominated by *Aphodius* and *Onthophagus* dung beetles (Robinson, 2000a; Robinson, 2013a, 2013b; Smith et al., 2019). The 'facultative' group could perhaps include the 'farmyard' taxa in full, but we have limited the taxa in this group to those listed by Kenward (Hall and Kenward, 1990; Kenward, 1997). Obligate 'strong synanthropes' (e.g. Ty*phaea stercorea, Tenebrio molitor* and *Aglenus brunneus*) all are recorded for the first time in Iron Age deposits. The blind and flightless salpingid *Aglenus brunneus* is a common component of faunas from Romano-British and Anglo-Saxon house

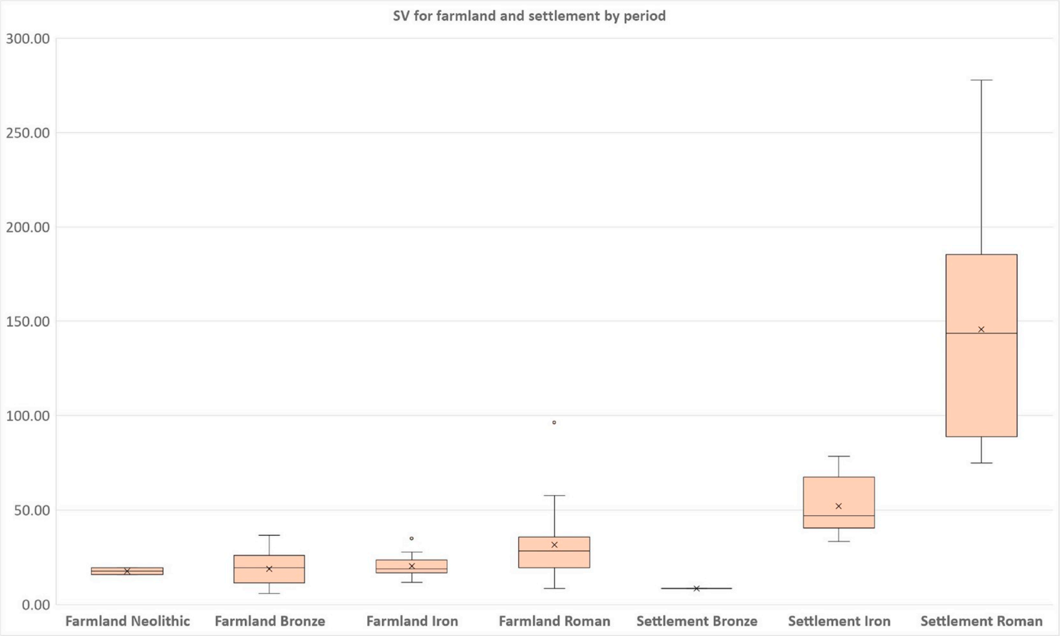


Fig. 7. Synanthropic Values arranged by site type and them by archaeological period.

floors (Kenward, 1975; Hall and Kenward, 1990; Kenward and Hall, 1995; Carrott and Kenward, 2001; Smith, 2012a), and today is frequently found within deep layers of rotting material. These strong synanthropes also are associated with settlement sites, rather than farmland (e.g. Cults Loch, the Goldcliff sites and Glastonbury Lake Village). However, there is one exception to this pattern, the field ditches from the rural site of Mingies Ditches, Oxfordshire (Robinson, 1993) has produced several of these synanthropes; however, it is believed a farmstead was located nearby or settlement waste was dumped into the ditches.

