The Landscape Ecology of Hedgerows with particular reference to Island Biogeography

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"Once again I see,
These hedgerows, hardy hedgerows,
Little lines of sportive wood run wild."

William Wordsworth

Abstract

Hedgerows constitute a major wildlife habitat in many areas of Britain. The theory of *island biogeography*, and in particular the equilibrium model, is often invoked to explain the characteristics of communities inhabiting habitat patches. The particularly interesting feature about hedgerows is that they are both a *linear*, and often an *interconnecting* patch-type. *Landscape ecology* addresses the spatial and temporal relationship between patch and matrix habitats and may, therefore, contribute to an understanding of species distributions in hedgerows.

Hedgerows on arable land in North Yorkshire and Oxfordshire were studied to assess which factors influence community characteristics and to determine the relevance of island biogeographic and landscape ecological concepts. Three contrasting wildlife groups were studied. First, a plant study addressed the extent to which *habitat area* can be used to predict species richness. Only in Oxfordshire did a significant *species-area effect* exist. Hedgerow *isolation* was also investigated by using indices of connectivity and with the formulation of a *hedgerow accessibility* index that attempted to measure the degree of physical connectance of a hedge to the surrounding hedgerow network. These indices were only of minor interpretive value and both their conceptual limitations and the difference between *functional* and *physical* habitat connectance is recognised.

Second, a small mammal study investigated the habitat preference of species and the movements of individuals in and around hedgerows that were either *isolated* or well *connected* to others. Species-specific patterns in field/hedgerow preference and movement behaviour were observed. There appeared to be no reliance on hedgerow connections for inter-hedge movement although the presence of nearby roads and verges may have modified movement patterns.

Third, a study of millipedes and woodlice addressed both the effect of hedgerow connections and the influence of soil properties on species distributions. Soil pH appeared to be a major determinant of community composition. Hedgerow configuration history and the possibility of 'relic' communities are discussed.

It is considered that the role of hedgerows as habitats and corridors will depend upon the autecology of the species considered, the quality of the hedgerow habitat and the nature of both the adjacent fields and their surrounding hedgerow network. Island biogeographic concepts are unable to model adequately community characteristics in hedgerows both because of their often narrow and interconnecting nature and because of the temporarily variable land matrix in which they are set. Landscape ecology and *metapopulation dynamics* may be more profitable conceptual frameworks within which to address the community characteristics of hedgerows.

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Acknowledgments

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During the course of my studies, financial support to attend a Nordic Council of Ecology workshop on metapopulations in Finland was gratefully received from the British Ecological Society. Also on an appreciative note, I would like to mention the Yorkshire Mammal Group and the College of Ripon & York St. John who generously lent me their Longworth traps. The small mammal study was additionally aided by the York Tackle Shop who cheerily provided an endless supply of bait. Thanks are also due to the flotsam and jetsam of friends and colleagues who occasionally helped me to conduct fieldwork; their accompaniment was generally of assistance, sometimes a hindrance, but *always* a pleasure. After my displacement from the lab, Jean Williams and Lyn Minto deserve a special mention for allowing me to borrow their knick-knacks and for only grumbling about it sometimes.

My parents, and one or two notable teachers, deserve a sincere thank you for their encouragement and support throughout my education. With their help dyslexia has not

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Declaration

The work presented in this thesis reports original research carried out by myself. It is hitherto unpublished with the exception of Appendix 6.1 which is a duplicate of a chapter written primarily by myself that appears in *Habitat Conservation for Insects: A Neglected Green Issue* published by the Amateur Entomologists' Society (1991). It has relevance to several of the chapters and is, therefore, included as an appendix to the general discussion (Chapter 6). It does not report field research conducted by the author but is a synthesis of facts and ideas relating in particular to the conservation of insects in hedgerows.

Preliminary notes

Many of the chapters of this thesis are more or less self-contained and consequently each chapter is accompanied by its own list of references. Following suit, appendices are also included at the back of each relevant chapter. This arrangement makes referral to related material easier and has been adopted to facilitate the intended migration of certain chapters to the published page. For completeness, a composite reference list of work cited is also given at the back of the thesis.

The physical measurements used throughout are in metric units and statistical abbreviations follow Steel & Torrie (1981). The nomenclature for plants, mammals, woodlice, and millipedes follow Clapham *et al.* (1985), Corbet & Harris (1991), Harding & Sutton (1985), and Blower (1985) respectively.

To illustrate the mixed blessings of modern technology, I would like to advise readers that should there be any reference in this thesis to 'haggis', 'head-gear' or 'hetaerism' then this is due to incongruous substitutions made by the automatic spell-checker on the word processor used to type its many pages. In total, the words hedge(s) and hedgerow(s) have been mentioned 2,074 times and it is hoped that inadvertent and wayward key-strokes used in their typing have not prompted erroneous substitution by fanciful spell-check alternatives. Neither haggis nor head-gear, least of all hetaerism, are the subject of this thesis.

Chapter 1

General Introduction

Contents

> *"Hedges that lovers love, and orchards, shrubberies, walls*
> *Where the sun untroubled by north wind falls"*
>
> Edward Thomas

1.1 Overview and thesis structure

In whatever context, hedgerows can not be considered without recognition of their agricultural role for it is within this capacity that they largely owe their existence. Yet so integrated is their place in the rural landscape of lowland Britain, that their role as a haven for wildlife, their scenic contribution and their cultural heritage can all be mentioned in the same breath as any reference to past or present agricultural function. This thesis investigates just one of the diverse facets of hedged field boundaries; namely, their role as *habitats* and *corridors* for wildlife. In doing so, a broad comparative approach has been adopted that addresses the contrasting wildlife groups of plants, arthropods and mammals. In this consideration of the wildlife role of hedgerows the theories of *island biogeography* and *landscape ecology* have been drawn upon as a means to help elucidate the factors that determine the species richness and the composition of communities found within the hedgerow habitat.

Before the corner-stone concepts of island biogeography and landscape ecology are introduced in sections 1.3 and 1.4 respectively, it is important to place the discussion of hedgerow wildlife into an agricultural, historical and social context. Indeed, in any comprehensive review, the consideration of hedgerow wildlife is incomplete without an understanding of the place of hedgerows in our countryside and culture. Within this wider context, it becomes apparent that throughout history the planting and removal of hedgerows has been both a cause of discontent and social comment and a source of cultural enrichment. Along with an overview of the wildlife to be found in hedgerows, these perspectives will be outlined in the next section (section 1.2). The general aims of the thesis are outlined in section 1.5, and, importantly, an explanation of the terminology used in the subsequent chapters is given in section 1.6.

Chapter 2 of the thesis describes both the general study approach adopted and the selection of study sites. The studies of the three wildlife groups investigated are considered, in turn, in Chapters 3 to 5; while the composite picture of hedgerows as a wildlife habitat is presented in Chapter 6 with reference to the previous chapters and additional source material. This last chapter also addresses in general terms some of the shortfalls of the studies, indicates important areas where knowledge is lacking, outlines the genetic implications of population isolation, and looks towards a synthesis of disciplines as a fruitful future direction.

1.2 Background and related matters

1.2.1 History, agricultural role and status of hedgerows

The history of hedgerows can not be considered without reference to changes in agricultural practice for the two are inextricably linked. Throughout history, farming policy and land ownership has motivated both hedge planting and removal. Consequently, the configuration and extent of hedgerows that we see in the landscape today are a result of both historic and current agricultural policy (see Photograph 1.1).

Photograph 1.1 A typical lowland landscape in Oxfordshire with hedgerows bordering both arable and pasture fields.

The need for agricultural hedges first arose with the domestication of animals, and although the first 'hedges' were probably of dead wood they may have provided suitable conditions for the spontaneous growth of a living hedge. Indeed, this is one of the three possible origins of hedgerows; namely (i) deliberate planting, (ii) woodland clearance (remnant vegetation), and (iii) spontaneous growth (Forman & Baudry 1984, Rackham 1986). The balance of these methods of origin is likely to have changed dramatically over history, with the former mechanism certainly being the predominant from the start of the Parliamentary Enclosures, around 1750. The number of hedgerows that owe their existence to each process and the date of their origin is almost impossible to estimate because of the long time spans involved, the lack of documentary evidence, and the varying agricultural practices conducted in different parts of the country at any one time. It has been suggested, however, that as a result of periods of agricultural neglect (e.g. during the Dark Ages) approximately one-quarter of our hedgerows have arisen spontaneously (Rackham 1986) and that only one-third of extant hedgerows originate from the Parliamentary Enclosure period (Muir & Muir 1987). The assumption of many, that hedgerows predominantly date from the Parliamentary Enclosures, may simply be a consequence of the existence of a large number of historical records dating from this period that document both the planting of hedgerows and the social changes that the Parliamentary Enclosures both reflected and brought. Indeed, Rackham (1976) considers that "*few popular myths have been more pernicious than the notion that all hedges date from the Parliamentary Enclosures*". It is certainly the case that generalisations about the age of Britain's hedgerows as a whole are misleading. For instance, while many hedgerows in certain counties of the Midlands may indeed be of Tudor and Parliamentary Enclosure origin, a large proportion of those of South-West England may be of much greater antiquity (Hoskins 1955, Wilson 1979).

The agricultural impetus for such landscape change is ever present but the history of change is often complex and, consequently, no detailed account will be given here. The rise of the woollen industry, the abandonment of the open-field system, the abolition of common land rights and an increasing urban population are, however, foremost in any consideration. It is without a doubt that one of the most dramatic changes to the landscape did come about as a result of the Parliamentary Enclosures. For although hedgerows were not a new feature within the landscape, the impact of the *c.* 1750-1860 enclosures was particularly great because the rate of planting was extremely rapid. Between these dates, some four to five thousand Acts of Parliament were passed that enabled the enclosure of approximately three million hectares of land (ADAS 1986, Dalyell 1990). The enclosure hedges tended to be linear and geometrically arranged within the framework of existing hedgerows that date from earlier agricultural periods.

Many of the hedgerows already existing were planted in piecemeal fashion by private agreement during the centuries before (Hoskins 1955, Taylor 1975, Butlin 1982).

Changes in agricultural practice in the latter half of this century have again been the impetus for landscape change. Since the Second World War, there has been a dramatic reorganisation of fields and farming practice that has involved the removal of hedgerows to both free unproductive land and also to enable the use of larger and more efficient farm machinery (Photograph 1.2). The decline in mixed farming (facilitated at least partially by the widespread introduction of inorganic fertilisers) and the introduction of more flexible methods of fencing has also been contributory to landscape change because hedges are no longer needed to the same degree as a means to impede the movement of stock. A detailed discussion of the changes in agricultural policy and their influence on wildlife will not be given here and readers are directed towards the work of, for example, Edwards (1968), Coppock (1968), Sturrock & Cathie (1980), Mellanby (1981) and O'Connor & Shrubb (1986). It should be noted, however, that concern has been expressed regarding the disadvantages of hedgerow removal which in the long run may off-set the advantages. Included among these are the loss of scenic beauty and wildlife (Muir & Muir 1987, Mellanby 1981, Shoard 1980, Pye-Smith & Rose 1984), the loss of income and the associated problems of soil erosion (Dudley 1985, Arden-Clarke & Hodges 1987), reduced populations of predatory arthropods (Sotherton 1984) and pollinators, falling numbers of game birds (Sotherton 1982, Rands 1987) and ergonomic factors (Dowdeswell 1987).

In the drive to increase agricultural efficiency (Sturrock & Cathie 1980), the grubbing up of hedgerows has occurred extensively since the 1940s and it has been estimated that 22 % of the hedgerows in England and Wales have been lost during the period 1947-1985 (CC 1985a) (see Photograph 1.3). Indeed, up until 1974 grants were available from the Ministry of Agriculture for hedgerow removal. Of the 1,600 km of hedgerows estimated by the Ministry of Agriculture to have been removed per year between 1957 and 1969, Hooper & Holdgate (1968) cite that approximately half of this was with the assistance of government grant aid.

A recent study undertaken by the Institute of Terrestrial Ecology estimated that 9.5 % of the hedgerows present in Great Britain in 1984 were lost during the six year period up to 1990 (Barr *et al.* 1991). This represents a total loss of 174,000 km, although only

Photograph 1.2 Tractor ploughing harvested wheat field in Oxfordshire: as farm machinery increases in size to reduce labour costs so too must field size increase to maximise machine efficiency.

Photograph 1.3 Hedgerow removal during road construction in North Yorkshire.

52,000 km of this total is attributable to direct hedgerow removal. Of the remainder, it is significant that 111,000 km is attributable to the deterioration of hedgerows as a result of management neglect and mis-management. As a consequence these former hedgerows are changed considerably from their original character and more closely resemble lines of trees or shrubs than hedgerows. It is apparent, therefore, that indirect hedgerow loss as a consequence of management neglect has become a greater threat to the hedgerow habitat than the grubbing out of hedgerows *per se*. This increasing incidence of neglect and mis-management is despite the advice available to farmers and landowners in the form of pamphlets (e.g. CC 1980, ADAS 1986) and through the Demonstrations Farm Project (CC 1985b).

Prior to this study, the Ministry of Agriculture estimated that combined hedgerow removal in England and Wales continued at a gross rate of about 1,600 km per year between 1980 and 1985 (a total loss of 8,000 km) with net hedgerow loss being half this figure (MAFF 1985). While for the period 1978 to 1984, hedgerow loss was estimated by *Barr et al.* (1986) to be 28,175 km for Great Britain as a whole. Allison (1989) remarks that there is little evidence of a decline in the rate of hedgerow removal for the 1980s, with the possible exception of parts of eastern England where few hedges remain. The latest available figures suggest that there are approximately 428,000 km of hedgerows remaining in Great Britain, with 378,500 of these being located in England and Wales (Barr *et al.* 1991). Hunting Technical Services estimated that in 1947 there were 796,600 km of hedgerows in England and Wales (CC 1985a) and so for the period 1947 to 1990 it would appear that about 52% of hedgerows in England and Wales have been lost. The differing methodologies used by the two studies mean, however, that this figure is an over estimation of hedgerow loss (as is evident from the discrepancies between estimations of hedgerow length for periods that both studies cover).

In the last decade there has been a change in Britain's agricultural policy from that of *intensification* to that of *extensification*. Over-production within the European Community's Common Agricultural Policy and the expense of both guaranteed prices and the storage and destruction of food surpluses (Rose 1986, Crabtree 1982) has seen the introduction of a *set-aside* policy and promotion of less intensive farming practices within designated regions (Environmentally Sensitive Areas). With particular reference to hedgerows, recent policy change has brought about the introduction of hedgerow planting and management grants (MAFF 1987). In England and Wales, for the five years up to 1985 an estimated 8,000 km of hedgerows were planted (MAFF 1985), while between 1984 and 1990 an estimated 23,100 km of new hedgerows were created (Barr *et al.* 1991). This apparent increase in the rate of hedgerow planting between the first and second half of the 1990s (1,600 km yr^{-1} to 3,850 km yr^{-1}) may indicate that the fortunes of the hedgerow have to some extent turned full circle. It is the case, however, that newly planted hedgerows are generally a poor substitute for established ones that have greater historical, wildlife and scenic value.

The loss of hedgerows with particular value has been a matter of concern for many years, although as yet there is no legislation for their protection. Individual hedgerow trees may be protected by a Tree Preservation Order but such designation does not offer protection for the hedgerow of which the tree is a part. This lack of statutory protection is despite the continued efforts of some Members of Parliament (Hardy 1982, 1983, 1989) and conservation bodies, such as the Royal Society for the Protection of Birds (Morgan 1988), to introduce a system of hedgerow preservation. Under such legislation it would be a finable offence to grub up designated hedgerows without prior permission (Hardy 1982, 1983).

The present Conservative Government has favoured a system of voluntary co-operation with financial incentives, although until very recently such a scheme has received lip-service only. An indication that a policy on hedgerow protection may be forthcoming is that the Government's recently published 'green manifesto' states that local authorities may be granted powers to protect hedgerows of key importance by "*making preservation orders, with appropriate payments to farmers to look after them properly*" (DoE 1990). This position has been affirmed more recently in both the House of Lords and the House of Commons by government representatives (Darke 1992) whose statements confirm that a policy of incentive payments to encourage hedgerow rejuvenation is being formulated (Blatch 1991). In addition, proposals were revealed of a scheme requiring both the registration of hedgerows of key importance and the mandatory notification to local authorities of the intention to remove hedgerows (Baldry 1991).

It is of note that hedgerow loss and laws relating to their protection are not a phenomenon confined to recent decades. In 1792 it was reported to the House of Commons Journal that

> *"The grubbing up of hedgerow become general, and the growth of timber in them is thereby totally destroyed, owing to the great price of corn and beer, which gives every farmer encouragement to grub hedgerow up, and convert them into cornland."*
>
> (from Rackham 1976).

Indeed, if a hedgerow preservation policy involving penalties is introduced in the near future, it is implausible that it would be empowered with the ability to punish and humiliate in the manner that the law carried some 400 years ago in the county of Essex. Rackham (1986) cites that in 1600 those found damaging hedges in Ingatestone were to be whipped until they "*bleed well*", and three years earlier in Felsted it was passed that

> *"any person breaking a hedge or stealing wood be put next Sunday or holyday in the stocks for two hours at the least, and the wood be placed before them, signifying the cause of their punishment."*

The last prosecution for hedgerow destruction was in 1926 when a Parliamentary Enclosure hedge was removed; under the Enclosure Acts hedges were to be maintained in perpetuity, although today the act is seldom interpreted as such (Hardy 1983, Dalyell 1990). With any system of hedgerow protection, it is vital that the goodwill of farmers and landowners be harnessed for without sympathetic management the wildlife and scenic value of hedgerows can be diminished regardless of any gross destruction (Dowdeswell 1987, Jones *et al.* 1991). It is both their realised and potential habitat value and their ability to enhance the landscape that is considered in the next sub-section.

1.2.2 Wildlife and scenic value of hedgerows

The intensification of farming that has taken place in recent decades has greatly reduced the area of a number of major wildlife habitats on farmland (Lowe *et al.* 1986). Coupled with the increased agrochemical inputs to land already under cultivation or pasture, this has meant that the potential value of hedgerows as a wildlife habitat is now greater than ever. Although no national plant rarities are restricted to hedgerows, ten rare species are found within the hedgerow habitat (Hooper 1970). Moreover, out of approximately one-thousand plant species that have been recorded in hedgerows, some 250 of these are inextricably associated with this habitat (NCC 1979). In addition, some 80% of our woodland birds, 50% of mammals, 30% of butterflies and all our species of amphibians and reptiles have been recorded from the hedgerow habitat (ADAS 1986). The habitat value of hedgerows for invertebrates is as yet unquantified in terms of number of species even within particular orders. Their value as breeding, feeding and overwintering habitats is, however, likely to be considerable (see Pollard 1968a & b, Lewis 1969a & b, Cameron *et al.* 1980, Sotherton 1982 & 1984, Sotherton *et al.* 1985, Morris & Webb 1987, Wratten 1988 and Jones *et al.* 1991). Under proper management it is beyond doubt that hedgerows can be valuable 'island' habitats for many plant and animal species that are unable to inhabit the highly disturbed adjacent farm land. However, it is interesting to note that certain poets writing around the time of the Parliamentary Enclosures documented the view that hedgerows were detrimental to wildlife. For example, John Clare, the nineteenth century poet, wrote of the enclosures

> *"And bird and tree and flower without a name,*
> *All sighed when lawless laws enclosures came."*

and in 1857 Chandos Wren Hoskyns wrote of hedgerows "*hideous and useless strong holds of roots, weeds, birds and vermin that afflict the farms of merry England*" (from Mellanby 1981).

In addition to the established insular habitat value of hedgerows, they are popularly perceived to have another wildlife function; that of facilitating the *movement* of plants and animals through the landscape. Indeed, much lip-service has been paid to the idea that they act as '*corridors*' for movement and dispersal. Although intuitively appealing, their true value as movement corridors is uncertain. This frequently stated function is introduced more fully in section 1.4. At this stage, however, it is important to note that if under certain circumstances the structural connections between hedgerows do indeed create an integrated series of corridors, then the inter-patch movements of individuals that these connections facilitate may have far reaching implications for the genetic characteristics of inhabitant populations. The maintenance of genetic diversity is vitally important for it enables a greater flexibility of response to environmental and biotic disturbances and so facilitates the persistence of at least some individuals within a population.

It is a widely held view that hedgerows and hedgerow trees have considerable scenic value (Hooper 1991). They both create a variety to the eye and a sense of intimacy and seclusion that makes many appreciative of their presence in the landscape. Indeed, so familiar are we with the hedged landscape of lowland Britain that the mosaic pattern of hedgerow and field is typically seen to be the hallmark of the English countryside (Muir & Muir 1987). Despite this they are not solely an English feature for the landscapes of Scotland (Tozer & Taylor 1978), Ireland (Webb 1988), and Wales (MAFF 1985) all benefit from the presence of hedgerows. Moreover, hedgerows are not even particular to Britain for they form the "*bocage*" (hedgerow landscape) of Normandy and Brittany in western France (Terrasson & Tendron 1975), and can even be found on cultivated slopes of the Peruvian Andes (Rackham 1986) and forest clearings in Indonesia. Nevertheless, hedgerows are synonymous with the English countryside and in many peoples' eyes they continue to enrich the landscape, contributing to the aesthetics of the countryside and enhancing rural recreational and leisure activities (Hardy 1983, Biber 1988) as well as nurturing a kindredship and even a spirituality with nature (Porritt & Winner 1988).

The scenic value of hedgerows is, however, a matter of taste, or perhaps more correctly, a matter of familiarity. For instance, during the eighteenth and nineteenth century enclosures, when many hedgerows were planted across the country in rapid succession, the poet John Clare wrote of the change in landscape appearance:

> "*No fence of ownership crept in between*
> *To hide the prospect from the gazing eye.*
> *Its only bondage was the circling sky.*"

and

> "*Enclosure, thou'rt a curse upon the land,*
> *And tasteless was the wretch who thy existence plann'd.*"

(from Muir & Muir 1987).

Clearly then, hedgerows have not always been considered a landscape asset and while locally their aesthetic value may be great, their ubiquitous presence throughout the landscape would create a uniformity that in itself would diminish regional character and scenic variety. Nevertheless, the significance of hedgerows in our landscape is clearly seen by their manifestation in a variety of artistic, literary and vernacular forms. Some of these are considered briefly in the next sub-section.

1.2.3 Cultural heritage

The values associated with hedgerows have perhaps undergone a reversal over history. Initially, their value will have largely been practical in that they delimited changes in land ownership, impeded the movement of stock, and provided timber, coppice wood, fruits and medicinal herbs. Today there is less reliance upon them as barriers to stock and the harvesting of hedgerow produce is more a quaint pastime than a necessity (although the hedgerow 'harvest' is advocated by Mabey (1975), Richardson (1980) and Orchard (1988)). With increasing urbanisation, agricultural intensification and the destruction of natural and semi-natural habitats, most people in Britain have never been more alienated from nature. Therefore, although not a monopoly of the present age, today it is perhaps both the subjective aesthetic and recreational roles of hedgerows (Biber 1988) that are popularly held to be their greatest cultural value (Photograph 1.4).

There is a vast and scattered literature documenting the loves and loaths of hedgerows and the enclosures that they brought. Indeed, testament to their influence on our culture is the broad spectrum of people who have made reference to them throughout history. From the commoner to royalty, from the playwright to the poet, and from the saintly to the absurd, hedgerows have been referred to in a multitude of literal and metaphorical contexts. For instance, the following popular rhyme of the enclosure periods expressed a widely felt injustice about the enclosure of common land:

> *"They hang the man and flog the woman,*
> *Who steal the goose from off the common.*
> *But let the greater criminal loose,*
> *Who steal the common from the goose."*
>
> (from Muir & Muir 1987).

Prince Philip, H.R.H. the Duke of Edinburgh, commented upon the removal of hedgerows and the changing shape of the landscape in the 1989 Richard Dimbleby *Lecture. Shakespeare in his Passionate Pilgrims* conveys a sense of blind devotion

Photograph 1.4 A layed hedge at the 1987 national hedge laying competition, held near Doncaster, South Yorkshire. In many instances the presence of hedgerows increases the recreational and leisure potential of the countryside; hedges that are traditionally managed are of additional interest (the two countryside crafts of fencing and dry-stone walling can also be seen).

"*I will but look upon the hedge and follow you*" and Wordsworth expresses the welcome familiarity of a hedged landscape (from Richardson 1980)

> "*Once again I see,*
> *These hedgerows, hardy hedgerows,*
> *Little lines of sportive wood run wild.*"

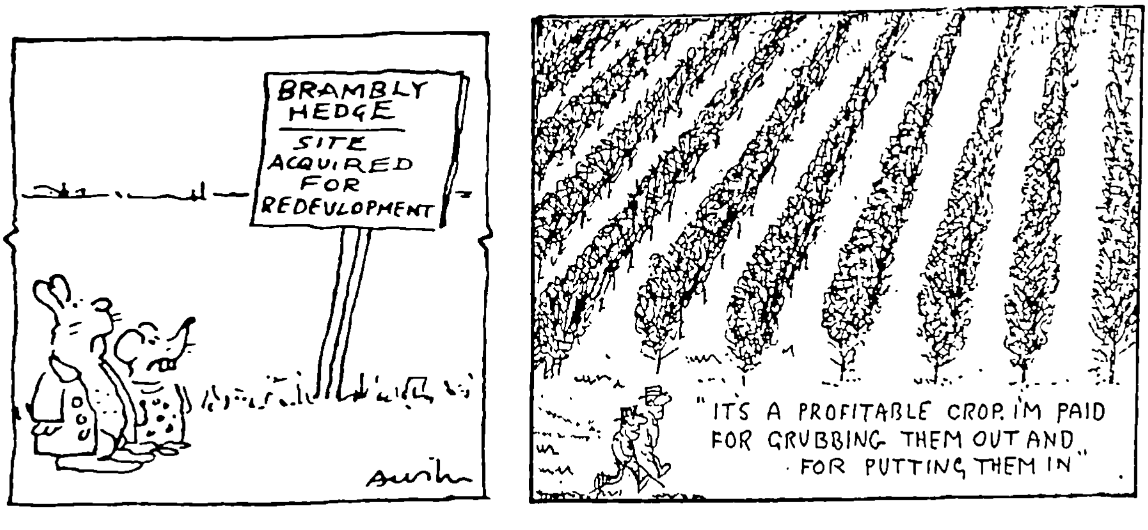
St. Luke in the Bible evangelises "*Go out into the highways and hedges, and compel them to come in*". While on the side of absurdity, in the ludicrous *Viz* comic an enquiring reader writes

> "*I have often wondered why bushes grow around the outside of fields and never in the middle?*".

To which the editor's answer is equally ridiculous

> *"...you seem to have us beaten this time. We rang the Ministry of Agriculture who told us that bushes or 'hedgerows' are always grown around the sides of fields and never in the middle. However, this is certainly not a result of recent EEC farming regulations. One farmer we spoke to told us that bushes had been growing around the edges of fields on this farm for over three generations, although he did not know why."*
>
> (Donald 1986).

If hedgerows are enigmatic in some respects then, contrary to the editor's facetious reply, this particular question is of course rhetorical. That hedgerows are the subject of popular humour, however, shows that they have come a long way to becoming a part of our culture. And if many a true word be said in jest, then the social comment of the two cartoons (Figure 1.1) appearing in recent issues of the *New Scientist* journal need no explanation; except perhaps to reiterate that the grubbing up of hedgerows is detrimental to many wildlife species, and that grants from the Ministry of Agriculture have now turned full circle from financial assistance for hedge *removal* to assistance for *planting*.



(a) (b)

Figure 1.1 Social comment made about hedgerow loss and the reversal of grant policy; (a) *New Scientist*, 21 January 1989 and (b) *New Scientist*, 17 December 1989.

The word hedge itself is thought to have a complicated derivation for the Anglo-Saxon words *haeg* (hurdle), *hecg* (a territorial boundary) and *hega* (a living or bordered boundary) (Dowdeswell 1987) and the word hedgerow is now taken by most to be more or less synonymous although I propose that the two words can beneficially be employed to define different aspects of the hedged field boundary (see section 1.6).

So integral have hedges become within our society that a large number of proverbs and sayings draw on their imagery. From the well known and cautious "*hedging your bets*" to the personified "*hedges have eyes and walls have ears*", from the philosophical "*one man may steal a horse, while another may not look over a hedge*" to the patriarchal "*I have cured her from lying in the hedge, said the man when he had wed his daughter*", and from the territorial "*hedges between keep friendships green*" to the judgmental "*he was on the wrong side of the hedge when the brains were given out*", hedgerows and their imagery have coloured the English language (Wilson 1970, Beale 1978, Simpson 1984). This influence is also manifested in the vernacular names of plants and animals and alludes to the close association between certain species and the hedged habitat. Among animals, the hedgehog (*Erinaceus europaeus*), hedge-sparrow (*Prunella modularis*) and the hedge brown (*Pyronia tithonus*) all fall into this category, as do plants such as the hedge bedstraw (*Galium mollugo*), hedge bindweed (*Calystegia sepium*), upright hedge-parsley (*Torilis japonica*), hedge mustard (*Sisymbrium officinale*) and the hedge woundwort (*Stachys sylvatica*).

Although hedges appear to be an integral part of the landscape and rural life today, they of course owe their existence to either the direct or the indirect activities of man. Their planting often caused much social and cultural discontent because of the changes in land ownership and agricultural practice that this often heralded. This contrasts dramatically with the romanticised view of hedgerows in much subsequent literary prose. For example, John Keats writes in *On the Grasshopper and Cricket*

> *"The poetry of earth is never dead...*
> *a voice will run from hedge to hedge about the new-mown mead"*

and Edward Thomas writes in *If I were to Own*

> "*Fields where plough-horses steam and plovers fling and whimper,*
> *Hedges that lovers love, and orchards, shrubberies, walls*
> *Where the sun untroubled by north wind falls*".

In reality, large scale enclosure both in Medieval and Georgian times was the cause of much social upheaval and hardship for it often resulted in the eviction of peasant farmers from their small holdings and common land. In 1549 a manifesto was drawn up to protest about common land enclosure in Norfolk, part of which bitterly read

> "*Shall they, as they have brought hedges about common pasture, enclose with their intolerable lust also all the commodity and pleasure of this life, which Nature the parents of us all, would have common, and bringeth forth everyday, for us, as well as for them?*".

The confrontation was lead by Robert Kett and resulted in his gruesome execution (Muir & Muir 1987). Some two hundred and fifty years later an anonymous lament to the enclosure of the Buckinghamshire parish of Thornborough (1798) expressed similar sentiments

> "*Time alas will soon approach,*
> *When we must all our pastures yield;*
> *The wealthy on our rights encroach,*
> *And will enclose our common field.*"
>
> (from Muir & Muir 1987).

Over the centuries, however, hedgerows have become a familiar and welcome feature of the landscape and hardships are forgotten. Now, both as children and adults, there is opportunity to participate in and learn about the nature, history and management of hedgerows. For instance, in the 1970s a national scheme was set-up to enable school children to survey hedges (Pollard *et al.* 1974) and in 1984 *The Times* newspaper ran a competition for young people to describe and draw their history and wildlife and received a "*happy deluge of material*" (Anon. 1984). Over the years numerous junior books have been published bringing the plants, creatures and seasons of the hedgerow to life for the young ecologist; worthy of particular note is *Hedgerow* by Thomas & White (1980) with its informative text and magnificent illustrations. The British Trust for Conservation Volunteers and the Field Studies Council both offer adult education courses in various aspects of hedgerows and the BTCV has, indeed, published an authoritative handbook on the traditional craft of hedge laying (Brooks 1980).

As indicated by the emotive language used in the press when reporting hedgerow removal (e.g. Young 1984, Lean 1989, Morrison 1990), the publication of popular journals and books on the hedgerow (e.g. Angus 1987, Young 1989) and the high profile of hedgerows in artistic expression of the countryside (e.g. Common Ground's Parish Maps Project (Greeves 1987)), hedgerows are popularly seen to enrich our culture. It is upon this broad social back-cloth of agricultural, aesthetic and literary considerations that the study of hedgerow wildlife is set.

1.3 Island biogeography

1.3.1 Conceptual development and the equilibrium theory

The geographical distribution of species has long attracted the attention of biologists and has become encompassed by the multi-disciplinary field of *biogeography* which includes elements of biology, geography, ecology, evolution and palaeontology (Pielou 1979, Brown & Gibson 1983). In the 1960s a quantitative as well as qualitative step was taken in earnest away from the large geographic and temporal scales addressed by biogeographers to the comparatively small area and time scales of those studying the distribution of species on *islands*. The study of *Island Biogeography* has now become a huge field in itself, being advanced immeasurably by the work of MacArthur and Wilson (1963, 1967). They moved the focus of attention away from the study of the origin, history or taxonomic development of a particular species, or group of species, within a geographical region to the study of the *number* of species on islands in general.

As initiated by their own work, and as built extensively upon by subsequent workers, the conceptual framework of island biogeography includes both water-locked and habitat islands. Indeed, the theory has been applied widely to many types of 'islands', including water-locked islands (Ebenhard 1987, Kelly *et al.* 1989), nature reserves (Diamond 1975, Miller 1978, Higgs 1981), woodland (Helliwell 1976), individual plants that are host to phytophages (Ward & Lakhani 1977, Davis & Jones 1986), lakes (Keddy 1976), urban habitats (Davis & Glick 1978, Crowe 1979) and even to caves (May 1977). The uniting feature of all these 'islands' is the dissimilarity of the surrounding habitats. Using this criterion, hedgerows can also be viewed as islands because they are set in a matrix of farmland that differs greatly in its physiognomy, management, micro-climate, nutrient status and disturbance regime. Despite the wide variety of island types studied, however, hedgerows are of particular interest because of their *linear* and often *interconnecting* nature. Except for other field boundaries, these two structural habitat features are generally uncommon, although water courses, railway embankments and the architecture of trees may be partially analogous).

MacArthur and Wilson were interested in recognising and modelling processes that would allow generalisations to be made regarding species distributions. The processes that they considered to be most influential in determining species richness on islands were those of immigration and extinction. Their observations lead them to propose that these processes were determined by the *area* of the island and its *isolation*. They considered that

(i) larger islands had lower species extinction rates because the increased resource availability on larger islands enable larger populations to be supported, and that

(ii) islands that are less isolated from a mainland or source population experience greater immigration because of an increased ability of dispersing species to reach them.

As influenced respectively by island area and isolation, the processes of extinction and immigration were seen then to be two opposing forces that determined species richness as a *balance* between the rate of addition and removal of species from an island. The theory was, accordingly, called the *Equilibrium Theory of Island Biogeography* (MacArthur & Wilson 1967). By way of illustration, Figure 1.2 shows how the equilibrium number of species on an island is modified both by its size and its degree of isolation; small islands that are far from a mainland species source have a low species richness in comparison to large islands that are near to a species source.

This model is intuitively appealing on account of its simplicity (McCollin *et al.* 1988, Williamson 1989) and a large number of studies have shown that species richness on both water-locked islands and habitat patches is, at least partially, explained by island area and isolation (e.g. Davis 1975, Crowe 1979, Ward & Lakhani 1979, Westman 1983, Opdam *et al.* 1985, Usher 1985). Such correlations are not, however, proof of the equilibrium theory for a number of other explanations are possible. Proof of the equilibrium model entails the empirical observation of more or less balanced rates of extinction and immigration that result in species turnover in the absence of gross changes in species richness (Faeth & Connor 1979). However, both because the dynamics of the system may operate over large time spans and because the existence of an equilibrium will depend upon the perturbance history of the island, proof of the MacArthur & Wilson model may be a long time coming. It is generally the case that static observations can offer only limited insight into the validity of the equilibrium theory although Kelly *et al.* (1989) provide a rare illustration of how such an approach can be informative (see next sub-section).

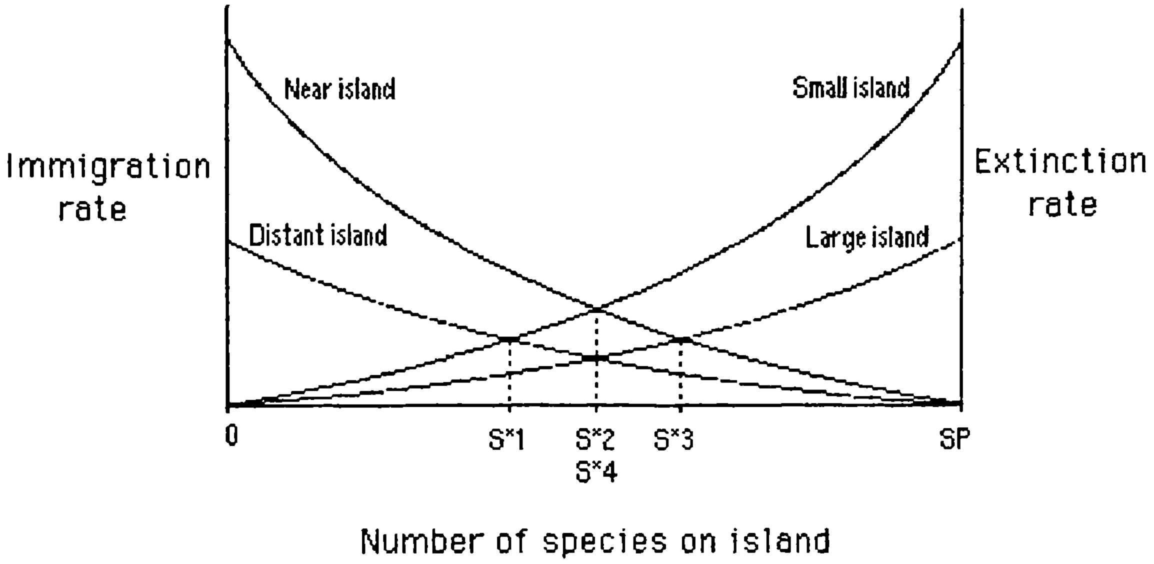


Figure 1.2 MacArthur & Wilson's (1967) equilibrium theory of island biogeography: the curves represent rates of immigration and extinction on islands of different size (small and large) and isolation from a mainland source (near and far); the equilibrium number of species for each island combination is reached when rates of immigration and extinction are in balance (S*1 to S*4); SP, the number of species in the species pool.

