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Dead wood matters:
the ecology and conservation of
saproxylic invertebrates in Britain

Edited by K J Kirby & C M Drake

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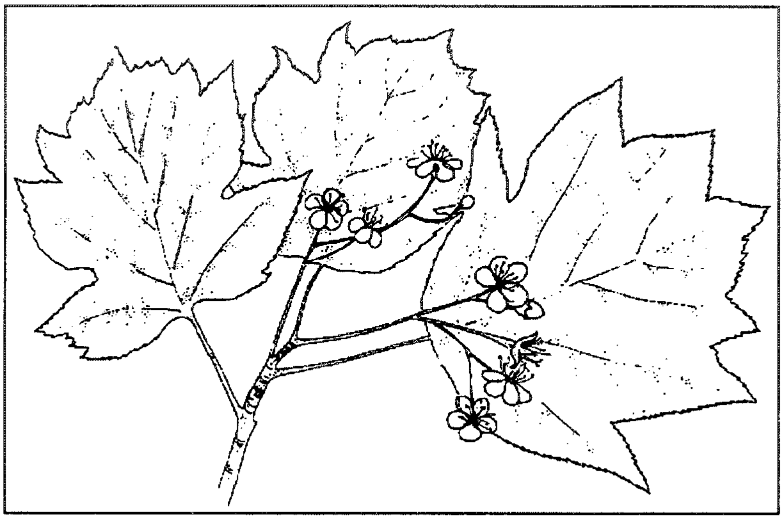

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INTRODUCTION

Keith Kirby & Martin Drake, English Nature, Northminster House, Peterborough, PE1 1UA

Insects and other invertebrates dominate the earth, but have often been under-represented in discussions and papers about nature conservation in British woods. There have however been considerable improvements in our knowledge of their needs over the last 15 years. In the early 1980s much attention was focused on the species found in the open spaces and young growth stages within woods. The reduction in coppicing this century had caused many of these species to decline greatly in abundance. Using initially butterflies as a marker, ways were proposed of incorporating permanent and temporary glades within commercially managed forests and reserves, with considerable success.

Another group of woodland species has however been equally threatened by changes in land use: those that depend on old trees, and dead and dying wood. Having 'sorted out' one end of the woodland cycle there was a need to raise the profile of species at the other end - fungi, lichens and saproxylic invertebrates. A symposium organised by the Parks Department of the Corporation of London on pollards, veteran trees and their management attracted over 200 people. To carry this enthusiasm forward we decided to organise this meeting, which concentrated just on the invertebrate perspective.

The contributors were chosen to cover a wide range of aspects. The first two papers set the scene in terms of the historical origins of our saproxylic fauna and the significance of our sites and species in Europe as a whole. The third is a detailed study of species in one wood and illustrates how scanty is our knowledge of the ecology of even some common species. The fauna of parkland is probably better understood but further survey is still needed, and this and the management needs of such sites are considered in the fourth paper.

Those concerned with conservation must however be aware of the conflicts that may (or may be perceived to) exist between looking after these special invertebrates and other uses of woodland or parks. The possible threats to commercial timber production and public safety questions are the subjects of the fifth and sixth papers.

The final paper pulls together some of the practical ways in which conservation of deadwood invertebrates can be furthered, and we have supplemented this by two annexes on guidelines for surveys and the treatment of storm-damaged woods.

In *The pattern of animal communities*, Charles Elton wrote ".... dead and dying timber provides one of the two or three greatest resources for animal species in a natural forest, and .... if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna".

Dead wood matters!

Acknowledgements

We thank the National Trust and its staff for allowing us to use Dunham Massey for the meeting. This contributed greatly to the success of the day. Richard Ferris-Kaan of the Forest Ecology Group (under whose auspices the meeting was run) helped with the organisation, and financial support came from the British Ecological Society. We must also thank the authors for their timeliness in providing texts and the referees who commented on them. Finally thanks to Stefa Kaznowska who had the task of steering the volume through to production.

WHAT ARE SAPROXYLIC INVERTEBRATES?

Roger Key, English Nature, Northminster House, Peterborough, PE1 1UA

Saproxylic species are those that depend on wood, usually but not always dead wood, for some part of their life-cycle. Many of them are invertebrates but some other groups of organisms also depend on dead wood, most notably the fungi, but also birds and mammals that use holes in trees in which to nest or roost. A large number of bark-living bryophytes and lichens are common on the old trees that are important for fungi and invertebrates although they cannot actually be called saproxylic.

Saproxylic invertebrates include not only those that feed on the wood itself, but also predatory and parasitoid species, species feeding on fungi, both within dead wood and in their fruiting bodies, species using sap exudates from trees and even species that use empty insect emergence holes in which to nest. The adult stages of many of the insects do not live in dead wood but are pollen or nectar feeders on flowers or are predatory on other invertebrates.

By far the majority of the actual wood-feeders are beetles and their larvae or the larvae of flies, although there are also a few sawfly and moth larvae that feed usually on healthy wood. Many beetles, flies, springtails, millipedes, woodlice, mites, bugs and earthworms feed on wood mould or fungal fruiting bodies on wood. Saproxylic predators include, again, large numbers of beetles, some fly larvae, bugs, ants, snakefly larvae, spiders, false scorpions and mites, while the majority of parasitoids are ichneumons or other parasitic wasps as well as a few flies. Obligate sap feeders are found entirely among the flies and beetles, some depending on exudates from the burrows of the goat moth larva. Many species of solitary wasp and bee also use beetle emergence holes for nesting sites.

Although there are many common saproxylic species, a high proportion are now very scarce and restricted to niches present only on very ancient trees. Many are now found only in areas where there has been a very long continuity of "overmature timber", such as pasture woodland and parkland with ancient pollards and old forests such as Windsor, Epping and the New Forest. Some are particularly vulnerable as their highly specialised niches may be present on only a tiny proportion of trees at a site at any one time, or they may have poor powers of dispersal and so not colonise new sites, or even new trees very easily. Throughout Europe, saproxylic species have been identified as the most threatened community of invertebrates.

Until recently, saproxylic invertebrates and their habitats have been given little consideration either in the selection of conservation sites or in the management of forests, woodland and parkland. This is slowly changing and Sites of Special Scientific Interest and National Nature Reserves have now been designated to conserve this fauna and information on their needs made available to conservation workers, foresters and others working with old trees. Many saproxylic invertebrates are brightly coloured and conspicuous or have bizarre and fascinating life histories and they have much to offer in interpreting their plight to a wider audience.

HOLOCENE WOODLANDS, THE FOSSIL INSECT EVIDENCE

P C Buckland and **M H Dinnin**, Department of Archaeology & Prehistory
University of Sheffield

Introduction

In one form or another, the history of the last ten thousand years, the Holocene Interglacial, is written in a rapidly diminishing resource, the wetlands. Their peats and organic silts preserve not only a record of the past flora, as both pollen and plant macrofossils (Godwin 1975), but also a significant proportion of the contemporary invertebrate assemblages, in particular the insect fauna (Buckland & Coope 1991). In addition, the wetlands also contain an archaeological record unparallelled in its detail outside the cold of the Arctic or the arid, drying sands of the deserts (Coles & Coles 1989). These waterlogged deposits contain a unique record of climatic, vegetational and faunal change, the implications of which have still to be fully appreciated.

Osborne (1965) was the first to point out the Old Forest element in early to mid-Holocene fossil beetle faunas, although as early as 1935 Blair had recorded the presence of the archetypal *Urwaldtier* - in the sense of an animal of the primary forest before it was disturbed by human activity - *Rhysodes sulcatus* F., from moorlog of early Holocene age from the coast of East Anglia. In common with the palynological evidence, entomological research by Osborne (1972), the late Maureen Girling (1982, 1985) and Buckland (1979) has shown that the first half of the present interglacial largely follows the pattern of previous interglacials, with the progressive rise to a largely forested landscape, with its associated fauna. Insect faunas from Cromerian (Osborne 1980), Hoxnian (Shotton & Osborne 1965) and Ipswichian (Gaunt *et al.* 1972; Girling 1980; Beesley 1988) interglacial deposits, despite their great temporal separation, display remarkable similarities to those of the first half of the Holocene. The slightly warmer climate of the Ipswichian (last) and the stochastic effects of biogeographic accident account for the small differences in biota. Despite the major disruptions caused by multiple glaciation and long periods when the norm was cold, arctic tundra, the forest fauna successfully reassembled itself each time. During the last 5,000 years, this established pattern has been disrupted. The late Holocene is unique in several ways, not least in the progressive impoverishment of biota, as forest has given way to culture-steppe. When glaciation again tidies up the European slate, there will be a much reduced genetic reservoir to re-occupy the land.

Fossil evidence for the forest insect fauna

As the West European insect fauna evolved through the Tertiary in a landscape of continuous forest with a scattered mosaic of other habitats, it is hardly surprising that it is the forest fauna that has suffered most from human impact; the natural forest has wholly disappeared from Britain and the few fragments claimed elsewhere in Europe all betray evidence of some human utilisation or inadvertant pressures in the past. The elements of the *Urwald* fauna survive either in scattered, much damaged fragments or in poor analogues to their primary habitats (Speight 1989). The nature of the *Urwald* - preferred to Rackham's (1976) term Wildwood since Badger's Wildwood contained clear evidence of human activity (Grahame 1908) - has been the subject of considerable debate. In the lowlands of England, the idea of oak being the dominant tree in the natural succession (e.g. Tansley 1949) has been superseded by the recognition of the importance of lime (Greig 1982), and the suggestion that fragments of primary forest may have survived as late as the seventeenth century (Kirby 1974) has been replaced by the widespread realisation that human impact upon the woodland was sufficient to lead to its wholesale modification in prehistory; as a conservative estimate, Greig (1982) suggests that there remained no natural forest in Europe by a thousand years ago. In England, aerial photographic evidence from some of the remaining refuges for old forest insects, for example

Sherwood in Nottinghamshire, show a managed landscape of rectangular fields from the pre-Roman Iron Age (Riley 1980). Any remaining woodland would have been heavily managed to ensure maximum yields.

In Britain, forest reached its maximum extent during the mesolithic, pollen zone VIIa (Bennett 1986). Although a plethora of pollen studies cover this period, *ca.* 10,000-5,000 bp, there are as yet only a handful of published beetle assemblages, and the list of extinct species is likely to be expanded considerably when further sites are studied. The palynological record itself suggests other areas where extinctions will inevitably have occurred, because of changes in the abundance of different tree species.

Since Kelly and Osborne's (1965) publication of plant macrofossil and insect evidence from a site at Shustoke in Warwickshire, dated to 4,830+/-100 B.P., the importance of lime in the English Forest has become increasingly apparent and the one clear lime indicator in the fossil insect record, the Scolytid *Ernoporus caucasicus* Lind, has been found on mid-Holocene sites as far apart as West Heath Spa in outer London (Girling 1989) and Thorne Waterside in South Yorkshire (Buckland 1979). Osborne (in Kelly & Osborne 1965) found this Scolytid as a fossil before Allen (1970) added it to the British list from specimens from Moccas Park, Herefordshire, taken in 1954, and its distribution has now been shown to extend to a number of other managed park woodland localities, including Swithland, Leicestershire (Cooter 1981), and Chatsworth, Derbyshire (Johnson, in Garland 1983). This pattern is typical of many of the surviving *Urwaldtier*, hanging on by the tips of their tarsi in areas of parkland with old pollards (Harding & Rose 1986), a managed habitat which is perhaps the oldest in Britain. *E. caucasicus* appears to disappear from the fossil record by the early Bronze Age, by which time the frequency of lime had already been seriously reduced, becoming even further restricted by the end of the period (Turner 1962). Oak-alder woodland, itself largely a result of human interference in the succession, became the most frequent forest type thereafter.

The most recent site which contains a recognisably *Urwald* assemblage of insects belongs to the Late Bronze Age, some 3,000 years ago. Buckland (1979) describes an insect fauna from the base of the peat at Thorne Moors, S. Yorks, containing seven species no longer found in the British Isles. *Rhysodes sulcatus* F. for example is recorded in Britain from several sites (Blair 1935; Kelly & Osborne 1965; Girling 1980; Buckland 1979) but is now extremely rare and mainly a south-east European species (Speight 1989). It is regarded as extinct in Sweden, being last recorded in 1863, and the few German records are old. In 1935, the German entomologist K Dorn coined the term *Urwaldrelikt*, a relict species of primary, wholly undisturbed forest, to describe this beetle. This species is found only in thoroughly rotten wood, where it is thought to feed on fungi (Crowson 1981). Although Horion (1935) notes a preference for beech, as in most of the saproxylic fauna, specialisation is towards a very particular microhabitat, rather than the species of tree. A similar preference for beech is suggested for the Eucnemid *Isorhipis melasoides* (Lap.), although the Thorne specimens were dug out of their pupal chambers in alder; additional fossil records are from Misterton Carr, Nottinghamshire, West Heath Spa, London, and the Somerset Levels (Girling 1982). Superficially, this beetle's continental distribution suggests that the species is relatively thermophilous, so that climatic deterioration might account for its extinction from Britain. However, its absence from a large area of central Germany seems to indicate also that old, established forest is a necessary part of the species ecology (Buckland 1979).

One of the most frequent fossils in the Thorne assemblage is the Cucujid *Prostomis mandibularis* (F.), and this has also been found in the Somerset Levels (Girling 1982). Horion (1960) and Palm (1959) describe *Prostomis mandibularis* as *Urwaldrelikt*, the former anticipating its extinction from Central Europe within a few years, although surprisingly it has established itself in southern British Columbian forests, where it has been accidentally introduced (Campbell 1978). In Europe, it is limited to a handful of isolated semi-natural forest remnants, where it lives in wet rotten wood (Dajoz 1974). Moist/wet wood in a highly advanced state of decay also forms the habitat of the fungal feeder *Mycetina cruciata* (Schall.), now extinct in Britain, whose only record is from Thorne Moors. The insects associated with fungal fruiting bodies on trees have also suffered severe decline. The Cisid *Rhopalodontus bauderi* Ab. which develops in fungal fruiting bodies growing on rotten wood has again only been found in Britain as a fossil from Thorne Moors.

Fires, both natural and of human origin, created other habitats. The Ostomid *Zimioma grossum* (L.) is apparently associated with birch damaged by forest fires, and its presence at Thorne, three thousand years ago, may reflect the "slash and burn" clearance of the region's woodland cover. The virtual disappearance of the burnt woodland habitat since, because surviving woodland types in the lowlands are generally less flammable, could have led to its extinction from Britain.

The Thorne list, from an area of forest killed by clearance and a rising water table, also includes many species whose British distribution is now particularly limited. Some, like *Dryophthorus corticalis* (Payk.) and *Eucnemis capucina* Ahr., have a southern distribution, but there are also species with a disjunct northern distribution in the same samples, such as the birch bark beetle, *Scolytus ratzeburgi* Jans. Girling's (1982) work in the Somerset Levels has produced similar patterns of change in the beetle fauna. This suggests that, although vagaries in climate have contributed to the changes (Osborne 1976, 1982), other factors such as reduction in habitat abundance are also important.

The Thorne Moors site provides the longest individual site list of extinctions from the British list and severe restrictions in distribution, since Hammond (1974) reviewed the changes in the British beetle fauna. The number of apparently extinct species found fossil in British Holocene deposits has risen to at least 30 (Table 1). *Porthmidius austriacus* (Schrk.) was recovered from mid-Holocene deposits near Church Stretton in Shropshire (Osborne 1972), and *Cerambyx cerdo* L., is known from two Cambridgeshire fenland bog oaks (Buckland & Kenward 1973; Harding & Plant 1978). One of the latter was such a good fossil that Duffy (1968) refused to believe its 3000 year radiocarbon age! *Pycnomerus terebrans* Ol. is recorded from Minsterley, Shropshire, the Somerset Levels and West Heath Spa, London (Osborne 1972; Girling 1985, 1989), whilst the Pselaphid *Batrisus formicarius* (Aub.) and *Bothrideres contractus* F. are only known in the Holocene from the Stileway site in the Somerset Levels (Girling 1985). Recently, Robinson (1991) has found the Eucnemid *Dromaeolus barnabita* (Villa) in late Neolithic deposits at Runnymede, Surrey and Wagner (pers. comm.) has added the woodboring Lucanid *Platyceris caraboides* (L.) to this list from mid-Holocene deposits at Melton in east Yorkshire. Several others not infrequent as fossils have not been found alive in the last fifty years (Foster 1991; Warren & Key 1991). The majority of extinctions and many gross retractions in range are among taxa which have an association with woodland, in particular with mature forest and its deadwood habitats. The relative ease with which fossil Coleoptera may be identified inevitably leads to a biassed list of extinctions from the British list; however other old forest indicators, particularly amongst the Diptera, are likely eventually to be added to the catalogue.