In total, 123 synanthropic taxa were identified from the Romano-British sites surveyed (a percentage increase of 55.7%). The range of strong synanthropes (**ss**) has increased radically and now includes species such as *Dermestes lardarius, Attagenus pellio, Anthrenus* spp. and *Tenebrio obscurus*, which all favour intensive settlement and urban 'heat islands' (Kenward, 1997). Similarly, the ground beetle *Laemostenus terricola* and the tenebrionid *Blaps* are regarded today as predominantly synanthropic (Lindroth, 1974; Brendell, 1975; Luff, 2007). The presence of artificially warm, urban habitats also favours the oriental cockroach (*Blatta orientalis* L.), which was recovered from early first century AD deposits in central London (Smith and Goddard, 2015). Grain and storage pests occur for the first time in the Romano-British period and include the saw-toothed grain beetle (*Oryzaephilus surinamensis*), the rust-red flour beetle (*Cryptolestes ferrugineus*), the small-eyed flour beetle (*Palorus ratzburgi*), the lesser mealworm (*Alphitobius diaperinus*) and the granary weevil (*Sitophilus granarius)*. Two grain pests, the cadelle (*Tenebrioides mauretanicus*) and the red flour beetle (*Tenebrio castaneum*), seem to require very sheltered or even heated areas in the British Isles (Solomon and Adamson, 1956).

By contrast, the rural sites which either date to just after the end of the Roman occupation or are not from the area of the Roman occupation (Buiston Crannog and Deer Park Farms) contain a much more limited range of strong synanthropes and, most notably, grain pests are entirely absent.

6.2. Changes in the relative proportion of the synanthropic groupings by period

The changing values for the synanthropic groupings are outlined by archaeological period in Fig. 2 and SV value by period in Fig. 5. The averages for synanthropic value (**SV**) (<50) and the proportion of the 'house fauna' (**h**) (<10%) are comparatively low for the Mesolithic, Neolithic and Bronze Age periods (with SV higher in the Bronze Age due to raised values for facultative species (**sf**) at Perry Oaks and Wilsford Shaft). The Iron Age data shows a slight rise in **SV** and the relative proportion of **h**, with a wider range of values when compared to earlier prehistoric results. For the Romano-British faunas, **SV** is markedly higher than in the prehistoric periods, often between 50 and 100; with several sites scoring above 200, suggesting that the 'superabundance' of strong synanthropes is a major aspect of these faunas. In the Roman period, the value for **h** varies from 1%–23.7% (it is worth remembering that **h** does not include grain pests) and both the **SV** and **h** statistics now show considerable variation between sites.

A similar overall pattern can be seen in the relative proportions of the facultative (**sf**) and typical synanthropes (**st**) recovered. Throughout the Mesolithic and Neolithic relative proportions of both groupings are usually below 10% of the fauna, with little variation in range. However, there is a clear increase in the relative proportion and range of facultative synanthropes from the Bronze Age onwards, with values > 10% common.

The variation in the relative proportions of strong synanthropes recovered over time is very striking. Values for this grouping remain very low (often negligible) until the Romano-British period. Grain pests are completely absent until the start of the Romano-British period (with the exception of the more eurytopic *Stegobium paniceum*).

There are, however, very high values for all synanthropic groupings, except strong synanthropes (**ss**) and grain pests (**g**), at the two Early Medieval rural sites of Deer Parks Farm and Buiston Crannog, most likely as a result of the sampled material coming directly from house floor deposits (Kenward et al., 1994; Kenward and Allison, 1994; Smith, 2012a).

6.3. Distribution of synanthropes by type of archaeological site

Fig. 3 indicates how the synanthropic groups differ between types of archaeological site and Fig. 6 displays the value of **SV** across site type.

For 'Urwaldrelikt' sites with little human activity, the values for the synanthropic groupings are very low (**SV** < 10; **h** <5%). One exception is Neolithic Langford (**SV** 21.1; **h** 6.8%), where, as discussed above, the higher values result from the faunas coming from rot holes and the boles of large trees (Howard et al., 1999).

SV and **h** are similarly low at farmed landscape sites in all periods. Slightly more elevated results for **SV** and **h** occur at Roman Perry Oaks, Northfleet and St. Loyes, probably due to disposal of settlement waste into ditches or pits (Robinson, 2006;. Romano-British urban sites produce synanthropic values that are comparatively high (**SV** 74.9–277.8; **h** 3.5%−23.7%).