1.3.2 Species-area effects

It is particularly worthy of note that although the often observed positive correlation between species richness and habitat area (the *species-area effect*) can be explained within the framework of island biogeography, it is the case that this does not prove the validity of the theory. Two other explanations are widely put forward as possible explanations of the species-area effect (Connor & McCoy 1979, McGuinness 1984). These are the

(i) *Random Placement* (or *Passive Sampling*) *Hypothesis* (Arrhenius 1921, Coleman 1981, Coleman *et al.* 1982) which recognises that if species and individuals are distributed randomly then the probability of recording a particular species is positively correlated with area, and

(ii) *Habitat Diversity Hypothesis* (Williams 1943, 1964) which states that as the area of land surveyed increases so will the number of habitats and hence the number of species that are recorded.

From a wildlife conservation viewpoint, the existence of a species-area relationship is of particular importance given that the area of a habitat may determine its conservation value. This is the case because species richness is often a major consideration when making decisions about habitat conservation (Margules & Usher 1981). The nature of any relationship between species richness and habitat area is best investigated with reference to a taxonomic group of high diversity. With hedgerows a suitable group to study is the flowering plants because they are both easily identified and, with approximately 250 species commonly associated with hedged field boundaries (NCC 1979), there is considerable scope for quantitative response to changing area.

By determining the nature of the species-area relationship when recorded using a fixed-sample size it is possible to gain an insight into its cause and thus an indication of the validity of the various theories of island biogeography (Kelly *et al.* 1989). With the constraint of a fixed sampling effort that is independent of habitat area, the random placement hypothesis explanation of the species-area relationship is not invoked. Furthermore, if sampling is conducted within only one habitat type then the habitat diversity hypothesis is obviously also untenable (Kelly *et al.* 1989). Under these circumstances, therefore, an area *per se* hypothesis is favoured and as such indicates that the effects of immigration and extinction as perceived by MacArthur & Wilson may be deterministic of species richness. The investigation of the species-area relationship is, therefore, not only a means of description, it may also further an understanding of species distributions and allow decisions on hedgerow management to be made.

1.4 Landscape ecology principles

1.4.1 Isolation and structural connectance

As formulated by MacArthur & Wilson (1967), species richness will also be dependent upon the degree of isolation from source populations that the island habitats experiences. The mechanisms and the degree of isolation that *habitat patches* experience are likely, however, to be poorly modelled by their water-locked counterparts. Insular habitats may experience considerably less isolation both because *corridors* and *stepping-stones* may increase the permeability of the surrounding land matrix and because of the effects of species not being confined within discrete habitat patches (Merriam 1988). As such, habitat patches are both set in a 'sea' that is more permeable and heterogeneous than true islands and they have much 'fuzzier' outlines than true islands.

Perhaps the greatest limitation to the applicability of island biogeographical theory to the hedgerow habitat, however, is that hedgerows are generally *not structurally isolated* from one another. As such, the physical connections between them may greatly influence the degree of isolation that they experience. For any number of hedged field boundaries there will, therefore, be a significant fraction that will not be isolates in the sense conventionally applied to habitat patches. For these hedgerows, the physical connections of like with like creates a *network* of habitat 'patches'. The isolation of any hedgerow on this network will, therefore, depend upon both the *permeability* of the adjacent field matrix and the *number* of hedgerows that abut to them. In addition, to the 'island-sea' model, therefore, a model incorporating structural connections (or corridors) between habitat 'patches' needs to be envisaged. Such a framework is seen in the emerging discipline of *Landscape Ecology* (Forman & Godron 1986) which addresses the spatial configuration of landscape elements, their function interactions and the changes in these structural and functional interactions with time (Forman & Godron 1984).

Although landscape ecology incorporates many principles of traditional biogeographical hypothesis, it extends and adds to them and emerges as the *terra firma* equivalent to island biogeography of the seascape. In addition to recognising both the structural and functional connections that exist between habitat patches (Baudry & Merriam 1988), landscape ecology recognises the heterogeneous nature of the landscape matrix. It seeks to understand species patterns that may extend on a scale from tens to thousands of metres depending on the size and nature of the habitat patches under consideration and the hierarchical level of the questions posed (e.g. patch to matrix movements of an individual or the landscape-wide dynamics of an entire population). It is the recognition of structural connectivity between habitat patches, and the implication that these connections have for the interaction of populations, that sets landscape ecology apart from traditional island biogeographical thinking (McDonnell & Pickett 1988). As such, it may be especially valuable as a means to investigate the distribution of wildlife in hedgerows which by their very nature are interconnecting. Despite this recognition, the structural relationship between habitat patches has rarely been addressed in functional ecological terms by empirical studies (Forman & Godron 1984, Bridgewater 1987). Considerable scope exists, therefore, for the study of such connections and their implications for species distributions. Hedgerows provide an excellent opportunity for an assessment of the connection attributes of the landscape.

1.4.2 Patchy habitats and metapopulations

A further example of how island biogeography can not readily be applied to the habitat setting is the notion of a 'mainland' source and an 'island' sink (Merriam 1988, Hanski & Gilpin 1991). While entirely reasonable in many oceanic settings, the source-sink relationship in habitat patches may be more ambiguous. Intensively farmed agricultural land typically consists of a multitude of habitat patches that may exist within a relatively restricted size range. As such, major source and sink habitats may not be easily defined. Rather the role of donor and recipient may be much more evenly spread between patches and may, indeed, fluctuate markedly depending on the specific local conditions that prevail at any one time.

This possibility has been formulated into the concept of the *metapopulation* (Levins 1970, Hanski 1989) which is defined as a population of interacting sub-populations which have a finite life (Hanski & Gilpin 1991). When applied to the agricultural setting (Baudry & Merriam 1988, Opdam 1988), the hypothesis proposes that a landscape-wide population that inhabits a series of patches existing within a fragmented environment (such as hedgerows or woods on farmland) may operate as a series of interacting sub-populations. Such sub-populations have strong intra-patch interactions on a *local scale* but weak inter-patch interactions on a *metapopulation scale.* The between-patch interactions are, nevertheless, vitally important because they allow the movement of individuals and genetic information that may facilitate the existence of the population at the landscape level. As such, sub-populations inhabiting patches may undergo *local extinctions* without long-term detriment to the population as a whole so long as recolonisation of uninhabited patches occurs at a greater rate than that of patch-population extinction (Hanski 1989). A metapopulation is, therefore, crucially dependent upon the dispersal and movements of individuals between habitat patches.

Obviously, the survival of the metapopulation is determined by the extinction rates experienced by the sub-populations within the habitat patches, the ease of dispersal between patches, and the establishment success once patches have been reached (Hansson 1991). Depending on the hierarchical level considered (Burel 1989) hedgerows can, therefore, be viewed both as features linking up habitat patches (such as farm woodlands) and as patches themselves that differ in their degree of isolation depending upon the heterogeneity and permeability of the surrounding matrix and upon their degree of connectance with other hedgerows. Again, therefore, it is necessary to extend and adapt the island biogeographical model in order for a transition to be made to the terrestrial setting. The metapopulation concept is a comparatively well researched aspect of the population dynamics of fragmented habitats; the considerable empirical and theoretical basis upon which it is built (Hanski & Gilpin 1991) means that it is at the forefront of research into landscape ecological principles.

1.4.3 Landscape scale

The possible role of hedgerows as islands and corridors is both a particularly fascinating possibility and one that is likely to afford few generalisations. It is likely to be crucially dependent upon the *scale* of enquiry (Merriam 1988, Burel 1988, 1989) and on both the habitat requirements of the species under consideration and their dispersal rates and mechanisms (Opdam 1988). For instance, species that need shady and/or relatively undisturbed ground in which to live but which are not reliant upon directional habitats for movement or dispersal will use hedgerows solely as 'island' habitats. Species that are restricted to woodland but which require directional features through which to disperse may use hedgerows solely as 'corridors'; while species that inhabit hedgerows and which have limited powers of dispersal may use them both as 'islands' and 'corridors'.

From an ecological viewpoint, it is interesting to address the study of hedgerows from a number of hierarchical levels (Burel 1989). At least initially, however, the most important scale is that which addresses the interactions between one hedgerow and another. By extension, it is then possible to address hedgerows at a network level and ultimately at a hierarchical level that addresses the role of hedgerow corridors and networks in connecting habitats of a different type with one another (i.e. the connection of two woodlands by a series of interconnecting hedgerows).

At all levels of consideration, however, the season of the year may have great bearing upon the functional role of hedgerows (Opdam 1988). Agricultural landscapes, and in particular arable ones, have extremely abrupt changes in habitat characteristics as fields are ploughed, planted and harvested. With these changing patterns in field characteristics there are also likely to be changes in habitat use and resource utilisation by many species. The role of hedgerows is seen, therefore, to be highly convoluted depending upon the autecology of the species, the structural characteristics of the hedgerow network, the hierarchical level of consideration and the temporal variability of agricultural landscapes.

1.5 General aims of research

The specific aims of the three studies presented here are explained in Chapters 3 to 5 respectively. The general aim of the research is to assess the role of hedgerows on arable farmland in providing both habitats and corridors for wildlife. To this end, the conceptual frameworks of island biogeography and landscape ecology will be drawn upon extensively. In contrast to many studies of hedgerows, it is the intention that the present research recognises the repeating and structurally connected pattern of hedgerows in an attempt to determine which factors influence the distribution of *inhabitant* and *transient* species. Therefore, although the study takes as a starting point the framework of island biogeography, the interconnecting nature of hedgerow 'islands' in a 'sea' of agricultural land means that the broader principles of landscape ecology are incorporated to help explain species distributions. It seeks, therefore, to explain species distribution with reference to holistic as well as the more traditional reductionist approaches.

In order that the value of hedgerows for a wide-spectrum of wildlife can be assessed, three varied taxonomic groups will be studied. These are (i) vascular plants, (ii) small mammals (mice, voles and shrews), and (iii) two soil arthropod groups, the woodlice and millipedes. The functional roles of hedgerows are likely to be many depending on the species, or group of species, considered and the particular characteristics of both the hedgerow habitat and the matrix of land that they intersect. As a consequence of this latter point, the study's aims were addressed solely towards inter-arable field hedgerows both because the grazing activity of stock is likely to be highly disruptive and because hedgerows are a feature particularly common in lowland areas where arable farming now predominates.

1.6 Terminology

The hedgerow habitat consists of many structural components and it is important to define the terms used here both to avoid confusion with other authors and to emphasis
that these distinctions are important when referring to the wildlife of hedgerows. Th
terms *hedge* and *hedgerow* are often used rather loosely although Bates (1937), Polla
et al. (1974), Tozer & Taylor (1978), Dowdeswell (1987), and Greaves & Marsh (1987) have all offered definitions of what constitutes a hedge/hedgerow and structural components. Unlike Dowdeswell (1987) and many other authors, I have fo
it particularly useful, however, not to use the terms 'hedge' and 'hedger
synonymously. I propose that they can be used with effect to refer to specific conc
a related issue is the importance of making clear the distinction between the *hedge* and its *hedgerow verges*. These terms are illustrated in Figure 1.3 and explained

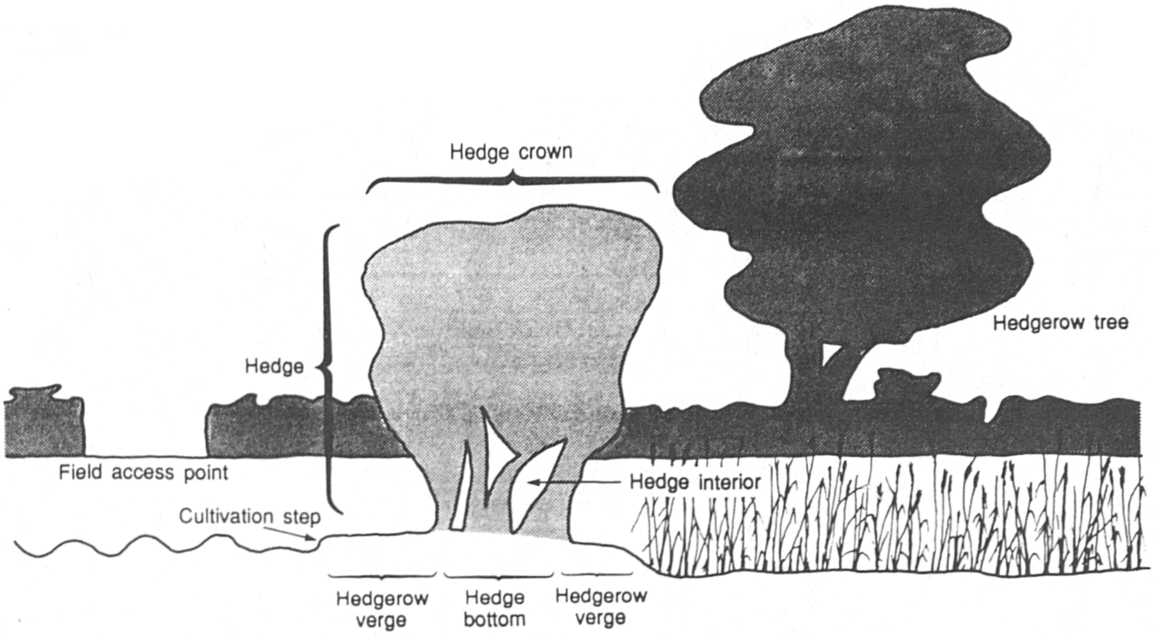


Figure 1.3 Schematic representation of cross-section and longitudinal views of a hedgerow showing its various structural components.

Hedge: any more or less continuous row of bush and tree species which are typically managed in such a way as to reduce the extent of their vertical and/or horizontal growth by periodic cutting; many such hedges were originally planted either to delimit changes in land ownership or to act as a barrier to the movement of stock. They are now also occasionally planted for wildlife, landscape and game bird interests.

Hedgerow verge: the relatively undisturbed area of land located between the edge of the field (which on arable land is usually marked by a cultivation step (*q.v.*)), and the side of the hedge; the hedgerow verges often support a well developed ground flora.

Hedgerow tree: a tree whose trunk is positioned in the line of the hedge and which grows significantly above the level of the hedge crown *(q.v.)*.

Hedgerow: an all inclusive term used to refer to the hedge itself, the hedgerow verges, trees and any ditch or bank that is associated with the hedge.

Hedgerow network: refers to several hedgerows that physically join onto one another and so form a series of connecting hedgerow habitats; the *network length* refers to the summed distance of these hedgerows.

Hedge crown: the main aerial body of the hedge characterised by the greatest lateral extension of its foliage.

Hedge interior: the sheltered region inside the hedge that experiences reduced temperature, illumination and humidity fluctuations.

Hedge bottom: the area of ground physically occupied by the hedge and greatly influenced by the hedge crown above; a distinctive ground flora will often be associated with the hedge bottom when foliage is dense and extends down to ground level.

Field access point: the gap in a hedgerow where farm machinery gains access to a field, such gaps are usually highly disturbed with sparse vegetation and compacted soils.

Cultivation step: the discontinuity in soil surface height at the juxtaposition of a cultivated field with the hedgerow verge; the cultivation step is formed by the action of ploughing and soil erosion carrying soil away from the comparatively undisturbed hedgerow verge.

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Chapter 2

Design of Studies and Selection of Field Sites

Contents

"Shall they, as they have brought hedges about common pasture, enclose with their intolerable lust also all the commodity and pleasure of this life, which Nature, the parents of us all, would have common, and bringeth forth everyday, for us, as well as for them?"

Robert Kett, 1549

2.1 Choice of studies

The study of hedgerow wildlife, and communities in general, can be of either a 'static' or a 'dynamic' nature. Static studies make observations at a single point in time and, although primarily descriptive, can be used to draw inferences about past events and present circumstances. Dynamic studies, by contrast, seek to recognise current processes by continuous observation or by monitoring at point intervals over time and are primarily of an explanatory nature. Such studies can be made either on experimentally manipulated or on unperturbed communities and habitats. When deciding on the nature of the hedgerow studies there were, therefore, two major considerations. First, the study organism or group of organisms had to be chosen. In the broadest of terms this meant deciding between the plant or animal kingdoms, but at a finer level the importance of hedgerows as a habitat and/or a possible dispersal route for a given species or species group had to be considered. Second, the survey approach had to be chosen, i.e. a trade-off had to be made between the study of a large number of hedgerows at one point in time only (static approach) or the repeated survey of a small number of hedgerows over the course of time (dynamic approach).

Given that a maximum of three summers are available for fieldwork these two considerations are not unrelated. For instance, it is not possible to study population characteristics of hedgerow shrubs using the dynamic approach unless these populations can be followed for relatively long time periods (say 5-10 years). The nature of the chosen studies is summarised in Table 2.1 and the practical constraints considered when selecting them are outlined below. The nature and aims of the studies are dealt with more fully in Chapters 3 to 6 inclusive.

2.1.1 Dynamic study approach

In order for dynamic studies to recognise ongoing processes they need to be conducted over time spans that enable changes to be detected by the particular survey methods used. The length of this time period will depend on the nature of the observations being made (e.g. the fate of a particular individual or changes in community structure) and the life history strategy of the organism being studied, e.g. r- or K-selected (Pianka 1970). The time constraint of having three field seasons available necessitates, therefore,

Table 2.1 The four hedgerow studies undertaken.

	Plant	Animal
Static	Island biogeography of hedgerow flora	Woodlouse and millipede distributions
Dynamic	Persistence of hedgerow verge flora	Small mammal movements and habitat choice

that the dynamic studies undertaken should seek to observe relatively rapid processes. These processes may range from a particular facet of an individual's behaviour (e.g. movement and dispersal) or the cumulative consequences of a species' life history strategy (the survival of the population within the community).

Animal populations that are highly mobile or that have short generation times can respond quickly to changing circumstances through immigration/emigration and mortality/natality processes respectively. As such, aspects of their population dynamics can be studied over relatively short periods of time. Small mammals (shrews, voles and mice) were chosen as a suitable study group both because they are mobile enough to allow their movements to be observed over the course of a single field season and because they lend themselves to live capture. The movements made by hedgerow small mammals were studied from the end of July to mid October in the second field season (see Figure 2.1).

Plant communities can respond to changing environmental circumstances at a slower rate than animal communities because they have no direct means of emigration and immigration. As a consequence the study of their dynamic nature can require relatively long periods of time. In order to study the dynamic nature of hedgerow plant communities it was, therefore, necessary to conduct point surveys on a small number of hedgerows over the course of two years, i.e. visit them on all three field seasons available (1988 to 1990 inclusive). Woody vegetation generally has a more stable community structure when judged over a period of a few years and slower population processes than herbaceous vegetation. It was decided, therefore, to study the dynamics of the hedgerow verge flora (i.e. herbs and grasses) rather than the hedge shrubs themselves. Figure 2.1 illustrates the timing of the verge flora study in relation to the other studies. The study of verge flora dynamics will not be presented in this thesis, although a discussion of its relevance to island biogeography and its significance to nature conservation is given in Chapter 6. It is planned to investigate the results of the survey at a later date.