Table I **Coleopteran species no longer extant in Britain** (not including recent extinctions)

Taxa	Most recent fossil record
Chlaenius sulcicollis (Payk.)	*ca.* 5,150 BP
Oodes gracilis Vil.	*ca.* 5,150 BP
Gyrinus colymbus Er.	*ca.* 600 BP
Rhysodes sulcatus (F.)*	*ca.* 3,000 BP
Batrisus formicarius Aube*	Late Neolithic / Early Bronze Age
Porthmidius austriacus (Schrk.)*	Neolithic
Isorhipis melasoides (Cast.)*	*ca.* 3,000 BP
Dermestes laniarius Ill.	3,160 +/- 60 BP
Zimioma grossum (L.)*	*ca.* 3,000 BP
Airaphilus elongatus (Gyll.)	4th Century AD
Prostomis mandibularis (F.)*	2,980 +/- 100 BP
Leucohimatium sp.	9,420 +/- 200 BP
Pycnomerus terebrans (Ol.)*	pollen zone VIIb
Dromaeolus barnabita (Villa)*	Late Neolithic
Bothrideres contractus F.*	Late Neolithic / Early Bronze Age
Mycetina cruciata (Schall.)*	2,980 +/- 110 BP
Rhopalodontus baudueri Ab.*	980 +/- 110 BP
Anthicus gracilis (Panz.)	2,340 - 2310 BP
Onthophagus fracticornis Preyss.	3,160 +/- 60 BP
Aphodius quadriguttatus (Hbst.)	3,160 +/- 60 BP
Platycerus caraboides (L.)*	pollen zone VII
Cerambyx cerdo L.*	3,690 +/- 100 BP
Hesperophanes fasciculatus (Fald.)*	2nd Century AD
Cathormiocerus validiscapus Roug.	8,320 +/- 100 BP
Cyphocleonus trisulcatus (Hbst.)	9,420 +/- 200 BP
Eremotes elongatus Gyll.*	pollen zone VIIb
Eremotes punctulatus Boh.*	pollen zone VIIb
Eremotes strangulatus Perr.*	Late Neolithic / Early Bronze Age
Acalles sp.	*ca.* 3,000 BP

* denotes species associated with timber and/or dead wood

The virtual disappearance of pine from the lowlands of Britain during the late Holocene reflects both natural and anthropogenic changes in the forest cover. Significantly, before the Forestry Commission provided an unexpected bonanza, a number of pinicolous insects, including *Eremotes ater* (L.), appear to have made their last documented lowland appearance during the late Bronze age some three thousand years ago (Buckland 1979; Girling 1982). Three other members of the genus, *E. elongatus* Gyll., *E. strangulatus* Gyll., *E. punctulatus* Boh., are known as mid-Holocene fossils, the first two from Church Stretton (Osborne 1972) and the last from Stileway, Somerset (Girling 1985). These weevils are not restricted to pine but demonstrate an aspect evident in much of the fauna, that of increased host-specificity at the climatic margins of their range; two Anobiids, *Gastrallus immarginatus* (Mull.) on field maple at Windsor (Donisthorpe & Allen 1936) and the death watch beetle *Xestobium rufovillosum* (Deg.) on oak in the north midlands, oak and willow in the south and a range of trees in Germany (Buckland 1975) provide further examples of this in the Thorne assemblage. A clearer casualty of the decline in mature pine forest, however, is the Scolytid, *Pityogenes quadridens* (Hartig), which occurs in the early to mid Holocene at Girton, Notts (Dinnin 1992). It is now restricted to the Scottish highlands and is listed by Shirt (1987) as rare.

Decline of the *Urwald* fauna in a changing landscape

The original fauna of western Europe was an *Urwald* one, evolved in a virtually continuous forest. With almost contiguous dead wood habitats, effective dispersal by flight was unnecessary to the bulk of the fauna and the microclimate of the forest was relatively uniform and stable. By contrast the open-ground elements required a high dispersal potential to seek out their patchy transient habitats amongst the trees. As axe and fire removed the forest, the uncommon became the common and the opportunists of the forest became the denizens of the growing culture steppe. At West Heath Spa, the environmental record spans this period of forest clearance (Girling & Greig 1977; Girling 1989; Greig 1989). The pollen zone VIIa samples yield both pollen and beetle evidence of the importance of lime. At these levels the beetle fauna is dominated by species associated with woodland, containing, for example, the Eucnemid *Isorhipis melasoides*, now extinct in Britain, six species of Scolytid, three different Anobiids and several tree-dependent weevils including *Dryophthorus corticalis* and *Eremotes ater*. There is little indication of ground vegetation other than pondside plants and herbs (Girling 1989). Coinciding with and succeeding the elm decline in the pollen record is a significant change in the insect fauna. Tree-dependent species decrease, although dead wood inhabitants survive, perhaps because large trees were killed by ring barking by the first Neolithic farmers. There is an increase in species that feed on light-demanding plants in the ground flora, and groups of beetles associated with herbivore dung appear for the first time. In higher (more recent) levels, the beetle and plant record documents a move towards an open landscape with open woodland. The whole succession clearly illustrates the process of replacement of an established *Urwald* fauna by an opportunist one. Much of this open ground element, however, appears to have required a certain amount of continuity and stability of habit conditions. Perhaps in natural clearings maintained by large herbivores (Buckland & Edwards 1985) or by fungi, the open ground species merely increased their populations as the openings got bigger. Such continuity and stability is lacking in the modern ploughed and reseeded grasslands, which are better suited to a more limited group of eurytopes and species of edaphic steppe, progressively introduced through the last few millenia (cf. Hammond 1974). The earlier opportunists of the cleared woodland have themselves begun to require refuges. Areas of old grassland, particularly pasture woodland (Harding & Rose 1986) traditionally managed by grazing, provide succour for some of these open ground elements now in decline. For example, the dung beetle *Aphodius scrofa* (F.), identified from West Heath Spa, is exceedingly rare in Britain; Jessop (1986) records it from Strathclyde, Lancashire and Cornwall, and it is not common on the continent (Paulian 1959). It, like many of Britain's rarer dung beetles and the extinct *Aphodius quadriguttatus* (Hbst), *Onthophagus fracticornis* Preyss. and *O. nutans* (Er.) (Osborne 1989), has suffered to a great extent from the ploughing up and "improvement" of old pasture. The decline of these and other relatively thermophilous coprophages, which is parallelled on the Continent, may be at least partly climatic (Osborne 1982), but only one, *Aphodius zenkeri* Ger., appears to be expanding its range in the current phase of "Greenhouse" warming and this may be more due to an apparent preference for the dung of deer in scrubby woodland, where roe deer are now becoming more frequent (Skidmore, pers. comm.).

Increasingly tidy forestry has had the greatest impact upon the dead wood fauna, but loss of species is not restricted to the strictly saproxylic fauna. Several species which relied on the microclimate of forest, buffered against extremes, have also declined. The water beetle *Agabus wasastjernae* Sahl., listed by Osborne (1972) from pollen zone VIIb deposits at Worldsend, Salop, may have become extinct in England as a result of the decline in native pine forest (Buckland 1979). The species inhabits rotholes, acid pools and marshy areas in coniferous woodland and has recently been discovered by pitfall trapping in Speyside, Scotland (Owen *et al.* 1992). Similarly, fen woodland, perhaps the refuge for many species between the cleared Roman landscape and the medieval parklands, has virtually disappeared from the lowland landscape. This might account for the decline of other waterbeetles, including the once widespread *Hydroporus scalesianus* Steph. (Buckland 1979), although widespread wetland drainage must in part be to blame.

It is significant that the most recent old forest fauna from Britain comes from 3,000 year old Bronze Age peat at the base of Thorne Moor, South Yorkshire. The archaeological evidence increasingly suggests a largely, if often intermittently, managed landscape by the late Iron Age (see Chowne *et al.* 1986; Dinnin 1992; Osborne 1969, 1979; Robinson 1979, 1981). Over most of the countryside, woodland was reduced to that which was economically necessary for the maintenance of communities, a rough balance which continued to the early modern period. By the Roman period in lowland Britain, most fossil insect assemblages have a distinctive element typical of open landscapes, which makes them not dissimilar from rural faunas of the recent past before the widespread use of pesticides. The similarity between records from the Roman period and collections made earlier this century, before the advent of modern mechanised farming had reduced habitat diversity, is very striking. Research upon the entomology of the Holocene elsewhere in Europe is less advanced (but cf. Koponen & Nuorteva 1973), and there is a need for more intensive studies, even in Britain, where the post-Roman landscape and the localities which assured continuity to the surviving fragments of the *Urwald* fauna remain poorly known. However, by the turn of the first millenium, Europe, contrary to persisting popular belief, must have presented few "massed tree trunks of the primeval forest still waiting the axe" (Hoskins 1955). Secondary forest, different in species composition and with its essential habitat continuity broken, did not present the same aspect to the natural fauna.

Refuges for the *Urwaldrelikt*

The insect fauna of the forest, particularly the old wood element, largely lacks the ability to move through open country to disperse through the progressively greater gaps in habitat that were created by forest clearance. A distinction must be drawn between the primary colonisers of standing timber, which carry their own microflora to crack cellulose and lignin, and the processors of wood already beginning its progress back to the soil by fungal decay. Commensalism of the latter with commercial forestry is unlikely and their survival in conserved woodland is questionable where maintenance of that woodland involves management by coppicing. Wood pasture areas where the trees were managed by pollarding have more potential (Harding & Rose 1986). Pollarding allows the continuance of old trunks and it is perhaps ironic that many of Britain's *Urwaldrelikt* species, such as *Dryophthorus corticalis, Gastrallus immarginatus* and *Eucnemis capucina*, survive precariously in such heavily managed environments as Windsor Great Park, where their future rests on the few remaining ancient beeches and oaks. Many other species, like the Pselaphid *Batrisus formicarius* Aube, no longer found in Britain but recorded by Girling (1985) from a late Neolithic/early bronze trackway in the Somerset Levels, could, on the strength of their European distribution, survive in Windsor Forest today.

Although apparently suitable habitats do exist, stochastic factors, including a lack of continuity of suitable habitat within the range of existing populations, have prevented many species of limited dispersal potential from maintaining a foothold in Britain. Once they have been rendered extinct on the island, the Channel has proved to be a significant barrier to their re-immigration.

Although Windsor was a creation of the late Saxon kings, other refuges from forest clearance, like the New Forest, Epping and Sherwood, were largely the conception of England's greatest advocate of conservation, Duke William of Normandy (Rackham 1980). William I's lust for the chase was shared by both his nobles and his successors, and their hunting areas were (in theory) protected by draconian forest laws. Although some areas were disafforested by a frequently impecunious Crown, sufficient remained, sometimes neglected, to provide a corridor into the parks of Capability Brown and his successors. These hunting areas perpetuated abundant habitats which might otherwise have been lost several hundred years earlier. The aristocratic policies, however, were not directed towards overall conservation. In the medieval period, the term forest did not necessarily imply woodland, merely a place with deer, and even where woodland was present the clearance and sale of timber, mining and other use of resources took their toll upon the trees. However, in some at least, sufficient dead and dying timber must have remained to allow the survival of fragments of an insect fauna which three thousand years before had been commonplace. The successors of these private chases of the nobility are often now in the public domain. Parks, and those great houses with their grounds held by civic or charitable bodies, have inherited William's mantle but with the difference that public use is often encouraged. Increased access means increased management. Old trees are felled on the grounds of safety or tidiness and a community established over several hundreds of years is lost in a matter of hours. Local extinction is the prelude to total extinction. The *Urwald* forests cannot be recreated but the entomologist should maintain at least a centennial, if not a millenial perspective on conservation issues and take steps to ensure habitat continuity, a point only recently recognised by conservation bodies (Speight 1989; Warren & Key 1991).

Post-*Urwald* introductions

It has been argued that the destruction of the *Urwald* has led to increased variety of habitat, and hence species diversity, but the consequences of living on an island are that losses are only balanced by rare events of random dispersal and, more significantly, by human dispersal. Few of the later increments to the British fauna, perhaps with the exceptions of *Micropeplus tesserula* Curt. and the Kerry slug *Geomalacus maculosus* Allm., would require conservation. Identifying recent introductions is in itself fraught with difficulties. Duffy (1953, 1968) presumed both the longhorn beetles *Pyrrhidium sanguineum* L. and *Cerambyx cerdo* to be recent, casual introductions, despite the former's occurrence in the old parkland at Moccas, Herefordshire, and the latter in "bog oak". Subsequently reanalysis of existing data and further fossil records (Buckland 1981b; Harding & Plant 1978) have established their native status. The occurrence of the largely Mediterranean longhorn beetle *Hesperophanes fasciculatus* Fald. in second century Roman Alcester, Warwickshire (Osborne 1971), is interpreted as an accidental introduction with imported timber, but further studies of fossil forest insect faunas might add it to the Holocene *Urwald* casualty list. *Dermestes laniarius* Ill. is a member of a genus which has become cosmopolitan as pests of stored products; Osborne (1969, 1989) regards its fossil record from the Late Bronze Age Wilsford Shaft as an early casual introduction. Buckland (1979), however, highlights the xerophilous nature of the species and its preference for sparsely vegetated open ground. *D. laniarius* could have been a native open ground species, surviving in open refuges from the forest, which, having thrived during the earlier stages of forest clearance as woodland gave way to short grazed grassland, has latterly become extinct; only further fossil occurrences can resolve this debate. If these species prove to be native they will be added to that list of insects for whom conservation is too late. It is the ecological opportunists, evolved to exploit transient habitats and including many taxa once restricted to birds' nests and rodents' stores, for whom man has provided a massive habitat expansion and an extensive transport facility (Sadler 1991). Significantly, these anthropochores and synanthropes first appear in Britain during the Roman period (Buckland 1981a), although changing patterns of storage of everything from hay (Buckland *et al.* 1991) to biscuits have led to changes in species composition in these faunas within the last century.

The effects of climatic change

Whilst habitat destruction is seen as the over-riding influence on changes within the Holocene, climatic change, which might seem the most obvious explanation for extinctions, can account for the demise of only a few species. Girling (1984a) describes early Neolithic insect faunas from the Somerset Levels, some 5,000 years old, which suggest a climate slightly warmer than at present. The assemblages contain four wetland beetle species which in Britain are known only from archaeological deposits. Of these, the European distribution of the marshland ground beetle *Chlaenius sulcicollis* (Payk.) closely follows the 17°C mean July isotherm, and it is rare in areas with an oceanic climate. Likewise, the carabid *Oodes gracilis* Vil. is also highly thermophilous (Lindroth 1943). *Anthicus gracilis* (Panz.), apparently associated with reed litter, is recorded from several sites in the Somerset Levels (Girling 1976, 1984a) and from early to mid-Holocene deposits at Girton, Notts (Dinnin 1992); however, from its present European distribution, it would appear that this species could survive in southern Britain today. The Cucujid *Airaphilus elongatus* Gyll., also recorded in Britain during the Ipswichian Interglacial, appears to be widespread in late glacial and mid Holocene contexts (Coope & Brophy 1972; Shotton & Coope 1983; Osborne 1972, 1980; Girling 1984a); the most recent find is from a late fourth century well at Alcester in Warwickshire (Osborne 1971, 1974). The species, an inhabitant of flooded meadows and natural hay refuse, has a scattered continental distribution, the result perhaps of collecting bias rather than its true distribution, and it may have simply been overlooked in this country (Osborne 1972). Alternatively it may have become extinct since the Roman period. The early post-medieval Little Ice Age saw the most significant climatic deterioration since the end of the last glaciation (Grove 1988), and it is this which seems most likely to have precipitated the extinction of *A. elongatus*, if not of the three other species. Girling (1984b) cites the whirligig beetle *Gyrinus colymbus* Er., only known in this country from medieval deposits in Leicester, as another likely victim of the Little Ice Age. Once rendered extinct in Britain, these species could have been prevented from recolonising from the continent during the twentieth century climatic amelioration by the insurmountable barrier of the Channel. The impact of the Little Ice Age combined with habitat destruction during and after this period may also be reflected in the distributions of the death watch beetle *Xestobium rufovillosum* (Buckland 1975), the ground beetle *Odocantha melanura* (L.) and the greater silver diving beetle *Hydrophilus piceus* (L.) (Dinnin 1991), which the fossil records indicate were once more widespread.