Values from farmed landscapes sites for 'typical' and 'strong' synanthropes are usually low (<10% for **st** and <10% for **ss**) when compared with those for urban settlements (3.5%–35% for **st** and 12.8%–90.2% for **ss**, with some high outliers). However, 'facultative' synanthropes (**sf**) usually occur in similar proportions at both farmed landscape and urban settlement sites (around 5%–25%). This is probably because many **sf** taxa can occur in both animal dung in pasture and in settlement waste (i.e. Kenward and Hall, 1997; Smith et al., 2019). Again, this raises the issue of the degree to which members of 'farmyard' and 'facultative' synanthrope faunas overlap and which of these taxa should be included in particular synanthropic or ecological groups.

6.4. Distribution of synanthropic groupings between farm sites and settlement sites by period

Fig. 4 outlines the nature of the synanthropic groupings for farmland sites and settlement by archaeological period in order to assess how this may change over time. Fig. 7 presents the SV values for the same groupings of sites. The relative proportions (both mean and range) of synanthropic groupings at farmland sites from all chronological periods are very similar (**SV** 6–46; **h** <10% - with the exception of Romano-British Perry Oaks, Northfleet and St. Loyes – as discussed above in §5.3). The settlement sites show a dramatic increase in **SV** between the prehistoric rural settlements and the urban Roman sites (usually >50 rising to values of between 74 and 277) although the values for **h** remain fairly constant. The main difference in **SV** values between the rural prehistoric and Romano-British urban sites can be attributed to the larger proportions of 'strong synanthropes' and grain pests in the later set of sites. This must relate to the intensive occupation, waste generation and rubbish disposal in Roman towns. Although prehistoric settlements were part of wider trading networks, Roman towns were highly connected and actively participated in extensive trading networks transporting large volumes of grain and other materials and, also, the insects that came within them.

7. Conclusions

7.1. The timing of the introduction of synanthropes to the British Isles compared to the European continent

This study has confirmed that synanthropic species, including some exclusive and now cosmopolitan synanthropes, have been present in human settlement in the British Isles for a long period of time and are not a modern phenomenon. The relative timing of the first occurrence of synanthropes occurs later in the British Isles than in the Near East and

Central Europe, with the first occurrence of synanthropic taxa dated to between *c.* 9500–5000 cal. BC often associated with the spread of farming in the early Neolithic (Panagiotakopulu and Buckland, 2017; Panagiotakopulu and van der Veen, 1997; Panagiotakopulu, 2000, 2001; King et al., 2014).

The late introduction of synanthropes into the British Isles could be explained in any number of ways:

1) the result of the lack of sizeable and more permanent settlements in the Neolithic and Early Bronze Age in the British Isles when compared to Central Europe (Thomas, 2008; Stevens and Fuller, 2012).
2) the difference in the nature and intensity of arable farming in Neolithic and Early Bronze Age Britain as compared with continental Europe. Agriculture in early prehistoric Britain seems to have remained comparatively small-scale and non-intensive (Moffett et al., 1989; Whittle, 1997; Robinson, 2000b) or was partly driven by ritual and social needs, rather than subsistence (Richmond, 1999; Thomas, 2008; Stevens and Fuller, 2012).
3) Robinson (2000a) suggested that rearing domestic animals during the British Neolithic may have been akin to 'wildwood ranching' rather than more intensive patterns of stock raising in continental Europe; a situation which could delay the development of the 'farmland fauna' and its associated 'quasi-synanthropes' or at least make it less archaeologically visible.

7.2. *The temporal pattern of the introduction of synanthropes*

There appears to be three distinct phases evident in the data.