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      1988                1989               1990
<-------------><-----------------------><---------->
M J J A S O N D J F M A M J J A S O N D J F M A M J J
|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|-|
                               <---->                   Small mammal study
    <->                      <->                    <->  Verge flora dynamics
  <------->                                             Biogeography of flora
                          <->                           Soil fauna distributions
```

Figure 2.1 Fieldwork schedule of the four hedgerow studies.

2.1.2 Static study approach

Although static studies are unable to discern cause and effect relationships, they do, nevertheless, fulfil a valuable descriptive role allowing inferences about processes that are difficult to study in the short-term to be drawn. Their advantage over dynamic studies is that they allow many samples to be surveyed because each sample location is only visited once. The slow response of hedgerow perennial vegetation to changes in environmental parameters, such as area and isolation, means that direct observations of community change are not feasible in the short-term. It was decided, therefore, to investigate the island biogeography of hedgerow flora by recording the presence or absence of species in a large number of hedgerows over the course of the 1988 field season (see Figure 2.1).

The static approach to the study of hedgerow communities can also be used to investigate the distribution of relatively sedentary animal groups, e.g. certain flightless arthropods. Such a group may provide a comparison with small mammals which are relatively mobile. It may be possible, therefore, to assess the significance of hedgerow connections for a relatively sedentary animal group that might have greater reliance on hedgerows as routes for movement and dispersal (Duelli 1990). Woodlice and millipedes were chosen as a suitable study group because of their comparatively poor dispersal ability (Cloudsley-Thompson 1988), their important decomposition role (Middleton & Merriam 1983) and because little is known about their distribution in hedgerows (but see Harding & Sutton 1985). The small size and habit of woodlice and millipedes means that they do not lend themselves to direct or repeated observation in the field and, consequently, they were sampled by a point survey early on in the summer of 1989 (Figure 2.1).

2.2 Selection of farms

Although nationally the density of hedgerows varies between regions (Allison 1989), they can, nevertheless, be found throughout lowland Britain from Essex (Mason *et al.* 1986; Conyers 1986) to Shropshire (Cameron *et al.* 1980), from Yorkshire (Sutton & Ecclestone 1977) to East Lothian (Tozer & Taylor 1978) and beyond. The availability of study sites was, therefore, not limited. Consequently, practical considerations concerning travel and facilities heavily favoured the study of hedgerows in North Yorkshire and Oxfordshire because these counties are home to the University of York and Cobham Resource Consultants (Abingdon Offices), the co-supervising body of the research, respectively. The study of hedgerows from two geographically isolated counties also allowed regional comparisons to be made.

In order to increase the general applicability of the survey findings to the lowland agricultural landscape, only those farms using conventional agrochemicals were included. The selection of the farms themselves was partially governed by their accessibility, both in terms of physical locality and in terms of obtaining permission for right of way.

Farms in the immediate vicinity of the University of York were easily accessible without the use of a vehicle and so farmers were approached with the request to allow their hedgerows to be included in the survey. The research project had from the outset been formulated with the co-operation of farmers participating in the Demonstration Farm Project (CC 1987). This meant that in North Yorkshire access was additionally granted to Hopewell House farm near Harrogate (CC 1985). In both Oxfordshire and North Yorkshire the county Farming and Wildlife Advisory Group (FWAG) officers were contacted and they were able to forward addresses of farmers who might be prepared to allow their farms to be included in the survey. An additional source of farms in Oxfordshire was those known to Cobham Resource Consultants. In total 23 farms were selected to be included in the survey; twelve from North Yorkshire (Figure 2.2) and eleven from Oxfordshire (Figure 2.3).

2.3 Selection of hedgerows

The selection of hedgerows was governed by the need to allow their area, degree of isolation and age to vary freely while keeping certain other parameters relatively constant. This approach was taken because in terms of equilibrium island biogeographical theory the area, isolation and age of a habitat isolate are perceived as being important variables in determining species richness. In order to assess the relevance of these three parameters to the hedgerow habitat (and hence to assess the significance of certain aspects of island biogeographical theory) it was, therefore, desirable to gauge their influence by either reducing or determining the variation of certain other parameters. Consequently, it was decided to include only those hedgerows that met the following five criteria.

(i) There must be arable land on both sides of the hedgerow: the intention of the hedgerow vegetation survey was to study the shrub, verge, climbing and understorey floras. Consequently, only hedgerows undisturbed by livestock were included because the grazing activity of stock on the hedge shrubs and herb flora was thought likely to be highly disruptive and variable. This is clearly seen in Photograph 2.1.

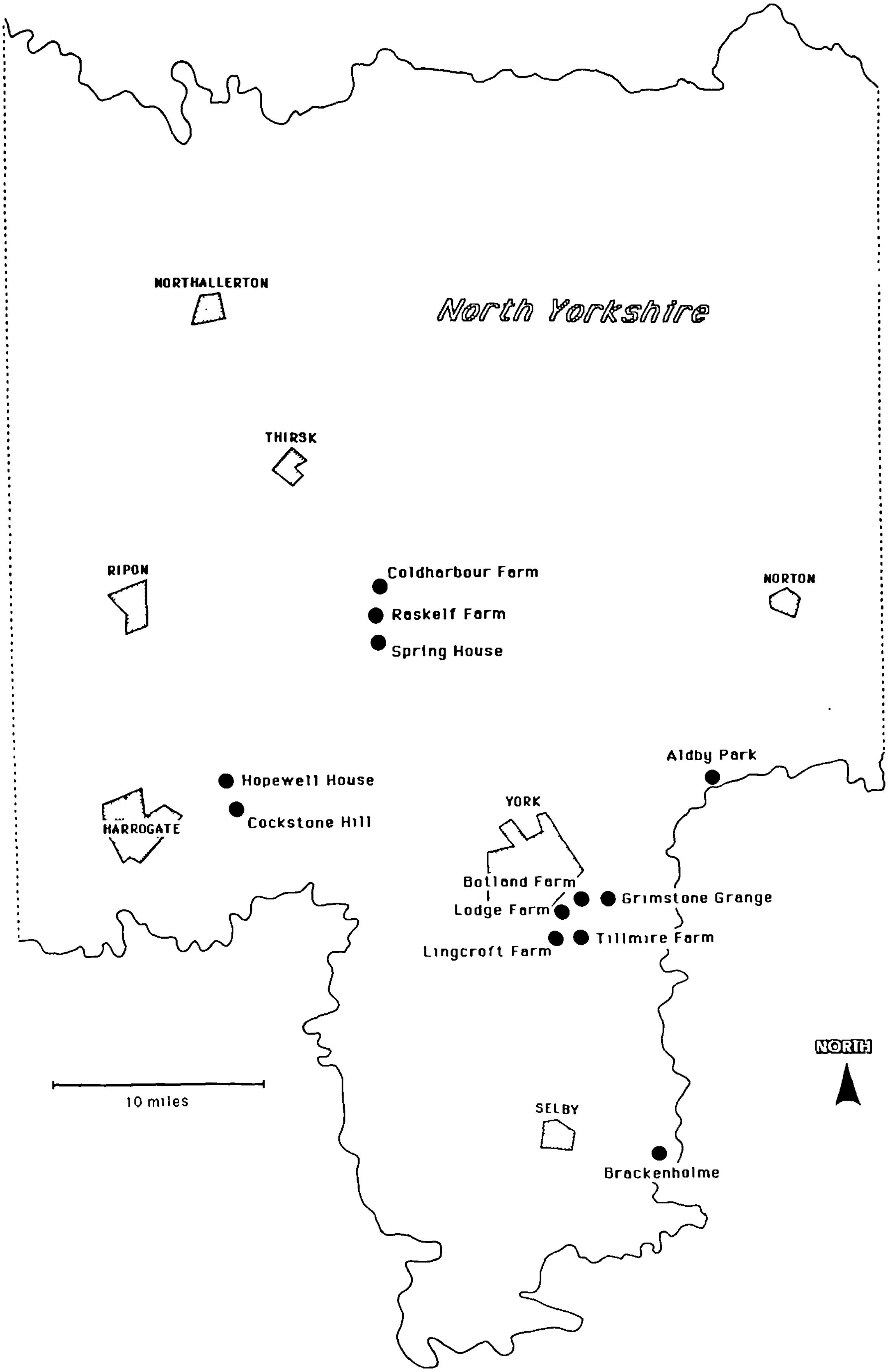

Figure 2.2 Location of the North Yorkshire farms included in the hedgerow surveys.

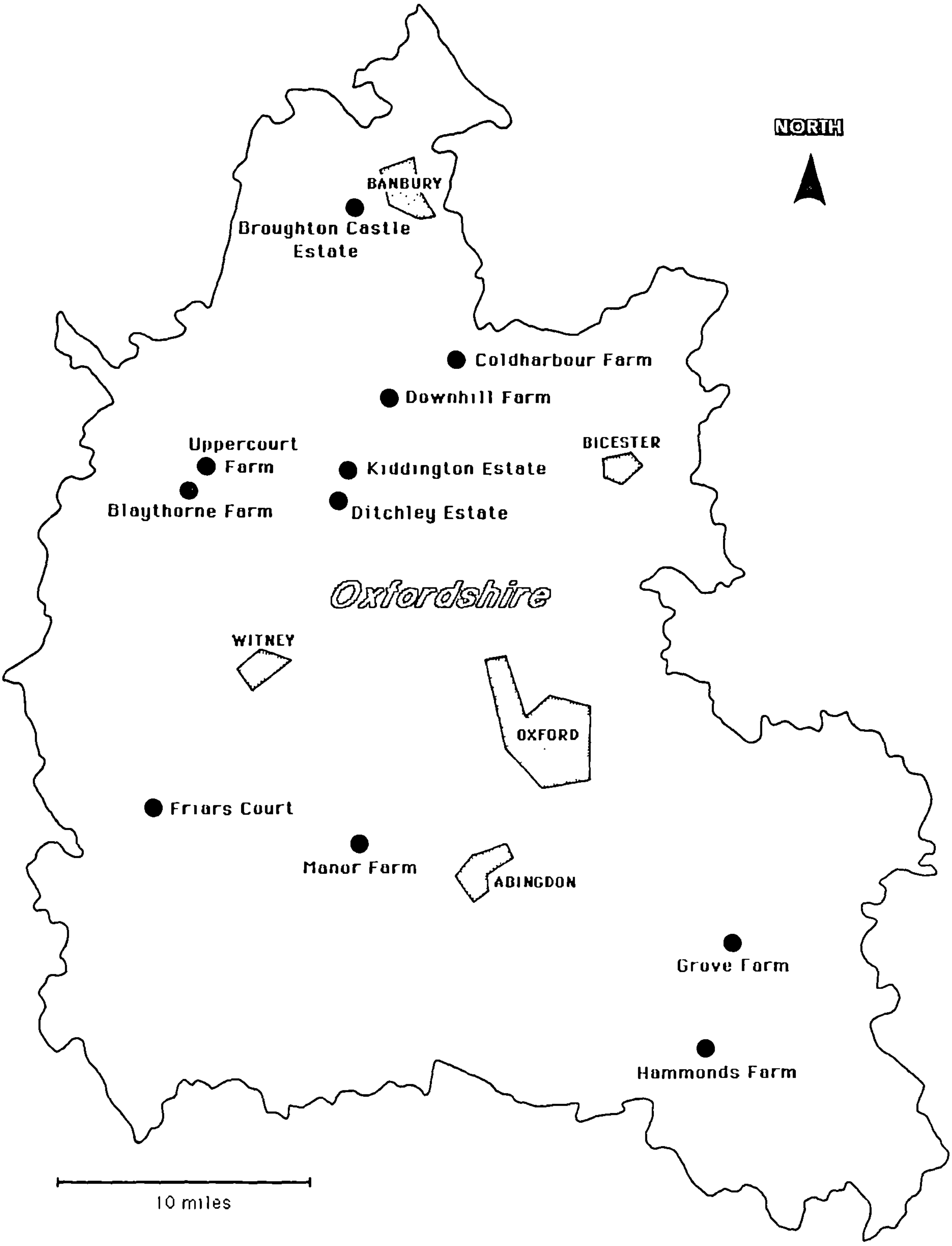

Figure 2.3 Location of the Oxfordshire farms included in the hedgerow surveys.

(ii) There must be no associated track or road: roadside verges have their own characteristic management, history and flora (Bates 1937; Dowdeswell 1987) which may influence the vegetation and fauna of hedgerows when hedge and road run parallel to one another.

(iii) There must be no associated ditch: hedgerow ditches are relatively common on agricultural land that has a high water table and, as with roadside verges, their history, management and microclimate may influence the species composition or richness of the associated hedgerow (Arnold 1983).

(iv) Hedgerow verges should be unsprayed with agrochemicals: the wilful or accidental application of herbicides, pesticides and fertilisers to hedgerow verges detrimentally effects many resident communities (Pollard 1968a, 1968b, Marshall 1986, Deane 1989). Consequently, hedgerows that were known to have recently been disturbed by such applications were excluded. The effect of herbicide application to hedgerow verge flora is illustrated in Photograph 2.2.

(v) The gaps along the length of the hedge must not exceed 20% of the total hedgerow length. When individual hedges become greatly disjointed by lateral gaps changes in habitat structure and microclimate may mean they resemble a number of short hedges or a series of isolated bushes and shrubs rather than a continuous hedgerow habitat.

On the basis of these five criteria, 180 hedgerows from the 23 study farms were selected to be included in the survey (93 from North Yorkshire and 87 from Oxfordshire). The number of hedgerows selected from each farm, as well as the National Grid Reference and county parish of each farm, is given in Table 2.2. The physical properties of the study hedgerows and their biota as recorded during the surveys are described in the relevant chapters (see Chapters 3 to 5 inclusive).

Photograph 2.1 The flora of hedgerows bordering pastures are subject to disturbances that inter-arable field hedgerows are not. In this extreme example, the disturbance to the hedgerow verge flora caused by the grazing and trampling activities of pigs is clearly evident.

Photograph 2.2 The chlorotic colourisation of hedgerow verge flora after herbicide application in spring.

Table 2.2 The number of hedgerows selected from each farm and the farms' parish and National Grid Reference (to the nearest km).

Farm	Number of hedgerows selected	County parish	National Grid Reference
Yorkshire:			
Aldby Park	2	Buttercrambe with Bossall	SE 73 59
Botland Farm	5	Heslington	SE 63 50
Brackenholme	7	Hemingbrough	SE 70 30
Cockstone Hill	5	*Goldsborough*	SE 38 56
Coldharbour Farm	3	Raskelf	SE 50 73
Grimstone Grange	11	Dunnington and Heslington	SE 65 50
Hopewell House	22	Knaresborough Outer	SE 37 59
Lingcroft Farm	14	Naburn	SE 62 47
Lodge Farm	9	Fulford	SE 62 48
Raskelf Farm	3	Raskelf	SE 49 71
Spring House	1	Raskelf	SE 49 69
Tillmire Farm	4	Fulford	SE 63 47
Oxfordshire:			
Blaythorne Farm	17	Chadlington	SP 32 22
Broughton Castle	8	Broughton and Tadmarton	SP 38 42
Coldharbour Farm	5	North Aston	SP 48 30
Ditchley Estate	11	Spelsbury and Enstone	SP 39 21
Downhill Farm	17	Westcot and Steeple Barton	SP 43 27
Friars Court	3	Clanfield	SP 29 01
Grove Farm	1	Brightwell Baldwin	SU 66 93
Hammonds Farm	3	Ipsden and Crowmarsh	SU 65 83
Kiddington Estate	10	Kiddington with Asterleigh	SP 42 23
Manor Farm	3	Fyfield and Tubney	SP 42 03
Upper Court Farm	9	Chadlington	SP 32 23

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Chapter 3

Species Richness and Composition of Hedgerow Flora

Contents

3.1 Introduction

The primary function of most hedgerows, that of a habitat originally intended to act as a barrier to the passage of stock, wild beast or man, necessitates that it is composed of a continuous and interlocked series of shrubs. Along with these shrubs, trees and climbing plants may also be present in large numbers. The physical presence of such woody species in the landscape can be considerable and the patchwork pattern of hedgerow and field has become the hallmark of the lowland English countryside. Moreover, the woody species comprising the hedge body give stability to the land and thus facilitate the development of a ground flora. This ground flora is comprised of the understorey flora of the *hedge bottom* and the edge flora of the hedge margins (the *hedgerow verges*). The very essence of the hedgerow habitat is, therefore, that of the plant community and as such most people value hedgerows through an appreciation of our natural flora or the varied and intimate landscape that they create.

It has been estimated that one-third of our native plants inhabit hedgerows and that approximately 250 of these are commonly or predominantly associated with the hedgerow habitat (Hooper 1968). Indeed, the vernacular names of many plants allude to this association, for example hedge woundwort (*Stachys sylvatica*) and upright hedge-parsley (*Torilis japonica*). It is generally a wide variety of the commoner plants that hedgerows provide a habitat for, although about ten of our rarest 300 plants also inhabit hedgerows (included in these are *Scrophularia scordonia*, *Lithuspernum purpurocaeruleum*, *Lonicera xylosteum and Stachys germanica*) (Hooper 1970a). With modern farming techniques, however, some of the so called 'commoner' species are themselves no longer so abundant and hedgerows can provide valuable refuges for these species (Deane 1989) (Photograph 3.1). As early as the 1930s the individuality of the hedgerow flora had been documented in the scientific literature (Bates 1937) and its characteristics continue to be recognised (Hooper 1968, Marshall & Smith 1987, Marshall 1988).

The safeguarding and conservation of wildlife habitats can be desirable for a wide variety of reasons (Margules & Usher 1981) and hedgerows are no exception. In addition to aesthetic and economic considerations, hedgerows can be viewed as worthy of conservation from a number of wildlife perspectives. Examples of these being the conservation of locally rare or increasingly rare plant species and the maintenance of a

Photograph 3.1 Many of the once commoner plant species that are now reduced in number by herbicides find a niche in hedgerows: here field poppy (*Papaver rhoeas)* is seen growing in an Oxfordshire hedgerow.

habitat reserve for a diverse community of commoner species that are, nevertheless, poorly represented in intensively farmed areas. The conservation of many arthropods, birds and small mammals is also directly related to the plant communities of hedgerows. Provided that hedgerows are managed in such a way as to enhance their quality there is considerable scope for them to represent a significant habitat resource within the farmed landscape given that it is estimated that there are 428,000 km of hedgerows remaining in Great Britain (Barr *et al.* 1991).

Depending upon management aims, the conservation of hedgerow plant communities is best achieved by establishing what factors determine the distribution of individual species, or groups of species, within hedgerows and/or by establishing which features contribute to the overall species richness of hedgerows. It is with this knowledge that management plans can be formulated. The factors that are likely to influence the species richness and composition of plant communities in hedgerows are:

(i) the area of land occupied by the hedgerow (Helliwell 1975),

(ii) their isolation from source populations (Elton 1966, Helliwell 1975, Forman & Godron 1984, Baudry 1988),

(iii) their origin, age and management history (Hooper 1970b & 1971, Pollard 1973, Cameron & Pannett 1980, Harris 1984, Deane 1989),

(iv) their habitat heterogeneity (Forman & Godron 1981 & 1984), and

(v) soil type and geographical location (Boatman 1980, Nau & Rands 1975, Willmot 1980).

3.2 Aims

The aim of this chapter is to elucidate the importance of some of the above factors for the plant communities of hedgerows bordering arable fields. The variables that will receive particular attention are outlined below.

First, the *area* of land occupied by the hedgerow will be determined to assess if a *species-area effect* exists for plants in the hedgerow habitat, and if so what might cause this frequently observed *positive correlation* between species richness and area. The relationship will be investigated for both the entire hedgerow plant community and for various plant subgroups. A comparative sampling approach will be taken to assess the strength of any species-area effect when considering both the number of species within the entire hedgerow habitat and the number of species when determined using a fixed sample size. Should the species-area effect still be in evidence with the fixed sampling technique, a more dynamic cause of the species-area phenomenon is implicated which suggests the validity of the MacArthur & Wilson's (1967) equilibrium theory of island biogeography (Kelly *et al.* 1989).

The species-area effect has been observed in many habitats for a variety of taxa (e.g. Usher 1979, Kitchener *et al.* 1980, Rigby & Lawton 1981, Opdam *et al.* 1985, Davis & Jones 1986, Rafe *et al.* 1988) although its cause and implications are still uncertain (Boecklen & Gotelli 1984, McGuinness 1984, Kelly *et al.* 1989). Species-area curves are frequently modelled by the power function

$$S = cA^{z} \qquad [3.1]$$

where S is the number of species, A is the habitat/island area and c and z are fitted constants. The power function can be linearised by logarithmic (either natural or base ten) transformation of both the dependent and independent variables to give

$$\log(S) = \log(c) + z\log(A) \qquad [3.2]$$

where c is the intercept of the species axis (species richness at unit density) and z is the slope of the species-area line (the rate of increase in species richness with increasing area). The exponential function, and its semi-logarithmic linear form

$$s = \log_{c}(c) + z\log_{c}(A) \qquad [3.3]$$

has also been used to model species-area relationships (Gleason 1922), although in a wide-ranging comparison Connor & McCoy (1979) found it to be inferior to the double-logarithmic power function. Whatever model is used (arithmetic, semi-logarithmic or double-logarithmic) it is important that there is a consistency in approach if comparisons are to be made because the parameters of each model are not necessarily interchangeable (Loehle 1990).

Second, the *isolation* of the hedgerow habitat from source habitats will be assessed. Habitat isolation has almost exclusively been estimated by determining the quantity of source habitats in the surrounding landscape or by the linear distance between source and recipient habitats (e.g. Helliwell 1975, Opdam & Schotman 1984, Osborne 1984).

In contrast, the configuration and connectivity between interacting habitat patches has rarely been assessed systematically (Golley 1989). The linear and interconnecting nature of hedgerows may create the situation where the structural relationship between hedgerows is vitally important in understanding the distribution of species and assessing the conservation value of particular hedgerows (Baudry 1988, Forman & Godron 1984). To address this, particular attention will be paid to the *connectance* attributes of the study hedgerows and the surrounding hedgerow network. To this end, complexity and relational indices derived from graph theory will be used (Taaffe & Gaulthier 1973, Bridgewater 1987) to assess landscape complexity and connectivity between habitat patches.

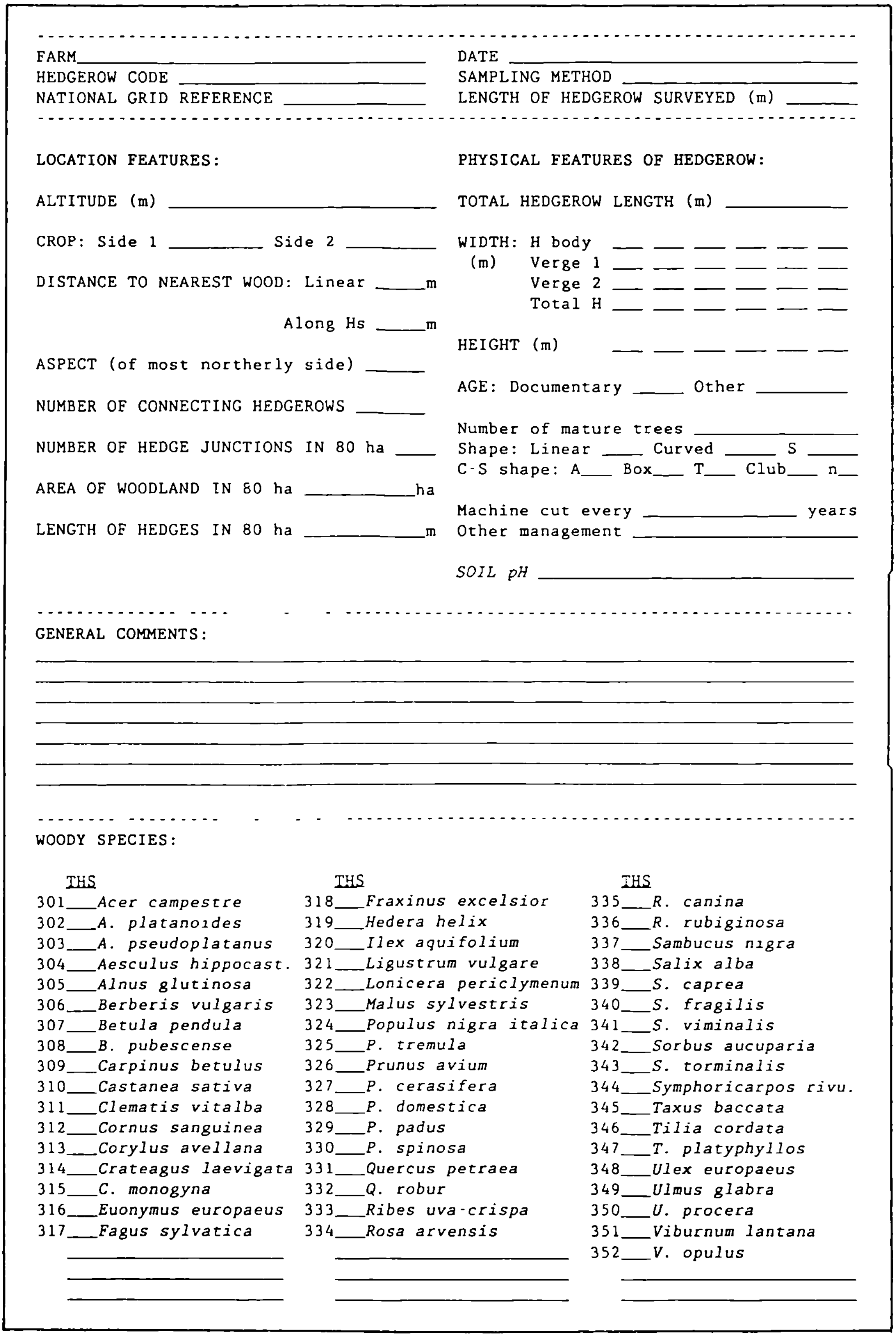
Third, hedgerow *age* will be estimated. The successional stage of a community is often directly related to habitat age (MacArthur & Wilson 1967, Crowe 1979). The species richness and composition of hedgerows has been found to be partially explained by the age of the hedgerow itself (Hooper 1970b & 1971, Pollard 1973, Cameron *et al.* 1980, Cameron & Pannett 1980) and this relationship for plants will be assessed with reference to documentary records.

Fourth and last, *habitat diversity* of the study hedgerows will be assessed by the recording of hedgerow soil pH. Mean soil pH and its variability within a hedge will be determined to assess both the occurrence of particular plants with specific edaphic requirements and the possible importance of variability in soil condition in providing a larger number of potential niches for habitation by plants.

3.3 Methods

3.3.1 Recording of hedgerow physical properties

The physical properties measured for each of the study hedgerows were their dimensions, shape, aspect and soil pH. These physical properties and the inhabitant plant species of the study hedgerows were recorded onto a survey sheet (Figure 3.1). The most important dimensions of the study hedgerows were their length and width so that an estimate of their area could be obtained. A number of other dimensions were also recorded and all measurements are described below; height and width dimensions are illustrated in Figure 3.2.



FARM________________________ DATE ________________________
HEDGEROW CODE ________________ SAMPLING METHOD ________________
NATIONAL GRID REFERENCE __________ LENGTH OF HEDGEROW SURVEYED (m) ______

LOCATION FEATURES:

ALTITUDE (m) ____________________

CROP: Side 1 _______ Side 2 _______

DISTANCE TO NEAREST WOOD: Linear _____m

Along Hs _____m

ASPECT (of most northerly side) ______

NUMBER OF CONNECTING HEDGEROWS ______

NUMBER OF HEDGE JUNCTIONS IN 80 ha ____

AREA OF WOODLAND IN 80 ha __________ha

LENGTH OF HEDGES IN 80 ha __________m

PHYSICAL FEATURES OF HEDGEROW:

TOTAL HEDGEROW LENGTH (m) __________

WIDTH: H body ___ ___ ___ ___ ___ ___
(m) Verge 1 ___ ___ ___ ___ ___ ___
Verge 2 ___ ___ ___ ___ ___ ___
Total H ___ ___ ___ ___ ___ ___

HEIGHT (m) ___ ___ ___ ___ ___ ___

AGE: Documentary _____ Other ________

Number of mature trees ______________
Shape: Linear ____ Curved _____ S _____
C-S shape: A___ Box___ T___ Club___ n__

Machine cut every ____________ years
Other management __________________

SOIL pH ______________________

GENERAL COMMENTS:

WOODY SPECIES:

THS
301___*Acer campestre*
302___*A. platanoides*
303___*A. pseudoplatanus*
304___*Aesculus hippocast.*
305___*Alnus glutinosa*
306___*Berberis vulgaris*
307___*Betula pendula*
308___*B. pubescense*
309___*Carpinus betulus*
310___*Castanea sativa*
311___*Clematis vitalba*
312___*Cornus sanguinea*
313___*Corylus avellana*
314___*Crateagus laevigata*
315___*C. monogyna*
316___*Euonymus europaeus*
317___*Fagus sylvatica*

THS
318___*Fraxinus excelsior*
319___*Hedera helix*
320___*Ilex aquifolium*
321___*Ligustrum vulgare*
322___*Lonicera periclymenum*
323___*Malus sylvestris*
324___*Populus nigra italica*
325___*P. tremula*
326___*Prunus avium*
327___*P. cerasifera*
328___*P. domestica*
329___*P. padus*
330___*P. spinosa*
331___*Quercus petraea*
332___*Q. robur*
333___*Ribes uva-crispa*
334___*Rosa arvensis*

THS
335___*R. canina*
336___*R. rubiginosa*
337___*Sambucus nigra*
338___*Salix alba*
339___*S. caprea*
340___*S. fragilis*
341___*S. viminalis*
342___*Sorbus aucuparia*
343___*S. torminalis*
344___*Symphoricarpos rivu.*
345___*Taxus baccata*
346___*Tilia cordata*
347___*T. platyphyllos*
348___*Ulex europaeus*
349___*Ulmus glabra*
350___*U. procera*
351___*Viburnum lantana*
352___*V. opulus*

Figure 3.1 Field survey sheet used to record the flora of the study hedgerows and various physical properties of each hedgerow and the surrounding landscape; the most northerly and the most southerly side of each hedgerow are referred to by the numbers 1 and 2 respectively (see reverse for grass and herb species lists).

1 2 GRASS SPECIES

01_ _*Agrostis canina*
02_ _*A. gigantea*
03_ _*A. stolonifera*
04_ _*A. tenuis*
05_ _*Alopecurus myosuroides*
06_ _*A. pratensis*
07_ _*Anthoxanthum odoratum*
08_ _*Arrhenatherum elatius*
09_ _*Avena fatua*
10_ _*Brachypodium sylvaticm*
11_ _*Bromus mollis*

1 2

12_ _*B. ramosus*
13_ _*B. sterilis*
14_ _*Cynosurus cristatus*
15_ _*Dactylis glomerata*
16_ _*Danthonia decumbens*
17_ _*Deschampsia flexuosa*
18_ _*Elymus caninus*
19_ _*E. repens*
20_ _*Festuca gigantea*
21_ _*F. pratensis*
22_ _*F. rubra*

1 2

23_ _*Holcus lanatus*
24_ _*H. mollis*
25_ _*Hordeum secalinum*
26_ _*Lolium perenne*
27_ _*Phleum pratensis*
28_ _*P.p. ssp. bertolonii*
29_ _*Poa annua*
30_ _*P. pratensis*
31_ _*P. trivialis*
32_ _*Trisetum flavescens*

1 2 HERBACEOUS SPECIES

51_ _*Achillea milefolium*
52_ _*Aegopodium podagraria*
53_ _*Aethusa cynapium*
54_ _*Ajuga reptans*
55_ _*Alliaria petiolata*
56_ _*Allium ursinum*
57_ _*A. vineale*
58_ _*Anagallis arvensis*
59_ _*Angelica sylvestris*
60_ _*Anthriscus sylvestris*
61_ _*Arctium lappa*
62_ _*A. minus*
63_ _*Armoracia rusticana*
64_ _*Artemisia vulgaris*
65_ _*Arum maculatum*
66_ _*Barbarea vulgaris*
67_ _*Bellis perennis*
68_ _*Bilderdykia convolvls*
69_ _*Bryonia dioica*
70_ _*Calystegia sepium*
71_ _*Capsella bursa-pastrs*
72_ _*Cardamine hirsuta*
73_ _*C. pratensis*
74_ _*Cardaria draba*
75_ _*Carduus acanthoides*
76_ _*Centaurea nigra*
77_ _*C. Scabiosa*
78_ _*Chamomilla recutita*
79_ _*Chaerophyllum temlntm*
80_ _*Chenopodium album*
81_ _*Chrysanthemum segetum*
82_ _*Cirsium arvense*
83_ _*C. vulgare*
84_ _*Clinopodium vulgare*
85_ _*Conicum maculatum*
86_ _*Conopodium majus*
87_ _*Convolvulus arvensis*
88_ _*Crepis capillaris*
89_ _*Cruciata laevipes*
90_ _*Daucus carota*
91_ _*Digitalis purpurea*
92_ _*Endymion non-scriptus*
93_ _*Epilobium angustifolm*
94_ _*E. hirsutum*
95_ _*E. montanum*
96_ _*Equisetum arvense*
97_ _*Eupatorium cannibinum*
98_ _*Euphorbia pepius*
99_ _*Euphrasia officinalis*

1 2

100_ _*Fragaria vesca*
101_ _*Fumaria officinalis*
102_ _*Galeopsis tetrahit*
103_ _*Galium aparine*
103_ _*G. mollugo*
105_ _*G. vernum*
106_ _*Geranium robertianum*
107_ _*Geum urbanum*
108_ _*Glechoma hederacea*
109_ _*Heracleum sphndylium*
110_ _*Humulus lupulus*
111_ _*Hypericum perforatum*
112_ _*H. pulchrum*
113_ _*Knautia arvensis*
114_ _*Lamium album*
115_ _*L. purpureum*
116_ *Lapsana communis*
117 _*Lathyrus pratensis*
118_ _*Leontodon hispidus*
119_ *Leucanthemum vulgare*
120_ *Linaria vulgaris*
121 *Lotus corniculatus*
122 *Matricaria matricar*
123_ *Medicago lupulina*
124 *Mentha arvensis*
125_ *Mercurialis perennis*
126_ _*Myosotis arvensis*
127_ *M. sylvatica*
128_ _*Myrrhis odorata*
129_ *Origanum vulgare*
130_ *Oxalis acetosella*
131_ *Papaver rhoeas*
132_ *Pimpinella majus*
133_ *Plantago lanceolata*
134_ *P. major*
135_ *Polygonum aviculare*
136_ _*P. lapathifolium*
137_ _*P. persicaria*
138_ *Potentilla anserina*
139_ *P. erecta*
140_ _*P. reptans*
141_ _*Primula veris*
142_ _*P. vulgaris*
143_ _*Prunella vulgaris*
144_ _*Pteridium aquilinum*
145_ _*Ranunculus auricomus*
146_ _*R. ficaria*
147_ _*R. repens*

1 2

148_ _*Raphanus raphanistrm*
149_ _*Reseda lutea*
150_ _*Rubus caesius*
151_ _*R. fruticosus agg.*
152_ _*R. idaeus*
153_ _*Rumex acetosa*
154_ _*R. conglomeratus*
155_ _*R. crispus*
156_ _*R. obtusifolius*
157_ _*R. sanguineus*
158 _*Senecio jacobaea*
159 _*S. squalidus*
160 *S. vulgaris*
161 *Silene alba*
162 *S. dioica*
163 *S. vulgaris*
164 *Sinapis arvensis*
165 *Sisymbrium officinale*
166 *Solanum dulcamara*
167 *S. nigrum*
168 *Sonchus asper*
169 *S. arvensis*
17 *S. oleraceus*
171 *Spergula arvensis*
172 *Stachys sylvatica*
173 *Stellaria graminea*
174 *S. holostea*
17 *S. media*
176 *Symphytum officinale*
177 *Tamus communis*
178 *Tanacetum pratheni*
179 *T. vulgare*
180 *Taraxacum officinale*
181 *Teucrium scorodonia*
182 *Torilis japonica*
182 *Tragopogon pratensis*
184 *Trifolium pratense*
185 *T. repens*
186 *Tussilago farfara*
187 *Urtica dioica*
188_ *Veronica chamaedrys*
189_ *V. hederifolia*
190 *V. persica*
191_ _*Vicia cracca*
192_ *V. sativa*
193 _*V. sepium*
194_ *Viola arvensis*
195_ _*V. odorata*

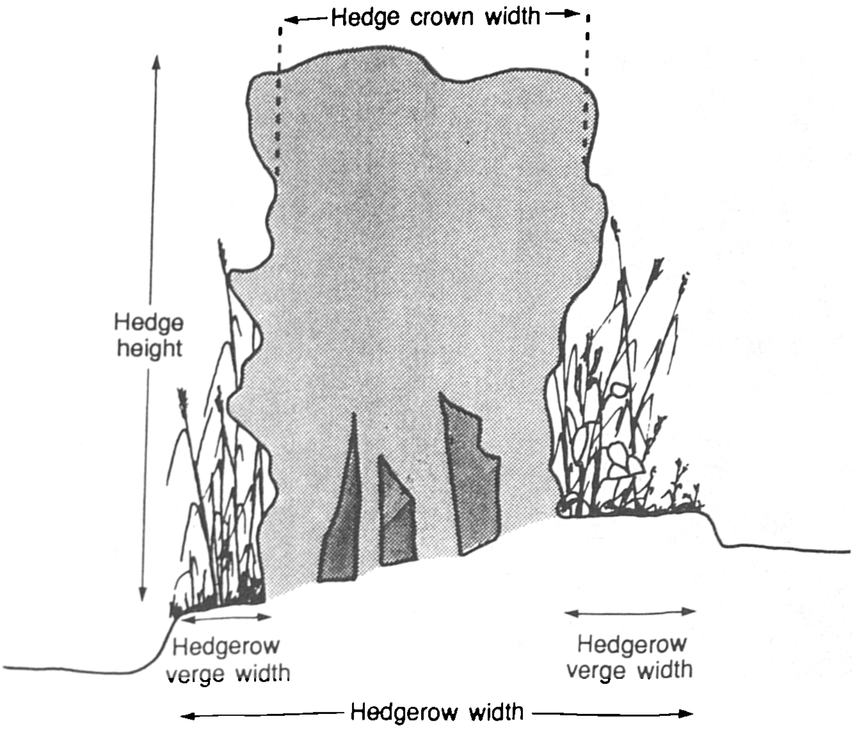


Figure 3.2 Cross section of hedgerow showing the height and width dimensions measured.

The physical dimentsions recorded for each study hedgerow were:

(a) *Hedge length* - the distance between the two end points of a hedge or adjacent junctions, measured by pacing the hedge and converting to the nearest meter;

(b) *hedgerow width* - measured as the total distance between the outer edge of each hedgerow verge (generally delimited by a cultivation step); the extent of hedgerow verge and hedge bottom habitats are therefore described by this measurement;

(c) *hedgerow area* - estimated by multiplication of the hedge length and mean hedgerow width measurement;

(d) *hedgerow verge width* - for each side of the hedgerow this was measured as the distance between the outer edge of the hedgerow verge and the side of the hedge at ground level;

(e) *hedge crown width* - measured as the distance between the opposite sides of the hedge crown at breast height (1.5 m), or at 10 cm from the top of the hedge when its height was less than breast height; and

(f) *hedge height* - measured as the height from the base of the hedge trunks to the top of the bulk of the hedge crown.

With the exception of the hedge length, all the dimensions were measured to the nearest 10 cm using 1.5 m survey poles. All these dimensions were recorded six times for each hedgerow to enable an average to be calculated and so to account for variations in structure along the hedge's length. The measurements were taken on a stratified random basis by dividing the hedgerow length into three and randomly selecting two survey points within each section.

In order to assess the influence of both soil pH and the variability of soil pH conditions along the length of an individual hedgerow, ten pH readings were taken in a stratified random manner from each hedgerow. On the more southerly side of each study hedgerow, ten 10 g samples of soil were collected at a depth of 5 cm at the juxtaposition of the hedgerow's verge with the side of the hedge. In the field, each sample was diluted in approximately 20 cm^3 of distilled water and shaken vigorously for 1 minute. The sample was then left to stand for a further 2 minutes before the pH of the supernatant solution was recorded using a portable pH metre (resolution 0.01 units). This procedure was adapted for the field situation from White (1979). One pH measurement was also taken in a central position 6 m into the adjacent field. This measurement allows for a comparison to be made between the hedgerow and field pH conditions. The variation in soil pH within each hedgerow was determined by calculating the coefficient of variation of the ten pH measurements recorded. The coefficient of variation is extensively used to compare the variability of sample populations independent of their means; it is commonly expressed as a percentage and is calculated as

$$CV = (s/\bar{Y}) \times 100 \qquad [3.4]$$

where CV is the coefficient of variation and s and $\bar{Y}$ are the standard deviation and mean of the sample respectively.

3.3.2 Hedgerow vegetation survey

The vegetation survey recorded all vascular plant species growing within the hedgerow habitat. The presence or absence of species was recorded on a survey sheet (Figure 3.1) that listed 220 plant species cited as inhabiting hedgerows in the literature. Species growing in the hedgerow were recorded by walking at a slow pace along either side and examining the hedge itself as well as the hedgerow verges and hedge bottom.

Three sampling methods were used in the survey; they were designed to obtain an indication of the total species richness of a hedgerow, the density of species in a hedgerow, and the number of species in a sample proportional to the hedgerow's total length. The three sampling techniques were:

(i) *Complete* - the entire length of the hedgerow was surveyed to obtain a measure of the total species richness;

(ii) *Fixed* - in order to obtain a measure of the density of species within a hedgerow a fixed sample length of 30 m was surveyed; it was randomly located along the hedgerows' length; and

(iii) *Proportional* - a proportional sampling technique allows for the species richness of a hedgerow to be determined as a function of its total length and so an estimate of its species richness can be obtained that reflects the size of the habitat while avoiding the necessity to survey the entire hedgerow. Three proportions were surveyed to allow comparisons to be made between their efficiency; these were 10%, 20% and 30% of the total hedgerow length. Equal fractions of each sample were located randomly within each third of the hedgerow to allow variation along the hedgerow's length to be surveyed.

3.3.3 Survey of adjacent landscape features

To investigate the influence of adjacent landscape features on the species composition of hedgerows it is necessary first to determine which features are to be recorded and then to select a scale of investigation. Habitats that are likely to be of importance are neighbouring hedgerows, additional boundary habitats (fencelines, stone dykes, roadside verges) and woodland area and perimeter habitats (classified as deciduous, mixed and coniferous). The area of land considered when estimating these parameters in the arable landscape is crucially dependent upon the scale at which hedgerows and other source habitats repeat themselves. To study the interactions between habitats at the landscape level a large number of similar habitat types must be included. An area of 80 ha (enclosed by a circle with a diameter approximately equal to 1 km) centred upon each hedgerow was considered large enough to allow landscape-wide processes to be investigated because hedgerows generally range from a few tens to several hundreds of metres long and woodlots are commonly smaller than a few tens of hectares in area. This area is slightly smaller than the 100 ha sample used by Helliwell (1975) in the form of a 1 km x 1 km square. The circular sampling area employed here is, however, more robust in that the quantification of adjacent landscape features is not affected by the orientation of the sampling area.

With confirmatory visits to the study farms, and using a colour coding system, these habitat features were recorded on 1:25000 scale maps which show all woodland and field boundaries. This was achieved quickest by surveying the landscape with binoculars from a high vantage point (usually a hedgerow tree).

3.3.4 Landscape isolation and connectivity

Using the encoded maps, three approaches to estimating the relationship between the study hedgerows and their neighbouring landscape features were used; respectively dealing with an estimate of source habitat *quantity*, the *complexity* of the landscape, and the *connectivity* of a hedgerow to its neighbours (the reciprocal of isolation) within each 80 ha region. There is little precedent for the estimation of the latter two parameters and, consequently, they will be explained at some length. The three measures of isolation used are described below.

(i) *Quantity of source habitats*

Within each 80 ha region the length of the encoded field boundaries (hedgerows, fencelines, stone dykes and roadside verges) and the perimeter and area of the woodland (deciduous, mixed and coniferous) was calculated using a digitising board and an image analyser.

(ii) *Landscape connectivity*

The complexity of a landscape can be assessed by enumerating the physical connections between its component habitats. The connectivity of a network or graph can be expressed with the use of indices derived from graph theory (Taaffe & Gaulthier 1973). Two such indices that are commonly used to describe networks are the *gamma* and *alpha* indices of connectivity. *Gamma* and *alpha* can be calculated for both planar (two-dimensional) and non-planar (three-dimensional) networks. With planar networks, intersecting linkages always cross at a node; whereas if a graph is abstracted in three dimensions then crossing linkages may not actually intersect. This latter, non-planar, situation is illustrated well by aviation flight paths. In the case of hedgerows, however, we are obviously dealing with the former, planar, situation. *Gamma* and *alpha* are best illustrated with reference to Figure 3.3 that depicts a simplified hedgerow network in the form of a planar graph.

The *gamma* index expresses connectivity as the ratio of the number of linkages in the network (in this case hedgerows) to the maximum number possible, thus

$$gamma = L \,/\, L_{max} \qquad [3.5]$$

where L is the actual number of linkages on the network and L_{max} is the maximum number of linkages. L is obtained simply by counting, while L_{max} can be determined from the number of nodes. As seen with reference to Table 3.0, the incorporation of each additional node to a *planar* network results in an increase in the maximum number of linkages by 3 (Taaffe & Gaulthier 1973). This is the case for all planar graphs consisting of more than two nodes. The relationship between L_{max} and the number of nodes can be expressed as

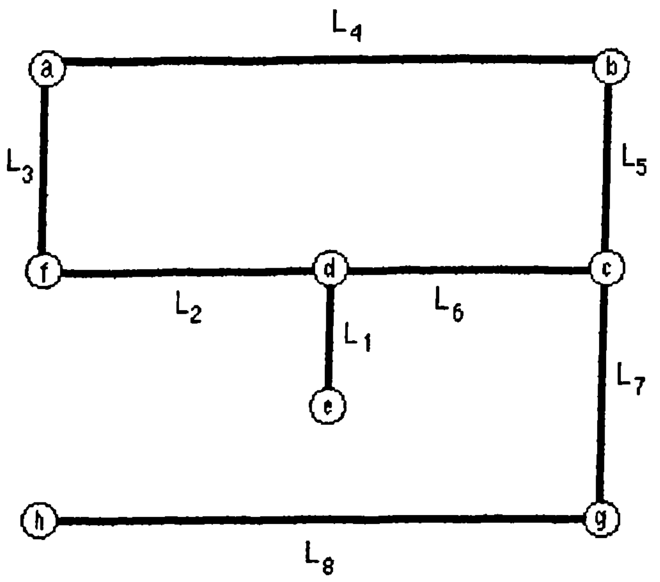


Figure 3.3 A simple graph depicting the topological relationship between hedgerows that form a network; there are eight linkages (L_1 to L_8) which represent hedgerows (hedge L_1 is the hypothetical study hedge) and eight nodes (*a* to *h*) which represent hedgerow junctions or endpoints; the *radius* of the graph (the number of hedgerows, including the study hedge, between the study hedge and the most distant hedge on the network) is three.

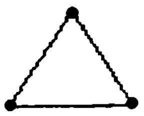
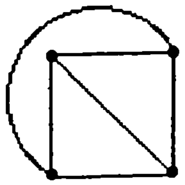
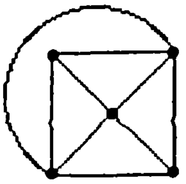
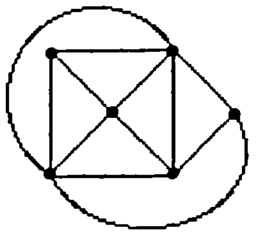
$$L_{max} = 3(n - 2) \qquad [3.6]$$

where *n* is the number of nodes. The *gamma* index is, therefore, defined as

$$gamma = L \,/\, 3(n - 2) \qquad [3.7]$$

In the case of the example network, the *gamma* index is 8/3(8-2)=0.44. *Gamma* never exceeds unity because the actual number of linkages can never exceed the maximum possible and is, therefore, conveniently expressed as a percentage. The example network is 44% connected.

Table 3.0 The maximum number of linkages on a planar network increases by 3 with the incorporation of each additional node (linkages intersect only at nodes); this relationship is modelled by 3(n - 2).

Number of nodes (n)	Planar graph	Maximum number of linkages (L_{max})	3(n - 2)
3		3	3
4		6	6
5		9	9
6		12	12

By contrast, the *alpha* index of connectivity is a measure of the number of alternative paths between nodes on the network. An alternative path is defined as a *circuit* and the index, therefore, is a measure of the network's *circuitry*. It is calculated as the ratio between the actual number of circuits within the network to the maximum possible number, thus

$$alpha = c \,/\, c_{max} \qquad [3.8]$$

where c is the number of circuits and c_{max} is the maximum number of circuits. The network shown in Figure 3.3 has one circuit that is composed of the nodes a, b, c, d and f and their associated linkages (L_4, L_5, L_6, L_2 and L_3). This circuit can be illustrated by taking nodes *a* and *b* as an example. In addition to this pair of nodes being directly connected to one another, they are also connected along the linkage sequence *a* to *f* to *d* to *c* to *b*, i.e. there is one circuit. The number of circuits (*c*) can, in fact, be derived from the number of nodes and linkages on the network. *c* is calculated as the difference between the number of linkages in a network (*L*) and the number of linkages needed to connect all nodes on a network once, and only once, such that there is only one path between any pair of nodes (i.e. there are no circuits). In such a *minimally connected* network, the number of linkages is always the number of nodes minus one ($L_{min} = n - 1$). Hence the number of circuits can be expressed as

$$\begin{aligned} c &= L - L_{min} \\ &= L - (n - 1) \\ &= L - n + 1 \end{aligned} \qquad [3.9]$$

Using this formula, and as already seen empirically, the value of *c* in the network shown in Figure 3.3 is 1 (i.e. 8-8+1). The maximum number of circuits (c_{max}) is simply the difference between the maximum possible number of linkages within the planar network (L_{max}) and the number necessary to form a minimally connected network (L_{min}). Hence,

$$\begin{aligned} c_{max} &= L_{max} - L_{min} \\ &= 3(n - 2) - (n - 1) \\ &= 3n - 6 - n + 1 \\ &= 2n - 5 \end{aligned} \qquad [3.10]$$

Thus, the *alpha* index of circuitry is calculated as

$$alpha = (L - n + 1) \,/\, (2n - 5) \qquad [3.11]$$

In the working example, *alpha* is (8-8+1)/(2x8-5)=0.09. The ratio is again conveniently expressed as a percentage, i.e. the graph has a circuitry of 9%.

This equation to calculate *alpha* can be directly applied to graphs where there are no isolated nodes or linkages, i.e. the graph is not composed of *subgraphs*. The hedgerow networks studied, however, frequently consisted of a number of subgraphs within each 80 ha area. In these cases, the actual number of circuits was calculated separately for each subgraph using equation 3.9 and then summed to obtain the total number of circuits for the delimited network as a whole. Therefore, in the case of fragmented hedgerow networks consisting of a number of subgraphs, *alpha* can be expressed as

$$alpha = [\ \sum_{i=1}^{s}(c)\ ]\ /\ c_{max}$$

$$= [\ \sum_{i=1}^{s}(L - n + 1)\ ]\ /\ (2n - 5) \qquad [3.12]$$

where s is the number of subgraphs within each 80 ha area.

The *alpha* and *gamma* indices were calculated for all of the hedgerows that were surveyed using the complete sampling technique. The number of linkages (hedgerows) and nodes (junctions and end points) were counted within each 80 ha area; both the hedgerows extending beyond the perimeter of the 80 ha area and their end points were excluded from the calculation.

Both the *alpha* and *gamma* indices describe the general connectivity characteristics of a hedgerow network that may consist of a single connected graph or two or more unconnected subgraphs. To look at the specific relationship between a particular hedgerow and the other points on a network an alternative approach is needed. Here the interest is in the relationship between the study hedge and all other hedgerows on the graph or subgraph of which it is a part. Using matrices, graph theory again offers a way to determine this characteristic of a network. It is described below and is the third index used to assess the degree of hedgerow isolation.

(iii) *Hedgerow accessibility*

Graph theory has formulated procedures for calculating the degree of topographical connectivity between two points on a network or, by its extension, between a given point and all other points. The perspective taken is usually that of assessing the degree of linkage between *nodes* on a network (e.g. the number of flight paths between airports). For each node it is possible to calculate the number of direct and indirect linkages that it has with all other nodes on the network; this is conventionally termed *nodal accessibility* (Taaffe & Gaulthier 1973). This perspective may find application in landscape ecology at a larger landscape scale than is being directly considered here (such as the connectivity between farm woodlands where the woodlands are perceived as nodes and the hedgerows between them as linkages). At the present hierarchical scale, that of inter-hedgerow relationships, it is necessary to shift the emphasis so that the connectivity between the *linkages* themselves (the hedgerows) can be assessed. This is the case because the flux of individuals and genes between hedgerows is of importance rather than the movements between nodes on the network (defined as the hedgerow junctions and end points). By analogy this parameter will be termed *hedgerow accessibility* and it can be calculated as a modification of the procedure used to calculate nodal accessibility. To explain the procedure the accessibility of the linkages in Figure 3.3 will be calculated.

The direct connections of all the eight hedgerows in Figure 3.3 can be recorded in a matrix to form the so-called *connectivity matrix* shown in Figure 3.4, matrix A. The matrix columns and rows represent the hedgerow linkages; it is convenient to consider the rows as representing *origin* linkages and the columns as representing *destination* linkages. A *unit entry* in the connectivity matrix indicates the presence of a *direct connection* between two hedgerows, while a *null* entry indicates the *absence* of such a connection. Taking hedgerow L_1 in Figure 3.3 as an example, it can be seen that its relationship to the other hedgerows is recorded in the first row of matrix A; its direct connections with hedgerow L_2 and L_6 are recorded by unit entries and the absence of direct connections with hedgerows L_3, L_4, L_5, L_7 and L_8 are recorded by null entries. The concept of a hedgerow being directly connected to itself is meaningless and, consequently, the leading diagonal axis is composed of null entries. The first column of matrix A records the same information as the first row because if hedgerow L_1 is connected to hedgerow L_2, then hedgerow L_2 is of course connected to L_1. The connectivity matrix is, therefore, symmetrical around the leading diagonal. The summation of each row (or column) of the connectivity matrix gives the total number of hedgerows directly connecting with the hedge in question. For example, the sum of the entries in row L_1 is 2, i.e. there are two hedgerows connecting directly to hedgerow L_1.

A. Direct connections
(connectivity matrix)

	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8
L_1	0	1	0	0	0	1	0	0
L_2	1	0	1	0	0	1	0	0
L_3	0	1	0	1	0	0	0	0
L_4	0	0	1	0	1	0	0	0
L_5	0	0	0	1	0	1	1	0
L_6	1	1	0	0	1	0	1	0
L_7	0	0	0	0	1	1	0	1
L_8	0	0	0	0	0	0	1	0

B. One-step indirect
connections

	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8
L_1	2	1	1	0	1	1	1	0
L_2	1	3	0	1	1	1	1	0
L_3	1	0	2	0	1	1	0	0
L_4	0	1	0	2	0	1	1	0
L_5	1	1	1	0	3	1	1	1
L_6	1	1	1	1	1	4	1	1
L_7	1	1	0	1	1	1	3	0
L_8	0	0	0	0	1	1	0	1

C. Two-step indirect
connections

	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8
L_1	2	4	1	2	2	5	2	1
L_2	4	2	4	1	3	6	2	1
L_3	1	4	0	3	1	2	2	0
L_4	2	1	3	0	2	2	1	1
L_5	2	3	1	4	2	6	5	1
L_6	5	6	2	2	6	4	6	1
L_7	2	2	2	1	5	6	2	3
L_8	1	1	0	1	1	1	3	0

D. Total indirect and
direct connections
(summation matrix)

	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8
L_1	4	6	2	2	3	7	3	1
L_2	6	5	5	2	4	8	3	1
L_3	2	5	2	4	2	3	2	0
L_4	2	2	4	2	5	3	2	1
L_5	3	4	2	5	5	8	7	2
L_6	7	8	3	3	8	8	8	2
L_7	3	3	2	2	7	8	5	4
L_8	1	1	0	1	2	2	4	1

Hedgerow accessibility:

Non-scalar	Scalar (0.2)
Σ = 28	Σ = 0.832
Σ = 34	Σ = 1.104
Σ = 20	Σ = 0.704
Σ = 21	Σ = 0.712
Σ = 36	Σ = 1.152
Σ = 47	Σ = 1.496
Σ = 34	Σ = 1.104
Σ = 12	Σ = 0.384

Figure 3.4 Hedgerow accessibility matrices describing the relationships between the eight linkages (L_1-L_8) shown in Figure 3.3; *A*, the *connectivity matrix* recording the number of direct connections between hedgerows; *B*, one-step indirect connections; *C*, two-step indirect connections; *D*, the *summation matrix* recording the total number of direct and indirect connections between hedgerows; *hedgerow accessibility* is the sum of the rows in the summation matrix, the example shows both non-scalar and scalar values (scalar matrices not shown).

The number of *indirect connections* can be derived by manipulation of the connectivity matrix. For example, the multiplication of the connectivity matrix with itself generates a second matrix that enumerates a network's *one-step indirect* connections (i.e. connections between any two hedgerows that exist through one intermediary hedgerow). This can be seen with reference to hedgerow L_1 and hedgerow L_3 of Figure 3.3. As seen from matrix A, hedgerow L_1 is directly connected to hedgerows L_2 and L_6, and hedgerow L_3 is directly connected to hedgerows L_2 and L_4. It is evident that L_1 and L_3 share a common direct connection with L_2 and, therefore, they must be indirectly connected to one another. This relationship is enumerated by multiplying the matrix row vector L_1 by the column vector L_3 because such a procedure generates a unit cell entry when two values of unity in the connectivity matrix are paired. Complete multiplication of the connectivity matrix with itself, therefore, generates a second matrix that records all the one-step indirect connections that exist between each and every hedgerow on the network (matrix B in Figure 3.4).

The number of *two-step indirect* connections can also be determined in a similar manner, i.e. the multiplication of matrix A with matrix B to form matrix C. This multiplication procedure (which is equivalent to the powering of the connectivity matrix) can be repeated until the desired number of indirect connections has been considered. This desired number is the number of steps that need to be taken to travel from the study hedgerow to the hedgerow furthest away on the network. If any fewer steps are considered then the connectance of outlying hedgerows with the study hedge will not be enumerated. Since the study hedgerow is located centrally within its network, this minimal connectance distance can be called the *radius* of the graph (this is analogous to the term *diameter* used in graph theory to calculate the accessibility of all nodes on a network). The network illustrated in Figure 3.3 has a radius of three, i.e. L_1 to L_6 to L_7 to L_8 (there are also two two-step paths from L_1 to L_4). Hence, by raising the connectivity matrix to the power of 3, all direct and indirect connections with the study hedge are enumerated (matrices A, B and C).

Summing these intermediate matrices gives a *summation matrix* (matrix D) that tabulates the total number of direct and indirect connections (up to the value of the radius) between each hedgerow on the network. Hedgerow accessibility is, then, the sum of each row of the summation matrix; the larger the value the more 'accessible' the hedgerow, i.e. the greater its degree of connection with the other hedgerows on the network. In the example shown in Figure 3.3, hedgerow L_6 is the most accessible to all other hedgerows on the network and hedgerow L_8 is the least accessible (see non-scalar hedgerow accessibility column of Figure 3.4).

If the connectivity matrix is raised to a power greater than the network's radius then *redundancies* are enumerated which represent paths between two hedgerows that pass through an intermediary hedgerow more than once. For example, if the hedgerow accessibility of hedge L_1 in Figure 3.3 is calculated using a radius of four, then paths such as L_1 to L_6 to L_7 to L_8 to L_7 would be enumerated (this path is obviously not the shortest one available to link L_1 to L_7). Even with this criterion, redundancies are enumerated in the form of repeated paths below the network's radius. These redundant paths are illustrated and discussed in sub-section 3.5.6.

One problem with the accessibility approach described so far is that all linkages are treated as being of equal importance, i.e. all direct and indirect connections contribute equally to the summation matrix. From an ecological view point this may be unrealistic because it can be postulated that more distant hedgerows are likely to have a smaller influence on the species composition of a given hedgerow than its immediate neighbours. This can be modelled by incorporating a *scaling factor* that introduces a *distance-decay relationship* into the calculation. With such a scaling factor the contribution made to the hedgerow accessibility measure decreases as the number of linkages away from the study hedgerow increases; more distant hedgerows contribute less to the accessibility measure. In addition to the incorporation of a distance-decay parameter being more ecologically realistic, it is also highly desirable because it reduces the contribution that redundancies have on the accessibility measure (see sub-section 3.5.6).