Maintaining habitat continuity in future

Losses and severe retractions in distribution have occurred mainly where habitats have been lost. A measure of habitat continuity (a Quaternary perspective precludes the use of the term permanence) is essential. Unfortunately, the maintenance of the *status quo* within existing nature reserves cannot provide the only answer. Whether such populations are liable to extinction by the postulated mechanism of genetic drift is open to question, but one legacy of the MacArthur-Wilson model of island biogeography (MacArthur & Wilson 1967) is a recognition of the precarious nature of survival in an isolated locality.

This point is illustrated by recent work on South Uist in the Outer Hebrides. Although once at least partially covered by mixed woodland (Fossitt 1990; Bennett *et al.* 1990; Wilkins 1984, but see also Birks & Madsen 1979), the islands are now, with the exception of modern plantations and a handful of localised scrub thickets, almost entirely treeless. Analysis of fossil insect assemblages from a woody peat from a site on the southern end of South Uist has yielded several beetle species associated with trees no longer recorded in the islands (Dinnin 1992). Modern collecting in a remnant of rowan, birch, willow and juniper scrub, protected from grazing sheep, on a small island in Loch Druidibeg SSSI failed to recover modern specimens of these beetles but did find three old woodland species, the woodboring weevils *Mesites tardii* (Curtis) and *Caulotrupodes aeneopiceus* (Boh.), and the Elaterid *Melanotus erythropus* (Gmel.). These occurred in the rotting branches of large derelict coppiced rowan and birch stools. The former two species have previously only been recorded from drift wood on the Outer Hebrides, whilst the latter is not included on the islands' faunal list (Waterston 1981). Although *M. tardii* has been presumed to be an introduction, the fossil record may confirm it as native to the islands. The small size of the island, less than 0.5 hectare, holds out some hope for further discoveries, yet the conservation of this isolated woodland beetle fauna necessitates the careful management of the remnant habitat. The single rowan tree, host to all three beetles, requires recoppicing in order to ensure habitat continuity. Without this measure the tree will eventually die, and like the pollards of Windsor, take its lichen and invertebrate community with it.

Conclusion

The last 5,000 years have seen the progressive impoverishment of the British insect fauna, primarily as the result of anthropogenic habitat destruction, combined with subtle climatic change. The transformation of Britain's landscape from one of primary undisturbed forest to its present heavily managed and relatively unwooded state has resulted in the severe decline, and in some cases extinction, of many woodland taxa. Many species survive only in a handful of sites, sometimes only a handful of trees, that are relicts of former land use patterns. Today's modern forestry management provides few suitable habitats for these woodland specialists and it has been shown that even where the right conditions exist another over-riding aspect, that of habitat continuity, is required to ensure their survival (Harding & Alexander 1993).

It is regrettable that the amount of research on Holocene fossil insect faunas is still insufficient to provide detailed histories of particular groups or particular localities, perspectives which are fundamental to the conservation of the surviving faunas. The creation of a fossil insect data base, containing habitat information, lists of fossil occurrences, sites and dates has greatly improved the ease of comparison between sites and proved a useful tool for analysis. Deposits spanning the post Roman period to the present are required to clarify the relative impacts of climatic change, for example The Little Ice Age, and human activity on the native fauna. Analysis of material of this age could help identify vulnerable species and have important implications for the management of nature reserves. Unfortunately, the deposits which might contain this information are themselves under threat from drainage and lowering of water tables. The destruction of these waterlogged deposits will result in the loss of a valuable and irreplaceable repository of palaeoecological information for archaeologists, geographers, Quaternary scientists and conservationists.

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SAPROXYLIC INVERTEBRATES - THE EUROPEAN CONTEXT

I F G McLean, English Nature, Northminster House, Peterborough PE1 1UA.

M C D Speight, Research Branch, National Parks and Wildlife Service, 51 Saint Stephen's Green, Dublin 2, Eire.

Preamble

Windsor-Forest

Thy forests, Windsor! and thy green retreats,
At once the Monarch's and the Muse's seats,
....
While by our oaks the precious loads are born,
And realms commanded which those trees adorn.

Alexander Pope (1713)

When Pope wrote these lines on Britain's premier site for saproxylic fauna, he recognised the importance of Royalty in maintaining the character of forests used for hunting and other noble pastimes. Although Pope was unaware of the significance of ancient oaks for saproxylic invertebrates, nevertheless, he unknowingly identified the principal factor which enabled these highly specialised animals to survive in Britain and some other European countries. By isolating substantial areas of forests or parklands from changes in land use, royal families and nobility initiated the first conservation measures for saproxylic invertebrates. These measures were of course incidental to their primary interests in growing large timber trees, hunting deer and other game, and creating attractive settings for their other recreational pursuits.

By ensuring greater abundance and continuity of ancient trees, forests and deer parks, the survival of many saproxylic invertebrates was assured in places such as the New Forest and Windsor Forest, England, the Forest of Fontainebleau, France, and some sites in the vicinity of Vienna, Austria. Although the survival of saproxylics until now has been by chance, their future depends upon their distinctive needs becoming recognised more widely and their remaining sites receiving better protection and, where appropriate, positive management (Key & Ball 1993; Kirby 1992). The conservation problems that we face in Great Britain are, as this paper will describe, mirrored elsewhere in Europe.

Introduction

Buckland & Dinnin (1993) summarise the changes which are known to have taken place in the status and distribution of saproxylic invertebrates over the last 10,000 years in Europe. The history of human treatment of forests in Europe has been of extensive tree clearance for farming and intensive management of forests to supply timber of various sizes. Thus the small number of forests that remain have had the great majority, or even all, of their trees removed at "middle age", well before they have reached their splendid biological maturity, when the increase of decaying wood and the presence of fungi allow the establishment of saproxylic invertebrate populations.

The major difficulty in reviewing the current status and distribution of saproxylic invertebrates in Europe is the lack of recent information about many forests and pasture woodlands of known or potential interest. The small number of entomologists, compared with ornithologists or botanists, is compounded by the fact that few entomologists study groups containing saproxylic species. The activities of entomologists wishing to study saproxylic invertebrates are also hindered by taxonomic impediments, namely the lack of well-illustrated keys to enable accurate identification of adults, let alone the early stages, of these often elusive species. The difficulties of finding many saproxylic invertebrates within any reasonable timescale is the consequence of several factors. First, they typically have long periods of development (sometimes several years), when they are hidden within decaying timber as larvae or pupae, which are difficult (or impossible) to identify. Secondly, they cannot be found as larvae or pupae without at least disrupting, if not destroying, their fragile habitat. Thirdly, they are characteristically found in only a proportion of potentially suitable trees, which in turn are only a small fraction of the total tree population in most forests. Fourthly, they usually have only short adult lifespans, when they are often hard to find (with the exception of those insects that feed at flowers). These factors have resulted in a lack of knowledge of threatened species and significant sites, thereby limiting awareness of the conservation needs of this fauna. The absence of popular guides has resulted in a poor (or non-existent) public profile for these species. To conclude this catalogue of problems, there is no organisation with the responsibility and resources capable of coordinating and funding surveys, receiving information from entomologists throughout Europe, and then collating and summarising this for ecological, conservation and educational purposes.

Speight (1989a) reviewed the status and conservation of saproxylic invertebrates throughout Europe, and Warren & Key (1991) gave an account of the conservation of woodland insects, contrasting the hazards faced by early and late successional stage species. There is no general descriptive account of saproxylic invertebrates throughout Europe. The treatment of the status of species in taxonomic texts is variable in quality, and usually has been compiled for only one country or a few adjacent countries. Many saproxylic species are cited in national Red Data Book lists, though the different standards in coverage and state of knowledge make detailed comparison and interpretation of these accounts difficult.

The size of the saproxylic fauna in Great Britain in relation to continental Europe

The number of saproxylic invertebrates in Europe and their distribution within the major orders and their constituent families is not accurately known; a comprehensive checklist of the European species would enable faunal and biogeographic comparisons to be made between countries. Thus the following examples can only be a preliminary assessment.

Some recent key works and catalogues have been consulted to derive estimates of numbers of species in selected groups of saproxylic beetles and flies (Tables 1 & 2). Great Britain has a smaller saproxylic invertebrate fauna than Scandinavian or Central European countries, though it is on a par with Belgium or Denmark. We have a smaller proportion of warmth-demanding species in groups such as Buprestidae, but a higher proportion of species associated with cool and damp conditions in groups such as Mycetophilidae.

Table 1 Examples of selected families of saproxylic beetles, total known species in Great Britain, Europe and the world. (Note: Some Cerambycidae and Buprestidae are not saproxylic as the larvae feed on other plant tissues).
[Sources: Bílý 1982b; Bílý & Mehl 1989; Lucht *in* Freude, Harde & Lohse 1987; Zahradník 1985]

Cerambycidae	World	20,000 plus	
	Central Europe	250	100%
	Great Britain	62	25%
Buprestidae	World	12,000 plus	
	Central Europe	100	100%
	Great Britain	12	12%
Lucanidae	World	930	
	Central Europe	6	100%
	Great Britain	4	67%
Elateridae: *Ampedus*	Central Europe	27	100%
	Great Britain	14	52%

Table 2 Examples of selected families of saproxylic Diptera, total known species in Great Britain, Europe and the Palaearctic.
[Sources: Chandler (GB Mycetophilidae *pers. comm.*); Soós & Papp 1988a, 1988b, 1989]

Mycetophilidae	Palaearctic	1012	
	Europe	759	100%
	Great Britain	523	69%
Pachyneuridae	Palaearctic	2	
	Europe	1	100%
	Great Britain	0	0%
Xylophagidae	Palaearctic	13	
	Europe	4	100%
	Great Britain	4	100%
Xylomyiidae	Palaearctic	26	
	Europe	7	100%
	Great Britain	3	43%
Syrphidae	Palaearctic	287	
	Europe	127	100%
	Great Britain	39	31%

The number of saproxylic invertebrates is smaller in Britain than, for example, in Central Europe because of our relatively isolated island position since the last glaciation (preventing some species from recolonising) and because of species losses due to forest clearance and intensive woodland management. There is evidence (Speight 1988, 1989b) that the saproxylics associated with the major boughs and trunks of large, long-lived trees like oak and beech, have been most adversely affected by such habitat loss and change. At present there are insufficient data to enable many significant comparisons to be made between sites in Britain and continental Europe in terms of their species richness for the same saproxylic groups. Thus, it is unclear whether the proportion of species found at the best sites in Great Britain is equivalent to the percentages for families given in Tables 1 & 2 in comparison with the best sites in continental Europe.

Biological characteristics of European saproxylic invertebrates

Beetles and flies dominate the European saproxylic fauna, with some species in other groups such as parasitic wasps, moths, bugs, sawflies and spiders. These insects typically have similar life cycles, in that the larvae feed within a patch of habitat selected by their mother, and the adults emerge and disperse to feed at flowers and to mate, the females then seeking out oviposition sites.

The mobility and dispersal potential of these invertebrates remains largely a matter of conjecture, though it is likely to be poorest in flightless groups (e.g. certain beetles). Even within winged insect groups the capacity for long distance dispersal is likely to be very limited. Saproxylic invertebrates evolved under conditions where there was almost continuous forest cover throughout the western Palaearctic, though the distribution of the different forest types has changed markedly during the Quaternary due to the alternation of glacial and interglacial periods (Buckland & Dinnin 1993). Examination of the few remaining areas of pristine forest in Eastern Europe indicates that here a very high proportion of trees is mature or post mature. Under circumstances where saproxylic invertebrates dispersing from a tree are likely to encounter another potentially suitable tree within a few metres, there is presumably little selection pressure to evolve the ability for effective long distance dispersal. As old trees became scarcer there would have been some advantage for species developing improved abilities for long-distance dispersal; whether the relatively rapid (in evolutionary timescales) clearance allowed such development of improved dispersal is unknown. Moreover, in the modern European landscape, where ancient forests remain only as isolated fragments, the pendulum has swung again. This is because there is likely to be no strong selection in favour of long distance dispersal, as almost all successful colonists will be moving within forest patches rather than moving between forests that are tens or hundreds of kilometres apart (see Figures 3 & 4). However, there are indications that when corridors of woodland of almost any sort link forests which may be kilometres apart, the saproxylics will use these corridors to move between sites (Speight, unpublished information from Malaise trap studies in gallery woodland along the banks of the River Loire, France).

Among saproxylic invertebrates there exist a range of adaptations for exploiting different niches associated with ancient trees. Within decaying wood itself they may feed in large trunks or in small twigs, depending on the invertebrate species; under bark, in rot holes or within sap runs and they may attack other saproxylic invertebrates (as predators or parasitoids), or consume fungal hyphae or fruiting bodies. In general, it appears that those species which exploit small pieces of dead wood (directly or indirectly) are more widespread and less threatened than those specialising in habitats associated with giant, veteran trees.

Biogeography of European saproxylic invertebrates and of important sites

Due to lack of distributional data, the biogeographical patterns of saproxylic invertebrates in Europe are not well defined. They are best understood for the more conspicuous beetles (Buprestidae, Carabidae, Cerambycidae, Cetoniidae and Elateridae), which have had more extensive recording and more publications in the entomological literature. There are two principal (and partly correlated) factors which determine the natural distribution patterns of saproxylic invertebrates in Europe. They are climate and the distribution of host tree or shrub species (or their associated fungi). The original natural distribution patterns have been extensively eroded by habitat loss, so only the commoner, less specialised saproxylic invertebrates show relatively intact ranges today.

Within each of the major European biogeographical zones (e.g. Boreal/Eurosiberian, Eurasian, Mediterranean) some species may be naturally restricted by climate or by the distribution of their hosts, particularly within the diverse assemblage of Mediterranean species. A few others may have evolved as island endemics, for example, some Buprestidae known only from Crete (Bílý 1982a).

Speight (1989a) compiled a list of 167 European forests and pasture woodlands identified as being of potential international importance for their saproxylic invertebrate fauna. This was compiled via correspondence with leading specialists throughout Europe. These specialists were asked to identify important sites using a list of 33 saproxylic insect species. Further sites were added by a second round of consultation when contributors were asked to identify additional forests which, on the best available information, were likely to contain saproxylic faunas as diverse as those already listed (Speight 1989a). Although this is a preliminary list, it represents the best available summary of the most important known sites, and it forms the basis of the description and analyses in this section. The location of 165 out of 167 of these sites is shown on the accompanying map (Figure 1). The absence of sites from some countries or areas reflects the lack of information (marked on the map), while for others (including Britain) this indicates the impoverishment which has occurred.

The distribution of these sites by country (Figure 2) shows that three countries, namely Sweden, France and Austria, contain half of the sites listed in the review by Speight (1989a). Eastern Europe was outside the scope of this review, but Poland, Czechoslovakia, Yugoslavia and other Balkan countries are known to have important sites for saproxylic invertebrates. A review of relevant sites in these countries is urgently required as a first step towards gaining recognition, protection and appropriate management for what may be some of the most important sites still remaining in Europe.

Although there are many other sites which are known to support significant assemblages of saproxylic invertebrates, the most threatened species are now largely concentrated within the forests and pasture woodlands mapped on Figure 1. Thus, the distances between the sites of greatest known or potential importance are an indication of the degree of isolation of the remaining populations from each other. On Figure 3 the distances from 165 of the 167 sites to its nearest neighbour are grouped into 4 categories.

Very few sites are less than 10 kilometres from the nearest forest of equivalent status. It seems very unlikely that many saproxylic invertebrates can colonise sites more than 10 kilometres distant, though information on the dispersal potential of saproxylic invertebrates is lacking at present. Because of their origins and evolutionary history, most saproxylics are unlikely to be adapted to disperse across non-forested terrain as well as invertebrates associated with ephemeral or early successional biotopes. A high proportion of sites are separated by more than 50 kilometres, and in the absence of suitable corridors or "stepping stones" these isolated sites must experience little faunal interchange. Therefore, a high proportion of populations of the most threatened species are likely to be completely isolated from conspecific colonies. The loss of any rare or threatened saproxylic species from a forest or pasture woodland site is therefore most unlikely to be made good by a subsequent recolonisation. In these circumstances the highest standards of management are required for internationally important sites if their saproxylic faunas are to remain intact for future generations to study and enjoy.