1) **prior to the Late Bronze Age:** synanthropic faunas in deposits associated with human activity are restricted to a range of Cryptophagidae and Lathridiidae.
2) **from the Late Bronze Age/Early Iron Age onwards:** synanthropic faunas expand to include a much wider range of facultative and typical synanthropes, along with a small number of strong synanthropes. These taxa are primarily associated with animal dung, stable waste, fodder and animal bedding. Their increased occurrence probably reflects the rapid expansion and intensification of pastoral and arable farming at this time in the British Isles, as well as increasing connectivity of settlements.
3) **from the early Roman period:** a third wave of synanthropic expansion is apparent from the early Roman period when a range of strong synanthropes (ss) and storage pests now are recovered more frequently. Romano-British synanthropic taxa are associated with dense, sheltered, urban habitation and many of these strong synanthropes/grain pests are unlikely to successfully overwinter in the wild in the British Isles. Importation and transport of goods on a massive scale was no doubt crucial in the dispersal of synanthropic beetles.

Notably, by the Romano-British period, this wider range of strong synanthropes is much broader than we expect to find in urban housing today (Kenward and Hall, 1995; Smith, 2012a). The permanent and widespread availability of decaying waste in ancient settlement probably produced an environment which was less ecologically 'patchy' than that of the modern urban landscape. This supports Blair (1999) and McKinney (2006) arguments that 'intermediate disturbance environments' are crucial for the development of synanthropy.

7.3. *Origins and the development of synanthropy*

This survey of British synanthropic data identifies several routes that beetles can take on the road to synanthropy:

Table 4
Quasi-synanthropic and synanthropic species recovered from the Neolithic tree bole (102) at Langford Quarry (Howard et al., 1999) and Medmerry tree bole (Allison, 2016, 2018). Numbers represent the Minimum Number of Individuals (MNI).

Coleoptera	Synanthropic coding	Member of house fauna	Tree bole sample 102 Langford Quarry (10)	Peat deposit associated with fallen tree Medmerry Sample 422
Hydrophilidae				
Cercyon melanocephalus (L.)	sf		1	–
Megasternum 'concinnum' (Marsh.)	sf		1	1
Histeridae				
Onthophilus striatus (Forst.)	sf		1	–
Paralister purpurasens (Hbst.)	sf		1	–
Staphylinidae				
Cordalia obscura (Grav.) or *Falagria*	sf		–	1
Dermestidae				
Attagenus pellio (L.)	sf	h	1	–
Monotomidae				
Rhizophagus picipes (Ol.)	sf		1	–
R. spp.			1	–
Cryptophagidae				
Cryptophagus scanicus (L.)	st	h	5	–
Cryptophagus spp.			8	–
Atomaria spp.	st		–	1
Lathridiidae				
Stephostethus angusticollis (Gyll.)	st		–	1
Lathridius minutus (Group)	st	h	1	–
Dienerella spp.	st		–	1
Corticaria spp.	st		1	–
Mycetophagidae				
Mycetophagus quadriguttatus Müll	sf		1	–
Anobiidae				
Grynobius planus (F.)	sf		1	1
Xestobium rufovillosum (Geer)	sf	h	2	–
Ptinidae				
Ptinus fur (L.)	sf	h	3	1
Tenebrionidae				
Tenebrio obscurus F.	ss	h	1	–

1) several 'generalist' members of the synanthrope fauna discussed here (mainly **rt** taxa) are associated with a range of short-lived and temporary ecologies (i.e. plant litter and organic-rich sediments). These occur patchily in unmanaged forest, grassland and disturbed habitats. Kenward and Allison (1995) and Kenward (1997) have hypothesised that these taxa naturally move from the local 'wildscape' into farmland and settlement (by 'accretion'). Once in settlement they are able to exploit the rich range of more permanent resources and are able to develop significant populations. Though Kenward (1997) initially indicated that the speed of this 'accretion' might be decadal in formation, work at the coastal, isolated,

seasonally-occupied and short-lived Iron Age site of Goldcliff, Gwent has indicated that large and diverse synanthropic faunas can establish over short periods of time, perhaps in a matter of weeks or months (Smith et al., 1997, 2000). Importation of materials containing abundant synanthropic beetles also may have been significant.