One way to incorporate a distance-decay relationship is to multiply the intermediate matrices by a powered scalar before they are summed to form the summation matrix. The decay effect is created by progressively increasing the power of the scalar as consecutively more distant linkage paths are considered. Thus in our example

$$D' = s^1A + s^2B + s^3C \qquad [3.13]$$

where D' represents the summation matrix, A, B and C the intermediate matrices, and s a powered scalar with a value between 0 and 1. The influence of the indirect hedgerows can be lessened by selecting smaller s values. In the case of hedgerow networks, the introduction of a scalar is a realistic assumption based upon the contention that close proximity hedgerows exert a greater influence than distant hedgerows. However, the precise balance of influence is unknown and the selection of a working scalar value is therefore somewhat arbitrary. In order to place a greater emphasis on the importance of the nearer hedgerows, a scalar of 0.2 was selected and the amended hedgerow accessibility calculated (see scalar hedgerow accessibility column in Figure 3.4).

This approach of assessing hedgerow isolation will be used to determine the relationship between the study hedgerow and all other hedgerows on the *immediate* network to which it belongs. It is then possible to compare the hedgerow accessibility of each study hedgerow in order to assess if their degree of isolation influences the species richness of the inhabitant plant community. This measure of isolation can not be used to determine the accessibility of a hedgerow to fragmented parts of a network (subgraphs) because there are no structural linkages between these component networks and hence there is no topological accessibility. The existence of large tracts of uninterrupted agricultural land and roads means that fragmented networks are common on farmland.

3.3.5 Estimating hedgerow age

The most accurate method of dating hedgerows is to use map and documentary evidence (Hoskins 1971). The problem with this approach, however, is that such evidence does not always exist or that it is not in a form that allows the age of a particular hedgerow to be estimated accurately. Nevertheless, this approach was used in an attempt to date all the Oxfordshire study hedgerows by consulting the Local Studies Library, the Bodleian Library and Oxfordshire Archives (the three repositories of maps relevant to the area). The documents consulted mainly consisted of Parliamentary Enclosure Awards and maps, tithe maps, private estate maps and Ordnance Survey maps. The North Yorkshire study hedgerows were not dated because the procedure proved to be very time consuming and was likely to be even more difficult in the Yorkshire instance because of the scattered location of the map repositories due to the changes in administrative boundaries in 1974.

Interpretation of the maps is sometimes difficult and often allows only a "planted before", "planted after" or "planted between" label to be given to a particular hedge. The most accurate age of a hedge can usually be derived from Parliamentary Enclosure maps because they show the hedgerows to be planted by the decree of the award. The enclosure maps, however, typically relate to the one hundred year period between the middle of the eighteenth century to the middle of the nineteenth century. It is necessary, therefore, to consult maps both before and after the time of the enclosure to obtain reference dates for the existence of the study hedgerows. The elapsed period between the publication of maps is sometimes considerable and so even when two reference points exist the precise dating of a hedgerow is problematic given that it could have been planted at anytime in between.

3.4 Results

3.4.1 Survey extent and summary of hedgerow characteristics

The vegetation survey included 93 hedgerows from North Yorkshire and 87 from Oxfordshire; for each survey technique (complete, fixed and proportional) this represents approximately 18 hedgerows from each county. The combined area of habitat that these hedgerows represent is 8.84 ha (approximately 36 km in length); the proportional and fixed sampling techniques mean that the actual area sampled was slightly under one-third of this (2.85 ha).

Taking the hedgerows studied using the complete sampling technique as a representative subset of all those hedgerows included in the study, it can be seen from Table 3.1 that the Oxfordshire study hedgerows tended to occupy a greater area of land due both to their greater length and to their greater width. Indeed, the Oxfordshire hedgerows were generally found to have larger physical dimensions, although the mean width of the hedgerow verges were the same for both counties.

Table 3.1 The mean physical dimensions and plant species richness of the North Yorkshire and Oxfordshire hedgerows surveyed by the complete sampling technique (ranges in parentheses).

	N. Yorks (*n*=17)		Oxon (*n*=19)	
Physical dimension:				
Hedge length (m)	134	(17-341)	183	(40-375)
Hedgerow area (m^2)	273	(51-528)	571	(129-1014)
Hedgerow width (m)	2.6	(1.3-5.6)	3.2	(1.9-4.6)
Hedgerow verge width (m)	1.8	(0.9-3.5)	1.8	(0.8-3.6)
Hedge crown width (m)	1.5	(0.6-2.4)	2.3	(1.5-3.9)
Hedge height (m)	2.2	(1.0-4.1)	2.5	(1.4-6.0)
Vegetation characteristics:				
Total number of species	25	(18-33)	36	(19-58)
Number of herb species	13	(8-19)	21	(13-34)
Number of grass species	6	(3-10)	7	(4-11)
Number of woody species	5	(2-10)	7	(1-15)
Number of individual trees	1.0	(0-7)	0.9	(0-8)

It can also be seen from Table 3.1 that the Oxfordshire hedgerows were more species rich than the North Yorkshire ones, this being particularly true with regards to the herbaceous plants. This may partially be due to the more southerly distribution of many plants and the fact that calcareous soils were encountered in Oxfordshire. It may also, however, be explained by the generally larger area of the hedgerows surveyed in Oxfordshire. This is investigated in the next sub-section. In total 120 plant species were recorded from North Yorkshire hedgerows and 136 were recorded from Oxfordshire hedgerows; these are listed in Appendix 3.1.

3.4.2 Species-area relationships

The relationship between hedgerow area and the number of species inhabiting that area can be assessed by either looking at all the species within the entire hedgerow habitat or by looking at groups of species within regions of the hedgerow depending on the *a priori* hypothesis.

In this study the number of species in a hedgerow can be meaningfully related to at least six physical dimensions of the hedge (length, width, total area, volume, verge width, verge area) and the species assessed can be grouped into at least five categories (the number of grass, herb and woody species and the composite groups of non-woody species and all recorded species). An investigation into the relationship between these variables and the plant species richness of hedgerows sampled from each county by the five survey techniques would, therefore, involve 300 (6x5x5x2) significance tests being conducted. Assuming a probability level of 0.05 as the level at which the null hypotheses in the regression analyses are rejected, the type I error (the wrongful rejection of the null hypothesis) will occur in 5% of the significance tests (i.e. on 15 cases). This undesirable situation can be counteracted by decreasing the level of significance or by conducting fewer significance tests. The latter option was chosen and in the first instance only the complete, fixed and 30% proportional survey techniques were considered with regard to the relationship between (i) the total number of species and the hedgerow area, (ii) the number of non-woody species and the hedgerow verge area, and (iii) the number of non-arable species and the hedgerow verge area. Preliminary analysis of the relationship between species richness and the physical dimensions of the study hedgerows revealed that a linear model between species richness and area was approximated most closely by the double-logarithmic transformation of the data. As such these three species-area relationships were investigated after double-logarithmic transformation. They are considered below.

(i) *Effects of area on total plant species richness*

The total species richness of a hedgerow includes all the herbaceous, grass and woody plants recorded as growing on the area of land occupied by the hedgerow verges and the hedge itself. As such, the species included are those inhabiting the hedgerow verges and hedge bottom as well as the woody species comprising the hedge (hedgerow trees included). The species-area data were linearised by a double-$\log_{(10)}$ transformation and the relationship was investigated by correlation and linear regression analyses. For each county and survey technique (complete, fixed and 30% proportional) the characteristics of the species-area regression line are summarised in Table 3.2.

Table 3.2 Summary of species-area regression lines obtained from the complete, proportional (30%) and fixed (30 m) survey techniques (double-logarithmic transformation of data); *r*, correlation coefficient; *z*, slope of regression line (rate of increase in species richness with area); *c*, intercept of regression line (species richness per unit area); *p*, statistical significance of regression line (n.s., not significant (p>0.05)); R^2, coefficient of determination (percentage of variation in species richness accounted for by regression line).

County	Survey technique	*r*	*z*	*c*	*p*	R^2
North Yorkshire	Complete	0.25	0.07	17.0	n.s.	6.3
	Proportional	0.22	0.13	9.7	n.s.	4.8
	Fixed	-0.06	-0.05	19.5	n.s.	0.3
Oxfordshire	Complete	0.54	0.18	11.2	≤0.05	28.9
	Proportional	0.64	0.27	5.2	≤0.01	41.4
	Fixed	-0.20	-0.10	45.7	n.s.	3.8

It can be seen that none of the species-area relationships from the North Yorkshire hedgerows were significant (p>0.05). However, two of the associations between area and species richness in Oxfordshire hedgerows were significant, i.e. a *species-area effect* (a positive correlation between area and species richness) was in evidence. As measured by the complete survey method, approximately 29% of the variation in plant species richness (R^2) was accounted for by the area of the hedgerow ($F_{[1,17]}$=6.9). Surprisingly, the amount of variation accounted for by the 30% proportional survey technique was greater (41%) ($F_{[1,15]}$=10.6). In each county, the density of species in the hedgerows (sampled by the fixed 30 m section) appears to bear no significant or positive relationship with total hedgerow area.

Analyses of covariance were conducted to determine whether or not the characteristics of the species-area relationship differ between counties. If the regression lines do not differ significantly from one another then it is possible to pool the data from each county to increase the effective sample size. The analysis allows the rate of increase, *z*, (the slope of the regression line) and the initial density, *c*, (the species richness per unit area) of the species-area relationships to be compared. The statistical significance of the difference in the slope (rate of increase) and intercept (initial density) of the North Yorkshire and Oxfordshire regression lines are shown in Table 3.3.

Table 3.3 Comparative species richness of Oxfordshire and North Yorkshire hedgerows; *p*, level of statistical probability; n.s., not significant; *F*-ratio, the variance ratio value derived from the analysis of covariance; d.f., the associated degrees of freedom.

Survey technique	Rate of increase (slope)			Density (intercept)		
	p	*F*-ratio	d.f.	*p*	*F*-ratio	d.f.
Complete	n.s.	1.35	1,32	≤0.01	11.70	1,33
Fixed	n.s.	1.17	1,31	≤0.001	26.13	1,32
Proportional	n.s.	0.05	1,30	≤0.001	17.91	1,31

It can be seen that, although the rate of accumulation of species with increasing area does not differ significantly, the unit density of species in North Yorkshire and Oxfordshire hedgerows are significantly different for each of the survey techniques and, therefore, it is not possible to combine the data from each county.

(ii) *Effect of area on non-woody plant species richness*

The lack of an overall species-area effect in hedgerows surveyed from North Yorkshire prompted a more detailed investigation. An important region of the hedgerow habitat is the hedgerow verge on either side of the hedge. This habitat supports herb and grass species and may exhibit a species-area relationship in its own right. This was investigated by assessing the nature and significance of the relationship between the hedgerow verge area and the species richness of the non-woody species recorded from the hedgerow. Regression and correlation analyses were conducted and Table 3.4 summarises the nature and strength of the relationships.

Table 3.4 Statistical significance (*p*), correlation coefficient (*r*) and the coefficient of determination (R^2) of the species-area relationship between non-woody plant species richness and hedgerow verge area as recorded using the complete, proportional (30%) and fixed (30 m) survey techniques (double-logarithmic transformation of data).

County	Survey technique	*p*	*r*	R^2
North Yorkshire	Complete	n.s.	0.24	5.6
	Proportional	n.s.	0.32	10.5
	Fixed	n.s.	-0.10	0.9
Oxfordshire	Complete	n.s.	0.32	10.1
	Proportional	≤0.05	0.48	22.6
	Fixed	n.s.	-0.08	0.6

Again, none of the species-area relationships observed in the North Yorkshire hedgerows was significant, while of the Oxfordshire hedgerows only the proportional (30%) sampling method revealed a significant species-area effect ($F_{[1,15]}$=6.6). Overall, therefore, the proportional sampling technique most consistently identified area as accounting for a significant amount of the variation of plant species richness in hedgerows. The density of species appears not to be significantly related to hedgerow area and the weak correlations that do exist are all negative and so there is an indication that if a relationship exists at all it is an inverse one. Given that the strength of the expected species-area relationships are weaker than that generally observed in many other habitats (e.g. Crowe 1979, Usher 1979, Jarvinen 1982), the nature of the relationship was investigated further by the ecological classification of the hedgerow flora into habitat groups. This classification and the reassessment of the species-area relationships are discussed below.

(iii) *Effect of area on non-arable plant species richness*

The relationships examined so far between hedgerow area and plant species richness have predominantly been weak or absent. One possible explanation for this is that the regression analyses include plant species that are not 'true' hedgerow species; one such group are the arable weeds and plants of other disturbed ground. The presence of these casual colonisers is less likely to be influenced by the area of the hedgerow than by the management of the adjacent fields and by the degree of disturbance caused by agricultural operations. It was decided, therefore, to exclude these opportunistic species from the data set and hence to assess the influence of area on the 'true' hedgerow plant community. This community is likely to consist of species adapted to moderately shady habitats such as the woodland edge (and the woodland interior in particularly wide or dense hedgerows) and species of meadows where the hedgerow verge is particularly wide or undisturbed.

The primary interest was to identify the plants characteristic of disturbed ground so that they could be excluded from species-area regressions. However, it was also of interest to identify the species typically associated with shady habitats and those typically associated with meadow habitat. Consequently, four broad categories were chosen. These were

(i) arable species (arable, disturbed and waste-ground habitats),
(ii) shade tolerant species (woodland edge and woodland interior habitats),
(iii) meadow species (dry and wet meadows and other open, undisturbed areas), and
(iv) other species (those not falling into the above categories).

In order to classify the hedgerow species into the above categories, questionnaires were sent out to 25 people familiar with the flora of England (particularly the plants of the lowland agricultural landscape). They were asked to assign the plants recorded in the survey to one or more of the habitat categories depending on their own personal observations and experience; the use of reference books was discouraged. Three main groups of individuals were approached, they were:

(i) those employed within the university setting conducting academic research into botanical/plant ecological subjects,
(ii) those employed by the Farming and Wildlife Advisory Group (FWAG) as county advisors to farmers on wildlife matters, and
(iii) those working for environmental and ecological agencies.

Twenty of the questionnaires (80%) were returned completed; eight from universities and six each from FWAG advisors and consultancies. The frequency of assignment of each plant species to the four categories was converted to a percentage and any plant that was assigned to a given category more than 50% of the time was then classified as belonging to that group.

The plant species classified to each of the categories are listed in Table 3.5. Of the 131 non-woody plants recorded in the survey, 28% were classified as belonging to the 'arable' category, 24% to the 'shade' category, 27% to the 'meadow' and 1% to the 'other' category. The remaining 20% of the plant species were not assigned to any one of these four groups on more than half of the occasions and, therefore, were considered to have a wide ecological range. The main objective of the classification was, however, to separate species of disturbed ground from species of undisturbed habitats and because of this a fifth 'shade and meadow' category was created. This category contained those species that were not predominantly assigned to either the 'shade' or the 'meadow' category but which could, nevertheless, be assigned to a combined 'shade and meadow' group if their combined frequency of occurrence within these two individual categories was greater than 50%. This category accounted for a further 10% of the plant species, leaving 10% that were neither predominantly assigned to any of the single categories nor to the merged category.

The questionnaire identified 37 species that were considered to have a strong affiliation with disturbed habitats. These were removed from the species data set, as recorded by the complete survey technique, and the species-area relationships were re-analysed for (i) the total hedgerow habitat area and (ii) the hedgerow verge habitat area for both

Table 3.5 Classification of flora recorded during the hedgerow vegetation survey into habitat categories; classification based upon assignment of a species to a given category by more than 50% of the questionnaire participants; values in parentheses are the proportion of species assigned to each category.

Shade species (24%)	Meadow species (27%)	Arable species (28%)	Other species (1%)	Shade & meadow spp.(10%)	Unassigned species (10%)
Alliaria petiolata	*Achillea millefolium*	*Aethusa cynapium*	*Carex riparia*	*Angelica sylvestris*	*Conium maculatum*
Allium ursinum	*Agrimonia eupatoria*	*Agrostis gigantea*	*Nepeta cataria*	*Anthriscus sylvestris*	*Dipsacus fullonum*
Arum maculatum	*Agrostis stolonifera*	*Alopecurus myosuroides*		*Arctium lappa*	*Epilobium hirsutum*
Bromus ramosus	*Allium vineale*	*Amsinckia lycopsoides*		*Arctium minus*	*Epilobium montanum*
Bryonia dioica	*Alopecurus pratensis*	*Anchusa arvensis*		*Ballota nigra*	*Equisetum arvense*
Calystegia sepium	*Arrhenatherum elatius*	*Artemisia vulgaris*		*Cirsium vulgare*	*Galeopsis tetrahit*
Chaerophyllum temulentum	*Centaurea nigra*	*Bilderdykia convolvulus*		*Heracleum sphondylium*	*Geranium pusillum*
Circaea lutetiana	*Centaurea scabiosa*	*Bromus sterilis*		*Lamium album*	*Impatiens glandulifera*
Digitalis purpurea	*Cerastium fontanum*	*Chamerion angustifolium*		*Pteridium aquilinum*	*Lapsana communis*
Elymus caninus	*Clinopodium vulgare*	*Chamomilla recutita*		*Ranunculus repens*	*Montia perfoliata*
Festuca gigantea	*Dactylis glomerata*	*Chenopodium album*		*Silene album*	*Potentilla reptans*
Galium mollugo	*Festuca rubra*	*Cirsium arvense*		*Taraxacum* aggr.	*Rumex conglomeratus*
Geranium robertianum	*Filipendula ulmaria*	*Convolvulus arvensis*		*Urtica dioica*	*Veronica hederifolia*
Geum urbanum	*Geranium dissectum*	*Elymus repens*			
Glechoma hederacea	*Holcus lanatus*	*Fumaria officinalis*			
Holcus mollis	*Hypericum perforatum*	*Galeopsis speciosa*			
Humulus lupulus	*Hypochaeris radicata*	*Galium aparine*			
Hyacinthoides non-scripta	*Knautia arvensis*	*Lamium hybridum*			
Mercurialis perennis	*Lathyrus pratensis*	*Lamium purpureum*			
Montia sibirica	*Lolium multiflorum*	*Matricaria matricariodes*			
Ranunculus ficaria	*Lolium perenne*	*Myosotis arvensis*			
Rubus caesius	*Odontites verna*	*Plantago major*			
Rubus fruticosus	*Papaver rhoeas*	*Poa annua*			
Rubus idaeus	*Pastinaca sativa*	*Polygonum aviculare*			
Silene dioica	*Phleum pratensis*	*Polygonum persicaria*			
Solanum dulcamara	*Plantago lanceolata*	*Reseda lutea*			
Stachys sylvatica	*Poa trivialis*	*Rumex crispus*			
Stellaria holostea	*Rumex acetosella*	*Rumex obtusifolius*			
Tamus communis	*Senecio jacobaea*	*Senecio vulgaris*			
Torilis japonica	*Trifolium pratense*	*Sherardia arvensis*			
Viola odorata	*Trifolium repens*	*Sisymbrium officinale*			
	Veronica chamaedrys	*Sonchus asper*			
	Vicia cracca	*Sonchus oleraceus*			
	Vicia sativa	*Stellaria media*			
	Vicia sepium	*Tripleurospermum inodorum*			
		Veronica persica			
		Viola arvensis			

Oxfordshire and North Yorkshire. The strength and nature of the relationships are summarised in Table 3.6. It can be seen that although there is a consistent positive correlation between species richness and habitat area none of these are significant ($p>0.05$). The two habitat area measurements (total hedgerow area and the hedgerow verge area) are, however, themselves positively correlated ($r=0.98$ and 0.94 for the North Yorkshire and Oxfordshire hedgerows respectively) and therefore the consistency of this positive correlation can be expected.

Table 3.6 Statistical significance (p), correlation coefficient (r), and the coefficient of determination (R^2) of the species-area relationship of non-arable herb and grass species found growing in hedgerow and hedgerow verge habitats in North Yorkshire and Oxfordshire.

County	Habitat region	p	r	R^2
North Yorkshire	Total hedgerow	>0.05	0.145	2.1
	Hedgerow verge	>0.05	0.128	1.6
Oxfordshire	Total hedgerow	>0.05	0.355	12.6
	Hedgerow verge	>0.05	0.165	2.7

3.4.3 Species-isolation relationships

The influence of the adjacent landscape elements in the surrounding 80 ha on the number of plant species inhabiting the study hedgerows was assessed using regression and correlation analysis. The results of the regressions between species richness and the three methods of enumerating the adjacent landscape features (quantity of source habitats, landscape connectivity and hedgerow accessibility) are given below. Only those hedgerows in North Yorkshire and Oxfordshire surveyed using the complete sampling technique are considered because the species recorded using this survey method best represent the true species richness of the hedgerow habitat.

(i) *Quantity of source habitats*

For the hedgerows studied in North Yorkshire there were no significant relationships between the number of species and the various estimations of the quantity of neighbouring source habitats (length of adjacent field boundaries and the perimeter and area of woodland). There were, however, a number of significant correlations with the equivalent set of Oxfordshire hedgerows. Hedgerow plant species richness showed a significant positive correlation with both the total perimeter and the total area of woodland (respectively, r=0.56, $F_{[1,17]}$=7.90, R^2=31.7 and r=0.70, $F_{[1,17]}$=16.37, R^2=49.1). This is to be expected because the area and perimeter of the Oxfordshire woodlands are closely correlated with one another (r=0.82). As with North Yorkshire there was no significant increase in the species richness with an increasing density of hedgerows in the surrounding landscape. There was, however, a significant ($p \leq 0.05$) *negative* correlation between species richness and the density of all field boundaries ($F_{[1,17]}$=5.79, R^2=25.4). This is contrary to what was expected given that, all other factors being equal, the more neighbouring habitats there are that are inhabited by hedgerow plants, the greater the opportunity that any given hedgerow will have of being colonised by a species dispersing from such source habitats.

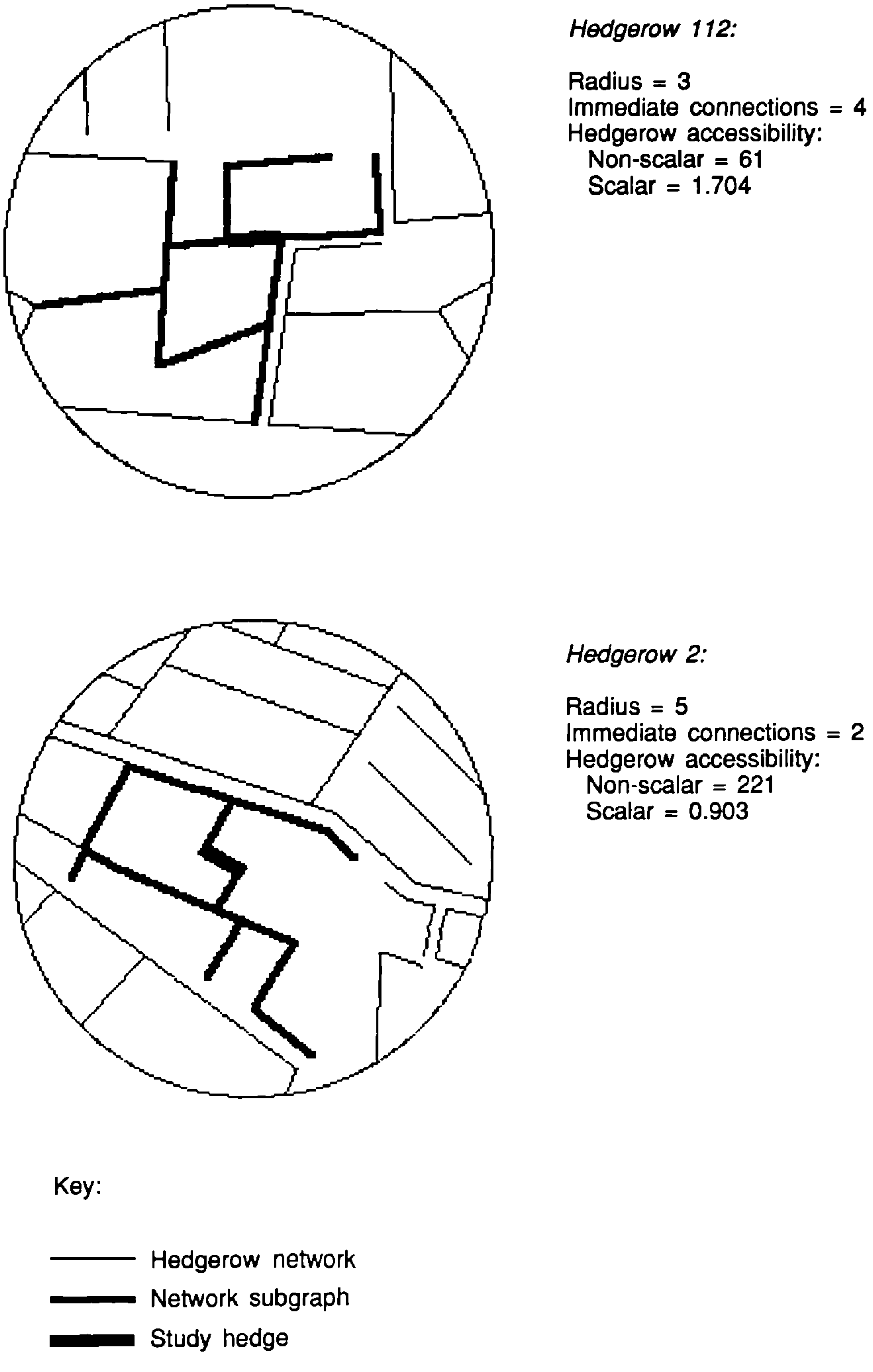
(ii) *Landscape connectivity*

The connectivity of the hedgerow networks, as determined using the *gamma* and *alpha* are given in Appendix 3.2. Although the *gamma* index of the North Yorkshire set of hedgerows and both the *gamma* and *alpha* indices of the Oxfordshire hedgerows were positively correlated with species richness, the level of significance was not below the 5% probability level. Comparing counties, there were no significant differences between the connectivity of the hedgerow networks surrounding the North Yorkshire and Oxfordshire study hedges (p>0.05). There was a close correlation between the *gamma* and *alpha* indices calculated for the North Yorkshire hedgerows (r=0.76), although this correlation was less pronounced with the Oxfordshire hedgerows (r=0.53).

(iii) *Hedgerow accessibility*

The degree of connectance (calculated both with and without a scalar multiplication to create a distance-decay effect) between the study hedgerows and all others on the network to which they belong are given in Appendix 3.2. When calculated in its crudest form, hedgerow accessibility was not significantly correlated with species richness of the hedgerows from either of the counties. This may be because the accessibility measure so calculated makes unrealistic assumptions. This is illustrated by one of the hedgerows from North Yorkshire (hedgerows coded 114) which has a very large accessibility measure when no account of the distance (measured in number of links) between the study hedge and the connecting hedgerows was considered. Thus, the anomalous situation can arise whereby hedgerows that have several close proximity connections are calculated as having a *lower* hedgerow accessibility than hedgerows with only a limited number of near hedgerow connections but which, nevertheless, have an extended network of distant connections (i.e. a high network *radius*). To counter this, a more realistic model was created by using a scaling factor in the calculation of the intermediate matrices (see equation 3.13). The closer the scalar to unity the greater the emphasis that is placed on the more distant hedgerows. Consequently, a scalar of 0.2 was chosen to place a greater emphasise on the importance of the nearer hedgerow connections. Figure 3.5 illustrates how the hedgerow accessibility measure is modified when a scalar is introduced to emphasise the relative importance of close-proximity hedgerows. Without the use of a scalar, the hedgerow coded 112 is calculated to have a lower accessibility than the hedgerow coded 2 despite it having a greater number of immediate connections (four compared to two). This is due to hedgerow 112 having a smaller radius than hedgerow 2. However, with the introduction of a 0.2 scalar into the calculation this order is reversed and as such may well reflect a more realistic situation.

Despite the introduction of a distance-decay effect to create a more realistic model, the amended accessibility measure did not account for a significant proportion of the variation in species richness. The scalar accessibility measure was positively correlated with species richness in the case of the Oxfordshire hedgerows, while negatively correlated in the case of the North Yorkshire hedgerows. The reverse situation is the case when the accessibility measure is calculated without a scaling factor. The number of direct and indirect hedgerow connections did not, therefore, appear to influence in a significant or consistent manner the plant species richness of the study hedgerows when measured by this hedgerow accessibility approach. In a comparison between counties, there was again no difference in the degree of connectance between the North Yorkshire and Oxfordshire study hedgerows.


Hedgerow 112:

Radius = 3
Immediate connections = 4
Hedgerow accessibility:
Non-scalar = 61
Scalar = 1.704

Hedgerow 2:

Radius = 5
Immediate connections = 2
Hedgerow accessibility:
Non-scalar = 221
Scalar = 0.903

Figure 3.5 Illustration of the hedgerow network subgraphs surrounding study hedgerows 2 and 112 used to calculate their hedgerow accessibility; hedgerow 112 has a greater accessibility than hedgerow 2 when calculated using a 0.2 scaling factor.

3.4.4 Species-age relationships

Figure 3.6 illustrates the approximate time of planting of the 87 Oxfordshire study hedgerows. Although it was possible to find maps that covered all the necessary estates and parishes, it was often the case that these maps were less than 150-200 years old. As such, many do not predate the planting of the study hedgerows and it is not possible accurately to determine an upper limit to their age. Consequently, the age of 38% of the study hedgerows could not be determined more accurately than by placing a 'planted before' label on them. For example, hedgerow (UC)410 was recorded as an 'old enclosure' hedgerow on a Parliamentary Enclosure map of Chadlington County Parish dated 1812. No earlier maps exist for this parish and, therefore, it is not possible to say anything more definite than that the hedgerow is at least 178 years old (i.e. planted before 1812). In contrast, 14% of the study hedgerows could be dated to within a few years of their planting because they were recorded on enclosure maps as hedges to be planted under the enclosure award (e.g. hedgerow (DH)446 was planted as part of a 1795 enclosure award). A large number of hedgerows (48%) fell between these two extreme categories, i.e. they can be dated within a broad time-span. For example, hedgerows (MF)403 and (MF)404 were absent on both an 1811 enclosure map and a 25 inch 1881 Ordnance Survey map, but were present on a 6 inch 1911 Ordnance Survey map. These two hedges must, therefore, have been planted between 1881 and 1911.

Of the hedgerows that were determined to have been planted in a given year or between two known dates, hedgerow (BC)537 is the oldest. It is recorded on a 1685 estate map of Broughton Castle and is, therefore, at least 305 years old. In contrast, hedgerow (FC)492 was not recorded until 1980 and its absence from a 1967 Ordnance Survey map indicates that it is between 10 and 23 years old (discussions with the farmer revealed that the hedge has, in fact, grown up spontaneously along the line of a wire fence).

Both the unknown lower limit of the date of planting of many of the hedgerows and the wide time-span over which many could have been planted mean that it is not possible to assess how the species richness of the study hedgerows changes over a continuous time scale. An alternative approach is to create a number of age categories and to compare the species richness of the hedgerows classified into each. Even this, however, did not allow a satisfactory assessment of the influence of age because the imprecise nature of the data meant both that the age categories were very broad and that

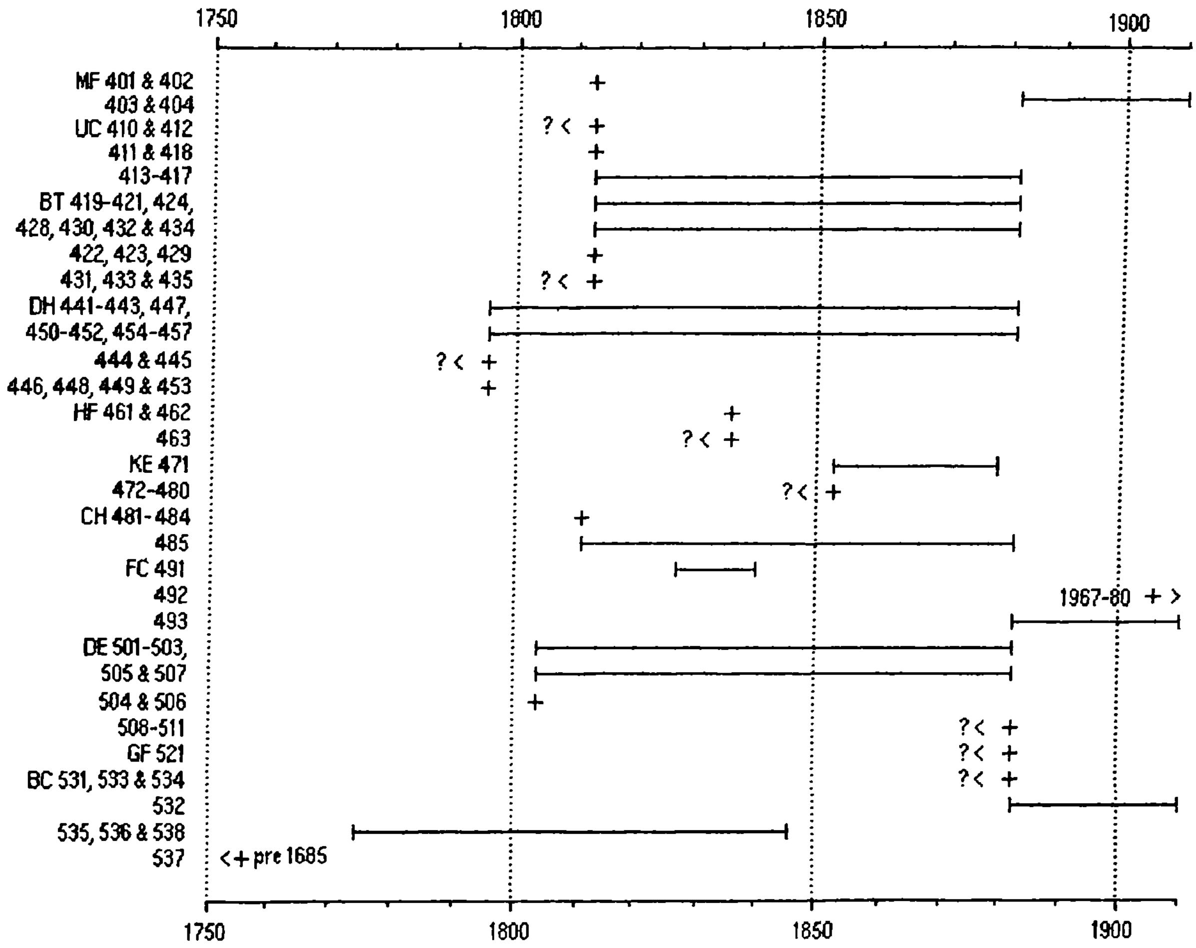


Figure 3.6 Approximate date of planting of the Oxfordshire study hedgerows determined from enclosure, tithe and estate maps; hedgerow codes are given on the left (the hedgerows from each farm are identified by the first being labelled by the farm's initials); +, year of hedge planting; ├─┤, planted between these dates; +>, planted after 1910; <+, planted before 1750; ?<+, planted at an unknown date but at least as old as date specified.

hedgerows were unevenly distributed within them. Table 3.7 lists the Oxfordshire study hedgerows surveyed by the complete sampling technique that fall into three broad age categories that divide the data best. The groups are (i) planted before 1800, (ii) planted between 1800 and 1900, and (iii) planted after 1900. Seven of the 19 study hedgerows could not be placed in these categories and are not included. The number of plant species inhabiting each hedge and the area of the hedge are also tabulated.

The small number of hedgerows in both the planted before 1800 and the planted after 1900 age category mean that only a limited number of species-age comparisons can be

Table 3.7 The Oxfordshire hedgerows surveyed by the complete sampling technique that were planted either (i) before 1800, (ii) between 1800 and 1900, or (iii) after 1900; species richness and hedgerow area are also tabulated.

Before 1800			Between 1800 and 1900			After 1900		
Hedge code	Species richness	Area (m^2)	Hedge code	Species richness	Area (m^2)	Hedge code	Species richness	Area (m^2)
448	36	772.8	401	37	342.0	492	19	128.8
537	36	892.4	411	42	937.5			
			415	32	518.0			
			418	30	241.4			
			430	36	326.0			
			461	35	952.0			
			471	33	680.4			
			501	58	612.6			
			505	37	210.9			

made. These straight comparisons are, however, misleading because they do not take into account the influence of hedgerow *area* on species richness. The influence of hedgerow area is important for these hedgerows because (as shown in sub-section 3.4.2) a significant species-area effect exists. For instance, although hedgerow 492 is both the youngest and the most species poor, it also occupies a smaller area of land than the other hedgerows under consideration. Consequently, its paucity of species may reflect *area* and not age. To assess this it is necessary to compare the deviations of the observed species richness of the study hedgerows from the expected species richness as derived from the species-area regression line for the data set. The hypotheses is that older hedgerows have a greater positive difference between observed and predicted species richness; and conversely, that younger hedgerows have a greater negative difference. The effect of hedgerow age can most clearly be seen by plotting the *residuals* (the difference between the observed and the predicted number of species) of the species-area regression against the independent variable (area). Such a plot is shown Figure 3.7 for the log(species)-log(area) regression analysis of the Oxfordshire hedgerows surveyed by the complete survey technique (Table 3.2).

By comparing the differences between the predicted and the observed species richness (rather than by comparing absolute species richness) it is apparent that hedgerow age, as defined by the three said categories, does not appear to influence consistently species richness in the manner predicted. Figure 3.7 illustrates that when the effect of hedgerow area is accounted for, the two oldest hedgerows (codes 448 and 537) have a lower species richness than expected, while many of the hedgerows of an intermediate age (i.e. those planted between 1800 and 1900) have a greater species richness than expected. In contrast to these findings, an observation that is consistent with the predicted outcome is that the youngest hedge in the sample (hedgerow 492) is indeed the most species poor after the effect of its small area has been accounted for.

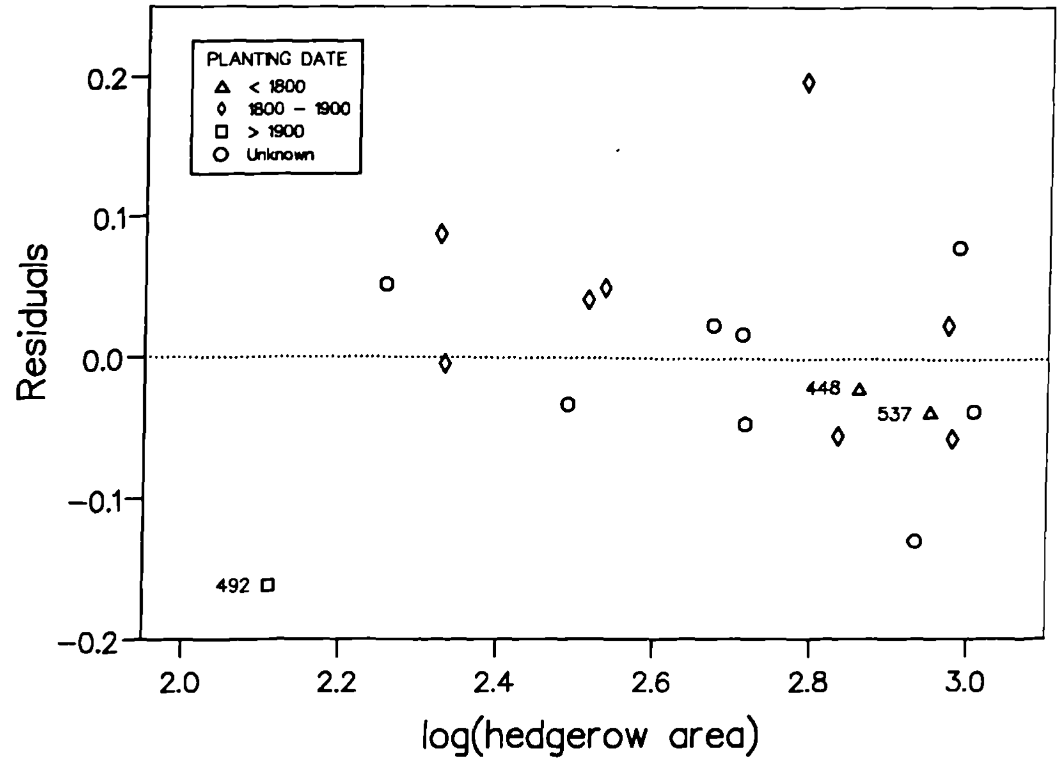


Figure 3.7 A plot of the residuals of the linear regression between log(hedgerow area) and log(species richness) of the Oxfordshire study hedgerows surveyed using the complete sampling technique; the greater the positive or negative deviation from zero (horizontal line) the greater the difference between a hedgerow's predicted species richness (calculated from the regression line) and the observed species richness; hedgerows that are identified by their numeric code are referred to in the text; marker symbols indicate hedgerow age category (see legend).

Assessing the effect of hedgerow age on the *density* of plant species (recorded by the fixed 30 m sampling technique (n=17)), as opposed to the absolute species richness, proved to be even less successful in that only two mutually exclusive age categories could be created from the dating information at hand. The two categories created contained those hedgerows (i) planted before 1850 and (ii) planted after 1850. Even with this broad division only one hedgerow recorded by the fixed sampling method could be confidently placed in the younger hedgerow category, while eight hedgerows could be placed in the older hedge category. The paucity of the data mean that little can be concluded about the effect of hedgerow age on the density of species in the Oxfordshire hedgerows.

Until the age of the study hedgerows can be determined more precisely, or until a larger data set is available, it is not possible to partition adequately the influence that the passage of time has on the number of species inhabiting a hedgerow from other possible species richness determinants. The age of hedgerows is, however, likely to be important because it largely determines the time that immigration and extinction processes have been in operation.

3.4.5 Soil pH characteristics

The hedgerow soils in North Yorkshire were much more acidic than those of Oxfordshire (the majority of North Yorkshire soils being in the pH range of 4.0 to 5.5 while Oxfordshire soils were generally in the range 7.5 to 8.5). Table 3.8 summarises the pH characteristics of the study hedgerows in each county. In contrast to Oxfordshire, the majority of North Yorkshire hedgerow soils were more acidic than the adjacent fields indicating the wide-spread use of lime to ameliorate the field pH conditions. The Oxfordshire hedgerows also tended to vary less along their length as indicated by the smaller coefficient of variation of the pH measurements.

3.4.6 Predicting hedgerow plant species richness

The simple linear regression models used do not appear to explain a satisfactory amount of the variation in species richness, i.e. no one variable has an exceptional predictive power. To investigate further what factors determine species richness a multiple regression technique was employed. Plotting the residuals of the single linear regression variables did not indicate curvilinearity of the underlying relationship and, therefore, the equation for a straight line could be used to model the underlying association. The model is

Table 3.8 The pH characteristics of hedgerow and adjacent field soils in North Yorkshire and Oxfordshire; *n*, number of hedgerows surveyed; CV, coefficient of variation; tabulated frequencies are the number of instances that a hedgerow soil had a pH significantly greater than (>) or less than (<) its adjacent southerly field (Student's *t*-test, significance level *p*0.05); n.s., no significant difference between hedgerow and field pH.

				Frequency			
Country	*n*	Mean hedgerow pH	Mean hedgerow ph CV	Hedge pH significantly > field pH	Hedge pH significantly < field pH	n.s.	Field pH unknown
Yorks	93	4.89	11.29	1	85	7	0
Oxon	87	7.27	6.18	24	17	18	28

$$y = c + z_1x_1 + z_2x_2 \ldots + z_tx_t \qquad [3.14]$$

where y is the number of species, x_1 to x_t are the predictor variables, z_1 to z_i are the slope coefficients, and c is a fitted constant. The data were double-$\log_{[10]}$ transformed. The predictor (independent) variables used in the multiple linear regression are (i) the area of land occupied by the study hedgerow, (ii) the hedgerow accessibility (0.2 scalar), (iii) the *gamma* index of connectivity, (iv) the total length of hedgerows in the surrounding 80 ha, (v) the length of woodland perimeter and field boundaries in the surrounding 80 ha, (vi) the area of woodland in the surrounding 80 ha, (vii) the network length of hedgerows in the surrounding 80 ha, (viii) the coefficient of variation in soil pH, (ix) the mean soil pH, and (x) the coefficient of variation in hedge height.

The analysis of covariance revealed that the species data from each county could not be pooled and a multiple regression analysis was, therefore, conducted separately for a subset of the North Yorkshire and Oxfordshire study hedgerows. By including all ten predictor variables in the model, 74.7% and 85.4% of the variation in species richness of the North Yorkshire and Oxfordshire hedgerows was accounted for respectively. In this instance, the sample size of hedgerows for North Yorkshire was 17 and for Oxfordshire 16 (although 19 Oxfordshire hedgerows were, in fact, surveyed for this study there were three missing values in the data set and, consequently, the effective sample size was 16 when conducting the multiple-linear regression using all the explanatory variables). Both the small sample size of hedgerows and the large number of independent variables included in the initial analysis meant that the variance accounted for by the regression line is not significant at the 5% probability level for either county.

Further examination of the relationship between species richness (y) and the ten predictor variables (x_i to x_{10}) was carried out to identify those predictors that account for the largest amount of variation in species richness. A simplified model can then be reconstructed by omitting those predictor variables that are of little interpretive value. To determine which predictor variables are of greatest explanatory power it is necessary to calculate the Student *t*-statistic associated with each. The *t*-statistic is calculated as

$$t = (z_i - Z_i) / s_i \qquad [3.15]$$

where t is Student's *t*-statistic, z_i is the regression line slope coefficient of predictor variable x_i, Z_i is the slope coefficient of the regression line of the population under the null hypothesis (in this instance Z_i=0 because the null hypothesis is that population species richness (y) is independent of the predictor variable x_i), and s_i is the estimated standard deviation of z_i. The probability of obtaining this *t*-statistic by chance is then obtained from the *t*-distribution with the required probability level and associated degrees of freedom. The smaller this probability the greater the likelihood that Z_i does not equal zero, and hence the greater the confidence that can be placed in its explanatory power.

In the case of the Oxfordshire hedgerows,
inspection of the *t*-statistic calculated for each predictor variable reveals that the only slope coefficient (z) that differed significantly from zero was that describing the regression line between species richness and study hedgerow area (p=0.016, $t_{[5]}$=3.58). The z value of the regression line between species richness and the area of woodland in the surrounding 80 ha just failed to reach significance (p=0.051, $t_{[5]}$=2.56). The probability value associated with the remaining predictor variables were all in excess of 0.195 and, therefore, had poor explanatory power. Upon reforming the model to include

only the two area measurements (the most powerful predictors) slightly less variance in species richness (62.9%) was explained than with the complete model. The relationship did, however, attain significance ($p \leq 0.001$, $n=17$, $F_{[2,14]}=11.87$). The simplified regression equation is

$$\log(S) = 0.600 + 0.228 \log(A_h) + 0.0771 \log(A_w) \qquad [3.16]$$

where S is the species richness of the study hedgerow, A_h is the area of the study hedgerow, and A_w is the area of woodland in the surrounding 80 ha.

For the North Yorkshire hedgerows, the same procedure proved unsuccessful because of the poor explanatory power of the predictor variables ($z=0$ was accepted in all instances with p ranging from 0.108 to 0.798). It was not possible, therefore, to eliminate independent variables of poor predictive value while at the same time maintaining the explanatory power of the model and increasing the confidence (and hence the significance) of the model.

3.4.7 Plant assemblages

Particularly in the case of the North Yorkshire hedgerows, the lack of pronounced relationships between the *number of species* inhabiting the study hedgerows and various environmental parameters thought on an *a priori* basis to be of interpretive value prompted the investigation of which particular species (or assemblages of species) tend to inhabit hedgerows characterised by particular properties. It is possible that a *qualitative*, rather than a *quantitative*, association may exist between the inhabitant species and the hedgerow's physical characteristics. One way to investigate this is to use a mathematical clustering technique that groups samples (in this case individual hedgerows) together according to the similarity of their floral composition. The physical properties of the derived groups can then be compared (e.g. by analysis of variance) to determine if they differ markedly in their characteristics. The cluster analysis used for this procedure was Twinspan (two-way indicator species analysis) (Hill 1979). This ordination technique generates a two-dimensional table that groups samples which have similar species composition and abundance closer together than those with dissimilar composition and abundance. Species that behave similarly across samples are also grouped closer together. In this instance the data are in a presence or absence form and so the grouping of hedgerows is solely based on the species composition. This ordination approach is divisive and polythetic; divisive in that it divides the community data into progressively smaller groups of similar species/samples at each successive dichotomy (rather than the usual agglomerative methods of hierarchical cluster analysis), and polythetic in that the dichotomous groupings are made with reference to a suite of species rather than the presence or absence of a particular one (Hill *et al.* 1975).

Although the attributes of the hedgerow ordination groups can then be compared statistically to determine if significant inter-group differences exist, this technique does not indicate causality between a given hedgerow attribute and its floral composition. This is the case because the relationship may only be a correlative one. The technique does, however, indicate the possibility of an association and allows hypotheses to be formulated.

The Twinspan ordination was conducted on all North Yorkshire and Oxfordshire hedgerows whose floral composition was surveyed using the complete sampling technique (*n*=36). On the assumption that very rare and very common species would be of little interpretive value, only species occurring in more than 10% and less than 90% of the hedgerows were included. Table 3.9 illustrates the ordination table; the first four hedgerow groups identified by the analysis are emphasised by vertical lines, while the first two species groups are emphasised by a horizontal line. These groups, and those identified by subsequent divisions, can be referred to by the binary ordination coding for each dichotomy shown on the right and at the bottom of the ordination table for the species and hedgerow groups respectively. For instance, the two primary hedgerow groups (those identified by the first level division and separated by the solid vertical line) are labelled with the code 0 for the left hand side group and 1 for the right hand side group; taking the left hand side group as a further example, the two groups identified by the second level division are labelled 00 for the left hand side group and 01 for the right hand side group. Subsequent hedgerow groups and the species groups are labelled in a similar manner. This labelling system will be used in the text to refer to the ordination groups. The hedgerows included in the ordination are referred to by an ordination code (1 to 36) along the top of the table; the location of the North Yorkshire hedgerows (ordination codes 1-16 and 36) and the Oxfordshire hedgerows codes (18-35) are given in Appendix 3.3. The tabulated species (names abbreviated to the first four

Table 3.9 Annotated Twinspan ordination of plants inhabiting the North Yorkshire and Oxfordshire hedgerows surveyed using the complete sampling technique; hedgerow ordination codes at top of table, species abbreviations at left of table; tabulated symbols: '-' indicates absence of species, '1' indicates presence; successive dichotomous divisions of hedgerow and species groups are indicated by the binary codes at the right (species group codes) and bottom (hedgerow group codes) of the table; solid vertical line emphasises first hedgerow division (groups 0 and 1), dotted lines the two secondary divisions (groups 00, 01, 10 and 11); solid horizontal line emphasises the first species division (groups 0 and 1); species annotated by '*' indicate those common on, or preferential to, calcareous soils; '#', those characteristic of acid soils; and '+', those characteristic of arable, disturbed and waste areas; species annotated with '@' indicate those predominantly classified into the 'arable' category in the habitat questionnaire.