Comparison of five countries for the same nearest neighbour analysis (Figure 4) indicates that there is considerable variation in the degree of aggregation of sites. Austria has a substantial proportion of important saproxylic sites with their nearest neighbour less than 10 kilometres away (largely the result of nine sites being located in and around Vienna), while for Spain and Greece the majority of sites are separated by more than 100 kilometres. Even this simple analysis, based on a preliminary review of the most important European sites, suggests that there are few countries where sites are sufficiently close to allow the possibility of dispersal between sites.

Although the most important British sites are better documented than many in other European countries, in some cases they remain threatened through continuing losses of existing ancient trees, as well as lacking of cohorts of suitable trees to form future generations of old trees. In many cases, populations of the rarest and most threatened saproxylic species are likely to be small in Britain, and this may also be true for even the largest sites remaining in Western Europe. This is because only a small proportion of ancient trees will support niches for the most specialised species. The chances of local extinction from sites must be considerable in these circumstances.

Conservation priorities for European saproxylic invertebrates

European saproxylic invertebrates are threatened by continuing losses of ancient trees and their associated saproxylic niches (see also Harding & Alexander (1993) and Key & Ball (1993)). Both ancient living trees and standing or fallen dead wood are regarded as unsightly, unsafe and unwelcome by many foresters and managers of pasture woodland. Few of those working in, or supporting, wildlife conservation are aware of the special problems faced by saproxylic invertebrates. The limited number of specialists who can find and identify saproxylic invertebrates, means that many sites are poorly documented or are even unknown, and may be destroyed before their full potential is recognised.

These threats, combined with the practical problems identified in the introduction to this paper, must be addressed as a matter of urgency. If these issues are to be tackled at the European scale, then a coordinated approach to make best use of limited expertise and resources is essential. The suggestions made here are intended to contribute to the debate over how progress can be made. The Council of Europe could be approached to develop the ideas outlined here, building on their previous support for the work published by Speight (1989a).

An increasingly serious threat to saproxylics has arisen recently from a quite different origin. There have been well-meaning efforts of international bodies, essentially the Council of Europe in Strasbourg and the European Commission in Brussels, to gain an overview of European conservation and coordinate conservation activities. A European classification system for terrestrial and freshwater habitats has been developed, which has been incorporated within the EC Habitats Directive for selecting candidate sites for protection. This classification is part of the EC Corine database (see Anonymous 1991), which purports to list all sites of international significance for wildlife conservation within the European Community. Furthermore, discussion is now underway to extend the use of this classification system throughout Europe to the Urals. Far from helping to identify and catalogue sites important for saproxylics, use of this classification system is decreasing the likelihood that these sites will be protected because overmature trees and ancient forests are not even mentioned or differentiated as notable habitat types. Similarly, in the lists of organisms intended to help identify important examples of each habitat type, saproxylics hardly appear. A handful of insects, no fungi and no lichens are listed. Therefore, this classification of European habitats ignores saproxylics and their habitats so they are not recognised as worthy of protection. This serious flaw in the system must be rectified quickly.

Figure 1 The location of 167 forest and pasture woodland sites of potential international importance for saproxylic invertebrates.

Figure 2 The distribution by country of 167 forest and pasture woodland sites of potential international importance for saproxylic invertebrates.

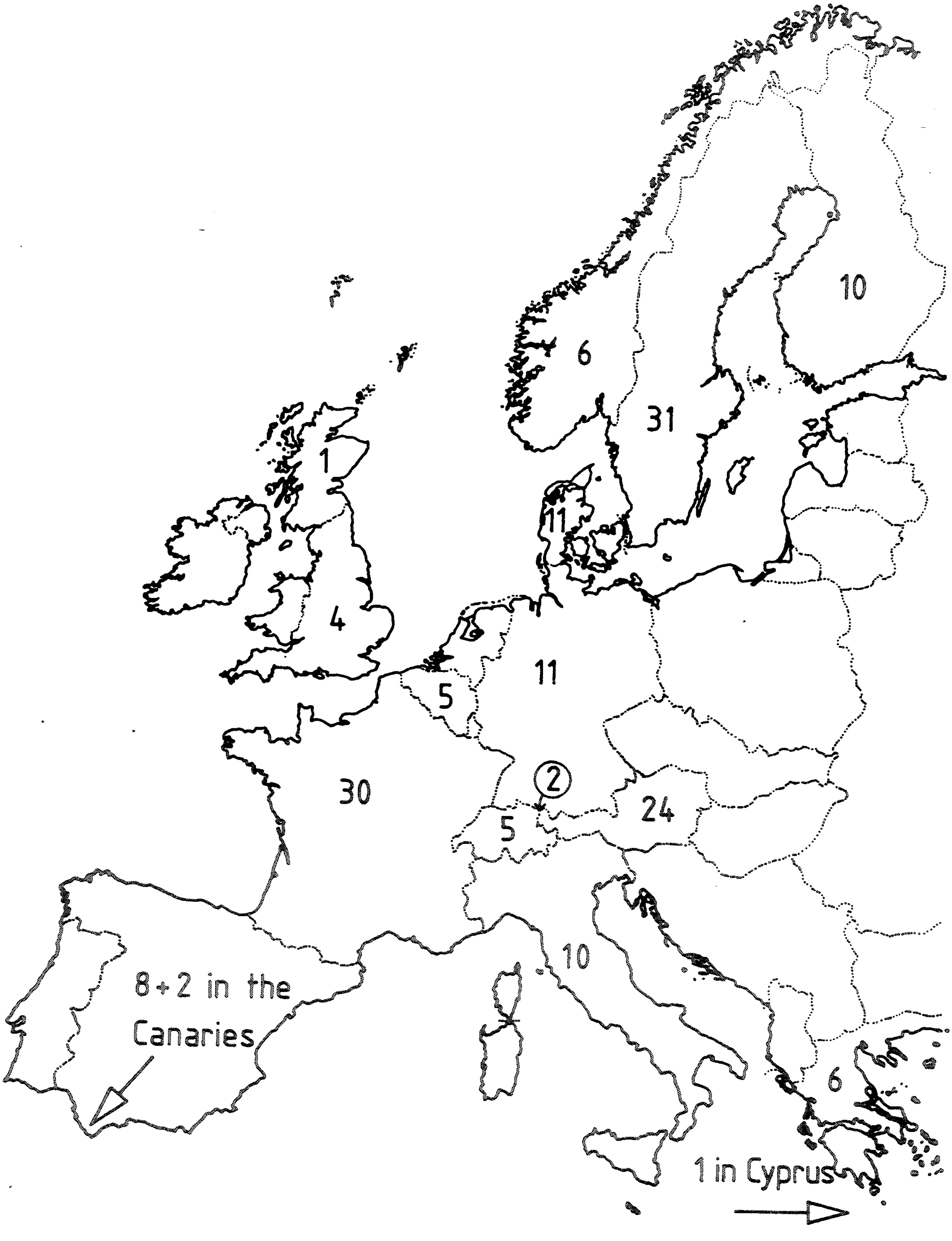


Figure 3 Nearest neighbour analysis for 167 forest and pasture woodland sites of potential international importance for saproxylic invertebrates.

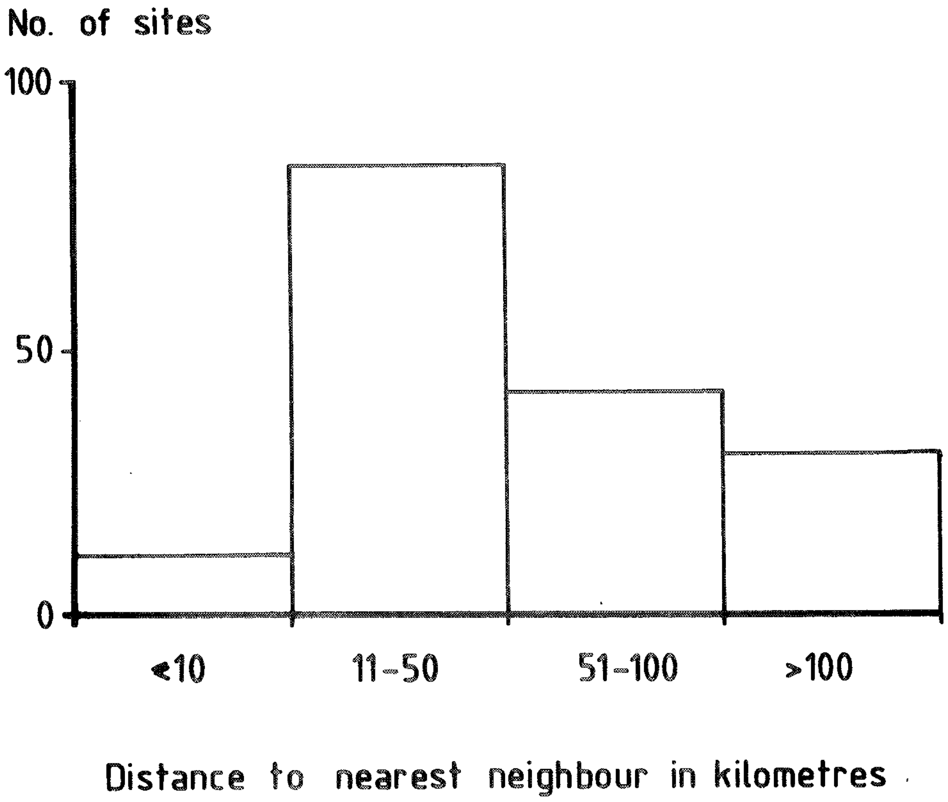
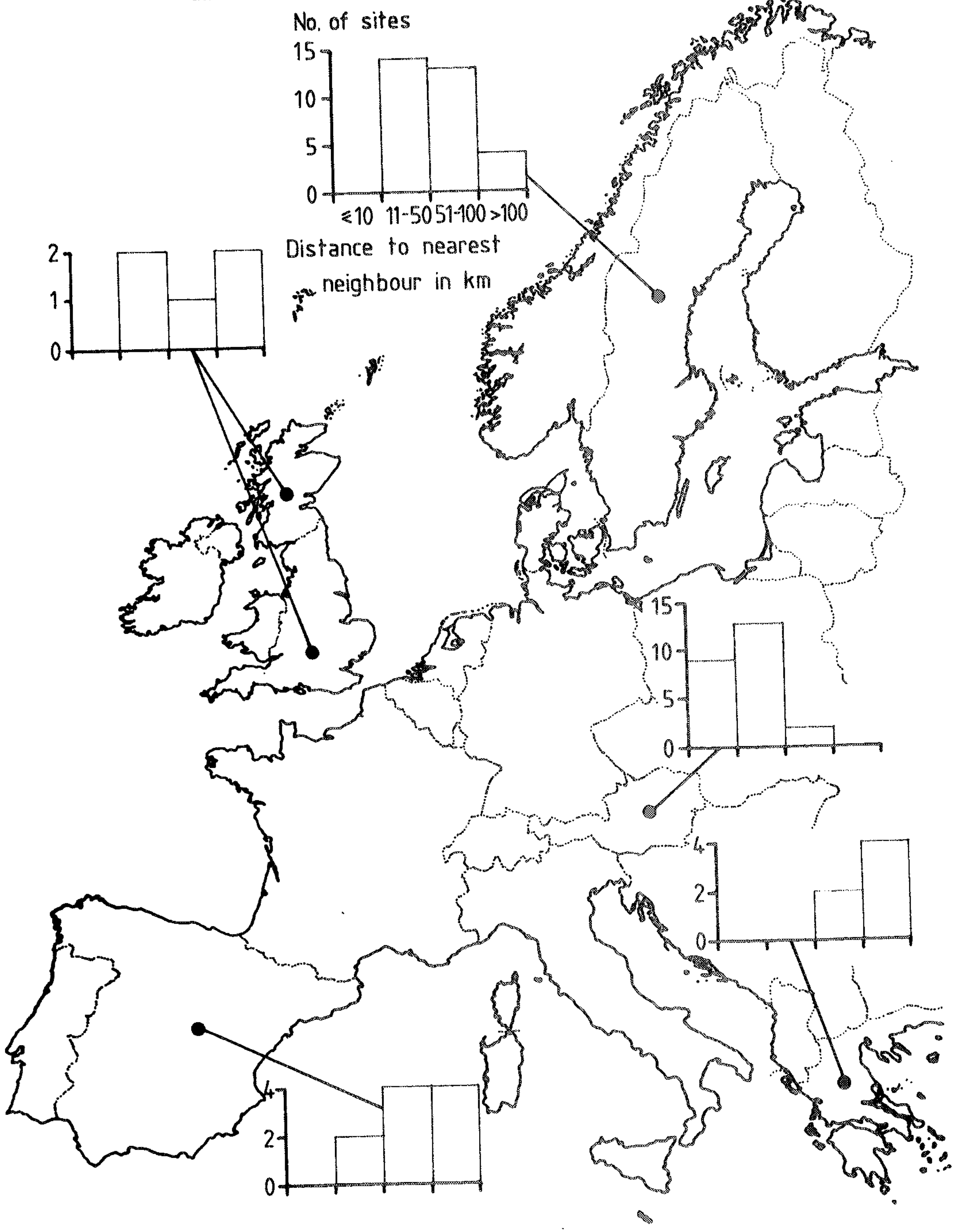


Figure 4 Nearest neighbour analysis for forest and pasture woodland sites of potential international importance for saproxylic invertebrates for five European countries.



A checklist of European saproxylic invertebrates is needed urgently in order to define which species are involved and to enable information on the status, distribution, ecology and conservation requirements to be compiled and used for conservation purposes. The checklist would be a first step to production of a European Red Data Book for saproxylics, in turn leading to international action plans to conserve the most threatened species and compilation of a realistic list of saproxylics for use in, for example, the EC Habitats Directive and Corine site evaluation processes.

Alongside the need for an overview of threatened saproxylic species is the requirement for information on sites with the largest assemblages of saproxylic invertebrates. Compilation of a register of the most significant sites would build on the work by Speight (1989a) and enable action to be concentrated where it is needed most. The species and site approaches should be combined in one integrated operation, preferably using a single database. At the same time, the whole question of how to integrate saproxylic habitats into the European habitats classification system must be addressed, to ensure recognition of important sites for saproxylics. A register of sites would be the first step towards informing those responsible for the management of these sites of their conservation interest. The next step would be preparation of management plans for each site of international importance, aimed at sustaining and enhancing the saproxylic fauna. The review by Harding & Rose (1986) and the work of the JNCC Invertebrate Site Register in Great Britain are illustrative of the approach required for documenting and managing the necessary information.

Similar conservation programmes are needed for other wildlife dependent upon continuity of ancient trees, notably lower plants, lichens and fungi. Recent proposals for management of Swiss forests by Broggi & Willi (1993) are relevant in this context. There, the need to adopt management procedures, appropriate for saproxylic species, is recognised for all protected woodland. A minimum of 3 ha in each 100 ha is recommended to be set aside for trees to live out their natural life span, in both nature reserves and commercial forests alike.

More information is needed on many saproxylic invertebrates and their sites. Many forests and pasture woodlands in Europe have not even been investigated for their saproxylic fauna. This applies particularly to the Mediterranean region. An international collaborative programme to survey the most promising candidate sites is needed to make best use of the limited available expertise. It is encouraging to note the recent initiative in France (led by Jean-Marie Luce, Ecology Laboratory, M.N.H.N. Brunoy) which seeks detailed information on the distribution of saproxylic Coleoptera from amateur entomologists. This is a model for what should be established for saproxylic invertebrates throughout Europe. In the longer term, more training and investment in invertebrate taxonomy is required to enable a new generation of user-friendly identification guides to be produced for use by professional ecologists and amateur naturalists.

If the plight of saproxylic invertebrates is to become more widely recognised then more publicity is essential. This should draw attention to the threats faced by this fauna, aim to increase sympathetic attention by demonstrating the colourful and attractive nature of many species, and indicate what is required for the survival of species and sites. Good colour photographs of saproxylic species in their natural environment are needed for publications and interpretive displays. The ancient trees themselves have considerable value for publicity and arousing public sympathy in their own right, both as wildlife and for their aesthetic appeal. Such approaches have the potential to capture the attention of many more people than have been concerned about invertebrate conservation in the past, and therefore should be welcomed as ways of creating better understanding for this hitherto largely neglected area of wildlife conservation.