2) another potential ‘wild’ origin for synanthropes was the interior of rotting timber and/or the burrows of animals and birds’ nests in the ‘wildwood’. This route may introduce several of the more specialised taxa; such as, woodborer, spider, darkling and hide beetles. For example, several synanthropic taxa have been recorded from Neolithic fallen tree boles at Langford, Nottingham and from peat associated with an old or dead tree at Medmerry, Surrey (Allison, 2016, forthcoming: see Table 4).
3) the development of intensive stock raising after the Late Bronze Age (Dark, 2006; Fyfe et al., 2015 Smith et al., 2019) seems to be a crucial step in the story of synanthropy in the British Isles. A large number of taxa which appear to be relatively rare or associated with spatially limited deposits (such as animal dung and plant litter in the ‘wildscape’ of the Early Holocene) appear to become common or dominant in farmland and settlement after the Late Bronze Age.
4) The importation of large volumes of grain and other traded goods form both local and international sources in the Romano-British period (Buckland, 1981; Smith and Kenward, 2011 Panagiotakopulu and Buckland, 2017) seems crucial. At the continental scale, Panagiotakopulu and Buckland (2017) have suggested that the spread of a range of synanthropic species across Eurasia results from the massive expansion of Roman maritime trade representing an example of ‘biological imperialism’. It also is clear that this introduction of ‘exotic’ synanthropes can be very rapid. In Britain, many ‘exotic’ synanthropes have been recovered in large numbers from deposits which are closely dated to within a few years of the Roman invasion (e.g. London - Smith, 2012a; Carlisle - Smith and Kenward, 2011; and York – Kenward and Williams, 1979).

Several of these possible routes to synanthropy are examples of an ecological theory known as ‘island isolation and biogeography’. This approach has been identified recently as key to explaining the richness and diversity of archaeoentomological fauna of the North Atlantic (Vickers and Buckland, 2015; Panagiotakopulu, 2014) and, specifically, also has been identified as key to the development of synanthropy by Kenward (1997).

7.4. Future research directions

This paper has outlined the development, timing and possible origins for the synanthropic coleopterous fauna of the British Isles. Obvious gaps in the data reviewed need to be filled (especially Early Prehistoric settlement deposits from the British Isles), but the general pattern seems clear. Internationally, it is important to determine if the nature, scale and timing of synanthropy is similar? Tracing the archaeological spread of synanthropic species in mainland Europe, in the post-colonial Americas and/or China would be fascinating. For example, Panagiotakopulu and Buckland (2017) suggest that the international spread of synanthropes in specific periods could be mediated by climate warming, an issue warranting further investigation.

Other orders of insects besides Coleoptera also merit investigation. For example, ectoparasites; such as, the body louse (*Pediculus humanus* L.), the pubic louse (*Pthirus pubis* L.) and the human flea (*Pulex irritans* L.), have a long and intimate association with humans. There are archaeological finds of the body louse dating back to at least 10,000 BC and the human flea dating to 5000 BC; though this relationship may be much older (Buckland and Sadler, 1989; Mumkuoglu and Zias, 1991; Araújo et al., 2000; Kittler et al., 2003; Reed et al., 2004; Amanzougaghene et al., 2016; Remicourt et al., 2014; Panagiotakopulu and Buckland, 2018). Panagiotakopulu and Buckland (2017) have recently outlined the archaeological history of the house fly (*Musca domestica* L.) and the lesser house fly (*Muscina stabulans* Fall.), suggesting an origin in the Nile valley and a subsequent spread alongside farming to middle Europe around 5000 BC.

At present, the detailed history of synanthropy presented here for the British Isles is not available for many areas of the world where archaeoentomology is relatively under-researched. If the history of synanthropes is to be researched world-wide, archaeoentomology needs to be adopted as a standard archaeological technique beyond Northern Europe. In terms of timescale required to generate appropriate datasets, it should be noted that this present survey represents nearly 50 years of research by just over a dozen archaeoentomologists.

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