```
   Species       2232232223112221133    1     133   1111
 abbreviation    363452789189012174512367893606450245      Hedgerow ordination code

 * Merc pere     ------11-11-1----------------------------    000000
 * Viol odor     1--111-111-------------------------------    000000
 * Clem vita     -------1111------------------------------    000000
   Gali moll     -----1---11111---------------------------    000001
   Knau arve     --1111-1-11-11---------------------------    000001
 * Rubu caes     -----1-1--111----------------------------    000001
 * Cent scab     -1111-----1-11---------------------------    00001
 + Rume sang     1---11---1----1--------------------------    00001
 + Sonc aspe     -11----111-------------------------------    00001
@+ Agro giga     -1-111-11111-111111----------------------    00010
 * Arum macu     --111-111111-11---1---11-----------------    00010
   Glec hede     ---11-11111111-111-----------------------    00010
 * Euon euro     -----111-1---------1---------------------    00010
 * Corn sang     1----1---1----1-----------1--------------    00011
   Alop prat     --------------1--1-1-----1---------------    0010
   Fest rubr     1--1---1-1-1-1-111-1---------------------    0010
   Hyac none     ----------------------1111---------------    0010
   Cory avel     ----1--111---1-11-----1111---------------    0010
 * Acer camp     ---11--1111111----1---111--------1---    0110
   Chae temu     --11---1-1-1111-1-11-1---1--------1--    0100
   Stac sylv     1--111111111-11-111111111--1---------    0100
   Tamu comm     1-111111111-11--11-1-11-1-1----------    0100
   Rosa cani     11-111111111-1--1111-11111-1-------1    0100
@+ Cirs arve     111-111111--1-111111-------11--------    010100
   Bryo dioi     -111-111111111-11--1-1111-11--11-----    010101
   Hede heli     -1--11-11111-1--111---1--1-------11-    010101
   Prun spin     11-1111111111111-11-1-1-111----1--1-1-    010101
   Samb nigr     11 1111111 11111-1111-11-1-----111111    010101
 + Poa  triv     111 -1111111111111111111111-1-----1111    01011
   Hera spho     1-111111111111111111111111-111--11111    01011
 + Laps comm     11-111--111-------1---1--1--------1-1    0110
 + Sile alba     --11---11111----1----1-----1-1-------    0110
 + Arct minu     1-1--1-------------------------1------    01110
   Conv arve     -1111111111111111--11--------1-1-11----    01110
   Gera robe     1--------11- 1-----------------1------    01110
   Sola dulc     1111-111--111------11---------1----1--    01110
   Alli peti     1111111111111111-----1-------11--------    01111
   Geum urba     1---1--1-1---1------------------------1---    01111
   Myos arve     --11-1-1-1-------------------1--------    01111
 ---------------------------------------------------------------------
   Loli pere     ---------------11-1------1------1---    100
@+ Rume obtu     -11-1-11--1---111111---111--11-1-1---    100
 + Tara offi     1--11----1-----1---------1-1------1--1    100
   Ulmu proc     --------------1 1 1------1-------1-    100
 + Holc lana     --------------111-111---111----1111-11    101
 # Holc moll     1-1-------------111111-1111-1-1111111    101
 + Ranu repe     1 1  -  -1--     --111    -      -    -1 1-    101
   Ilex aqui     -------1-1-----1-1-----11- --1--1---    101
 + Anth sylv     -11111111111111- -111-11-11-11-1-1111    110
 + Lami albu      11-111111--1 11111 11--1 1111 11-1--    110
 * Frax exce     1 -1111 -1 -1    --11 11- 11 1  11-    110
@+ Brom ster     -111111111-1-11111-1-11--11111111111    11100
 + Cirs vulg     --1---1111---1----1111-----1-1--1111    11100
   Malu sylv     ---------1-----1-------------11-----    11100
@+ Sonc oler     ---1-1---------1------------1---1----    11101
@+ Stel medi     ------------------1-1----1---11-1-1    11101
 + Equi arve     ----------------1------------1---11-    111100
   Malu dome     ----------1---1--------------1------11    111100
@+ Arte vulg     -11---------------------------1---1-    111101
@+ Chen albu     --------1- -----------------1-11111----    111101
 + Coni macu     --- ---------- -------------1111------    111101
 # Pter aqui     ------- -  -------------1--11--11------    111101
@+ Sisy offi     -11--------------------------11--1-----    111101
   Acer pseu       ----1- -----   ------1------111----    111101
   Quer robu     -1-----1-----------------1 ----11------    111101
 + Gale tetr     ----------1 ---------111 1--1-------    11111

                 000000000000000000000000001111111111
                 000000000000000111111111110000001111
Dichotomous      000111111111111000000011110000 11       Dichotomous
ordination          0000000000010000111                   ordination coding
coding for          00000001111                           for
hedgerow groups     0001111                               species groups
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letters of their genus and species) have been annotated to indicate their preferred habitat type as cited in Clapham *et al.* (1985). They have also been labelled to indicate which were considered to belong to the 'arable' category (cultivated, disturbed and waste ground species) by participants of the habitat questionnaire. The full names of these species are given in Appendix 3.4.

The physical characteristics of the primary (0 and 1) and secondary (00, 01, 10 and 11) hedgerow groups identified by the analysis were compared using analyses of variance. The parameters investigated for association with the identified groups were (i) area of land occupied by the hedgerows, (ii) *gamma* index of connectivity, (iii) *alpha* index of circuitry, (iv) hedgerow accessibility (a scalar value of 0.2 was used), (v) *network length* of the hedges (the summed length of hedgerows adjoining the study hedge in the surrounding 80 ha) as a measure of source habitat quantity, (vi) pH of the hedgerow soils, (vii) the variation in soil pH along their length as calculated using the coefficient of variation, and (viii) hedgerow age. The parameters that differ significantly between the paired ordination groups are shown in Table 3.10.

The first division appears to indicate that the hedges associated with the primary hedgerow group coded 0 have both a lower hedgerow accessibility and a shorter length of connecting hedgerows (network length) than the reciprocal group coded 1. Species identified by the ordination as being "*indicator*" (Hill 1979), i.e. highly preferential, species to this former group are *Agrostis gigantea, Arum maculatum, Glechoma hederacea, Stachys sylvatica, Tamus communis, Rosa canina* and *Prunus spinosa.* No one species was identified to be highly characteristic of the latter group. The secondary ordination groups 00 and 01 differ significantly both in their mean soil pH and in the hedge network length. The more alkaline soil conditions of hedgerows characteristic of group 00 appears to favour the occurrence of calcicole plants. Although none of the indicator species identified by the analysis (*Knautia arvensis, Convolvulus arvensis, Solanum dulcamara* and *Alliaria petiolata*) are calcicoles, there are a number of plants associated with calcareous soils that are characteristic of this hedgerow group (e.g. *Clematis vitalba, Centaurea scabiosa* and *Euonymus europaeus*). In contrast two species commonly associated with acid soils, *Holcus mollis* and *Pteridium aquilinum,* showed no association with the more alkaline subset of hedgerows. As seen from the soil pH coefficient of variation, it appears that the species classified into the groups 10 and 11 may be characteristic of hedgerows that differ in the variability of their soil pH, i.e.

Table 3.10 Physical properties of hedgerows classified into the primary (0 and 1) and secondary (00, 01, 10 and 11) ordination groups that differ significantly; (*s*, standard deviation; *p*, statistical probability; d.f., degrees of freedom).

Hedge property	Code	Mean	*s*	*p*	*F*-ratio	d.f.
Scalar hedgerow accessibility	0	1.07	0.48	≤0.05	7.28	1, 34
	1	1.54	0.44			
Network length	0	1854	602	≤0.05	5.88	1, 34
	1	2411	657			
Soil pH	00	9.85	4.59	≤0.01	11.75	1, 24
	01	5.40	2.84			
Network length	00	1640	566	≤0.05	5.27	1, 24
	01	2147	542			
Soil pH coefficient of variation	10	5.60	1.93	≤0.05	7.34	1, 8
	11	11.44	4.85			

group 10 may be inhabited by plants that require a more homogeneous spoil pH than the reciprocal group (the indicator species of group 10 are *Bryonia dioica* and *Chenopodium album*).

Both the habitat questionnaire and habitat preferences cited in the literature indicate that the plants inhabiting cultivated soils, waste ground and disturbed areas tend to pertain to the lower half of the ordination. There is a tendency, therefore, for a polarity to exist within the vegetation community; plants commonly associated with calcareous soils tended to be grouped at the top of the ordination table, and plants of acid soils and cultivated, waste and disturbed soils tended to be grouped towards the bottom.

3.5 Discussion

3.5.1 Predictive value of hedgerow area

The various comparisons of the number of plant species inhabiting hedgerows of differing area do not show area to be consistently a significant determinant of species richness. There is, however, a large difference in the amount of variation in species richness accounted for between counties and between methods of assessment. For example, in North Yorkshire area only accounted for 6.3% of the variation in species richness as recorded using the complete sampling technique. While in Oxfordshire the species-area relationship attained significance at the 5% probability level with 28.9% of the variability being accounted for. The correlation coefficient (*r*) of this relationship for North Yorkshire and Oxfordshire hedgerows is 0.25 and 0.54 respectively. The correlation coefficients of the various species-area relationships are generally lower (especially in the case of North Yorkshire) than in a number of other studies of plant species richness in habitat patches. For example, the correlation coefficient was 0.72 for nature reserves in Yorkshire (Usher 1979), 0.96 for the Aland Islands, Finland, (Jarvinen 1982) and 0.48 for vacant urban lots in Chicago, USA, (Crowe 1979). Why this should be the case may be related to the underlying causes of the species-area relationship and how these are modified by the special conditions that pertain to linear, and often interconnecting, habitats of different age within the intensively farmed landscape.

In terms of the rate of species accumulation, the effect that area does have on species richness does not differ significantly between the North Yorkshire and Oxfordshire hedgerows, i.e. the slope of the regression lines (*z*) are not significantly different for each survey technique (Table 3.3). Nevertheless, and in the instances where species richness is positively correlated with area, the Oxfordshire survey hedgerows do acquire species at a greater rate with increasing area than the North Yorkshire hedgerows (Table 3.2). It is this greater *z* value of the regression line derived from the complete sampling technique (0.18 for North Yorkshire compared to 0.07 for Oxfordshire) that explains why the observed species richness of the Oxfordshire hedgerows is greater than that of the North Yorkshire hedgerows (Table 3.1) despite the fact that by extrapolation those from North Yorkshire appear to have a greater unit density (a *c* value of 17.0 compared to 11.2) (Table 3.2). In reality, therefore, the constant *c* is seen to be of little value in assessing the species richness of hedgerows on a per area basis. As advocated by Connor & McCoy (1979), Jarvinen (1982) and Loehle (1990), care should be taken when interpreting the coefficients of the species-area relationship and their implications for the theory of island biogeography.

It appears that when considered by itself, area is a poor predictor of species richness and that both the strength and the nature of the species-area relationship differ between counties. The predictive power of area in combination with other hedgerow parameters, such as management, habitat diversity, isolation and age, is discussed in subsection 3.5.9. Before this, however, the significance of these additional parameters will be considered individually.

3.5.2 Hedgerow management and disturbance

Hedgerows are habitats that experience disturbance from a variety of sources because they both need to be managed in order for them to fulfil an agricultural role and because they are set in a matrix of highly disturbed agricultural land. Disturbance may take the form of mechanical disturbance caused by vehicle passage, hedge cutting or agrochemical disturbance (Roebuck 1987, Marshall 1988). As proposed in Figure 3.8, disturbance may act to increase or decrease the species richness of a hedgerow depending upon its level of intensity. For instance, at moderate levels of disturbance the composite number of perennial and biennial species may be unaffected by the disturbance which, nevertheless, provides a niche for invasive annuals to establish themselves within the perennial sward. Under these circumstances species richness might actually increase. At higher levels of disturbance, however, the established perennial species populations may suffer local extinction as a direct result of the disturbance or may be out-competed by weed species with high growth and reproduction rates. Under these circumstances, a situation can be envisaged whereby disturbance decreases species richness. This latter scenario appears to be the situation with three hedgerows on Grimstone Grange Farm, Heslington, North Yorkshire, which in the previous year had been sprayed with a broad spectrum herbicide to control weeds. Comparison of the observed species richness with the expected (as derived from the regression analysis for North Yorkshire hedgerows) showed that all three hedgerows were considerably less species rich than expected. The observed number of species were 11, 12 and 16 with the expected species richness for each hedgerow having 95% confidence intervals of 11.6-19.1, 19.8-25.0 and 15.7-26.3 species respectively. This evidence is inconclusive, however, because the species richness of the hedgerows before they were sprayed is not known and the 95% confidence interval around the regression line of the third hedgerow does not exclude the observed number of species. It seems likely, however, that incidental or direct disturbance will modify the species richness and composition from that characteristic of the undisturbed hedgerow habitat.

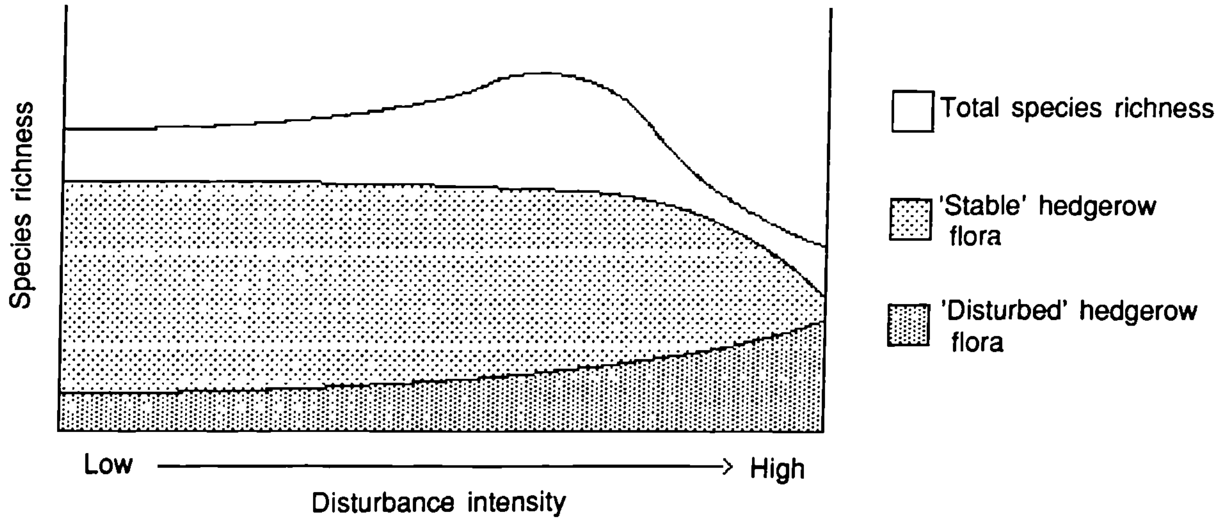

Figure 3.8 Changes in the species richness and composition of hedgerow flora with varying degrees of habitat disturbance.

In order to assess the species-area relationship of the plant community that might be more characteristic of the undisturbed hedgerow habitat, plants associated with cultivated, disturbed and waste ground (the 'arable' category in the habitat questionnaire) were excluded from the data set. This procedure, in fact, *lessened* the explanatory power of area for both counties, i.e. generally less than 10% of the variation in the amended species richness was accounted for by the hedgerow or hedgerow verge area. This may again indicate that the study hedgerows were subject to varying degrees of disturbance because, depending on the intensity of disturbance, varying fractions of the perennial and biennial floras may begin to be lost from the hedgerow.

3.5.3 Causes of the species-area effect

The theory of equilibrium island biogeography has central to it the premise that species richness is positively correlated with island area and that the number of species on an island will increase asymptotically with time. Yet neither of these observations are proof that the mechanisms behind the equilibrium theory are in operation (Williamson 1989). The envisaged mechanism was that the observed number of species on an island is brought about by the equilibrium between the rate of immigration (as determined by island isolation) and of extinction (as determined by the size of the island and consequently the size of inhabitant populations). There are a number of observations that would indicate that the processes that MacArthur & Wilson (1967) considered to determine the number of species on water-locked and insular islands are actually in operation. They are:

(i) empirically observed rates of immigration and extinction,

(ii) species turnover as a result of immigration and extinction in absence of changes in species richness,

(iii) an increase in extinction rate (with unaltered immigration rate) following a decrease in island area and a consequent 'relaxation' in species richness to a new equilibrium value, and

(iv) the continued presence of the species-area relationship when sampling *one habitat type* with a *fixed sampling effort* regardless of habitat area.