Finally, it needs to be stressed that the fate of saproxylic organisms should not be perceived as being of concern only to entomologists and other specialists. They are the means whereby nutrients in the woody parts of trees are recycled in natural forests. No forest nature reserve can be said to represent and conserve forest ecosystems without characteristic assemblages of saproxylic species. It is a salutary thought that before humans removed trees, all wood was recycled by large numbers of saproxylics. Their current impoverishment contrasts sadly with their past richness and abundance, and demonstrates their true conservation significance as part of Europe's natural heritage.

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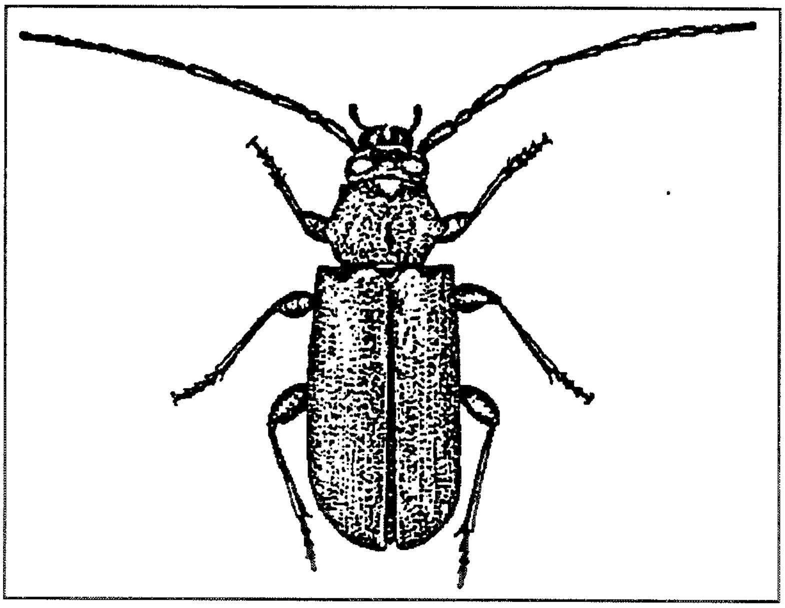

A QUANTITATIVE STUDY OF THE FAUNA OF SMALL DEAD AND DYING WOOD IN LIVING TREES IN WYTHAM WOODS, NEAR OXFORD

Kitty Paviour-Smith* and C A Elbourn**, Dept of Zoology (Animal Ecology Research Group), Oxford University, South Parks Road, Oxford

Introduction

The conservation of dead wood sites in Wytham Woods, near Oxford, was first actively promoted by Charles Elton. He had realised, in the early 1950s, that this so-called 'derelict' woodland (recently acquired by the University) was being depleted of suitable habitats for the rich fauna of dead and dying wood and for the special fauna of wood-inhabiting fungi (Paviour-Smith 1971), during the process of cleaning-up and replanting which had been embarked upon after the Second World War. These were habitats in which he had a special interest in his studies of the patterns of animal communities, which he was building up as the Wytham Ecological Survey (Elton 1966). The survey is however concerned mainly with the larger invertebrates, mostly of large dead wood mainly on the ground.

Elton's interest in this habitat inspired most of the detailed quantitative studies of dead wood invertebrates which have been done in Wytham Woods: Beaver's (1967a, b) elm bark beetle study, Fager's (1968) study of fallen small oak branches and oak box artifacts on the ground, Larkin & Elbourn's (1964) study of dead oak branches in trees and boxes of oak sawdust attached to trees, and similar oak boxes up trees by Elbourn (1970). Larkin & Elbourn (1964) gave a vivid description of the varied nature of natural dead branches as a habitat for animals. They also gave a species list and, for each order, the mean number of organisms per sample and a grand mean (a third of the density of organisms found in Fager's ground logs). However, they gave no frequency or abundance data at the species level. Elbourn (1970) reported on only the commonest 12 species and a few higher taxa, but mites were omitted from both these studies of aerial dead wood in Wytham Woods.

When dead wood is being conserved, on the ground or in trees, we ought to know which invertebrates are actually, as opposed to potentially, being conserved. A picture of the regular fauna is needed, not just of the rarities, since the status of both rare and common species may change because of alterations in habitat management, competition with introduced species or because of long-term climatic changes.

The main purpose of this paper is to record the list of invertebrate species found in a study of aerial dead wood on oak, ash, sycamore and hawthorn in a partly ancient woodland (Gibson 1988) in southern Britain 23 years ago, with the frequency and abundance of each species. It represents a solid body of data on what was actually being conserved in 1969, for future comparisons and the monitoring of change. We discuss in more detail 'scarceness' or 'relative rarity' e.g. in a fungus beetle, *Cis vestitus*; the distribution of a 'real rarity' (the wood-feeding larva of the mordellid beetle, *Tomoxia bucephala*) which may be on the edge of its range; and the changes in status revealed in two species of lathridiid beetles (six spp. found) when long-term records are kept for one area, as in the Wytham Ecological Survey.

Footnote:

* Work done partly in Hope Dept of Entomology, University Museum, Oxford University. Present address: 89 Bainton Road, Oxford, OX2 7AG.

** Present address: Forestry Dept, CAB International, Wallingford, Oxon, OX10 8DE.

Table 1 Tree species and amounts of dead/dying wood on them on the 1.2 ha study area, Holly Hill Copse (part of Wytham Woods), March-May 1968.

			All wood		Dead/dying wood		
	No. of canopy trees	No. in understorey > 1 cm diam	Vol. m^3	Vol. as % of total	Vol. m^3	Vol. as % of total	% dead of all wood in each species
Oak *Quercus robur* L. introgressed with *petraea* (Mattuschka) Liebl.	29	11	107.36	32.7	29.45	55.8	27.6
Sycamore *Acer pseudoplatanus* L.	65	1872	140.52	42.9	11.40	21.6	8.1
Ash *Fraxinus excelsior* L.	7	3266	54.51	16.6	8.43	16.0	15.5
Hawthorn *Craetaegus monogyna* Jacq.	6	75	6.67	2.0	1.76	3.3	30.5
Beech *Fagus sylvatica* L.	1	7	14.57	4.4	0.73	1.4	5.0
Field maple *Acer campestre* L.	2	62	1.57	0.5	0.22	0.4	14.0
Scots pine *Pinus sylvestris* L.	1	0	0.60	0.2	0.21	0.4	35.0
Elder *Sambucus nigra* L.	12	22	0.34	0.1	0.20	0.4	59.0
Spindle *Euonymus europaeus* L.		106					
Hazel *Corylus avellana* L.		38					
Willow *Salix* sp.		26					
Dogwood *Thelycrania sanguinea* (L.) Fourr.		14	1.82	0.6	0.42	0.8	23.0
Birch *Betula pendula* Roth		7					
Wayfaring tree *Viburnum lantana* L.		2					
Horse chestnut *Aesculus hippocastanum* L.		1					
Total (all species):	123	5509	327.96		52.82		

By the present study we hoped to throw new light on the fauna of this habitat by sampling quantitatively the most abundant kinds of *small* dead wood in several species of trees at different heights. In the process we did indeed reveal new facts about the behaviour and habitat distribution of the commonest two spider species found (Paviour-Smith & Elbourn 1978).

Methods

A relatively undisturbed area of 1.2 ha in the oak-ash-sycamore woodland of Holly Hill Copse was chosen in 1968 (National Grid Reference SP 461086 - 461087). This was fifteen years after myxomatosis had eliminated rabbits on the Wytham estate, resulting in a dense regrowth of young understorey ash and sycamore beneath the canopy trees. These two species are divided in many of the tables which follow into 'canopy trees' and 'understorey'. All the oaks and hawthorns sampled were 'canopy trees' (Table 1) since only large trees of these two species had any dead wood on them. The vertical layers into which the data are divided are those used by Elton & Miller (1954) in their habitat classification, viz. Ground Zone: up to 0.15 m (not sampled); Field Layer: 0.15-1.85 m; Shrub Layer: >1.85-4.6 m; Canopy: >4.6 m. Only two oak samples were from the Field Layer, and only two hawthorn samples from the Canopy.

The area was mapped and the amount of dead wood on both canopy trees and understorey estimated (Table 1). Of the fifteen species of trees and shrubs on the study area, oak, ash, sycamore and hawthorn contributed about 97% to the available dead wood habitat. These were therefore the tree species sampled in a 'stratified' random manner, with relatively more samples being taken from the individual trees or grid squares which contributed most dead wood. Not all the samples which should have been taken could in fact be reached by us. We sampled from measured heights up to 11.0 m, at weekly intervals over six weeks in February/early March 1969 ('winter samples') and over four weeks in August 1969 ('summer samples').

Dead wood samples were about 400 cc in volume, a convenient size for extraction of the animals using the Tullgren heat extraction apparatus that was already available. Samples varied in length according to their diameters (2-12 cm). The larger species of epiflora were identified and the amount of cover provided for animals by the epiflora and by loose bark estimated. Also the degree of rot and 'burrowedness' of the wood were assessed. Of 253 samples, 152 had some sort of cover, but only 57 had really loose bark.

Results

Though samples were collected according to diameter group (2-5 cm and >5-15 cm) and according to whether the wood was dead or had any living twigs attached, in practice, most samples were a mosaic of different stages of decay. As decay proceeded the rotten wood was more likely to fall to the ground. No clear-cut differences between the fauna of samples at different stages of decay could be demonstrated, except when one compared such extremes as oak staghorns on the one hand and mostly rotten wood on the other. Therefore, in the main, the results are presented as comparisons between just the four tree species and the vertical layers.

Overall richness and diversity in the mesofauna

Except for the Pseudoscorpiones, Opiliones and Aranea (see Paviour-Smith & Elbourn 1978), Appendix 1 lists the 368 invertebrate species found in all 253 samples and gives, for each species, the total number of individuals found, the life history stages known certainly to be present, the frequency of the species in the samples and the tree species on which it occurred. The data for the omitted arachnids are included in calculations of diversity of the whole fauna. The basic data for each sample and detailed quantitative results of the distributions and abundances of all species according to tree species, vertical layer and season are being deposited in the Wytham Ecological Survey now in the Hope Collections in the University Museum, Oxford; only a few detailed results, mainly for mites and beetles, are given here. The taxonomic problems with some groups were so great that compiling this Appendix list would have been impossible without help from many expert taxonomists, especially with the Acari, and with some Coleoptera and Collembola.

Table 2 summarises for the whole data and different subsets of samples, the species richness, abundance and a diversity index (∝) which combines the two (Fisher, Corbet & Williams 1943; Williams 1947, 1964).

Table 2 Summary of richness, abundance and diversity with different levels of identification of fauna for all 253 samples.

Determined to level of:	**Species**	**Genus**	**Family**	**Order**
a. **Whole data**				
No. individuals	46,635	48,073	48,467	49,143
% total individuals	95%	98%	99%	100%
No. taxa	368	268	149	24
∝ diversity	54	37	19	2.4
b. **Omitting young stages**				
No. individuals	40,748	40,920	40,947	
% total individuals	83%	83%	83%	
No. taxa	289	204	118	
% of total taxa (in (a) above)	79%	76%	79%	
∝ diversity	42	28	15	

Table 3 The first 30 species ranked by frequency in the samples with their actual frequency and abundance-ranking. * = The six species in the top 10 in both frequency and abundance; † = also in Fager's (1968) major recurrent group of 23 spp.

Code no. (Appendix 1)	Species name	Frequency in samples	Frequency ranking	Abundance ranking
77	†**Carabodes labyrinthicus* (Acari)	238	1	4
194	**Xenylla boerneri* (Collembola)	177	2	1
206	**Entomobrya albocincta* (Coll.)	152	3	8
107	†*Gamasellodes bicolor* (Acari)	96	4 =	17
203	†**Isotoma cinerea* (Coll.)	96	4 =	9
205	*Entomobrya nivalis* (Coll.)	94	6	18
202	**Isotoma arborea* (Coll.)	89	7	7
71	*Eremaeus oblongus* (Acari)	87	8	11
78	**Odontocepheus elongatus* (Acari)	85	9	2
237	*Limothrips cerealium* (Thysan.)	84	10	31
345	*Lestodiplosis* sp. (Dipt.) larvae	80	11	29
131	*Typhlodromus bakeri* (Acari)	79	12	19
195	†*Xenylla grisea* (Coll.)	78	13	3
201	*Isotoma sensibilis* (Coll.)	76	14	5
208	*Orchesella cincta* (Coll.)	63	15	26
89	*Oribella castanea* (Acari)	57	16	15
98	*Chamobates schutzi* (Acari)	54	17	13
358	*?Platypalpus* sp. (Dipt.) larvae	53	18	47
130	*Amblyseius (?silvaticus)* (Acari)	51	19	35
197	*Friesia claviseta* (Coll.)	45	20	14
79	†*Tectocepheus velatus* (Acari)	42	21 =	12
115	*Hypoaspis oblonga* (Acari)	42	21 =	34
264	*Malthodes marginatus* (Coleopt.) larvae	41	23	48
259	*Leptusa ruficollis* (Coleopt.)	40	24	59 =
133	*Typhlodromus rhenanus* (Acari)	37	25	51
236	*Thrips major* (Thysan.)	34	26 =	40
336	*Brittenia fraxinicola* (Dipt.) larvae	34	26 =	28
101	*Oribatella quadricornuta* (Acari)	30	29 =	22
219	*Reuterella helvimacula* (Psoc.)	30	29 =	38 =
228	*Loricula elegantula* (Hemipt.)	30	29 =	74 =

Gamasellodes bicolor = Fager's *Digamasellus oudemansi* (Halb.). Fager's voucher specimens re-examined by Prof G Owen Evans in the light of recent taxonomic changes.

The diversity estimate is very much affected by the level of identification adopted. Here 95% of the total 49,143 invertebrates extracted were identified to species, but the diversity estimate dropped dramatically if identification was taken only as far as genus. Acarine genera, such as *Phthiracarus, Dendrolaelaps, Tarsonemus* and *Tydeus*, each represented by six or more species, will have had a considerable effect on this drop. More information contributing to species diversity appears to be lost through identification only to genera or families than if young stages are omitted, even though in one large group, the Diptera, 78% of the 45 species found occurred only as larvae or pupae.

123 species occurred in five or more samples. The most frequent 30 species of invertebrates are ranked in Table 3 by frequency and by abundance, the fauna being dominated by mites and Collembola. There are six species in common between the top 10 species in the two methods of ranking.

Faunal diversity according to tree species

The lowest faunal diversity was found in the dead wood of understorey ash (∝ = 15) and the highest in oak and large canopy ash trees (for both, ∝ = 32), with hawthorn close behind (∝ = 29) (Table 4). That oak and hawthorn actually housed most species of invertebrates (197 and 184 species respectively) may reflect the fact that these two tree species appeared to have the richest epiflora (mosses, foliose lichens, macrofungi and myxomycetes) with 22 species recorded on each (Table 5). Ash canopy trees were close behind (20 spp.). The crustose lichen *Lecanora conizaeoides* Nyl. ex Cromb. was recorded on 30-60% of all samples taken in all tree categories. Oak was richest in species of psocids and of neuropterous larvae, and hawthorn for certain beetle larvae and mites.

Table 4 Richness, abundance and diversity of animals in the dead/dying wood of the four tree species

	Oak	**Ash**		**Sycamore**		**Hawthorn**
		Canopy trees	Under-storey	Canopy trees	Under-storey	
No. samples	71	39	20	43	30	50
No. of animal species	197	163	71	108	142	184
No. individuals	14,837	4,827	1,600	3,873	6,253	15,245
Diversity index ∝	32	32	15	21	26	29

Table 5 No. species of epiflora on samples from each tree category

	Oak	Ash		Sycamore		Hawthorn
		Canopy trees	Under-storey	Canopy trees	Under-storey	
Mosses	1	2	0	0	0	4
Foliose lichens	6	1	0	1	0	3
Ascomycetes	2	6	2	0	3	4
Basidiomycetes	13	10	1	1	6	9
Fungi Imperfecti	0	0	0	1	1	1
Myxomycetes	0	1	0	0	0	1
Total no. species	22	20	3	3	10	22

Table 6 Richness, abundance and diversity in five groups of invertebrates (from data in Appendix 1)

	No. species	**No. individuals**	$\propto$
Aranea	19	171	5.5
Coleoptera	49	414	14
Diptera	45	1,882	8.3
Acari	154	19,968	23
Collembola	19	23,020	2.0
Whole data	368	46,635	54

Richness, abundance and diversity in selected groups of invertebrates

Spiders, beetles and flies (three groups widely collected and studied by amateur naturalists) and mites and springtails (which are studied mainly by professional zoologists) have been selected to see how each group contributed to overall faunal diversity.