The first three points require the direct observation of changes in species composition and richness over time. Such changes may occur slowly over the course of many years and, consequently, the observation of such processes is problematical (Usher 1985). In contrast, the last point can be investigated by 'snap-shot' surveys with the dynamic nature of the underlying process being inferred from the inability of the *random placement hypothesis* (Arrhenius 1921, Coleman 1981, Coleman *et al.* 1982) and the *habitat diversity hypothesis* (Williams 1943, 1964) to explain a species-area effect under the constraints of the single habitat and fixed sampling effort specification (Kelly *et al.* 1989). The random placement explanation of the species-area effect is untenable under such criteria because its postulate is that the number of species will increase with increasing area if species and individuals are distributed randomly. Larger islands or 'quadrats' will have more species by default. This situation is obviously excluded by the fixed sampling effort constraint. The habitat diversity hypothesis is untenable because at its basis is the premise that with increasing area the number of habitats, and thus niche availability, increases with the result that more species are recorded because of the greater niche variety. This explanation is also excluded by sampling *within one habitat* type. By contrast, the equilibrium hypothesis predicts that larger islands will have lower local extinction rates and, therefore, the *density* of species will be positively correlated with area. Using this survey technique, Kelly *et al.* found that the variation in species richness accounted for by area dropped from 92% when species richness was determined by complete island surveys to 10% and 17% for the two vegetation types encountered. They concluded that immigration and extinction were not in operation in the manner that MacArthur & Wilson had hypothesised.

This survey technique has not been applied to insular isolates in the context of island biogeography and there is, therefore, considerable interest in such an approach. In the present study the use of a 30 m fixed survey length enables the density of plant species to be compared with total hedgerow area. The condition of a high degree of habitat homogeneity is, however, only partially satisfied, because although the hedgerows were all chosen (i) to be inter-arable, (ii) to not have an associated road or ditch, and (iii) to not have been managed in a way that increases disturbance, they were not chosen for a blanket-uniformity of characteristics. Treating the North Yorkshire and Oxfordshire hedgerows as two subsets, this technique accounted for a very small percentage of the species richness and, indeed, the correlation coefficients of the species-area association were both negative (Table 3.2). In addition, the absence of a significant species-area effect in the case of the North Yorkshire hedgerows surveyed by the complete survey technique makes the test for the mechanism of the species-area effect less meaningful or even inappropriate.

The possibility of a marked influence of habitat diversity on the observed species richness that may act to obscure any species-area effect can not be ruled out. If a variety of habitat parameters is available, one way to address this problem is to conduct a cluster analysis to identify habitat samples that are physically similar. The species-area relationships of the habitat subgroups can then be assessed (Kelly *et al.* 1989). For plants, important habitat variables are likely to include soil moisture, pH and nutrient status, disturbance intensity, habitat structural characteristics, and solar radiation. Only information about the variability of soil pH and hedgerow height was available and so an effective ordination of hedgerow properties was not possible. It is concluded, therefore, that the habitat diversity hypothesis can not be excluded as a mechanism with the potential to explain, at least partially, the species-area relationships observed. The effect of habitat heterogeneity is considered further below.

3.5.4 Habitat diversity

Within the framework of equilibrium island biogeography, any discussion about the effect of area on species richness must consider the role of habitat heterogeneity. As already noted, in the present study this parameter was measured by an edaphic variable (soil pH) and a structural variable (hedgerow height). The Twinspan cluster analysis (Table 3.9), and subsequent analysis of variance, identified that soil pH variability may be a factor influencing the species composition in the two reciprocal ordination hedgerow groups 10 and 11 (Table 3.10). Comparison of the species richness of the hedgerows characteristic of these hedgerow groups revealed that there was no statistically significant difference in the numbers of species characteristic of each (p=0.69, $t_{[8]}$=0.41). The qualitative differences between the two hedgerow groups are exemplified by the indicator species *Bryonia dioica* and *Chenopodium album* for the hedgerow group characterised by soils with a more homogeneous pH (group 10), and *Poa trivialis* for the reciprocal group characterised by a more variable soil pH (group 11). It can be postulated that the respective pH conditions may favour the establishment and reproduction of the species characteristic of each group.

The coefficients of variation for the hedgerow height did not differ significantly (p>0.05) between the primary or secondary hedgerow groups identified by the ordination. At the very coarse level considered here, therefore, any *a priori* hypotheses on the possible influences of variability in hedge height on species composition (such as those caused by differential shading, entrapment of airborne seeds and attractiveness to seed dispersing birds) are not substantiated in this instance. In addition to hedge height, differential shading may also result from the orientation of the hedgerow with respect to north. Hedges may have a greater niche variability if they run east to west because their northerly side will experience reduced irradiation and temperature in comparison to their southerly side. No account of this possible influence has been incorporated because orientation in itself is not a measure of microclimatic conditions (shading will also be determined by the *density* of hedge foliage and the *thickness* of the hedge).

The nature of habitat variability may not always be very obvious and the possibility arises that habitat differences may go unrecorded and yet may, at least partially, explain species-area relationships. This is illustrated by a study of phytophagous arthropods on patches of bracken that were initially selected for their uniformity (Rigby & Lawton 1981). The authors' subsequent investigations revealed, however, that the frond size of the bracken plants was positively correlated with habitat area. It was proposed, therefore, that differences in plant architecture may, in fact, account for the species-area effect and not area *per se*. Indeed, it is clear that habitats that appear similar when judged by top-level hierarchical considerations may, in fact, vary considerably lower down in the hierarchy. MacArthur & Wilson (1967) themselves recognised that larger habitats are likely to encompass a greater number of habitats due to increased environmental diversity. Therefore, although the equilibrium theory's explanation of the species-area effect is often cited as one based upon the *per se* influence of area on the extinction rate of populations, it is clear that MacArthur & Wilson (1967) did themselves acknowledge the importance of habitat heterogeneity; in their own words *"area itself is correlated with environmental diversity, which exerts a more direct effect on species number".*

3.5.5 Isolation: source habitat quantity

The role of habitat isolation has long been recognised as a factor determining the distribution of species. Isolation has generally been assessed with reference to the quantity of neighbouring habitats that may be inhabited by potential source populations or the linear distance between source and recipient habitats. Quantitative measures will be considered in this section, with distance measures being discussed in the following section.

Both the quantity of woodland and woodland edge habitats in the surrounding 80 ha were significantly correlated with hedgerow species richness in Oxfordshire. Hedgerows have variously been considered as 'woodland edge' or 'miniature woodland' habitats (Pollard *et al.* 1974) with many of the species being common to both woodland and hedgerow habitats (Hooper 1968). Such linear and two-dimensional source areas may then provide a valuable reservoir of species that are able to inhabit the hedgerow habitat. These species are likely to consist predominantly of woodland edge species because only very wide hedgerows will have "*interior*" habitats (Baudry 1988) suitable for colonisation by woodland species requiring conditions such as shade and high humidity. Despite the potential role of neighbouring hedgerows to act as source habitats for the study hedgerows, in quantitative terms, this influence did not appear to be great (although the correlation between the total length of neighbouring hedgerows was positive it was not significant at the 5% probability level). There may, however, have been an effect of the hedgerow *network length* (the summed length of hedgerows adjoining the study hedge in the surrounding 80 ha) on species composition because two of the ordination dichotomies identified hedgerow groups (0/1 and 00/01) with significantly different hedgerow network lengths (Table 3.10).

What is unexpected is the significant *negative* correlation between species richness and the density of field boundaries when considered as a whole. No *a priori* hypotheses were envisaged that would create such a relationship and no *ad hoc* ecological explanation seems feasible. It is considered, therefore, that this association is an anomalous situation resulting from the peculiarities of the data set or the incursion of a type II error (the wrongful acceptance of the alternative hypothesis). Further investigation is needed to assess the validity of this finding.

3.5.6 Isolation: landscape connectance

Isolation is commonly assessed by calculation of the linear separation distance between habitats. The assumption is that this distance is correlated with the ability of a species to move between fragmented habitats. This assumption is likely, however, to be the exception rather than the rule. Although this hypothesis is most realistic for wind dispersed plants, even here the Euclidean distance will need modification because source and sink areas are likely to be conditional upon their *orientation* and *location* with regards to the predominant wind direction. For plants that rely on (i) self-dispersal by dehiscent mechanisms, (ii) dispersal by animal vectors, and (iii) those whose movement is complemented by vegetative spread, the general structural connectance of the landscape may be important. The relationship between hedgerows might then be particularly important in determining the distribution of certain plants because of the potential that hedgerows have to function as "*ecological corridors*" (Colvin 1973).

The possible function that hedgerows might have in lessening the isolation between habitat patches (and indeed between other hedgerows and field boundaries) by acting as movement corridors first received serious attention in the 1970s (e.g. Colvin 1973, Pollard 1973, Hooper 1974a, Helliwell 1975). Predating this, however, the movement of plants along hedgerows was observed by Elton (1966) who concluded that hazel (*Corylus avellana*) spread from a coppiced wood along a connecting hedgerow. He writes that the occurrence of the hazel "*could only be attributed to the gradual carriage of nuts by red squirrels and birds along the hedge as a highway*". Even earlier than this, in the study of plant species inhabiting a farmland plantation, Woodruffe-Peacock (1918) considered *Acer campestre* to have dispersed "*from the south-west to this covert along the hedges*". He also lists a number of species that he considered to have been introduced to the plantation "*by wind drift along the hedges*". Although such anecdotal accounts are interesting, Helliwell (1975) was one of the first to apply a more scientific approach. Specifically concentrating on plants highly characteristic of the woodland habitat, he concluded that hedgerows were not efficient "*corridors*" for the movement of most woodland plant species. In contrast, Forman & Baudry (1984) comment that "*the evidence available leads us to conclude that hedgerows function as corridors for movement across a landscape by many species*". Clearly then, the particular species (or groups of species), the precise landscape configuration, and the *quality* (e.g. hedgerow width (Petto 1990, Baudry 1988) of the hedgerow habitat will determine to what degree hedgerows can be labelled '*movement corridors*'.

Although the possible value of assessing landscape connectivity in habitat terms has been discussed (Forman & Godron 1984, Bridgewater 1987) only one study was found that has actually employed any quantification (Braekevelt 1988). This study, however, addresses topographical changes in landscape connectivity over time and not the influence of hedgerow connectance on species distributions. Using the *gamma* and *alpha* indices of graph complexity to measure the degree of *connectivity* and *circuitry* in the hedgerow network respectively, no significant influence of hedgerow network complexity on species richness or composition was detected. These aggregate measures of network pattern did not, therefore, appear to offer an insight into the distribution of hedgerow flora. By using the *hedgerow accessibility* measure, the specific connectance attributes of each study hedgerow to their hedgerow network as a whole was assessed. In this instance there appears to be a *qualitative* influence on *species composition* (Table 3.10) rather than a quantitative effect on species richness. It might be expected that the species assemblage identified by the ordination that is characteristic of the well connected hedgerow subset would be characterised by species that are poor dispersers, or at least by those that require stretches of continuous, relatively undisturbed ground. The ordination, however, did not identify any species that were particularly characteristic of this group and so this hypothesis can not be readily validated even if the necessary ecological information were available.

The lack of a quantitative effect of isolation on species inhabiting the study hedgerows is contrary to the hypothesis of equilibrium island biogeography (MacArthur & Wilson 1967) that relates isolation to species richness through its effect on immigration rate. In addition, isolation may also affect species richness by an effect on *extinction.* This is the case because species populations that are locally vulnerable to extinction may acquire a degree of persistence through the immigration of same-species individuals from source areas, i.e. there is a 'topping-up' of populations and gene pools. This *"rescue effect"* (Brown & Kodric-Brown 1977) is likely to be less pronounced in more isolated habitat patches and islands and so local extinction may occur more readily. Moreover, area can be envisaged to affect immigration because larger areas offer a greater 'target' to dispersing species or propagules.

If immigration is a major factor determining the species richness of isolates, it can be hypothesised both that (i) well connected hedgerows will be inhabited to a greater degree by species with a lower dispersal capability than those that are less well connected, and (ii) that well connected hedgerows will have a greater species richness because their inhabitant community will be composed of species that are both good dispersers and those that possess lesser powers of dispersal. In addition to the possibility that the effect of isolation is subordinate to other more deterministic parameters, there is a number of other explanations as to why the connectivity measures used here do not indicate a significant species-isolation effect. These are discussed below.

First, the scale of inquiry might not adequately record the most important landscape features influencing species composition and richness of a particular habitat element. Second, no attempt has been made to screen out those species that are unlikely to rely heavily on the hedgerow network as a route for dispersal. They may, therefore, mask any influence of hedgerow connectance. Third, in the case of the hedgerow accessibility measure, the selection of the scalar value used to create the distance-decay effect was more or less arbitrary. Although the influence of nearby hedgerows is likely to be stronger than more distant ones, the desired actual weighting is unknown and is likely to be highly dependent upon the species, or group of species, under consideration. Fourth, although only paths with a number of linkages below the network's radius were enumerated, redundant paths are still included in the accessibility measure. Like the redundancies already described, these paths take the form of routes between hedgerows that pass through the same hedgerow more than once, i.e. non-shortest distance paths between two hedgerows. Two examples can serve to illustrate this. First, it can be seen that matrix C in Figure 3.4 records six two-step paths between L_5 to L_6, i.e. (i) L_5 to L_6 to L_5 to L_6, (ii) L_5 to L_7 to L_5 to L_6, (iii) L_5 to L_6 to L_7 to L_6, (iv) L_5 to L_6 *to* L_1 to L_6, (v) L_5 to L_6 to L_2 to L_6, and (vi) L_5 to L_4 to L_5 to L_6. These are obviously redundant paths because L_5 and L_6 are directly connected to one another. Second, the leading diagonal of each matrix records the number of connections that each hedgerow has with itself (*reflexive connections*). In terms of species movements and dispersal of individuals or genes from an origin hedge to a destination hedge, the quantification of such paths is spurious because the source and the sink hedgerows are one and the same.

To further illustrate this problem of reflexive connections the leading diagonal of matrix B in Figure 3.4 will be considered in greater detail. This axis records the number of one-step indirect connections that each hedgerow has with itself. This is the case because it is generated by the multiplication of each row vector in matrix A by its corresponding column vector. For example, L_1 in Figure 3.3 has two one-step indirect connections with itself along the paths L_1 to L_2 to L_1 and L_1 to L_6 to L_1. Because such one-step reflexive connections are equivalent to direct connections, it is the case that the leading diagonal in matrix B records the number of direct connections of each hedgerow. These direct connections have, however, already been enumerated by the connectivity matrix (matrix A) and are, therefore, represented twice in the summation matrix (matrix D). One way to eliminate the reflexive paths enumerated in each of the intermediary matrices is simply to set each element in the leading diagonal to zero. This however, only partially solves the problem of redundancies because, as already illustrated, non-shortest distance paths between different origin and destination hedgerows have also been enumerated in the matrices.

The implication of these redundancies for the calculation of an ecologically meaningful accessibility measure is unknown. If dispersal occurs serially along a hedge then the enumeration of the indirect connections between L_1 and L_2 is meaningless. However, if dispersal occurs in reversible steps (Forman & Baudry 1984) then the enumeration of such indirect routes is indeed important for the estimation of the accessibility of the study hedgerow.

A further weakness of the hedgerow accessibility measure as described here is that it has been formulated by counting the *number* of connecting hedgerows, i.e. it considers only the topological relationships. As such, a single broad and long hedgerow contributes the same 'accessibility' weight to the index as a narrow and short hedgerow. Obviously, this is unlikely to be a realistic assumption and the method described does, in fact, give a relatively crude idea of the degree of hedgerow connectivity that does not incorporate any measure of the 'quality' of the connecting hedgerows. A refinement of the hedgerow accessibility measure would be, therefore, to include a coefficient to express some measure of each connection's characteristics, rather than deriving the index solely from topological pattern. Such additional characteristics might be the length or area of the connecting hedgerow, its diversity of plant species, or the density of cover it provides. It can be envisaged, therefore, that each hedgerow will have an associated degree of resistance to movement. Moreover, it is likely to be the case that this resistance will be modified through time depending upon the season or the present stage of the hedgerow's management cycle.

It is apparent that there is a number of problems associated with using the hedgerow accessibility index as defined here. With further development, however, there may be scope to improve upon and apply connectivity measures as tools to aid in the understanding of plant distributions. It is important, however, not to use such indices to measure *functional connectivity* if species movements are not, in fact, facilitated by *structural connections* (Forman & Godron 1984). A fruitful first step may be to derive a community similarity index between hedgerows within a landscape unit based on species composition or richness and to compare this with a measure of hedgerow accessibility. A positive correlation between similarity in species characteristics and the degree of structural connectance would indicate the importance of structural proximity. A lack of correlation may indicate that functional processes are not necessarily dependent upon the physical connectance attributes of the network. This difference between structural and functional connectance of habitats and populations (Baudry & Merriam 1988) is a central principle of landscape ecology. Their relationship is both an important element in understanding the distribution of populations from an island biogeographical viewpoint and in allowing management decisions to be made on the basis of their ecological implications (Burel 1984, Baudry & Burel 1984).

3.5.7 Habitat shape and orientation

Perhaps equally important when talking about 'target-areas' is the shape and orientation of isolates. For individuals and propagules dispersing in a passive manner (e.g. airborne flightless or weakly flying arthropods and plant seeds), the apparent size of an island will depend on the shape of the island and its orientation to the dominant direction of the *species-rain*. Therefore, depending on the balance of immigration and extinction as modified by the shape of an isolate, species richness will either increase or decrease from the equilibrium level for isolates that are often 'idealised to the circular' in discussions about island biogeography. Game (1980) and Laurance & Yensen (1991) have both used an index of shape to measure the departure from circularity of isolates; the proposed index is

$$R = P/2(\pi A)^{0.5} \qquad [3.14]$$

where R is a shape index measuring the departure from circularity, P and A are the perimeter and area of the isolate respectively. Circular isolates have an R value of unity, with progressively less circular shapes having larger R values. Blouin & Connor (1985) assessed the influence of shape on species richness of five taxa on fourteen archipelagos and concluded that it did not account for a significantly greater amount of variation in species richness than area alone. The applicability of this finding to habitat islands is yet to be established.

The importance of shape, *per se*, is therefore uncertain and its consequences are likely to be highly dependent upon both autecology and habitat type. It can be envisaged, however, that shape may be an important predictor of species richness or composition. This is be seen particularly clearly with reference to the orientation of the isolate to the dominant flux of dispersal movements. For species that do not use linear features (such as adjoining hedgerows) to move and disperse the 'target size' of a 400 m^2 hedge, 2 m wide by 200 m long, can be envisaged to be 2 m at its lowest when it is parallel with the dispersal flux, or 200 m at its highest when it is perpendicular to the dispersal flux. For wind dispersed seeds and arthropods, hedgerow shape and orientation may differentially modify air currents and cause variable deposition of air-borne material depending on how the carrying capacity is altered. In this respect, hedgerows may be viewed as sinks or *barriers* to dispersal (Jones *et al.* 1991) in a similar manner to perch sites acting as "*recruitment foci*" of bird dispersed seeds (McDonnell 1984). The effect of shape and orientation on species richness of hedgerows is unknown. The study hedgerows range in their *R* value from 1.44 to 11.23 with a mean of 5.15. It is not known, however, what the *apparent* area of each study hedgerow is and how this will influence isolation and, consequently, immigration rates.

3.5.8 Species-age considerations

The available documentary evidence on the age of the Oxfordshire study hedgerows was found to be insufficient to assess adequately the effect of hedgerow age on species richness. The importance of hedgerow age in influencing species composition seems probable given that the longer a habitat has been in existence the greater the length of time that plants have had to disperse and successfully colonise it. However, the species composition of a 300 year old hedgerow planted with a single woody species is likely to differ both in composition and richness from a hedgerow of similar antiquity created during the felling of a woodland or planted with mixed seedlings. Clearly, the origin and subsequent management of a hedgerow will influence its species composition and richness. Consequently, hedgerow age may bear no direct relationship to vegetation characteristics. Despite the possible pitfalls, Hooper (1970b & 1971), using a combination of documentary evidence and fieldwork, found that the number of woody species in a hedgerow was linearly related to the age of the hedge (r=0.85). He observed that the average number of woody species in 27.5 m hedge sections was correlated with the age of the hedge in hundreds of years, e.g. a hedge with a mean density of five woody species per 27.5 m was likely to be in the order of 500 years old.

The validity of this linear relationship has been the subject of much debate (Johnson 1978, Muir & Muir 1987, Johnson 1980) and if it is tenable it is interesting for two reasons; first, because of the ecological mechanism responsible for the relationship and, second, because of the practical application of the correlation in aiding the dating of hedgerows for which insufficient documentary evidence exist. Since this technique was not used to date the study hedgerows a detailed discussion of these two points is out of context. Much of the discussion concerning the dating technique (see Hooper (1970b, 1971, 1974a and 1974b), Allen (1971), Johnson (1978), Cameron & Pannett (1980), Johnson (1980), Willmot (1980), Harris (1984), Dowdeswell (1987) and Muir & Muir (1987)) has arisen from it being interpreted as a *theory* rather than a *hypothesis* and it being applied unadjusted for local historical and biological circumstances; both are contrary to its original formulation (Hooper 1970b & 1971).

The value of the hypothesis can perhaps be measured in two respects. First, by its confirmation and structuring within an ecological framework; and second, by the interest it has generated in the hedgerow habitat and in local history. On the first point more research is needed before conclusions can be drawn, while on the second it has undoubtedly been a great success. If the form of the species-age relationship can be successfully formulated for local conditions, it may both facilitate the conservation of wildlife by aiding in the interpretation of species distributions and, in conjunction with landscape evidence, facilitate the conservation of the most historically valuable hedgerows.

The flora inhabiting hedgerows has been noted to differ qualitatively with hedgerow age as well as quantitatively, i.e. particular species have been observed to show an affiliation with hedgerows or woody habitats depending on the age or origin of the habitat. Pollard (1973) identified *Hyacinthoides non-scriptus*, *Anemone nemorosa* and *Mercurialis perennis* to inhabit "older" hedgerows in Huntingdon. In the present study only *M. perennis* was recorded in the dated (Oxfordshire) hedgerows (n=87); four of the hedgerows inhabited by this species were comparatively young (between 110 and 186 years old) while three were of an unknown age (but they were at least 109 years old). Hooper's (1970b & 1971) study of hedgerows in Devon through Gloucester to Cambridge, Huntingdon and Lincoln revealed that hedgerows with *Acer campestre* and *Euonymus europaeus* were rarely younger than 400 and 600 years old respectively. In Lincolnshire, *E. europaeus* was identified as an indicator of ancient hedgerows (Peterken 1974). In the present study these species did not appear to indicate hedgerows of particular antiquity in Oxfordshire. Of the twelve study hedges with *E. europaeus* ten were 109 to 266 years old and there were many instances of *A. campestre* in hedgerows younger than 400 years old. *Allium ursinum*, a species generally found to indicate primary woodland in Lincolnshire (Peterken 1974), was also found in a comparatively young hedgerow (planted 109 to 178 years ago). Clearly then, "indicator" species such as these are specific to local conditions and they can not been *used ubiquitously to aid* in the dating of hedgerows of uncertain age.

3.5.9 Determinants of species richness and composition

The factors influencing species richness in hedgerows appear to be many. It has proven particularly difficult to discern them given that these factors, or at least the magnitude of their importance, appears to differ between counties. The necessary separate treatment of the North Yorkshire and Oxfordshire hedgerow data has hampered the evaluation of determinant parameters because of the resultant small sample size. In the case of the North Yorkshire hedgerows, neither a single environmental factor nor a group of factors was identified to influence significantly the species richness of the study hedgerows. In Oxfordshire, the area occupied by the hedgerow combined with the area of woodland in the surrounding landscape appeared to be the best predictor of species richness. Presumably, neighbouring woodland provides a seed source for hedgerow populations. The underlying influence of hedgerow area could be one of several, but in reality a combination of processes is likely to be in operation. There is an indication that hedgerow area does not affect species number purely through its effect on local extinction rates and it seems very probable that habitat diversity will be important.

Hedgerow age, management history and disturbance regimes are also likely to be deterministic. Their adequate estimation may further the understanding of hedgerow species richness and community composition. Hedgerow isolation, in terms of landscape connectance, proved to be of only limited value in assessing the distribution patterns of plants in the study hedgerows and problems in the formulation of the index are recognised. It is possible that the physical connection between habitats is not necessary for dispersal of many plant species because wind and animal vectors (particularly by birds) are able to disperse seeds regardless of landscape connection attributes. The plants that do require connectivity between habitat patches may be few and, consequently, only a weak relationship would exist between species richness and the degree of habitat connectance as measured here. However, on the basis of hedgerow accessibility, there does appear to be a qualitative influence on species composition for the cluster analysis identified two major hedgerow groups characterised by hedgerows with contrasting hedgerow accessibility measures (Table 3.10). The one group that contained highly preferential species was, however, characterised by species with markedly different life-history strategies (one grass and one tree species, two climbing species and three herb species) and the ecological implications of this in terms of habitat connectance and dispersal are unknown.

If the influence of physical connection between habitats is weak for many plant species, there then remains the possibility that physical connections may facilitate the movement and dispersal of certain animal species which inhabit or utilise hedgerow. If so, the study of the movement of certain animal species may contribute to the interpretation of the distribution of those plant species whose dispersal is aided by an animal vector. The movement of two animal groups is examined in the forthcoming two chapters.

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Appendix 3.1 The plant species recorded from the 93 study hedgerows from North Yorkshire (Y) and the 87 study hedgerows from Oxfordshire (O).

Y	O	Species	Y	O	Species
*	*	*Acer campestre*	*		*Ligustrum ovalifolium*
*	*	*Acer pseudoplatanus*		*	*Ligustrum vulgare*
*	*	*Achillea millefolium*		*	*Lolium multiflorum*
	*	*Aethusa cynapium*	*	*	*Lolium perenne*
	*	*Agrimonia eupatoria*		*	*Lonicera periclymenum*
	*	*Agrostis canina*	*	*	*Malus domestica*
*	*	*Agrostis gigantea*	*	*	*Malus sylvestris*
*	*	*Agrostis stolonifera*	*		*Matricaria matricariodes*
*	*	*Alliaria petiolata*		*	*Medicago lupulina*
	*	*Allium vineale*	*	*	*Mercurialis perennis*
	*	*Allium ursinum*	*		*Montia perfoliata*
	*	*Alopecurus myosuroides*	*		*Montia sibirica*
*	*	*Alopecurus pratensis*	*	*	*Myosotis arvensis*
*		*Amsinckia lycopsoides*		*	*Nepeta cataria*
*		*Anchusa officinalis*		*	*Odontites verna*
	*	*Angelica sylvestris*		*	*Papaver rhoeas*
*	*	*Anthriscus sylvestris*		*	*Pastinaca sativa*
*	*	*Arctium lappa*	*		*Petasites hybridus*
*	*	*Arctium minus*		*	*Phleum pratensis*
*	*	*Arrhenatherum elatius*		*	*Plantago lanceolata*
*	*	*Artemisia vulgaris*		*	*Plantago major*
*	*	*Arum maculatum*	*	*	*Poa annua*
*	*	*Ballota nigra*	*	*	*Poa trivialis*
*	*	*Bilderdykia convolvulus*	*		*Polygonum persicaria*
	*	*Bromus ramosus*		*	*Polygonum aviculare*
*	*	*Bromus sterilis*	*	*	*Potentilla reptans*
*	*	*Bryonia dioica*		*	*Prunus avium*
*	*	*Calystegia sepium*	*		*Prunus domestica*
*		*Capsella bursa-pastoris*	*	*	*Prunus spinosa*
	*	*Carex riparia*	*	*	*Pteridium aquilinum*
	*	*Centaurea nigra*	*	*	*Quercus robur*
	*	*Centaurea scabiosa*	*		*Ranunculus acris*
*		*Cerastium fontanum*	*		*Ranunculus bulbosus*
*	*	*Chaerophyllum temulentum*	*		*Ranunculus ficaria*
*		*Chamerion angustifolium*	*	*	*Ranunculus repens*
*		*Chamomilla recutita*		*	*Reseda lutea*
*	*	*Chenopodium album*		*	*Rhamnus catharticus*
	*	*Circaea lutetiana*	*		*Ribes uva-crispa*
*	*	*Cirsium arvense*		*	*Rosa arvensis*
*	*	*Cirsium vulgare*	*	*	*Rosa canina*
	*	*Clematis vitalba*	*	*	*Rubus caesius*
	*	*Clinopodium vulgare*	*	*	*Rubus fruticosus*
*	*	*Conicum maculatum*	*		*Rubus idaeus*
*	*	*Convolvulus arvensis*	*		*Rumex acetosella*
*	*	*Cornus sanguinea*	*		*Rumex conglomeratus*
*	*	*Corylus avellana*	*	*	*Rumex crispus*
*	*	*Crateagus monogyna*	*	*	*Rumex obtusifolius*

Continued overleaf...

Appendix 3.1 *Continued from overleaf.*

Y	O	Species
*	*	*Dactylis glomerata*
*		*Digitalis purpurea*
	*	*Dipsacus fullonum*
	*	*Elymus caninus*
*	*	*Elymus repens*
*	*	*Epilobium hirsutum*
	*	*Epilobium montanum*
*	*	*Equisetum arvense*
	*	*Euonymus europaeus*
	*	*Festuca gigantea*
*	*	*Festuca rubra*
	*	*Filipendula ulmaria*
*	*	*Fraxinus excelsior*
*	*	*Fumaria officinalis*
*	*	*Galeopsis speciosa*
*	*	*Galeopsis tetrahit*
*	*	*Galium aparine*
	*	*Galium mollugo*
	*	*Geranium dissectum*
*		*Geranium pusillum*
	*	*Geranium robertianum*
*	*	*Geum urbanum*
*	*	*Glechoma hederacea*
*	*	*Hedera helix*
*	*	*Heracleum sphondylium*
*	*	*Holcus lanatus*
*	*	*Holcus mollis*
	*	*Humulus lupulus*
*		*Hyacinthoides non-scriptus*
	*	*Hypericum perforatum*
*		*Hypochaeris radicata*
*	*	*Ilex aquifolium*
*		*Impatiens glandulifera*
*	*	*Knautia arvensis*
*	*	*Lamium album*
*		*Lamium hybridum*
*		*Lamium purpureum*
*	*	*Lapsana communis*
	*	*Lathyrus pratensis*
	*	*Rumex sanguineus*
	*	*Salix alba*
*		*Salix caprea*
*	*	*Sambucus nigra*
*	*	*Senecio jacobaea*
*		*Senecio vulgaris*
*		*Sherardia arvensis*
*	*	*Silene alba*
	*	*Silene dioica*
*	*	*Sisymbrium officinale*
*	*	*Solanum dulcamara*
*	*	*Sonchus asper*
*	*	*Sonchus oleraceus*
*		*Sorbus aucuparia*
*	*	*Stachys sylvatica*
*	*	*Stellaria holostea*
*	*	*Stellaria media*
*	*	*Tamus communis*
*	*	*Taraxacum spp.*
*		*Teucrium scorodonia*
	*	*Torilis japonica*
	*	*Trifolium repens*
	*	*Trifolium pratense*
*	*	*Tripleurospermum inodorum*
*		*Tussilago farfara*
*	*	*Ulex europaeus*
*	*	*Ulmus procera*
*		*Urtica annua*
*	*	*Urtica dioica*
	*	*Veronica chamaedrys*
*		*Veronica hederifolia*
*		*Veronica persica*
	*	*Viburnum lantana*
*	*	*Viburnum opulus*
*	*	*Vicia cracca*
	*	*Vicia sativa*
*	*	*Vicia sepium*
*	*	*Viola arvensis*
	*	*Viola odorata*

Appendix 3.2 Measures of landscape connectivity (*gamma* and *alpha* indices (%), equations 3.7 and 3.11 respectively) and the degree of structural connectance between the study hedgerow and its neighbours (*hedgerow accessibility*) for each of the North Yorkshire and Oxfordshire hedgerows surveyed using the complete sampling technique.

Hedge code	*Gamma* index	*Alpha* index	Hedgerow accessibility	
			Non-scalar	0.2 Scalar
Yorks:				
2	31.6	5.3	221	0.903
55	37.5	6.7	6	0.560
61	34.4	5.1	4044	2.481
66	30.8	3.9	130	1.373
67	30.8	3.9	110	1.277
100	31.9	0	837	0.896
101	30.1	0	273	1.324
103	30.1	0	273	1.324
112	32.3	1.6	61	1.704
114	23.8	1.4	80061	1.469
120	31.7	2.5	823	1.033
134	37.5	6.7	12	0.960
203	25.9	0	23	0.760
208	30.8	4.8	159	1.739
251	33.3	4.8	2542	1.860
284	30.0	0	27	1.016
601	42.9	7.7	57	1.608
Oxon:				
401	28.8	4.3	77	0.859
411	28.6	0	30	1.072
415	30.8	0	82	0.679
418	24.2	0	36	0.666
430	29.2	0	654	0.983
435	28.3	1.6	46	1.264
443	33.3	0	93	0.596
448	31.9	4.8	136	1.350
455	33.3	2.7	7	0.624
461	20.5	0	1	0.200
471	29.2	0	5	0.520
476	40.0	5.9	22	1.680
478	37.0	7.6	12	0.960
492	40.0	5.9	53	1.576
501	33.3	11.8	23	1.720
505	23.8	0	25	0.968
521	38.1	9.1	39	1.176
536	35.1	9.1	292	2.246
537	34.8	12.9	69	1.800

Appendix 3.3 Location and codes of the hedgerows included in the ordination of hedgerow flora recorded by the complete sampling technique.

Ordination code	Hedgerow code	Farm	Parish	County
1	2	Botland Farm	Heslington	N. Yorks
2	55	Lodge Farm	Fulford	N. Yorks
3	61	Lingcroft Farm	Naburn	N. Yorks
4	66	Lingcroft Farm	Naburn	N. Yorks
5	67	Lingcroft Farm	Naburn	N. Yorks
6	100	Hopewell House	Knaresborough Outer	N. Yorks
7	101	Hopewell House	Knaresborough Outer	N. Yorks
8	103	Hopewell House	Knaresborough Outer	N. Yorks
9	112	Hopewell House	Knaresborough Outer	N. Yorks
10	114	Hopewell House	Knaresborough Outer	N. Yorks
11	120	Hopewell House	Knaresborough Outer	N. Yorks
12	134	Cockstone Hill	Goldsborough	N. Yorks
13	203	Grimstone Grange	Dunnington & Heslington	N. Yorks
14	208	Grimstone Grange	Dunnington & Heslington	N. Yorks
15	251	Brackenholme	Hemingbrough	N. Yorks
16	284	Tillmire Farm	Fulford	N. Yorks
17	401	Manor Farm	Fyfield and Tubney	Oxon
18	411	Upper Court Farm	Chadlington	Oxon
19	415	Upper Court Farm	Chadlington	Oxon
20	418	Upper Court Farm	Chadlington	Oxon
21	430	Blaythorne Farm	Chadlington	Oxon
22	435	Blaythorne Farm	Chadlington	Oxon
23	443	Down Hill Farm	Westcot & Steeple Barton	Oxon
24	448	Down Hill Farm	Westcot & Steeple Barton	Oxon
25	455	Down Hill Farm	Westcot & Steeple Barton	Oxon
26	461	Hammonds Farm	Ipsden and Crowmarsh	Oxon
27	471	Kiddington Estate	Kiddington with Asterleigh	Oxon
28	476	Kiddington Estate	Kiddington with Asterleigh	Oxon
29	478	Kiddington Estate	Kiddington with Asterleigh	Oxon
30	492	Friars Court	Clanfield	Oxon
31	501	Ditchley Estate	Spelsbury and Enstone	Oxon
32	505	Ditchley Estate	Spelsbury and Enstone	Oxon
33	521	The Grove	Brightwell Baldwin	Oxon
34	536	Broughton Castle	Broughton and Tadmarton	Oxon
35	537	Broughton Castle	Broughton and Tadmarton	Oxon
36	601	Raskelf Farm	Raskelf	N. Yorks

Appendix 3.4 Names of plant species abbreviated by the Twinspan analysis of the species inhabiting hedgerows surveyed using the complete sampling technique (Table 3.9).