Acari (154 spp., $\alpha = 23$) made the greatest contribution of these five groups to species diversity, and Collembola the smallest (19 spp., $\alpha = 2$) (Table 6). Of the amateur-favoured groups, Coleoptera were the most diverse ($\alpha = 14$). Only these groups are discussed below.

The Acari

Table 7 shows the habitat distribution in this study of the most frequent or most abundant species in each main order of this group, and also of one decaying-wood-feeding genus, *Phthiracarus*, represented here by six species.

The most abundant of the Astigmata, the elongate, xylophagous *Michaelopus corticalis*, which has been observed by us loosening the bark especially of oak twigs, was, along with other delicate, thin-skinned Astigmata, poorly extracted by the heat extraction technique used. We recorded it however from nine samples (11% of oak samples and 5% of understorey ash). It occurred in all layers but was found only in winter samples.

The Cryptostigmata were dominated by two widespread forest soil species, *Carabodes labyrinthicus* and *Odontocepheus elongatus*, the former of which was a member of Fager's major recurrent group in decaying oak wood on the ground, and the latter, though not found by Fager (1968), has been recorded by others from decaying ash and birch wood and from soil samples in Wytham. Together they made up 62% of all the oribatid mites counted. *C. labyrinthicus*, with 3,530 individuals spread over 94% of the total samples taken, was fairly evenly distributed over all four species of tree, at all heights, both in winter and summer. By contrast, *Odontocepheus elongatus*, which burrows into wood and is very sluggish (Michael 1884), had 5,068 individuals, apparently occurring very patchily, in only 34% of the total samples and mostly on oak and hawthorn.

Of the wood-feeding oribatid mites, the genus *Chamobates* was represented by five species, *C. schutzi* by 814 individuals in 54 samples, but there was some uncertainty about the true identity of three of these species. Instead, the habitat distributions are given for the six species of *Phthiracarus*, found less commonly in the samples - the most frequent being *P. clavatus* as 93 individuals in 24 samples. (This genus is usually considered as living in soil and litter.) It is one of the most difficult genera taxonomically (each specimen needing to be dissected, and drawings made, for identification). Adults and their thin-skinned, soft-bodied, sluggish young stages were found burrowing into decaying wood but the latter were not extracted by the present method. The most frequent and abundant species, *P. clavatus*, was not described till 1979 by Dr B Parry, who recorded it from mull soil and from *Phragmites* litter from four localities. Yet, in Wytham, it occurred in 38% of the hawthorn samples and in samples from large ash (8%), large sycamore (2%) and oak (1%). On hawthorn, it was distributed in the Field Layer, Shrub Layer and Canopy up to 5.6m, in the same proportion as that in which these layers were sampled. All six species occurred in the Field Layer, and *P. anonymum* was also recorded in the Shrub Layer. Two of the six species were found only as singletons, with *P. clavatus*, in one hawthorn sample.

Table 7 Distribution according to tree species, height and season of most frequent (or most abundant) mites in each major group and the most abundant springtail. The data for the genus *Phthiracarus* (discussed in the text) are also given. FL = field layer, SL = shrub layer, C = canopy, f = frequency.

	OAK	ASH		SYCAMORE		HAWTH.	VERTICAL LAYERS			SEASON		Total frequency in samples	No. individuals
		Canopy trees	Under-storey	Canopy trees	Under-storey		FL	SL	C	Winter	Summer		
No. samples: Frequency:	71 f (%)	39 f (%)	20 f (%)	43 f (%)	30 f (%)	50 f (%)	66 f (%)	137 f (%)	50 f (%)	156 f (%)	97 f (%)		
Astigmata													
Michaelopus corticalis	8(11.3)	0	1(5.0)	0	0	0	1(1.5)	4(2.9)	4(8.0)	9(5.8)	0	9	68
Cryptostigmata													
Carabodes labyrinthicus	71(100)	35(89.7)	17(85.0)	41(95.4)	25(83.3)	49(98.0)	61(92.4)	132(96.4)	45(90.0)	145(93.0)	93(95.9)	238	3,530
Odontocepheus elongatus	44(62.0)	3(7.7)	2(10.0)	4(9.3)	4(13.3)	28(56.0)	22(33.3)	56(40.9)	7(14.0)	47(30.1)	38(39.2)	85	5,068
Phthiracarus clavatus	1(1.4)	3(7.7)	0	1(2.3)	0	19(38.0)	12(18.1)	11(8.0)	1(2.0)	12(7.7)	12(12.4)	24	93
Phthiracarus murphyi	0	0	0	0	0	1(2.0)	1(1.5)	0	0	0	1(1.0)	1	1
Phthiracarus rectisetosus	0	0	0	0	1(3.3)	1(2.0)	2(3.0)	0	0	0	2(2.1)	2	2
Phthiracarus nitens	0	0	0	0	2(6.7)	0	2(3.0)	0	0	1(0.6)	1(1.0)	2	3
Phthiracarus affinis	0	0	0	0	0	1(2.0)	1(1.5)	0	0	1(0.6)	0	1	2
Phthiracarus anonymum	1(1.4)	0	0	0	1(3.3)	0	1(1.5)	1(0.7)	0	1(0.6)	1(1.0)	2	2
Prostigmata													
Tarsonemus bifurcatus	3(4.2)	0	1(5.0)	0	0	3(6.0)	3(4.6)	2(1.5)	2(4.0)	7(4.5)	0	7	1,502
Bdella ?iconica	8(11.3)	2(5.1)	0	0	0	10(20.0)	2(3.0)	14(10.2)	4(8.0)	1(0.6)	19(19.6)	20	34
Mesostigmata													
Gamasellodes bicolor	19(26.8)	23(59.0)	6(30.0)	13(30.2)	8(26.7)	27(54.0)	24(36.4)	54(39.4)	18(36.0)	63(40.4)	33(34.0)	96	483
Microsejus truncicola	5(7.0)	0	0	0	0	6(12.0)	6(9.1)	3(2.2)	2(4.0)	7(4.5)	4(4.1)	11	601
Typhlodromus bakeri	26(36.6)	10(25.6)	13(65.0)	12(27.9)	9(30.0)	9(18.0)	18(27.3)	44(32.1)	17(34.0)	47(30.1)	32(33.0)	79	424
Amblyseius ?silvaticus	21(29.6)	5(12.8)	1(5.0)	1(2.3)	1(3.3)	22(44.0)	16(24.2)	31(22.6)	4(8.0)	26(16.7)	25(25.8)	51	136
Collembola													
Xenylla boerneri	57(80.3)	26(66.7)	6(30.0)	25(58.1)	14(46.7)	49(98.0)	46(69.7)	99(72.3)	32(64.0)	112(71.8)	65(67.0)	177	12,203
No. individuals													
X. boerneri	2289	1165	10	1582	1715	5442							

The much more diverse Prostigmata (3,076 individuals of 54 species) were dominated by the 'algivorous or mycetophagous' *Tarsonemus bifurcatus* (Evans, Sheals & Macfarlane 1961). Nearly half (1,502, or 49%) of the individual Prostigmata counted were of this species but it occurred very patchily, in only seven winter samples (4% of oak samples, 5% of understorey ash and 6% of hawthorn samples). Much more widespread were the small numbers (only 34) of the predatory *Bdella ? iconica*, found in 20 (mostly summer) samples and thus the most frequently occurring species in this major group (in 20% of hawthorn, 11% of oak and 5% of canopy tree ash samples).

The Mesostigmata found were probably all predators and were equally represented in both summer and winter in all woodland layers. The most frequent species, *Gamasellodes bicolor*, (483 individuals) was present in 96 (38%) of the total samples, spread over all four species of tree, both large canopy trees and understorey (in as many as 59% of oak samples and 54% of hawthorn), while the most abundant species, *Microsejus truncicola* (601 individuals) occurred in only 11 (4%) of all samples (only on oak (7%) and on hawthorn (12%)). The two other frequent Mesostigmata, *Typhlodromus bakeri* and *Amblyseius ? silvaticus* (in 20% and 31% respectively of all samples) were spread over all tree species and are probably surface hunters over the whole tree. The former, according to Chant (1959), is "entirely bark-inhabiting and usually associated with mites of the family Tydeidae (17 species in our samples) and others. Probably feeds on algae and fungi as well as on mites".

Collembola

The most remarkable thing about the list of 19 species of Collembola in this study is that the most abundant species, *Xenylla boerneri* (comprising half of all the Collembola found) had not been recorded in the Wytham area before. While this could be a species liable to fluctuate violently, the most probable explanation is that this springtail is minute (0.4-0.7 mm in length), springless, and, when dead (i.e. after extraction into alcohol), very difficult to identify unless specimens are mounted in precisely the correct position to show the extremely minute diagnostic characters. It has therefore been identified previously almost entirely by professional taxonomists, who give as its habitat 'in moss and lichens on tree trunks and rocks chiefly in hilly country' (Gisin 1960), 'under loose bark' and in coniferous litter. Travé (1963) considers it to be a mountain species. Though collembolologists mostly study soil and litter, not trees, their work does indicate that *X. boerneri* is not a ground-dwelling species. Finally, ecologists, studying whole communities, have tended to confine their identifications to relatively large, easily identified species, and sensibly call the rest 'other Collembola'.

This species was most frequent and most abundant on hawthorn (Table 7), where it may act as a 'key-industry' animal (Elton 1927) serving as food for many predatory species such as the common predatory beetle larvae (*Malthodes marginatus* - Table 8) and predatory mites such as *Hypoaspis oblonga*, both of which lived principally in hawthorn in these samples.

Coleoptera

The frequency of occurrence on the four tree species, the vertical distribution and any seasonality of the beetle species present in five or more samples are shown in Table 8 and some general points from these are considered below.

The identification problem In order to discover what exactly is being conserved, the greatest problem, as we have seen in other groups, is one of precise identification. The polyphagous larvae (Duffy 1946) of the cerambycid *Grammoptera ruficornis* were identified by E A J Duffy, who said (1953) that they feed sub-cortically in 'slender recently dead or slightly decaying twigs and branches'. They occurred in samples from both large and small ash and sycamore trees, more in winter than in summer, and especially in the canopy - yet these larvae had not been recorded for the Wytham estate before. The adults however are commonly taken in spring from the woodland Field Layer, especially on flowering shrubs (Elton 1966).

Table 8 Habitat distribution of Coleoptera species present in 5 or more samples (+ *Anaspis* larvae).
FL = field layer, SL = shrub layer, C = canopy

	OAK	ASH		SYCAMORE		HAWTHORN	VERTICAL LAYERS			SEASON		Total frequency in samples	No. individuals
		Canopy trees	Under-storey	Canopy trees	Under-storey		FL	SL	C	Winter	Summer		
No. samples: Frequency:	71 f (%)	39 f (%)	20 f (%)	43 f (%)	30 f (%)	50 f (%)	66 f (%)	137 f (%)	50 f (%)	156 f (%)	97 f (%)		
Dromius quadrimaculata	1(1.4)	1(2.6)	0	1(2.3)	2(6.8)	3(6.0)	1(1.5)	4(2.9)	3(6.0)	2(1.3)	6(6.2)	8	9
Ptinella errabunda	5(7.0)	1(2.6)	0	0	0	2(4.0)	3(4.5)	4(2.9)	1(2.0)	7(4.5)	1(1.0)	8	35
Leptusa fumida	8(11.3)	10(25.6)	3(15.0)	0	2(6.7)	4(8.0)	9(13.6)	16(11.7)	2(4.0)	9(5.8)	18(18.6)	27	50
Leptusa ruficollis	4(5.6)	11(28.2)	3(15.0)	5(11.6)	7(23.3)	10(20.0)	14(21.2)	18(13.1)	8(16.0)	21(13.5)	19(19.6)	40	63
Euplectus fauveli	2(2.8)	3(7.7)	0	0	0	0	1(1.5)	2(1.5)	2(4.0)	3(1.9)	2(2.0)	5	5
Bibloporus minutus	3(4.2)	1(2.6)	0	0	0	1(2.0)	0	2(1.5)	3(6.0)	5(3.2)	0	5	6
Malthodes marginatus la.	10(14.1)	3(7.7)	0	3(7.0)	4(13.3)	21(42.0)	15(22.7)	21(15.3)	5(10.0)	23(14.7)	18(18.6)	41	82
Cyphon variabilis	1(1.4)	1(2.6)	0	1(2.3)	1(3.3)	4(8.0)	4(6.1)	4(2.9)	0	8(5.1)	0	8	8
Aridius bifasciatus	0	2(5.1)	1(5.0)	0	0	3(6.0)	4(6.1)	2(1.5)	0	4(2.6)	2(2.1)	6	6
Enicmus transversus	0	0	0	1(2.3)	2(6.7)	6(12.0)	4(6.1)	4(2.9)	1(2.0)	1(0.6)	8(8.3)	9	13
Grynobius excavatus incl. la.	0	0	0	0	0	6(12.0)	4(6.1)	2(1.5)	0	4(2.6)	2(2.1)	6	8
Ptilinus pectinicornis incl. la.	0	0	0	0	5(16.7)	0	3(4.6)	2(1.5)	0	3(1.9)	2(2.1)	5	21
Rhinosimus planirostris	0	3(7.7)	3(15.0)	1(2.3)	2(6.7)	2(4.0)	3(4.6)	7(5.1)	1(2.0)	5(3.2)	6(6.2)	11	16
Anaspis rufilabris	3(4.2)	1(2.6)	0	0	0	2(4.0)	1(1.5)	3(2.2)	2(4.0)	6(3.9)	0	6	6
Anaspis larvae ?sp. or spp.	31(43.7)	23(59.0)	4(20.0)	18(42.9)	8(26.7)	38(76.0)	30(45.5)	71(51.8)	21(42.0)	65(41.7)	57(58.8)	122	320
Grammoptera ruficornis la.	0	2(5.1)	1(5.0)	2(4.7)	1(3.3)	0	1(1.5)	2(1.5)	3(6.0)	5(3.2)	1(1.0)	6	6

Our material of the minute ptiliid genus *Ptinella* had to wait for some years for proper identification. Dr C Johnson, who described *Ptinella errabunda* only in 1975, found, when he examined our material, two species: *P. errabunda* in five samples from three tree species (all large trees), and the much less frequent *P. denticollis*. Ptiliid larvae, determined only to family, were counted but could not be included in figures for species diversity. The same problem, over larvae associated with adults but not certainly belonging to the same species, occurred in the genus *Anaspis*. Six adults of *Anaspis rufilabris* (Gyll.) (= *hudsoni* Donisthorpe) were found, all from winter samples. They occurred, one in each of five samples, associated with *Anaspis* larvae, and one teneral adult, without larvae, in another sample.

The importance of the *Anaspis* larvae in the present context is that they were the most frequent Coleoptera determined only as far as genus, 320 larvae occurring in 122 samples. If they could have been identified certainly as belonging, with the adults, to *A. rufilabris*, this would have become not only the most frequent beetle species, but also the fourth most frequent invertebrate species (following *Entomobrya albocincta* in the frequency ranking of Table 3). If, for the moment, we assume that the adults and larvae of the *Anaspis* found all belong to one species, we find that its apparent preference for hawthorn (Table 8) is highly significant (chi-squared = 23.15, 3 d.f., $p << 0.005$). *Anaspis* spp. are regarded as 'flower beetles' and adults are most frequently collected in spring from flowering trees and shrubs, including hawthorn (Fowler 1891; Palm 1959). The successful pollination of such trees and shrubs must therefore owe something to the conservation of small arboreal dead wood as habitats for thinly distributed larvae of some species of 'flower beetles' and other flower-visiting insects.

Hibernation sites In conserving dead wood in trees, we are also conserving hibernation sites for some species. We found the scirtid marsh beetle, *Cyphon variabilis*, in winter samples only, of all tree species; it is obviously common, yet had never been recorded from Wytham before. There was a small pond only 10 m south of our study area and a large marsh about 100 m north of it; four of the seven records were from three large hawthorns near the pond. Again, it belongs to a genus which is difficult taxonomically and 'is not a popular one with collectors' (Kevan 1962), so voucher specimens are essential.

Change in status An Australian lathridiid beetle, *Aridius bifasciatus*, has been spreading steadily in Britain since it was first recorded at Esher Common, Surrey, in 1950 (Allen 1951; Hammond 1974). By 1960, it was known also from Kent, Essex, Middlesex and W. Sussex (Lewis 1960), and was found first in that year in a bracket fungus in Wytham Woods (in the Watsonian vice-county of Berkshire). There are many records of lathridiids from dead wood and bracket fungi in Wytham from 1949-60 (including many of the very similar, but easily distinguishable, *A. nodifer*, originally also from Australia but now cosmopolitan (Horion 1961)) but none till 1960 of *A. bifasciatus*. In 1961-2, Larkin & Elbourn (1964) found only *A. nodifer* in their samples and boxes up oak trees; in 1965 *A. nodifer* was the commonest beetle in Elbourn's (1970) oak boxes up trees and only a single *A. bifasciatus* was found by him. In our study, of 1969, a single *A. nodifer* adult was found in an understorey sycamore sample, while six samples (three hawthorn and three ash) each contained one *A. bifasciatus*. The question is posed: has the new invader really been supplanting the earlier, now resident species? (Both have been found in similar 'General Habitats' (Elton & Miller 1954), viz. dead wood, fungi, vegetable debris, haystacks.) Or, are they by now sharing out the habitats, the new arrival perhaps surviving best in drier conditions up trees and in drier years, and the earlier species in the damper ones (as has happened with the Australian fungus beetle *Cis bilamellatus* Wood and the native British and European species *C. bidentatus* (Oliv.) (Paviour-Smith 1960))?

'Scarceness' or 'apparent rarity'. A species may appear to be rare because an appropriate sampling method remains to be discovered. *Cis vestitus*, belonging to a family of fungus beetles, was considered by Fowler (1890) and Joy (1932) to be 'rare' and, by the latter, 'on oak'. It is found in ones and twos whenever a large sample of dead oak wood is examined (e.g. in Fager's, 1968, and Larkin & Elbourn's, 1964, studies). Till recent years, it has almost never been found breeding. In this study, we found only a single specimen in an oak sample, but since then new collecting methods have been in use, and it has been recorded, clearly having been breeding, in a 'knock-down' sample from three ancient oaks in Silwood Park, Berks, in August 1979, by Professor T R E Southwood and his colleagues. The three oaks, smoked by pyrethrum (smoke penetrating up to 10 m on the trees) had a lot of dead branches and dead apices still attached. The collection included 30 adult (including a number of teneral) *Cis vestitus* and 12 adults (including several teneral) of *Cis alni* Gyll. - the latter also 'scarce' and rarely found breeding. "*Cis vestitus* adults (including tenerals) have in recent years been taken in numbers from oaks, by similar 'smoking' methods, in other sites in southern England" (P M Hammond & N E Stork, pers. comm.).

Real rarity Of all the 368 species found and tens of thousands of individuals counted in all 253 samples taken by us, only one beetle larva, that of *Tomoxia bucephala* is considered really as a 'rarity' and is listed as such in the *British Red Data Book 2: Insects* (Shirt 1987). It was in a 2 cm diameter x 127 cm long sample, collected on 25.2.69, from a height of 5.2 m on understorey ash; 95% of the sample's bark was loose and the rest gone; all the wood was solid, but showed a few zone lines indicating fungus infection. Firm records (Morley 1935; Duffy 1945; Johnson 1963; Nash 1972; Godfrey 1989) are all for the south of Britain (Hampshire, Hants-Surrey border, Berkshire and Hertfordshire), and all the above records, except for Duffy's, were for beech (large standing dead boles and stumps and logs). Duffy found abundant larvae in stumps of oak in September and adults in June.

There was one very large beech with some small dead branches about 90 m from the grid square in which we collected the *Tomoxia* larva, but two large oaks were only about 20 m and 30 m away. This beetle appears to need much larger-sized dead wood than we were sampling, and beech and oak seem to be its breeding headquarters in southern Britain, where it appears to be on the edge of its European range. However that could change with climate change.

Conclusions

There is understandable concern to protect sites for rare deadwood invertebrates (Stubbs 1972) and hence much effort goes into the identification of such areas. However, rare species must be placed in context, which means knowing more about the frequency of, and factors that affect, the populations of 'common' species as well. There is relatively little work of this nature from British woods apart from studies of pest species. Part of the difficulty of assembling such data, as this study has illustrated, is methodological - both in terms of sampling the populations and in identifying the beasts afterwards.

This study has also brought out the interrelationships between the deadwood habitat and other elements in the system, for example, the use of dead wood as hibernation sites by wetland species and the pollination of hawthorn flowers by adults of species whose larvae live in dead wood. More such links are likely to emerge as further studies are made.

The 'manicuring' of parkland trees to eliminate their small dead wood (so-called 'tidying up') and the removal of ancient hawthorns, which form rich habitats for dead wood faunas as well as for flower-visiting insects, indicate the likely impoverishment of the system. The latter may be done to open up the sides of woodland rides for improved visibility for shooting parties, after change in ownership or management of an estate (eg Wychwood Forest, Oxon, in the 1960s).

The study also shows the importance of long-term records for one site. Wytham Woods has now been designated a 'flagship' site for research into climatic change and the environment, and, as Buckland and Dinnin (1993) show, dead wood beetles are particularly useful indicators of such change. However, that requires good baseline studies of the type provided here.

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Appendix 1 Summary of whole data on animals determined to species level, in all 253 wood-samples. (A = adults, Y = immature, L = larvae, P = pupae, o = oak, a = ash, s = sycamore, h = hawthorn)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Pulmonata	1	*Marpessa laminata* (Montagu) (a, s)	4	A + Y	3
	2	*Oxychilus alliarius* (Miller) (s, h)	3		2
	3	*Limax maximus* L. (o, a, s)	3	Y	3
Oligochaeta	4	*Eiseniella tetraedra* (Savigny) (a, h)	7		2
Oniscoidea	5	? *Trichoniscus* sp. (a)	1		1
	6	*Oniscus asellus* L. (o, a, s, h)	41	A + Y	12
	7	*Porcellio scaber* Latreille (o, a, s, h)	57	A + Y	18
Polyxenida	8	*Polyxenus lagurus* (L.) (o, h)	105	A + Y	15
Iulida	9	*Isobates varicornis* (C L Koch) (o,a,s)	40		5
	10	*Proteroiulus fuscus* (Am Stein) (o, h)	25	A + Y	5
	11	*Tachypodoiulus niger* (Leach) (o, h)	3		3
Lithobiomorpha	12	*Lithobius variegatus* Leach (h)	3		3
	13	*Lithobius melanops* Newport (o, h)	7		7
	14	*Lithobius curtipes* C L Koch (h)	1		1
Pseudoscorpionida	15-16	2 species	6	Paviour-Smith & Elbourn (1978)	
Opiliones	17-19	3 species	16		
Aranea	20-38	19 species	171		
Acari-Astigmata	39	*Michaelopus corticalis* (Michael) (o,a)	68		9
	40	Species II, Acaridae (o, s)	4		3
	41	Species III, ?*Tyrophagus* Acaridae (h)	8		2
	42	Species IV, ?*Schwiebea* I Acaridae (s,h)	21		10
	43	Species IVA, ?*Schwiebea* II Acaridae (a,s)	12		7
	44	Species V, ?*Thyreophagus* Acaridae (a)	2		1
	45	Species VI, ?*Tyroborus* Acaridae (o,s,h)	32		5
	46	Species VIA, ?nr. *Tyroborus* Acaridae (o,a,s)	4		3
	47	Species VII, ?*Forcellinia* Acaridae (s)	1		1
	48	Species VIII, Acaridae (o)	1		1
	49	Species XI, *Acarus* sp.-long (o,a,h)	15		11
	50	Species XIA, *Acarus* sp.-fat (a)	1		1
	51	*Histiogaster* cf. *carpio* or *oudemansi* (o,s)	2		2
	52	*Calvolia hagensis* Oudemans (s)	9		2
	53	Species XII, ?*Histiostoma* (o)	1		1
	54	Species XIII, ?nr. *Wichmannia* Anoetidae (s)	1		1
	55	*Glycyphagus*, species X (o,a,s,h)	12		9
	56	*Glycyphagus* (?*domesticus* (De Geer)) Species XA (h)	2		2
	57	Species IX, ? Lardoglyphidae (a,h)	2		2

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Acari-Cryptostigmata	58	*Phthiracarus clavatus* Parry (o,a,s,h)	93	A	24
	59	*Phthiracarus murphyi* Harding (h)	1	A	1
	60	*Phthiracarus rectisetosus* Parry (s,h)	2	A	2
	61	*Phthiracarus nitens* (Nicolet) (s)	3	A	2
	62	*Phthiracarus affinis* (Hull) (h)	2	A	1
	63	*Phthiracarus anonymum* Grandjean (o,s)	2	A	2
	64	*Brachychthonius (?marginatus* Forss.)(o,s,h)	64		8
	65	*Camasia horrida* (Herm.) (o,a,h)	3		3
	66	*Camasia (?segnis* (Herm.)) (o)	7	A + Y	3
	67	*Damaeus clavipes* (Herm.) (o, h)	5	A	5
	68	*Damaeus (?gracilipes* (Kulcz.)) (h)	1	A	1
	69	*Damaeus (?onustus* C L Koch) (s)	7	A	2
	70	*Cepheus latus* C L Koch (s, h)	30	A	6
	71	*Eremaeus oblongus* C L Koch (o,a,s,h)	1061	A + Y	87
	72	*Adoristes ovatus* (C L Koch) (s)	1	A	1
	73	*Adoristes (?poppei* Oudemans) (h)	1	A	1
	74	*Xenillus latus* (Nic.) (a, h)	11	A + Y	2
	75	*Xenillus tegeocranus* (Herm.) (a, s)	18	A + Y	3
	76	?*Ceratoppia* sp. (a)	1	A	1
	77	*Carabodes labyrinthicus* (Michael) (o,a,s,h)	3530	A + Y	238
	78	*Odontocepheus elongatus* (Michael) (o,a,s,h)	5068	A + Y	85
	79	*Tectocepheus velatus* (Michael) (o,a,s,h)	835	A + Y	42
	80	?*Membranoppia* sp. (o)	1	A	1
	81	*Multioppia* cf. *wilsoni* Aoki (o,a,h)	251	A	12
	82	*Oppia falcata* (Paoli) (a,s,h)	151	A	9
	83	*Oppia minus* (Paoli) (a, s)	3	A	2
	84	*Oppiella (= Oppia) nova* (Oudemans) (s, h)	31	A	4
	85	*Oppia ornata* (Oudemans) (s)	3	A	1
	86	*Oppia* cf. *translamellata* (Willmann) (o)	1	A	1
	87	*Quadroppia quadricarinata* (Michael) (o, s)	3	A	2
	88	*Autogneta longilamellata* (Michael) (o)	8	A	1
	89	*Banksinoma lanceolata* (Michael) (= *Oribella castanea* (Herm.)) (o,a,s,h)	714	A	57
	90	*Cymbaeremaeus cymba* (Nic.) (o,a,s,h)	69	A + Y	20
	91	*Micreremus brevipes* (Michael) (o,a,s,h)	92	A + Y	24
	92	?*Oribatula tibialis* (Nic.) (h)	1	A	1
	93	*Phauloppia lucorum* (C L Koch) (o)	6	A	2
	94	*Zygoribatula exilis* (Nic.) (a, h)	365	A + Y	5
	95	*Chamobates borealis* (Träg.) (o,a,s,h)	92	A + Y	20
	96	*Chamobates* A (*"punctatus"*) (a,s,h)	6	A	4
	97	*Chamobates* nr. *pusillus* (Berlese) (o,a,s,h)	27	A	10
	98	*Chamobates schutzi* (Oudemans) (o,a,s,h)	814	A + Y	54
	99	*Chamobates* B (*"tridentatus"*) (o, h)	13	A	4
	100	?*Mycobates parmeliae* (Michael) (o)	3	A	1
	101	*Oribatella quadricornuta* (C L Koch) (o,a,s,h)	322	A + Y	30
	102	?*Oribatella* sp. (other) (o,s,h)	19	Y	5

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Acari-Mesostigmata	103	*Proctolaelaps pygmaeus* (Müller) (= *hypudaei* (Oudemans)) (h)	28		5
	104	*Arctoseius* sp. I (o, s)	47	A	2
	105	*Arctoseius* sp. II (h)	2	A	1
	106	*Asca squamulata* Athias-Henriot (a, s)	2		2
	107	*Gamasellodes bicolor* (Berlese) (o,a,s,h)	483	A + Y	96
	108	*Lasioseius confusus* Evans (h)	2	A	2
	109	*Lasioseius muricatus* (C L Koch) (o,a,h)	197	A + Y	14
	110	*Lasioseius ometes* (Oudemans) (o,a,s,h)	111	A	26
	111	*Lasioseius penicilliger* Berlese (o,a,s,h)	127	A	26
	112	*Dermanyssus gallinae* (De Geer) (a)	2	Y	2
	113	*Hypoaspis brevipilis* Westerboer (o)	13	A	2
	114	*Hypoaspis giffordi* Evans and Till (o,a,s,h)	29	A	11
	115	*Hypoaspis oblonga* (Halbert) (o,a,s,h)	140	A	42
	116	?*Dendroseius scotarius* Sheals (a)	2	A	1
	117	*Dendrolaelaps acornutosimilis* (Hirschmann) (o,a,s,h)	63	A + Y	12
	118	*Dendrolaelaps cornutulus* (Hirschmann) (a)	5	A	1
	119	*Dendrolaelaps cornutus* (Kramer) (o,a,s,h)	184	A + Y	8
	120	*Dendrolaelaps* nr. *fallax* (Leitner) (a)	7	A	1
	121	*Dendrolaelaps longulus* (Hirschmann) (o)	75	A	3
	122	*Dendrolaelaps punctulatus* (Hirschmann) (o,a,s,h)	175	A + Y	20
	123	*Microsejus truncicola* Trägårdh (o,h)	601	A + Y	11
	124	*Porrhostaspis lunulata* Müller (s)	1	A	1
	125	*Paragamasus alpestris* (Berlese) (s)	2	A	1
	126	*Paragamasus* nr. *cambriensis* (Bhattacharyya) (a)	1		1
	127	*Pergamasus crassipes* (L.) (o, h)	2		2
	128	*Pergamasus longicornis* Berlese (o)	1	A	1
	129	*Amblyseius* (?*graminis* Chant) (s)	1	A	1
	130	*Amblyseius* (?*silvaticus* Chant) (o,a,s,h)	136	A	51
	131	*Typhlodromus bakeri* (Garman) (o,a,s,h)	424	A + Y	79
	132	*Typhlodromus finlandicus* (Oudemans) (s)	1	A	1
	133	*Typhlodromus rhenanus* (Oudemans) (o,a,s,h)	75	A	37
	134	*Typhlodromus* (?*umbraticus* Chant) (o,s)	5	A + Y	5
	135	?*Veigaia* sp. (o, h)	4	Y	2
	136	*Zercon triangularis* C L Koch (s, h)	2	A + Y	2
	137	Uropodina I [*Leiodinychus-Oodinychus* group] (s)	2	A	1
	138	Uropodina II (s)	1		1