Abbreviation	Species	Abbreviation	Species
Acer camp	*Acer campestre*	Holc moll	*Holcus mollis*
Acer pseu	*Acer pseudoplatanus*	Hyac nons	*Hyacinthoides non-scriptus*
Agro giga	*Agrostis gigantea*	Ilex aqui	*Ilex aquifolium*
Alli peti	*Allium petiolata*	Knau arve	*Knautia arvensis*
Alop prat	*Alopecurus pratensis*	Lami albu	*Lamium album*
Anth sylv	*Anthriscus sylvestris*	Laps comm	*Lapsana communis*
Arct minu	*Arctium minus*	Loli pere	*Lolium perenne*
Arte vulg	*Artemisia vulgaris*	Malu dome	*Malus domestica*
Arum macu	*Arum maculatum*	Malu sylv	*Malus sylvestris*
Brom ster	*Bromus sterilis*	Merc pere	*Mercurialis perennis*
Bryo dioi	*Bryonia dioica*	Myos arve	*Myosotis arvensis*
Cent scab	*Centaurea scabiosa*	Pter aqui	*Pteridium aquilinum*
Chae temu	*Chaerophyllum temulentum*	Poa triv	*Poa trivialis*
Chen albu	*Chenopodium album*	Prun spin	*Prunus spinosa*
Cirs arve	*Cirsium arvense*	Quer robu	*Quercus robur*
Cirs vulg	*Cirsium vulgare*	Ranu repe	*Ranunculus repens*
Clem vita	*Clematis vitalba*	Rosa cani	*Rosa canina*
Coni macu	*Conicum maculatum*	Rubu caes	*Rubus caesius*
Corn sang	*Cornus sanguinea*	Rume obtu	*Rumex obtusifolius*
Cory avel	*Corylus avellana*	Rume sang	*Rumex sanguineum*
Equi arve	*Equisetum arvense*	Samb nigr	*Sambucus nigra*
Euon euro	*Euonymus europaeus*	Sili alba	*Silene alba*
Fest rubr	*Festuca rubra*	Sisy offi	*Sisymbrium officinale*
Frax exce	*Fraxinus excelsior*	Sola dulc	*Solanum dulcamara*
Gale tetr	*Galeopsis tetrahit*	Sonc aspe	*Sonchus asper*
Gali moll	*Galium mollugo*	Sonc oler	*Sonchus oleraceus*
Gera robe	*Geranium robertianum*	Stac sylv	*Stachys sylvatica*
Geum urba	*Geum urbanum*	Stel medi	*Stellaria media*
Glec hede	*Glechoma hederacea*	Tamu comm	*Tamus communis*
Hede heli	*Hedera helix*	Tara offi	*Taraxacum officinale*
Hera spho	*Heracleum sphondylium*	Ulmu proc	*Ulmus procera*
Holc lana	*Holcus lanatus*	Viol odor	*Viola odorata*

Chapter 4

Hedgerows as Habitats and Corridors for Small Mammals

Contents

> *"Hideous and useless strong holds of roots, weeds, birds*
> *and vermin that afflict the farms of merry England."*
>
> Chandos Wren Hoskyns, 1857

4.1 Introduction

The loss of permanent cover has lead to an increasing fragmentation of many habitats within the rural landscape. This process has lead to a *patchiness* that increasingly imposes problems for the dispersal and establishment of animals (Henderson *et al.* 1985, Hansson 1988). In many lowland areas, hedgerows are an important landscape feature and their role as a habitat for many wildlife species is well known (Pollard *et al.* 1974). The extent of their capacity to act as *ecological corridors* (Colvin 1973), enabling the maintenance of species diversity by allowing the dispersal of individuals or propagules along their length, remains an enigma. Given the increasing fragmentation of woodland and, indeed, the breakdown of the hedgerow network itself, the role of hedgerows both as habitats and as corridors facilitating the movement and dispersal of animals is of increasing interest (Dendy 1987, Hobbs *et al.* 1989). Such dispersal movements may be of considerable importance in allowing the survival of a species on a landscape level even if local sub-populations undergo periodic extinction (Noss 1987, Fahrig & Merriam 1985).

If hedgerows are important 'corridors', then it is likely that they will only be so for species that either need a relatively undisturbed habitat through which to move, or for those species that require dense ground vegetation to provide cover. It is of interest, therefore, to investigate small mammal communities because certain species have been observed to require varying degrees of ground cover (Pollard & Relton 1970, Boone & Tinklin 1988). Small mammals lend themselves to the study of dispersal movements because they are both easily marked and their movements are sufficiently rapid to allow observations to be made over relatively short time periods.

4.2 Aims

The aims of the study are to determine whether or not hedgerows are an important habitat for small mammals and to determine to what degree they allow the movement of small mammals within the agricultural landscape. To this end, the role of physical connections between hedges was investigated by the comparison of the movements made by small mammals in and around hedges that were well connected to other hedgerows with those that were isolated from all others.

4.3 Methods

4.3.1 Design of study and recording of movements

Small mammal movements were studied by capture, mark and recapture (CMR) trapping techniques using Longworth traps (Photograph 4.1). In order to obtain a large quantity of information on movements, caught individuals were removed from their site of capture and then released at a *displacement point* approximately 0.5 km away from the study hedge. The numbers in which these marked individuals subsequently recolonised the denuded hedge, and the rate at which they did so, was monitored over the following ten weeks. The displacement points were chosen so that they afforded some cover for the removed individuals. It was hoped that death by immediate predation, exposure or food shortage might, therefore, be reduced.

Photograph 4.1 Longworth mammal trap consisting of a tunnel which houses the trap door mechanism and a box that is set with food and bedding (*c.* 25 x 8 x 6 cm).

Caught individuals were fur clipped to allow for their subsequent identification. By clipping the fur on the back of an animal in one or in any combination of two letter-coded positions (out of a possible of eight) a total of 36 individuals for each sex could be marked with a unique pattern. Clipping areas in combinations of three allow a further 56 male and female individuals to be identified. Each individual could, therefore, be referred to by a unique letter code. General tips on trapping, handling and identification were taken from the informative guide book on live trapping by Gurnell & Flowerdew (1982). For this study, the following parameters were recorded for each animal that was caught: date, time (am/pm), farm, species, sex, code, weight, age (adult, sub-adult or juvenile), breeding state (lactating, perforate, imperforate, scrotal or non-scrotal), position of trap (field or hedge), position of trap in trapline, weather (sunny, fine, overcast or rain) and the fate of the individual (displaced or released).

The information gathered from each trap was stored on a database and analysed by selectively accessing the data through a series of questions that revealed the movements of the small mammal species for each of the study hedges.

4.3.2 Location of hedges

The logistics of live trapping meant that only four hedgerows could be studied, hence two hedges of each type (connected and isolated) were trapped. The two isolated hedges (codes IH1 and IH2) are shown in Figure 4.1 and 4.2 respectively, and the two connected hedges (codes CH1 and CH2) are shown in Figure 4.1 and 4.3 respectively. All four study hedges are located in the parishes of Heslington and Fulford in the Vale of York, North Yorkshire; study hedges CH1 and IH1 are on Botland Farm and their National Grid Reference is SE633496 and SE636496 respectively; study hedges CH2 and IH2 are on Grimstone Grange and Lodge Farm respectively and their respective National Grid Reference is SE648497 and SE622483.

4.3.3 Position of traplines

In total 63 traps were set at each study site, these being arranged in three traplines of 21 evenly spaced traps. The hedge trapline ran along the centre of the hedge, while the two adjacent field traplines ran parallel to the hedge and 5 m out into each field. Study

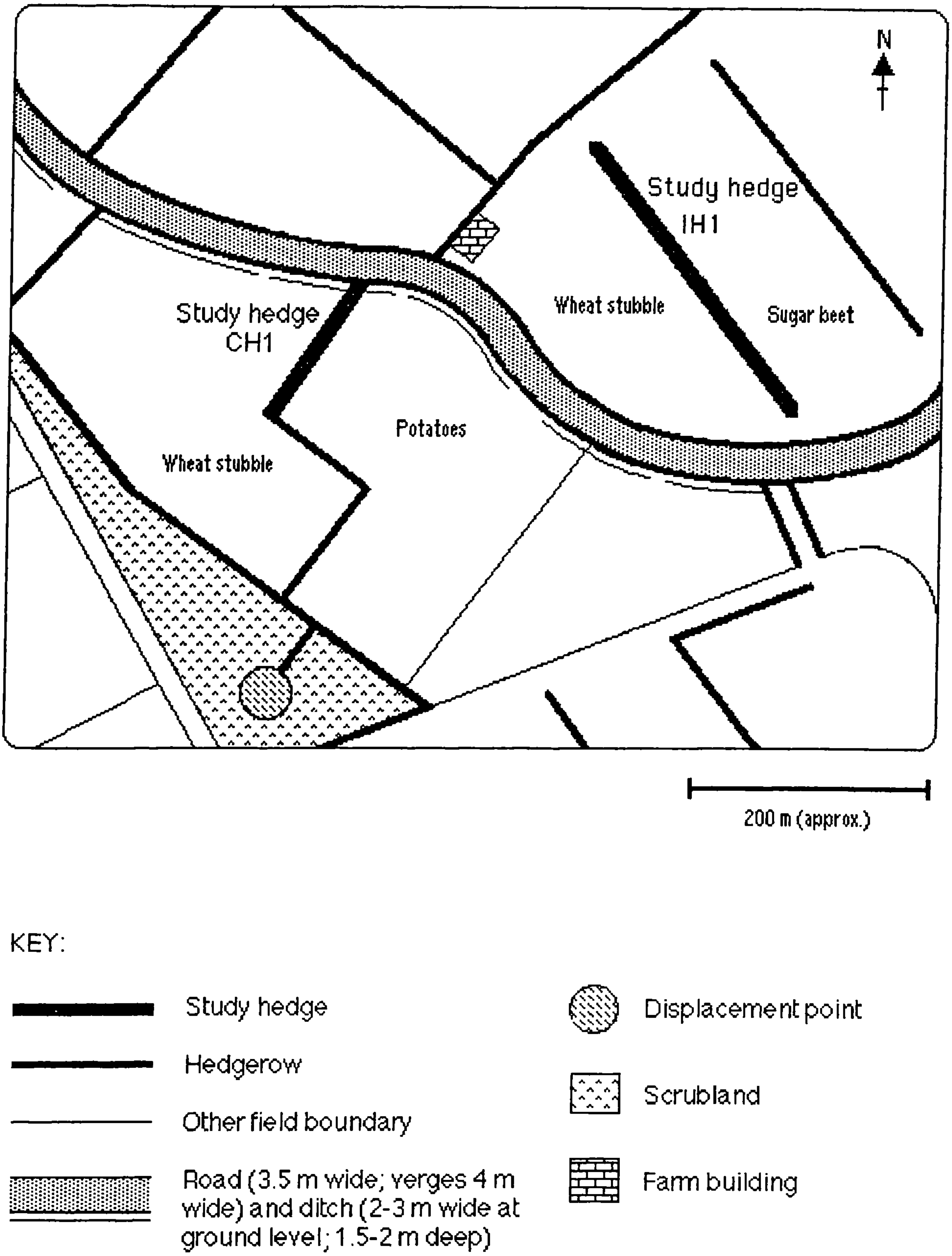


Figure 4.1 Study hedge CH1 & IH1, their displacement point and the surrounding landscape.

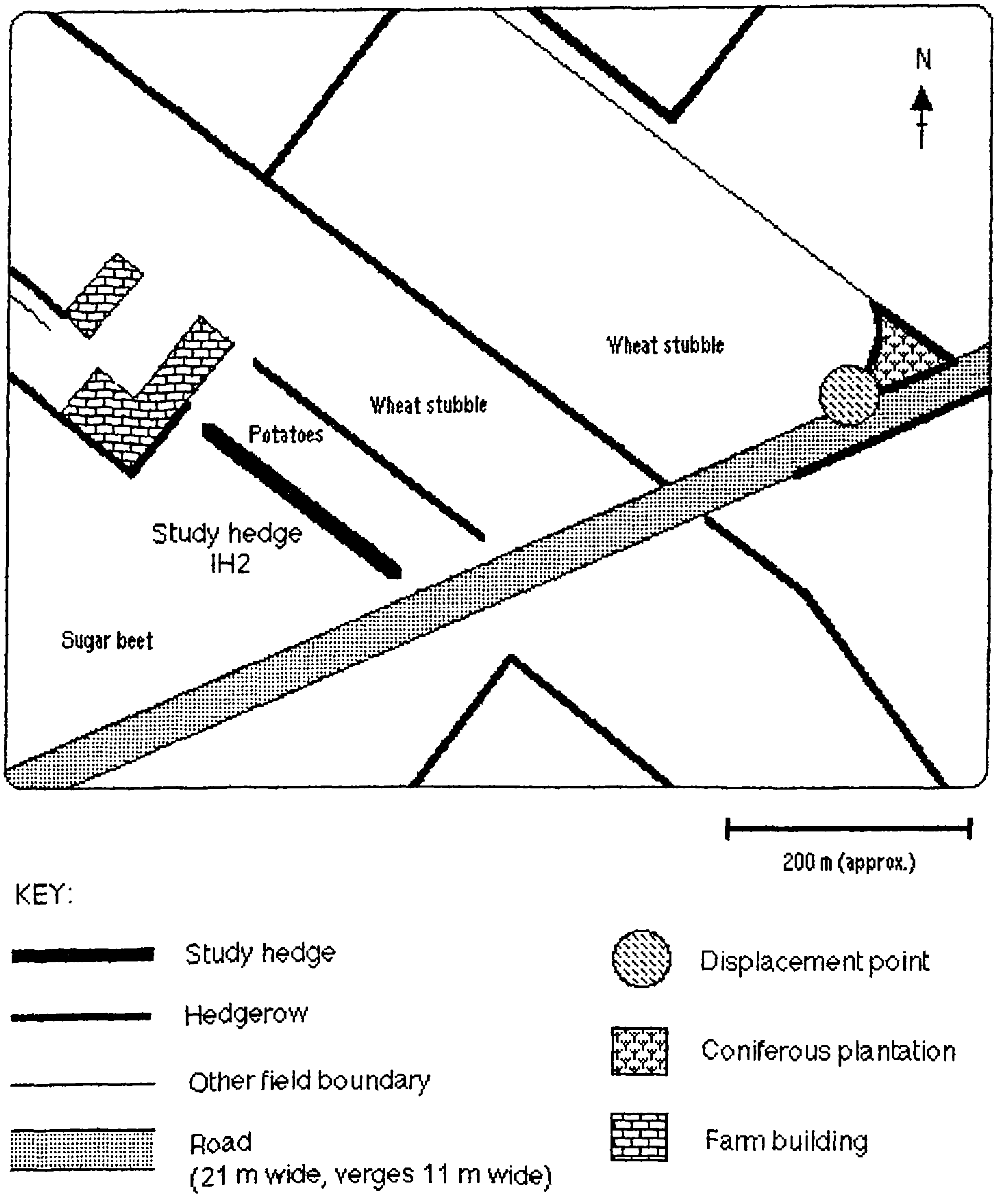


Figure 4.2 Study hedge IH2, its displacement point and the surrounding landscape.

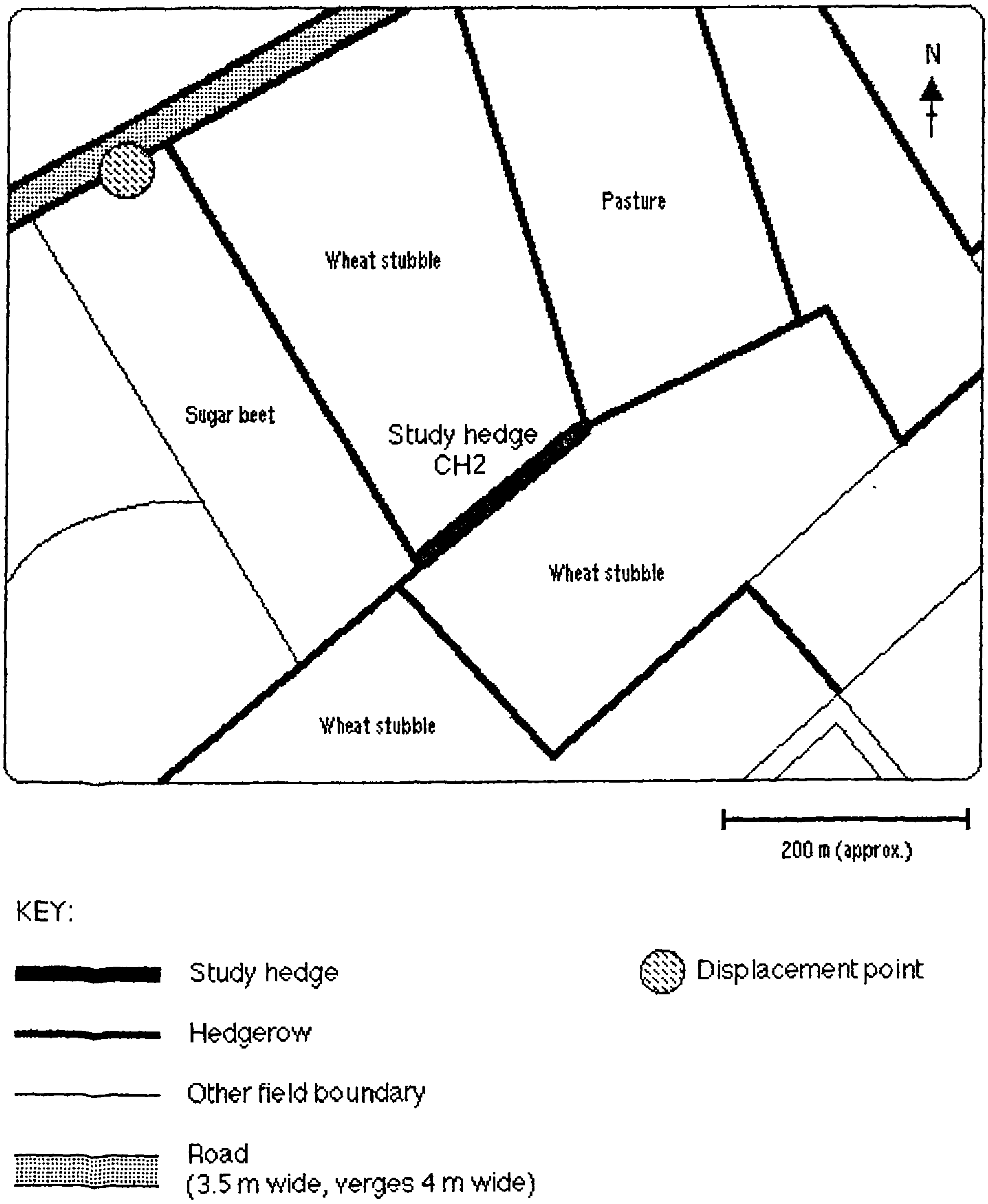


Figure 4.3 Study hedge CH2, its displacement point and the surrounding landscape.

hedge IH1 was the exception in that the traps were placed at 5 m intervals in the middle section of the hedge. Traps in fields that received no cover from the crop were covered with straw to lessen temperature fluctuations within the traps and to reduce the likelihood of theft.

4.3.4 Trapping schedule

The large number of traps used at each hedge meant that only two of the hedges could be trapped at any one time. By trapping non-continuously, however, the trapping of the hedges could be staggered to enable all four to be trapped in the same three month period. To this end, the trapping of hedges CH2 and IH2 was staggered three weeks behind CH1 and IH1. Three types of trapping were conducted, these are explained below and the timing of each trapping period is shown in Figure 4.4.

(i) *Displacement trap*

Most of the trapping undertaken was of this type which involved the removal of caught individuals to, and then their release at, the displacement point. This displacement trapping consisted of an initial trapping period of approximately one week (displacement trap I in Figure 4.4). The return of individuals displaced during this period was monitored by a further displacement trap (trap II) one week later (short term returns) and then by another two (traps III and IV) at subsequent three-week intervals (longer term returns). During the displacement trapping all individuals were removed except for lactating and pregnant females. This policy was adopted to avoid unnecessary suffering of offspring.

(ii) *Corridor trap*

The second type of trap was designed to investigate the route by which displaced individuals returned to the study hedges. This trapping consisted of a single night of trapping the hedges that connected the study hedges CH1 and CH2 with their respective displacement point. It was carried out immediately after the third displacement trapping period.

(iii) *Adjacent hedgerow trap*

This final type of trapping was conducted at the end of the study and involved the trapping of the study hedge and its nearest neighbour hedges. Animals caught during this period were released at their site of capture. The intention of this trapping session was to monitor the returning individuals from the last displacement trap and to assess the relatively undisturbed movements of individuals within a hedge.

Study hedges CH1 and IH1:

Jul	25	am pm	Displacement trap I
	26	am pm	
	27	am pm	
	28	am pm	
	29	am pm	
	30	am pm	
	31	am	
Aug	7	am pm	Displacement trap II
	8	am pm	
	9	am pm	
	31	am pm	Displacement trap III
Sept	1	am pm	
	2	am pm	
	3	am	Corridor trap
	26	am pm	Displacement trap IV
	27	am pm	
	28	am pm	
	29	am pm	Adjacent hedgerow trap
	30	am pm	
Oct	1	am pm	
	2	am pm	
	3	am pm	

Study hedges CH2 and IH2:

Aug	13	am pm	Displacement trap I
	14	am pm	
	15	am pm	
	16	am pm	
	17	am	
	25	am pm	Displacement trap II
	26	am pm	
	27	am pm	
Sept	19	am pm	Displacement trap III
	20	am pm	
	21	am pm	
	22	am	Corridor trap
Oct	12	am pm	Displacement trap IV
	13	am pm	
	14	am pm	
	15	am pm	Adjacent hedgerow trap
	16	am pm	
	17	am pm	
	18	am pm	
	19	am pm	

Figure 4.4 Schedule of mammal trapping - dates given are those that the traps were emptied; *displacement trap* I-IV, traps set in study hedges and their adjacent fields (caught individuals removed to displacement point); *corridor trap*, traps set in hedges CH1 and CH2 and in the hedges which connect them to their displacement point (caught individuals released at site of capture); *adjacent hedgerow trap*, traps in study hedges and their nearest neighbour hedges (caught individuals released at site of capture).

4.4 Results

4.4.1 General comments

The physical properties of the study hedgerows and estimates of ground cover provided by crops in their adjacent fields are summarised in Tables 4.1 and 4.2, respectively.

Table 4.1 Physical properties of study hedgerows (standard deviation of width and height measurements in parentheses).

Study hedge	Length (m)	Mean hedgerow width (m)	Hedgerow area (m²)	Mean height (m)	No. woody & climbing species	Number of connecting hedgerows
CH1	105	2.3 (0.5)	242	1.7 (0.3)	9	3
CH2	165	1.7 (0.2)	280	1.4 (0.2)	8	4
IH1	305	1.3 (0.1)	396	1.2 (0.1)	5	0
IH2	205	2.2 (2.2)	451	1.8 (0.1)	9	0

Table 4.2 Height and ground cover of crops in fields adjacent to the study hedgerows (standard deviation of crop height measurements in parentheses; estimated wheat-stubble height is given as a range).

Study hedge	Adjacent crops	Mean height of crop (cm)	Ground cover of crop
CH1	Potatoes	46 (39.8)	Dense
	Wheat-stubble	10-20	Sparse
CH2	Wheat-stubble	10-20	Sparse
	Wheat-stubble	10-20	Sparse
IH1	Sugar beet	42 (8.1)	Dense
	Wheat-stubble	10-20	Sparse
IH2	Sugar beet	36 (7.4)	Dense
	Potatoes	32 (9.4)	Dense

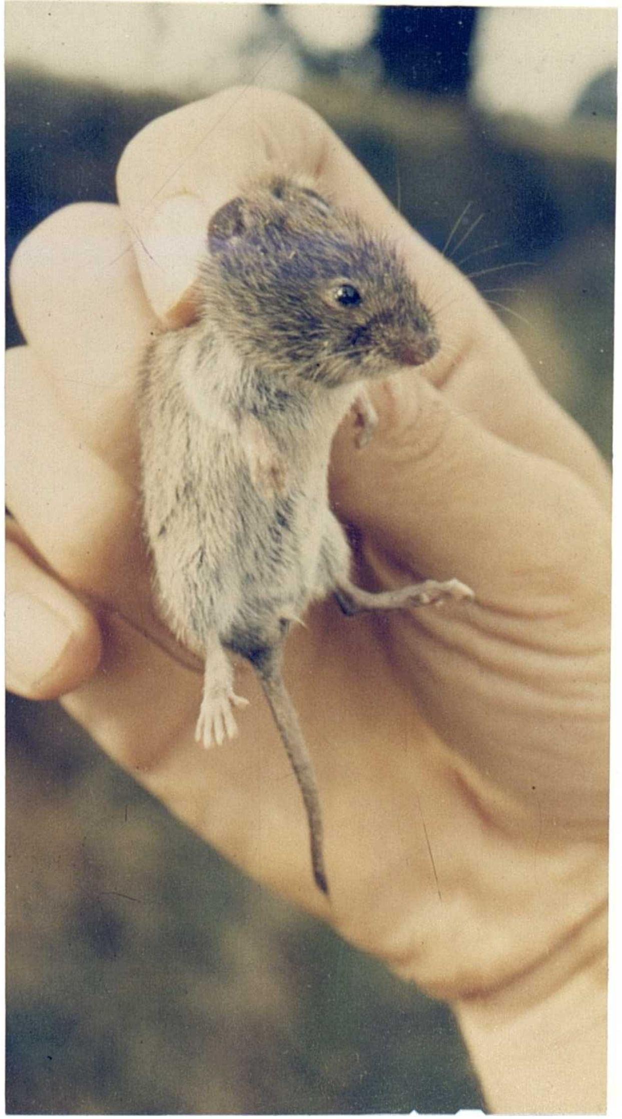
Seven species of mammals were caught during the three months of trapping. In order of abundance, these were *Apodemus sylvaticus* (wood mouse), *Sorex araneus* (common shrew), *Clethrionomys glareolus* (bank vole), *Sorex minutus* (pygmy shrew), *Microtus agrestis* (field vole), *Neomys fodiens* (water shrew) and *Mustela nivalis* (weasel). The three most commonly caught species are shown in Photographs 4.2 to 4.4. The number of individuals of each species caught at the four study sites is given in Table 4.3. Overall, 494 individuals were trapped a total of 933 times.

Table 4.3 Number of individuals of each species caught at the four study sites.

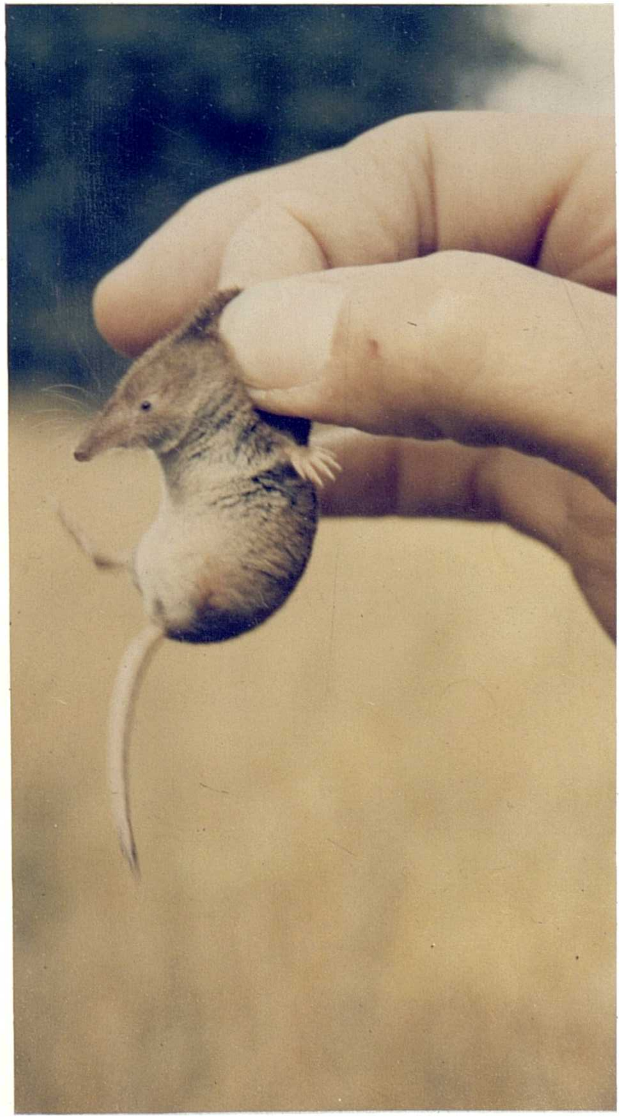
	Study site				
Species	CH1	CH2	IH1	IH2	Species total
A. sylvaticus	13	30	34	79	256
S. araneus	23	36	20	35	114
C. glareolus	13	16	9	56	94
S. minutus	4	13	4	2	23
M. agrestis	0	3	0	0	3
N. fodiens	0	0	0	2	2
M. nivalis	1	1	0	0	2
Study site total	54	99	67	274	494

It can be seen that *A. sylvaticus* was the most common species trapped in or near the isolated hedges, while *S. araneus* was the most common species trapped at the connected hedge study sites. Nearly three times the number of individuals were caught in or near IH2 compared to the next largest catch; this is largely due to the presence of a large population of *A. sylvaticus*. There appears to be an unusually large population of *S. minutus* at study hedge CH2.

Photograph 4.2 Woodmouse (*Apodemus sylvaticus*).



Photograph 4.3 Bank Vole (*Clethrionomys glareolus*).



Photograph 4.4 Common shrew (*Sorex araneus*).

4.4.2 Habitat preference and activity

Analysis of the time (night or day) and the location (study hedge or adjacent field) at which individuals were captured reveals clear species differences in both habitat preference and period of activity. Table 4.4 gives both the observed frequency of capture of species and the difference between this observed and the expected frequency of capture. The expected frequency is calculated assuming a hypothesis of mutual independence between variables. Under this hypothesis, and using the χ^2 test of association, the species caught is found to be significantly dependent ($\chi^2_{[10]}=300$, $p\leq0.001$) on one, or both, of the independent variables (i.e. the location of the trap and the time at which the trap was set). Similar tests of association, but assuming partial independence of each of the variables, reveal that the species caught is in fact dependent on both the location ($\chi^2_{[7]}=179$, $p\leq0.001$) and the time ($\chi^2_{[7]}=167$, $p\leq0.001$) of the trap (see Everitt 1977 for statistical method).

Table 4.4 Combined frequency of small mammal captures in the four study hedges and their adjacent fields for both the night and day trap periods; difference between these observed and the expected frequencies are given in parentheses; negative values indicate observed frequencies less than those expected, positive more than those expected; differences denoted by a '#' indicate those whose combined χ^2 values account for over half the overall χ^2 statistic.

Location of trap	Time of trap	*Apodemus sylvaticus*	*Clethrionomys glareolus*	*Sorex araneus*	*Sorex minutus*
Hedges	Night	123 (-52)	49 (+3)	174 (+18)	24 (+4)
	Day	0 (-31)	15 (+7)	74 (+47) #	7 (+4)
Fields	Night	188 (+95) #	18 (-6)	27 (-56)	4 (-6)
	Day	3 (-13)	1 (-3)	6 (-8)	0 (-2)

It can be seen that *A. sylvaticus* is caught in exceptionally large numbers during the night trap in the fields adjacent to the study hedgerows. In addition to the field and night trap of *A. sylvaticus*, the large number of *S. araneus* caught in the hedges during the day also contributes greatly to the overall χ^2 statistic (their summed individual contribution to χ^2 accounts for over half of the χ^2 statistic). It is evident from Table 4.4 that *C. glareolus* and *S. minutus* also prefer the hedge habitat to that of the field although this preference is not as pronounced as for *S. araneus.* The nocturnal/diurnal division of activity in these latter three species is not as pronounced as the activity pattern of *A. sylvaticus.* It appears, therefore, that these three species' activity is more evenly spread between day and night.

4.4.3 Return of displaced individuals

The return of animals that were removed to the displacement point can be measured both in terms of the *numbers* in which they returned and by the *time* it took them to return.

Taking the number of returns first, for each species a distinction can be made between the number of *individuals* that returned and the *total number* of returns. Obviously, an individual can return more than once provided that it is displaced after each capture, therefore the total number of returns of each species will always be equal to, or larger than, the number of returning individuals. Only *A. sylvaticus*, *C. glareolus* and *S. araneus* were caught in large enough numbers to allow significance testing, consequently it is only these species that will be considered further. For each study site, Table 4.5 lists both the numbers of individuals of each species that were displaced and subsequently recaptured and, conversely, those that were displaced but not recaptured.

The most striking feature of the data presented in Table 4.5 is that no returns were made to IH1. There is a number of reasons why this might be the case and these are discussed later. At this stage, however, it is enough to note that this hedge was separated from its displacement point by both a country lane (3.5 m wide with 4 m wide grass verges) and a deep V-shaped drainage ditch (2-3 m wide and 1.5-2 m deep) that ran along the side of the lane but which was subterranean in several places. Study hedge IH1 can also be classed aside from the other hedgerows because interpretation of the trap data for IH1 is problematic. Statistical reservations are based upon the possibility that the number of

Table 4.5 The number of returning and non-returning individuals of each species for the four study hedgerows.

Study Hedge	Species	Number of individuals not recaptured	Number of individuals recaptured
CH1	*A. sylvaticus*	7	1
	C. glareolus	6	1
	S. araneus	8	5
CH2	*A. sylvaticus*	16	4
	C. glareolus	12	1
	S. araneus	9	11
IH1	*A. sylvaticus*	17	0
	C. glareolus	5	0
	S. araneus	15	0
IH2	*A. sylvaticus*	81	21
	C. glareolus	21	3
	S. araneus	14	4

returns to this hedge is independent of the sample size. This is the case because there was a total absence of recaptures at study hedge IH1 and, consequently, it is not possible to say if increasing the sample size of individuals displaced from IH1 would in fact influence the number of returning individuals. On the grounds that (i) study hedge IH1 had associated characteristics that were not shared by the remainder of the hedgerows, and (ii) that there were statistical reservations about analysing the return data for IH1 in conjunction with the remaining three hedgerows, it was decided that hedge IH1 was in some respects aberrant and that it would be excluded from the analysis of the remaining three hedgerows.

A first step in the analysis of the return data was to see if there were significant differences in the behaviour of male and female individuals. For each hedgerow, Table 4.6 shows the number of male and female individuals of *A. sylvaticus* and *C. glareolus* that were (i) displaced and recaptured, and (ii) displaced but not subsequently recaptured. Due to the small and hidden nature of the genitalia of *S. araneus* it was not always possible to identify confidently the sex of captured individuals and, therefore, data for *S. araneus* are not presented.

Table 4.6 Frequency of recapture of male and female individuals of *A. sylvaticus* and *C. glareolus* after displacement from study hedgerows CH1, CH2 and IH2.

Study hedge	Fate	*A. sylvaticus* Male	*A. sylvaticus* Female	*C. glareolus* Male	*C. glareolus* Female
CH1	Recaptured	0	1	1	0
	Not recaptured	8	1	5	1
CH2	Recaptured	2	0	1	0
	Not recaptured	5	11	5	6
IH2	Recaptured	15	7	3	0
	Not recaptured	45	28	12	8

For each study site, a χ^2 analysis was conducted to allow the significance of the difference between the observed and expected male and female frequency of recapture/non-recapture to be determined. The expected frequency was calculated assuming mutual independence between variables. Only in the case of *A. sylvaticus* at study hedge CH1 was there a significant difference ($p \leq 0.05$) between the male and female return frequency ($\chi^2_{[1]}=4.44$). Further consideration of *A. sylvaticus* at study hedge CH1, however, casts doubt upon the confidence of the male/female difference. Only two female *A. sylvaticus* individuals were displaced from CH1 and, consequently, the sample size is very small. It is the case, therefore, that there appeared to generally be little difference between male and female behaviour with respect to recapture. It must also be remembered that the comparison made between the fate of male and female individuals excludes those females that were pregnant or lactating. Females in either of these breeding states were not removed from the hedgerows and, therefore, the inter-sex comparison made was in fact between all males and those females that were either juvenile, sub adult, adult imperforate, or adult perforate. Both because there was a lack of a robust statistical difference between the sexes, and because a comparison was being made between groups of differing age structure, it was decided to pool the data for each species and use the combined male and female frequency data in subsequent analysis.

Having combined these data, and with the inclusion of the data collected on *S. araneus*, a comparison of the fate of each species reveals that there is no significant influence of the hedge type on the number of returning individuals. The χ^2 statistic for *A. sylvaticus*, *C. glareolus* and *S. araneus* is 0.30, 0.26 and 4.27 respectively, none of which exceed the critical value of 5.99 at the 0.05 probability level with 2 degrees of freedom. It is not possible, therefore, to validate the hypothesis that a larger number of individuals would be able to return to the connected hedgerows. Since there is no significant difference between sites, it is possible to view the different hedges as replicates and pool the data in a comparison of the fate of each species. Table 4.7 gives the observed and the expected frequency of capture of each species when considering hedgerows CH1, CH2 and IH2 together. A χ^2 analysis of this contingency table shows that the null hypothesis of independence can be rejected at the 0.01 probability level ($\chi^2_{[2]}$=11.70).

Table 4.7 Observed and expected frequency of individuals recaptured and not recaptured after displacement from study hedgerows CH1, CH2 and IH2 (expected values in parentheses).