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Acari-Prostigmata	139	*Anystis* cf. *andrei* Oudemans (o)	1	A	1
	140	*Bdella ?iconica* Berlese (o,a,h)	34		20
	141	*Bdella ?muscorum* Ewing (o)	3		3
	142	*Neophyllobius* sp. (o)	4		3
	143	Calligonellidae (h)	1		1
	144	*Cunaxoides* sp. I (o,a,s)	9	Y	8
	145	Cunaxidae sp. II (o)	1		1
	146	*Ereynetes* (s.g. *Gymnereynetes*) (o,a,s,h)	37		12
	147	*Cocceupodes ?clavifrons* (*R. Canestrini*) (h)	1		1
	148	*Eupodes* sp. (o,h)	2		2
	149	*Linopodes* sp. (h)	4		2
	150	*Protereunetes* sp. (o,a,s,h)	62		17
	151	*Microdispus* sp. I (h)	27	A	1
	152	*Microdispus* sp. II (a)	2	A	1
	153	*Neopygmephorus* (s.g. *Neopygmephorus*) (a,h)	26	A	8
	154	Pyemotidae (*Pygmephorus* or *Microdispodides*) (a)	2		1
	155	*Rhagidia* sp. I (h)	4		3
	156	*Rhagidia* sp. II (o)	1		1
	157	*Diversipes* sp. (s)	4		1
	158	*?Imparipes* sp. (a)	6		1
	159	*Scutacarus* sp. (o,h)	5		3
	160	*Barbutia* sp. (o,a)	55		4
	161	*Mediolata acus* (Summers) (o,a,s)	22		10
	162	*Mediolata* nr. *chanti* Gonzalez-Rodriguez (a,s)	2		2
	163	*Mediolata californica* Gonzalez-Rodriguez (o,a,s)	21		12
	164	*Stigmaeus fusus* Summers (o,a,h)	25		11
	165	*Stigmaeus purpurascens* Summers (o,s)	12		7
	166	*Daidalotarsonemus hewitti* Mahunka (o,a,h)	42	A	12
	167	*Tarsonemus bifurcatus* Schaarschmidt (o,a,h)	1502	A	7
	168	*Tarsonemus* II (o,a,h)	67	A	8
	169	*Tarsonemus fusarii* Cooreman (a,h)	3	A	2
	170	*Tarsonemus* IV (o,a,h)	10	A	6
	171	*Tarsonemus* V (a,s)	3	A	2
	172	*Tarsonemus* VI (a)	273	A	2
	173	*Tarsonemus* nr. *ips* Lindquist (a)	1	A	1
	174	Tetranychoidea. indet. (a,s)	2		2
	175	*Coccotydeus* I (o,a)	326		4
	176	*Coccotydeus* II (a,h)	12		2
	177	*Lorryia* nr. *armaghensis* Baker (o,a,s)	21		8
	178	*Lorryia ?bedfordiensis* Evans (o,s)	76		12
	179	*Paralorryia* A (*?woolleyi* Baker) (o,a,s,h)	8		7
	180	*Paralorryia* B (a,s)	13		3
	181	*Paralorryia* C (s)	3		1
	182	*Paralorryia* D (s)	22		1
	183	*Paralorryia* E (a)	1		1

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Acari-Prostigmata (cont'd)	184	*Tydeus* I (h)	14		1
	185	*Tydeus* II (s)	150		1
	186	*Tydeus* III (o)	2		1
	187	*Tydeus* IV (o,a,s)	5		4
	188	*Tydeus* V (o,a,s,h)	13		9
	189	*Tydeus* VI (a)	92		1
	190	*Tydeus* VII (a,s,h)	6		4
	191	*Tydulosus lolitae* Baker (o,s,h)	35	Y	6
	192	Prostigmata, other, indet. (o)	1		1
Insecta					
Collembola	193	*Hypogastrura purpurascens* (Lubbock) (o,s,h)	22		7
	194	*Xenylla boerneri* Axelson (o,a,s,h)	12,203		177
	195	*Xenylla grisea* Axelson (o,a,s,h)	3,833		78
	196	*Xenylla* sp., other, indet. (o,a)	21		2
	197	*Friesea claviseta* Axelson (o,a,s,h)	783		45
	198	*Pseudachorutes asigillatus* Borner (o,s,h)	39		12
	199	*Neanura muscorum* (Templeton) (a,s,h)	16		3
	200	*Folsomia* cf. *candida* Willem (h)	6	Y	2
	201	*Isotoma sensibilis* Tullberg (o,a,s,h)	1762		76
	202	*Isotoma arborea* (L.) (o,a,s,h)	1308		89
	203	*Isotoma cinerea* (Nicolet) (o,a,s,h)	1120		96
	204	*Entomobrya albocincta* (Templeton) (o,a,s,h)	1143		152
	205	*Entomobrya nivalis* (L.) (o,a,s,h)	437		94
	206	*Lepidocyrtus lignorum* (F.) sensu Hale 1966 (a,s,h)	11		7
	207	*Willowsia nigromaculata* (Lubbock) (o,a,s)	46		19
	208	*Orchesella cincta* (L.) (o,a,s,h)	190		63
	209	*Tomocerus minor* (Lubbock) (o,a,s,h)	67		18
	210	*Bourletiella bicincta* (C L Koch) (h)	2		2
	211	*Sminthurus fuscus* (L.) (o,a,s,h)	11		6
Dermaptera	212	*Forficula auricularia* L. (o,a,s,h)	10		8
Psocoptera	213	*Cerobasis guestfalica* (Kolbe) (o,s,h)	7	A	5
	214	*Pteroxanium kelloggi* (Ribiga) (o,a)	3	A	3
	215	*Loensia fasciata* (F.) (s)	1	A	1
	216	*Trichadenotecnum sexpunctatum* (L.) (o,a,s)	3	A	3
	217	*Philotarsus picicornis* (F.) (a)	4	A	1
	218	*Pseudopsocus rostocki* Kolbe (o,h)	21	A	14
	219	*Reuterella helvimacula* (Enderlein) (o,a,s,h)	111	A	30
	220	*Peripsocus phaeopterus* (Stephens) (a,s)	3	A	2
	221	*Caecilius flavidus* (Stephens) (a)	2	A	1

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Heteroptera	222	*Empicoris vagabundus* (L.) (o)	1	A	1
	223	*Temnostethus gracilis* (Horvath) (o,a,s,h)	19	A	10
	224	*Anthocoris confusus* Reuter (a,s,h)	6	A	6
	225	*Anthocoris nemoralis* (F.) (a)	1	A	1
	226	*Anthocoris limbatus* Fieber (s)	1	A	1
	227	*Anthocoris nemorum* (L.) (a,s,h)	16	A	14
	228	*Loricula elegantula* (Barensprung) (o,a,s,h)	37	A	30
	229	*Deraeocoris lutescens* (Schilling) (o,s)	2	A	2
	230	*Phytocoris dimidiatus* Kirschbaum (a,h)	2	A	2
Homoptera	231	Cicadellidae (a)	1	A	1
	232	Aphididae (o,s,h)	3		3
Thysanoptera	233	*Dendrothrips degeeri* Uzel (o)	1	A	1
	234	*Taeniothrips vulgatissimus* (Haliday) (h)	2	A	1
	235	*Thrips fuscipennis* Haliday (o)	1	A	1
	236	*Thrips major* Uzel (o,a,s,h)	106	A	34
	237	*Limothrips cerealium* Haliday (o,a,s,h)	161	A	84
	238	*Limothrips denticornis* Haliday (o,h)	8	A	8
	239	*Phlaeothrips fungi* (Zetterstedt) (o,a,s)	131	A + Y	13
	240	*Phlaeothrips longisetis* (Baghall) (a)	2	A	2
	241	*Phlaeothrips ulmi* (F.) (o,a,s,h)	103	A + Y	17
	242	*Haplothrips subtilissimus* (Haliday in Walker) (o)	2	A	1
Neuroptera	243	*Raphidia* sp. (o,a,s)	5	L	5
	244	*Coniopteryx tineiformis* Curtis (o)	1	A	1
	245	*Kimminsia subnebulosa* (Stephens) (o,s)	8	L	7
Lepidoptera	246	Oecophoridae sp. (h)	1	P	1
	247	Tortricidae sp. (s)	2	L	2
Coleoptera	248	*Dromius quadrimaculatus* (L.) (o,a,s,h)	9	A	8
	249	*Agathidium varians* Beck (a)	2	A	2
	250	*Stenichnus* sp. (o,h)	2	A	2
	251	*Ptinella denticollis* (Fairmaire) (o,a)	5	A	3
	252	*Ptinella errabunda* Johnson (o,a,h)	35	A	8
	253	*Dropephylla ioptera* (Stephens) (s,h)	2	A	2
	254	*Atrecus affinis* (Paykull) (h)	8	A + L	2
	255	*Gabrius splendidulus* (Gravenhorst) (o)	3	A	1
	256	*Tachyporus chrysomelinus* (L.) (h)	1	A	1
	257	*Oligota apicata* Erichson (a)	1	A	1
	258	*Leptusa fumida* (Erichson) (o,a,s,h)	50	A	27
	259	*Leptusa ruficollis* (Erichson) (o,a,s,h)	63	A	40
	260	*Atheta* (s.g. *Mocyta*) (? *fungi* (Gravenhorst)) (h)	1	A	1
	261	*Ischnoglossa prolixa* (Gravenhorst) (o)	5	A	2
	262	*Euplectus fauveli* Guillebeau (o,a)	5	A	5
	263	*Bibloporus minutus* Raffray (o,a,h)	6	A	5

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Coleoptera (cont'd)	264	*Malthodes marginatus* (Latreille) (o,a,s,h)	82	L	41
	265	*Malachius bipustulatus* (L.) (o)	1	L	1
	266	*Denticollis linearis* (L.) (s)	3	L	1
	267	*Cyphon variabilis* (Thunberg) (o,a,s,h)	8	A	8
	268	Cucujoidea, larva Y (s)	1	L	1
	269	? *Dacne* sp. (a)	4	L	1
	270	*Cryptophagus ruficornis* Stephens (a)	4	A	3
	271	*Atomaria fuscata* (Schoenherr) (s)	1	A	1
	272	*Stephostethus lardarius* (Degeer) (s,h)	7	A	3
	273	*Aridius bifasciatus* (Reitter) (a,h)	6	A	6
	274	*Aridius nodifer* Westwood (s,h)	2	A	2
	275	*Enicmus transversus* (Olivier) (s,h)	13	A	9
	276	*Corticaria elongata* (Gyllenhal) (h)	1	A	1
	277	*Cortinicara gibbosa* (Herbst) (o,s)	2	A	2
	278	*Cerylon ferrugineum* Stephens (o)	2	A	2
	279	*Calvia quattuordecimguttata* (L.) (h)	1	A	1
	280	*Cis vestitus* Mellié (o)	1	A	1
	281	*Ennearthron cornutum* (Gyllenhal) (o)	2	A	1
	282	*Grynobius excavatus* (Kugelann) (h)	8	A + L	6
	283	? *Ochina ptinoides* (Marsham) (o)	2	L	1
	284	*Anobium ?punctatum* (Degeer) (h)	1	L	1
	285	*Ptilinus pectinicornis* (L.) (s)	21	A + L	5
	286	*Rhinosimus ruficollis* (L.) (s)	1	A	1
	287	*Rhinosimus planirostris* (F.) (a,s,h)	16	A	11
	288	*Anaspis rufilabris* (Gyll.) (o,a,h)	6	A	6
	289	*Tomoxia bucephala* Costa (a)	1	L	1
	290	*Orchesia minor* Walker (a)	1	A	1
	291	*Grammoptera ruficornis* (F.) (a,s)	6	L	6
	292	*Phyllotreta undulata* Kutschera (o,s)	2	A	2
	293	*Rhynchaenus fagi* (L.) (a,s,h)	3	A	3
	294	Curculionidae (not *Rhynchaenus*) indet. (o,a)	2	L	2
	295	*Hylesinus crenatus* (F.) (a)	3	A	3
	296	*Hylesinus ?oleiperda* (F.) (a)	2	A	1
Hymenoptera	297	Tenthredinidae, indet. (s,h)	2	L	2
	298	Braconidae, indet. (a)	1	A	1
	299	*Aphidius* sp. (o)	1	A	1
	300	Cryptinae, indet. (o,s)	3	P	2
	301	*Hemiteles* s.lat. *?aclastus* sp. (a)	1	A	1
	302	*Gelis arcator* Panzer (o)	1	A	1
	303	*Lissonota* sp. (o)	2	P	2
	304	*Xyalaspis* sp. (s)	1	P ← L	1
	305	*Macromesus amphiretus* Walker (a)	1	A ← P	1
	306	*Syrphophagus* sp. (s)	1	A	1
	307	Eulophidae sp. (o)	1	A	1
	308	*Trichogramma evanescens* Westwood (o,a)	6	A	6
	309	*Dicopus minutissimus* Enock (o,a,s)	25	A	10
	310	Proctotrupidae, indet. (h)	1	P	1
	311	*Ceraphron* sp. C (scutellum margined) (o,a,s,h)	8	A	7
	312	*Ceraphron* sp. D (scutellum not margined) (s)	1	A	1

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Hymenoptera (cont'd)	313	*Ceraphron* sp. E (v. flat scutellum) (a,s)	2	A	2
	314	*Lygocerus* sp. (Ceraphrontid sp.I, with stigma) (s)	1	A	1
	315	*Conostigmus* sp. (Ceraphrontid sp.III, with stigma) (h)	1	A	1
	316	*Atricomellus/Dendrocerus* (Ceraphrontid sp.IV, with stigma) (o)	1	A	1
	317	Ceraphrontid sp.II (with stigma) (o)	1	A	1
	318	*Leptacis* sp. (a)	1	A	1
	319	*Passaloecus* sp. (s)	1	A	1
	320	*Rhopalum clavipes* (L.) (s)	1	A	1
	321	*Rhopalum coarctatum* Scopoli (a)	1	A	1
	322	Crabronidae, sp.I (s,h)	2	P ← L	2
	323	Crabronidae, sp.II (o)	2	P ← L	1
Diptera	324	*Tipula irrorata* Macquart (h)	2	L	2
	325	*Tipula flavolineata* Meigen (a,s)	2	L	2
	326	?*Nephrotoma* sp. (h)	2	L	1
	327	Psychodidae, indet. (s)	2	L	1
	328	s.f. Orthocladiinae (a,h)	6	L	4
	329	*Forcipomyia* sp. (o,a,h)	14	P + L	7
	330	*Culicoides* sp. (a,h)	2	A	2
	331	Sciophilinae, sp. (o,s,h)	7	L	5
	332	*Sciara* sp.I (o,a,s,h)	8	A + P	8
	333	?*Mycophila* sp. (wingless female), sp,III (h)	1	A	1
	334	*Mycophila barnesi* Edwards, larva J (o,a,s,h)	64	L	15
	335	*Leptosyna nervosa* (Winnertz) larva B (o,a)	1081	L	17
	336	*Brittenia fraxinicola* Edwards (o,a,s,h)	177	L	34
	337	nr. *Brittenia* (?*Nikandria*) (a,s)	48	L	6
	338	??Heteropezinae - v. obscure (a)	3	L	1
	339	nr. *Camptomyia* sp.I (a,s)	2	L	2
	340	nr. *Camptomyia* sp.II (a,s)	11	A	5
	341	?cf. *Schizomyia* (a)	1	A	1
	342	nr. *Tricholaba* sp.I (a,s)	3	L	3
	343	nr. *Tricholaba* sp.II (h)	1	L	1
	344	nr. *Tricholaba* sp.III (o)	1	L	1
	345	*Lestodiplosis* spp. (o,a,s,h)	176	L	80
	346	nr. *Putoniella* sp. (a,s)	4	L	2
	347	*Echinella* (?*albiventris* Mamajev) (o,h)	10	L	2
	348	cf. *Karschomyia* (s)	1	A	1
	349	?nr. *Karschomyia*, larva N (a,s,h)	38	L	8
	350	nr. *Rhipidoxylomyia* (o,a)	34	L	2
	351	cf. *Winnertzia* (h)	2	A	1
	352	nr. *Winnertzia*, sp.I (a,s,h)	13	L	4
	353	nr. *Winnertzia*, sp.II (a)	2	L	1
	354	Trifila, indet. (h)	1	A	1
	355	s.f. Epiphiniinae (s)	1	L	1
	356	Stratiomyidae, other (o)	1	L	1
	357	Coenomyiidae, indet. (a,s)	5	L	2
	358	?*Platypalpus* sp. (o,a,s,h)	87	L	53
	359	?*Rhamphomyia* sp. (o,a,s,h)	14	L	10
	360	*Megaselia* sp. (o,h)	11	A	3

Appendix 1 (cont'd)

Order	Code no.	Species	Total abundance	Stages found	Total frequency
Diptera (cont'd)	361	Phoridae, other (s)	1	A	1
	362	Lonchaeidae (o,a,s,h)	23	L	11
	363	Sciomyzidae (s)	1	P	1
	364	*Bigonicheta setipennis* (Fallen) (o,s)	5	P	3
	365	*Orthellia caesarion* (Meigen) (o,s)	5	A	3
	366	?Muscidae, larva P (not *Orthellia*) (o)	1	L	1
	367	?Muscidae, larva B (not *Orthellia*) (s,h)	4	L	4
	368	Muscidae, true (not *Orthellia*) (s,h)	4	L	2
		Total animals = 46,635			
		Total species = 368			
		$\propto = 54$