Fate	*A. sylvaticus*	*C. glareolus*	*S. araneus*
Returned	26 (29.5)	5 (6.0)	20 (11.6)
Not returned	104 (100.5)	39 (34.0)	31 (39.4)

To investigate further this finding, and to see where the deviations from the expected frequency are greatest, the adjusted residuals can be calculated. These residuals are approximately normally distributed with mean 0 and standard deviation 1. Therefore, values lying above 1.96 or below -1.96 (the 5% standard normal deviate) represent significant departures from the null hypothesis. Similarly, absolute values above 2.58

and 3.29 represent departures from the null hypothesis at 0.01 and 0.001 probability levels respectively. These residuals can be calculated form Table 4.7 as

$$d_{ij} = e_{ij} / \sqrt{(v_{ij})}$$

where d is the adjusted residual, e is the standardised residual, v is an estimate of variance, and i and j identify the cell of the contingency table. A full explanation of the calculation of the standardised residuals and their associated variance is given in Everitt (1977). The adjusted residuals for each species are given in Table 4.8. It can be seen that *C. glareolus* was recaptured significantly fewer times than expected ($p \leq 0.05$), while *S. araneus* was recaptured a significantly greater number of times than expected ($p \leq 0.01$).

Table 4.8 Adjusted residuals from the χ^2 analysis of the fate of individuals displaced from study hedgerows CH1, CH2 and IH2.

Fate	*A. sylvaticus*	*C. glareolus*	*S. araneus*
Returned	-1.12	-2.00	3.21
Not returned	1.12	2.00	-3.21

The total number of returns (as apposed to the number of returning individuals) can be analysed in a similar manner. The χ^2 analysis again revealed that there is no significant difference in the return of each species between hedgerows ($\chi^2_{[2]}$ = 4.80, 2.21, and 0.70 for *A. sylvaticus, C. glareolus and S. araneus* respectively) and, consequently, it is again possible to pool the data across hedgerows and compare the differences between species. Table 4.9 gives the total number of observed and expected returns and non-returns for each species as well as the derived adjusted residuals.

Table 4.9 The observed and expected total number of returning and non-returning individuals of each species to study hedgerows CH1, CH2 and IH2 combined; expected frequencies are in parentheses; associated adjusted residuals are given in italics.

Species	Total number of recaptures	Total number of non-recaptures
A. sylvaticus	44 (63.2) *-4.35*	101 (81.8) *4.35*
C. glareolus	10 (21.8) *-3.66*	40 (28.2) *3.66*
S. araneus	85 (54.0) *7.17*	39 (67.0) *-7.17*

A χ^2 analysis of these return data gives an overall χ^2 statistic of 53.08 which is a highly significant departure from independence ($p \leq 0.001$, d.f.=2). From the adjusted residuals shown in Table 4.9, it can be seen that the total number of returns of both *A. sylvaticus* and *C. glareolus* are significantly less than expected ($p \leq 0.001$), while the total returns of *S. araneus* is significantly more than expected ($p \leq 0.001$). While this finding tends to support the observations made with regard to the number of returning individuals, caution needs to be taken because the total number of returns can be heavily weighted by a small number of individuals that return frequently.

The second measurement of return to the study hedges is that of the *speed* at which they return, i.e. the rate at which the displaced animals recolonise the hedges from where they were removed. Table 4.10 lists the time taken by displaced animals of each species to return to the study sites. Since trapping was not continuous, it is not possible accurately to assess the time it took for an individual to return unless it was displaced and recaught in the same trapping period. Consequently, all those return times of over one week are maxima.

Table 4.10 Rate of return (days) of displaced small mammals to study hedges (values in parentheses indicate the number of multiple returns); return rates indicated by the less than sign (<) are those of recaptures following displacement in a former trapping period, these return times are therefore maxima; there were no returns to hedge IH1 or to hedge IH2 by *S. minutus.*

Study hedge	*Apodemus sylvaticus*	*Clethrionomys glareolus*	*Sorex araneus*	*Sorex minutus*
CH1	2.0 <25.5	1.5 (2) 1.0 (5) 1.5 (2) 2.5 <24.0	0.5 (9)	<32.0
CH2	1.0 2.0 3.0 5.0 6.0	4.0 1.0 (13) 1.5 (2) 2.0 <8.0 <9.0 (2) <10.0 <25.0 <26.0 <59.0	0.5 (9) 4.0 <35.0	1.0
IH2	1.0 (24) 2.0 (3) 3.0 (2) 4.0 (2) <8.0 (2) <8.5 <10.0 <21.0 (2) <22.0 <23.0 <25.0 (2) <26.0 (2) <28.0 <49.0 <52.0 <53.0	0.5 (2) 1.0 2.0 (2) 3.0 <8.0 <65.5	0.5 (20) 1.0 (5) 1.5 2.0 (3) <8.0 <9.0 <22.5 <23.0 <48.0	-

Taking the return times of under one week, a weighted analysis of variance can be conducted to compare the mean length of time it took for individuals of each species to return to the connected and isolated study hedgerows. The lack of returns to study hedge IH1 necessitated its exclusion from the analysis of variance. The analysis reveals that return times to the study hedges are dependent on the species of the displaced individual

($F_{[2,36]}$=4.21; $p \leq 0.05$), but that there is no significant difference between the return times to the connected hedges CH1 and CH2 when compared with returns to the isolated hedge IH2. The mean return times are shown in Table 4.11. It can be seen that the species that returned quickest to the study hedges was *S. araneus* while the species that returned at the slowest rate was *A. sylvaticus.* For *A. sylvaticus* and *C. glareolus* there is a slight indication that individuals returning to the connected hedges did so at a *slower* rate than the isolated hedge; this difference, however, is not statistically significant.

Table 4.11 Mean return time (days) to the two connected and one isolated study hedge (standard deviation in parentheses; means are of returns made in the same trapping period that the individual was displaced; no returns were made to hedge IH1).

Study hedge	*Apodemus sylvaticus*	*Clethrionomys glareolus*	*Sorex araneus*
Connected hedges (CH1 & CH2)	3.72 (0.44)	2.33 (0.54)	1.20 (0.37)
Isolated hedge (IH2)	2.05 (0.30)	1.73 (1.09)	1.67 (0.80)

4.4.4 Connecting hedgerow trap

Trapping of the hedgerows linking study hedges CH1 and CH2 with their displacement points provided evidence that hedgerows are used as a route for *S. araneus* individuals to return to their site of capture. Although no individuals were caught in the 'corridor' hedges of CH2, there were three *S. araneus* individuals caught in hedgerows linking CH1 with its displacement point. Two of these captures were made during the corridor trap on 3 September (individuals AC and DE, Figures 4.5 and 4.6 respectively) while the third was caught during the adjacent hedgerow trap on 29 September (individual BD, Figure 4.7).

Taking individual AC as an example, it can be seen from Figure 4.5 that this individual was first caught in study hedge CH1 on 7 August. Up until 2 September it was caught a further four times having made its way back to CH1 after removal to the displacement point. Following a further displacement in the evening of 2 September, it was recaught in the morning of 3 September in a hedge linking CH1 with its displacement point. After immediate release, it then travelled nearly 160 m and was recaught in CH1 the same morning; the time between release and recapture was approximately 45 minutes. After the corridor trap, individual AC was caught in study hedge CH1 as soon as displacement trapping commenced again on the 26 September. It returned after displacement on a further two occasions before being caught a further four times between 29 September and 1 October having been released back into CH1 at its site of capture.

Turning to Figure 4.7, it is interesting to note that although individual BD was originally caught in IH1, it appeared to successfully establish a new territory in CH1 (study hedges IH1 and CH1 share the same displacement point (Figure 4.1)). Not only did individual BD return to CH1 after displacement, it was also repeatedly captured there following its immediate release.

4.5 Discussion

4.5.1 Habitat preference

The ability of *A. sylvaticus* to inhabit the fields adjacent to the study hedgerows may partly be explained by the fact that it is largely a nocturnal species (Ashby 1972, Flowerdew 1984). As such, the need for concealment in dense vegetation in order to avoid predation is lessened. This nocturnal habit of *A. sylvaticus* is, indeed, borne out by the present study. Predation may be an important factor in influencing the size of small mammal populations in the agricultural landscape because during the course of the study weasels, kestrels, an owl and domestic cats were all seen to stalk the study hedgerows and adjacent fields. The *A. sylvaticus* individuals that were trapped in the

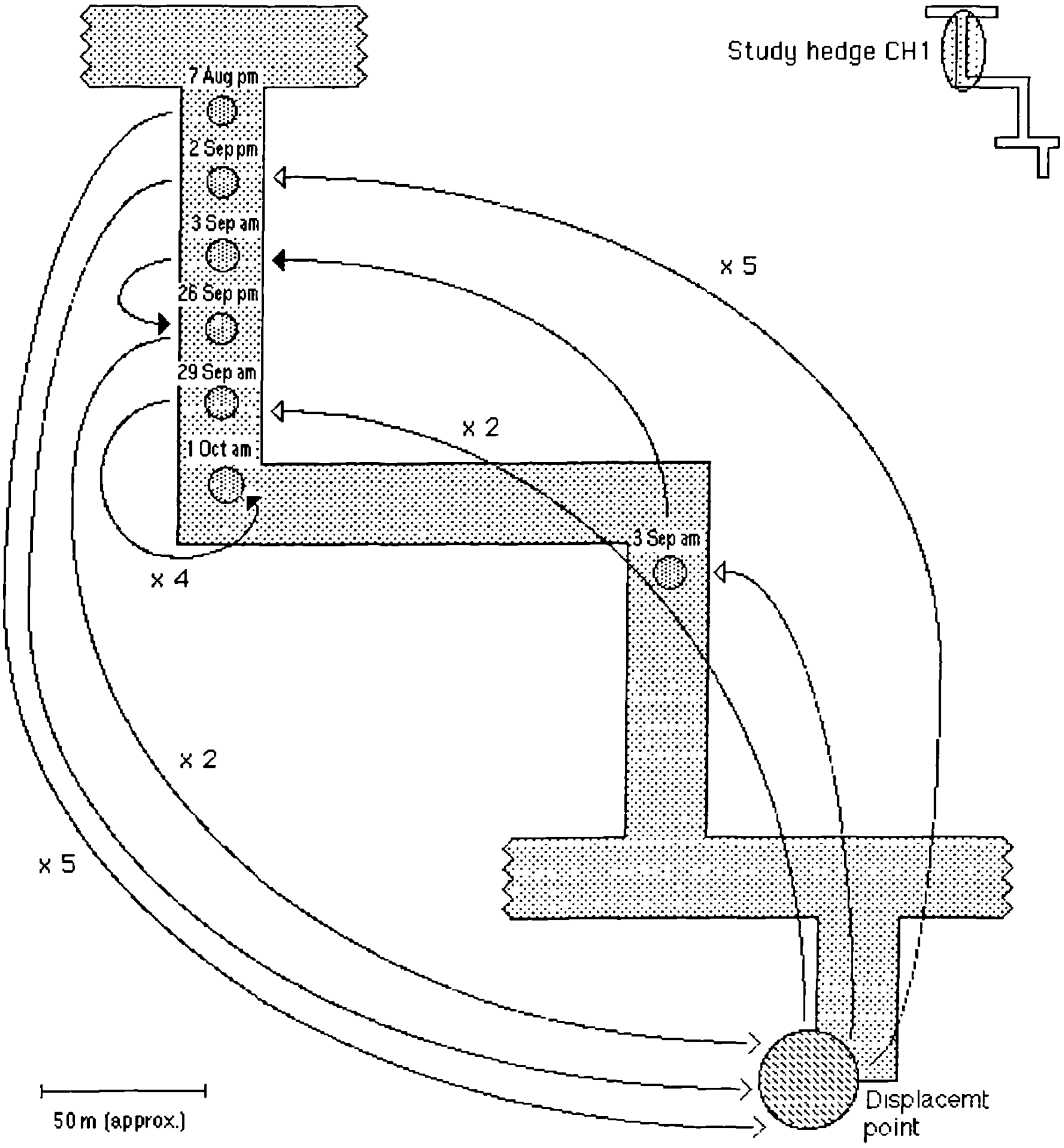


Figure 4.5 Movements and dates of capture of *Sorex araneus* individual AC at study hedge CH1 following transfer to displacement point and release at site of capture (—> , transfer to displacement point; —▷ , movement made after transfer to displacement point; —▶ , movement made after release at site of capture; arrows indicate direction and not route of movement; multiplier by arrows indicate the number of times movements were made between the specified dates; the site of capture (●) refers to the hedge and not to the exact trap location.

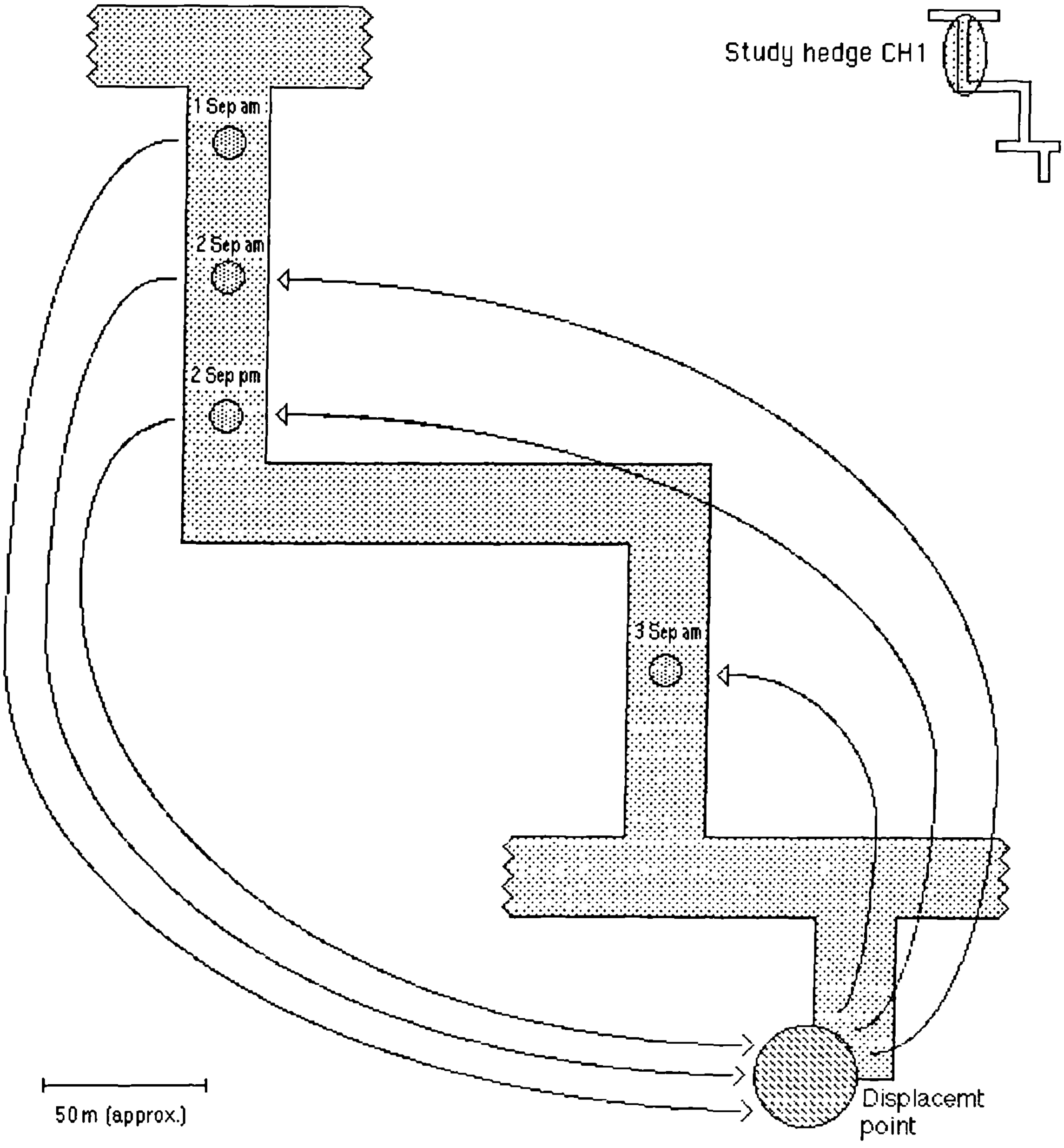


Figure 4.6 Movements and dates of capture of *Sorex araneus* individual DE at study hedge CH1 following transfer to displacement point and release at site of capture (—> , transfer to displacement point; —▷ , movement made after transfer to displacement point; —▶ , movement made after release at site of capture; arrows indicate direction and not route of movement; the site of capture (◍) refers to the hedge and not to the exact trap location.

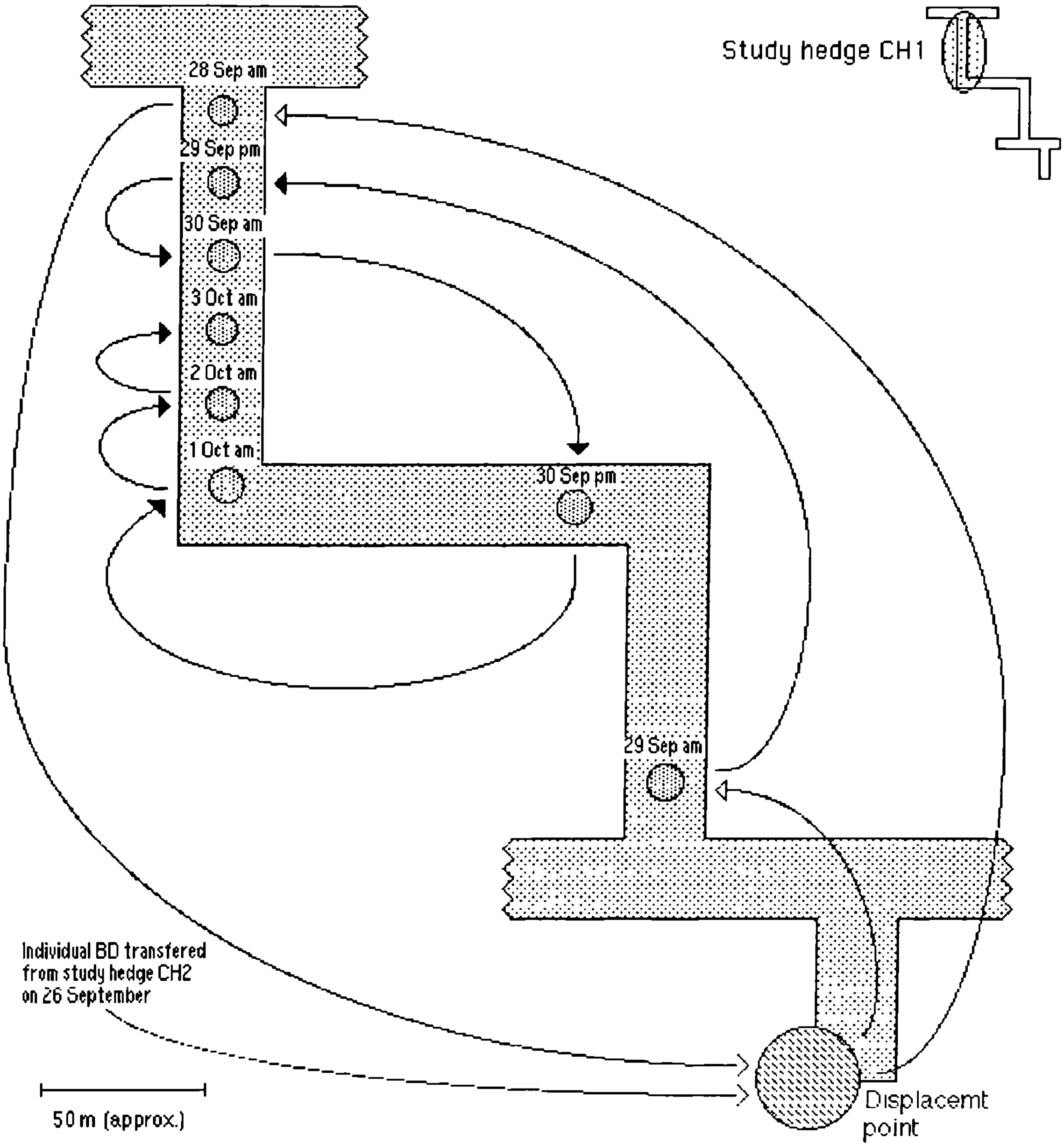


Figure 4.7 Movements and dates of capture of *Sorex araneus* individual BD at study hedge CH1 following transfer to displacement point and release at site of capture (—> , transfer to displacement point; —▷ , movement made after transfer to displacement point; —➔ , movement made after release at site of capture; arrows indicate direction and not route of movement; the site of capture (◍) refers to the hedge and not to the exact trap location.

study hedges are likely to be resident in the hedges themselves or to be foraging from the open fields where their burrows are common (Green 1979).

In addition to *A. sylvaticus*' preference for the field habitat over the hedge habitat, a preference for potato and sugar beet fields over wheat-stubble fields was also noticed. This may again be partly explained by the ground cover afforded by the crops in the fields for (as seen in Table 4.2) the cover provided by the wheat-stubble fields is very poor. Moreover, it was noted that when the above ground vegetation of the potato field adjacent to IH2 began to die back at the end of the growing season the number of catches declined dramatically.

In contrast to *A. sylvaticus*, it was observed that *C. glareolus* and the *Sorex* spp. have a preference for the hedgerow habitat. This may again be linked with their activity rhythms for their periods of activity are distributed more evenly through the day and night (Churchfield 1988, Corbet & Harris 1991). They may, therefore, confine themselves more to the hedgerow habitat in order to reduce the risk of predation by diurnal predators.

The use of hedgerows as movement corridors is discussed below, but it is worth noting here that the habitat preferences of small mammals may have bearing on their ability to disperse through the agricultural landscape.

4.5.2 Effect of isolation on recolonisation

(i) Isolation by roads

The most striking result of the survey was the complete lack of recolonisation by individuals displaced from study hedge IH1. The one feature of this hedge that sets it apart from the other study hedges is that it is separated from its mammal displacement point by both a country lane with a macadamised surface approximately 3.5 m wide and a drainage ditch 1.5-2 m deep and 2-3 m wide at ground level (see Figure 4.1). From the capture, mark and recapture data it is reasonable to propose that these features may impede the free movement of small mammals. Any barrier effect is not, however, absolute because during the course of the study two observations were made that indicate that study hedge IH1 is not totally isolated from small mammal populations on the far side of the lane. The first is that a *S. araneus* individual was actually observed running across the road, while the second is that a *S. minutus* individual that had been caught 5 days previously at study hedge CH2 was recaptured in IH1 (in addition to study hedges IH1 and CH2 being separated by the said lane, approximately 800 m of agricultural land and a 21 m wide four-lane trunk road also come between them). It is also uncertain to what degree the drainage ditch acts as a obstacle to movement. During the summer months the ditch retains no water and its sides are well vegetated. These features, coupled with the fact that the ditch is covered for short stretches, suggest that it may not hinder greatly the movements of small mammals. Clearly, therefore, the presence of the bisecting country lane and ditch can not wholly explain the observed lack of recolonisation of hedge IH1. A contributing factor may be that this hedge is approximately 85 m further away from its displacement point than IH2 which had the next greatest separation distance. Whether this additional distance is of significance is unknown. It is, however, thought unlikely because in the only other study that was found in the literature that monitored the recolonisation of displaced individuals, woodmice were observed to return to their site of capture some 800 m from the release point (Wallace 1961).

Although the strength of the lane's influence remains uncertain, it nevertheless appears to be substantial and a number of studies have, indeed , demonstrated that roads can offer a significant hinderance to the movements of various animals, e.g. small mammals (Oxley *et al.* 1974, Mader 1984), frogs (Reh & Seitz 1990) and arthropods (Duelli 1990, Mader *et al.* 1990). The effectiveness of roads as barriers will depend on the species being considered, the width of both the road verges and its carriageway, the surface of the carriageway (e.g. asphalt, gravel, dirt), the volume of traffic using the road, and, very importantly, the *orientation* of the road. Orientation is vitally important because associated road habitats have been found to aid the connectivity between otherwise isolated patches. Studying small mammals in forest patches connected by narrow roadside woodland strips, Bennett (1990) observed that verge habitats could act as a corridor for movement both of genes and of individuals. It is apparent, therefore, that the orientation of a road, its width and its associated verge habitat characteristics are all likely to influence whether or not small mammals perceive roads as either a *barrier to*, or a *corridor for*, movement and dispersal.

In the present study the *road clearance* (the combined width of the road verges and its carriageway) was approximately 12 m which is considerably narrower than the 20 m road clearance that was noticed to inhibit small forest mammal movements between the edges of bisected forests (Oxley *et al.* 1974). It is important that the consequences of habitat isolation by roads and arable land are considered because bisected habitats may effectively function as isolates for certain species (Mader 1984). If the gene pools of these isolated populations are small the effects of inbreeding may be observed (Reh & Seitz 1990). Ultimately, reduced genetic variation within populations may increase their vulnerability to localised extinction by a reduced phenotypic response to adverse conditions (Usher 1987).

(ii) Isolation by agricultural land

If study hedge IH1 is excluded from the analysis on the grounds that it is atypical (at least as far as the other study hedges are concerned), then an investigation of the number and the rate of return of displaced individuals to the remaining unconnected and two well connected hedgerows seems to indicate that the number of adjoining hedges does not significantly influence the recolonisation characteristics of displaced individuals. There is an indication, therefore, that hedgerows that are 'isolated', in the sense that they have no connections with other hedgerows, are not perceived by small mammals to be true isolates. Nevertheless, direct observations were made on a number of occasions when *S. araneus* individuals were seen to use connecting hedgerows to return to their site of capture. Consequently, it appears that although not necessary for the functional linkage between local populations, structural linkages between hedgerows are used by certain small mammal species to move through the agricultural landscape. Baudry & Merriam (1988) made this distinction between physical connections (*connectedness*) and functional connections (*connectivity*). This study provides evidence that connectedness between hedgerows is not necessary for the connectivity of local populations of small mammals on arable farmland.

From the habitat preference data, it seems likely that *C. glareolus*, *S. araneus* and *S. minutus* have a patchy distribution on arable farmland and consequently will exist as localised populations. The concept of *metapopulations* (Levins 1970) may help in understanding the dynamics and persistence of these localised populations in hedgerow and woodland habitats on agricultural land. Metapopulation theory has arisen as a means to understand the population dynamics of species that exist in patchy environments and whose sub-populations within that environment are functionally connected by dispersal events. The long-term survival of the population is assured provided that the rate of local extinction events at the sub-population level does not exceed the rate of recolonisation of denuded habitats (Hanski 1989). Should these sub-populations of hedgerow small mammals undergo extinction due to severe weather, predation, disease or through population stochasticity then it seems likely that recolonisation of the denuded hedgerow will occur regardless of its degree of *connectedness* with surrounding hedgerows. Recolonisation may, however, be impeded in the case of hedgerows surrounded by a matrix of fields providing very poor cover (such as harvested wheat fields) or where roads traverse the landscape.

The apparent lack of a role of hedgerows in facilitating small mammal movements in this study is in contrast with work by Wegner & Merriam (1979) who found that fencerows adjoining woodland were used as movement corridors by white-footed mouse (*Peromyscos leucopus*) and chipmunks (*Tamias striatus*). Additional work with the white-footed mouse, however, indicated that fencerows are not always used as corridors and that this species may perceive the farmland mosaic as a series of non-isolated islands (Middleton & Merriam 1981). The contrary findings of studies such as these indicate that the precise configuration the habitat elements may be of importance, as will be the species under investigation (see next sub-section).

The conclusion of this study, that of the apparent unimportance of structural connections between hedges, is a very tentative one because the logistics of trapping meant that replication was minimal. Moreover, although hedge IH2 had no hedgerow connections it was relatively near the 11 m wide grassy verge of a major trunk road (see Figure 4.2). This may in effect be acting here as a corridor along which small mammals could move before making the relatively short journey across open field to the study hedgerow (Photograph 4.5). The orientation of roads appears, therefore, to be a critical consideration. In the case of hedgerow IH1 the road may be acting as a barrier, while in the case of hedgerow CH2 the near-side road verge may be acting as a corridor.

Photograph 4.5 Hedge IH2 was isolated by disturbed ground at each end, the gaps being 13 m wide at the northerly end (foreground) and 7.5 m wide at the southerly end (background); a 10 m wide road embankment at the southerly end of the hedge may have facilitated the return of displaced individuals.

It appears, therefore, that certain specific characteristics of some of the study hedgerows and their associated features may not allow generalisations to be made about the significance of hedgerow connections. It should be noted, however, that both the hedgerows studies and the farmland in which they are set are not atypical. Consequently, the observations made during the study are likely to be representative of many movements occurring within the arable landscape.

4.5.3 Species- and sex-specific behaviour

From a number of the analyses it is apparent that *S. araneus* is able to return to the study hedgerows in greater numbers and at a faster rate than *A. sylvaticus* and *C. glareolus* (Table 4.7, 4.9 and 4.11). This is despite this species' preference for hedgerows and other habitats affording dense cover (Table 4.4). It appears able to return at a faster rate than even *A. sylvaticus* which has powerful hind legs and can readily be found in the open field habitats and, consequently, during dispersal movements made at night will be less likely to need to make convoluted journeys in order to keep to habitats that provide dense cover. *S. araneus* also typically has a home range one-eighth to one-quarter the size of *A. sylvaticus* and so its ability to return with such rapidity is even more notable. It is possible that its small size may be partially compensated for by its high activity. To what extent the magnitude and frequency of movements observed are characteristic of unperturbed communities, and the extent to which species may differ in this respect, is unknown. Since the communities were manipulated in a highly artificial manner in order to induce movement, the resulting behaviour is in some respects highly artificial. It is the case, however, that all species were treated similarly and as such it is possible to make comparisons between species.

Despite documented differences in the behaviour and home range size of male and female individuals, there did not appear to be a substantial difference in the return behaviour of males and female individuals of each species. This, however, may reflect the fact that pregnant and lactating females were not removed. Breeding *A. sylvaticus* females defend mutually exclusive home ranges (Flowerdew 1984) and, therefore, upon displacement there may be a strong requirement for them to return to their established home range in order to survive. This is in contrast to the overlapping home ranges of sexually mature males and the excursions made by males when looking for a mate (Flowerdew 1984). Due to the difficulty of sexing *S. araneus* individuals, an assessment of the behaviour patterns of male and female individuals is not possible. Churchfield (1988) notes, however, that although males and females have similar home range sizes (370-630 square metres) males can travel more than 100 m beyond the boundary of their normal home range in search of mates. This concords with the fact that the *Sorex* individual that moved approximately 800 m between study hedgerows CH2 and IH1 was a male. The occurrence of multiple paternity in *S. araneus* (Tegelstorm *et al.* 1991) may also have a bearing on the movement behaviour of male individuals for, while sexually receptive, females may not preclude additional males from entering their home range after an initial mating.

The correct interpretation of the number or rate of returning individuals is problematic because the behaviour of the displaced individuals upon their release at the displacement point is unknown. It is possible that *S. araneus* individuals that are released into a linear habitat (such as the roadside verge displacement point of hedge CH2) may, in fact, be funnelled along its length in one of two directions because of their preference for dense vegetation cover. Provided that such individuals do not 'head-off' in the direction away from the study hedge, the probability of them returning may, therefore, be greater than that of *A. sylvaticus* individuals which may disperse towards all points of the compass if released at night. The assumption here is that movement from the displacement point is not influenced by orientation behaviour or direction finding ability. It has, however, been shown that *A. sylvaticus* can orientate itself using the earth's magnetic field (Flowerdew 1984). Other location finding senses (e.g. sight, sound and smell) may enable homing if the terrain is recognised and, therefore, individuals are more likely to be recaught if they are familiar with areas beyond their normal home range. Such a familiarisation process may take place during movements associated with sexual behaviour or when dispersing from the territory in which they were reared. In the case of *S. araneus*, the observation that certain individuals were able to return with great frequency suggests either that the terrain between the study hedgerow and the displacement point was already familiar, or that some degree of familiarisation took place once it had been traversed for the first time. If no locational clues are available, then the return of individuals will be non-directional until familiar surroundings are reached.

An additional interpretive difficulty relating to the fate of displaced individuals is that if a species such as *A. sylvaticus* and *C. glareolus* are predated at a higher rate than *S. araneus*, or if they are better able to establish new territories, then their perceived ability to disperse through the agricultural landscape may be less than that of *S. araneus*. It is the case that differences in habitat orientation, in the habitat quality of the displacement point, and in the ability of the different species to establish new territories after removal or to avoid predation, may all bias both the observations made about the relative unimportance of maintaining hedgerow connections and the observations about which species are better able to return to the study hedgerows.

The analysis of the return rate of individuals is hindered because three types of error are included in the data. The first is that an individual may be in a hedgerow and yet not be trapped and so go unrecorded (this will particularly be so for trap shy individuals); the second is that traps were only emptied twice a day and so the precise length of time between displacement and recolonisation is not known; and the third, and potentially the most limiting for this non-continuous trapping approach, is that recolonisation can occur a particular trap period (i.e. displacement traps I to IV in Figure 4.4) in the analysis of variance this last source of error has been removed. The second source of error is constant for both hedges and species and so is standardised. It is, therefore, the first source of error that remains problematic. The use of radio tagging (Kenward 1987) may help to resolve this problem.

It is of note that there appears to be a very high density of *S. araneus* individuals associated with study hedge IH2, for it was not uncommon to trap five individuals at this hedge at any one time. The minimal territory size for *S. araneus* may be around 370 m^2 (Churchfield 1988), slightly less than the area of this hedge (see Table 4.1). There could be several explanations for the large number of individuals caught at any one time; these are (i) territory overlap (during the breeding season intraspecific exclusion is less pronounced) (Michielsen 1966), (ii) transient individuals may pass through the home range of other individuals in search of mates (Churchfield 1988), and (iii) although *S. araneus* may have its home range centred on the hedgerow, it is, in fact, caught to a lesser degree in the adjacent fields and so its home range may extend beyond the hedgerow habitat.

The distances moved by shrews in this study exceed those recorded by Michielsen (1966) who observed long distance dispersers moving 160-355 m. In a study of urban habitats by Dickman & Doncaster (1989), *C. glareolus* and *A. sylvaticus* were observed to move up to 500 m from source populations to habitats denuded of their small mammal communities. They found that, compared to *C. glareolus*, *A. sylvaticus* re-established quicker in patches furthest away from the source area. The characteristics of *A. sylvaticus* and *C. glareolus* in the present study are rather similar to one another and no information on *S. araneus* behaviour is given for the urban habitat study. The design of the present study meant that the recording of movements greater than the distance between the study hedge and its displacement point was very unlikely (although, as already mentioned, an individual was observed to move approximately 800 m between study hedge CH2 and IH1). Consequently, the very long dispersal distances observed by Tegelstrom & Hansson (1986) were not recorded. These authors observed individuals moving 3-5 km over a snow covered Scandinavian lake and so such extreme dispersal events may be unusual on arable farmland.

In summary, it can tentatively be said that for the hedgerows studied, and except for occasional extreme dispersal events, isolation caused by roads appears to impede the movements of small mammals more than a lack of hedgerow connections. This is at least the case where the gaps between hedgerows are not great and where the crops in the adjacent fields provide sufficient ground cover. It is also apparent that *S. araneus* can move quicker and in larger numbers than the other trapped species; as such it may be better able to reach fragmented farmland habitats. Like *C. glareolus* and *S. minutus*, however, *S. araneus* exhibits a strong preference for habitats that provide dense cover. Consequently, no matter how good this species' dispersal ability, its niche within the agricultural landscape will be weakened unless habitats such as hedgerows are retained. This study has shown that the small mammals found on arable farmland rely to varying degrees on hedgerow and field habitats and that the characteristic movements of certain species differ considerably. It is hoped that additional studies will investigate further the role of hedgerows in the dispersal of small mammals. The use of radio tagging may be particularly informative in the study of small mammal movements in hedgerows. It is the case that the conservation of small mammals on farmland is best achieved by first determining how they perceive the fragmented agricultural landscape and then conserving and improving those features that contribute most to their survival.

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Chapter 5

The Distribution of Woodlice and Millipedes in Hedgerows

Contents

5.1 Introduction

The cultivation of arable farmland necessitates mechanical operations that greatly disturb the soils' upper horizons. In addition to this mechanical disturbance, chemical disturbances in the form of pesticide, herbicide and fungicide application are also a frequent feature of fields cultivated under intensive farming regimes. These two forms of disturbance, as well as the depletion of soil organic matter by the yearly harvesting of crops, create a soil environment that differs greatly from adjacent uncropped areas (such as hedgerows and woodland). As a consequence, the distribution of cryptozoic species (soil and soil-surface living organisms) is greatly influenced by agricultural operations (Edwards 1929, Sutton 1980, Harding & Sutton 1985).

One result of agricultural intensification may be that undisturbed soil habitats become fragmented to such a degree that they eventually exist as isolates within the farm landscape. Such habitats may develop impoverished or specialised soil communities, this being especially so in the case of soil- and litter-living organisms that have limited means of movement and dispersal (Soesbergen & Mabelis 1989, Mader *et al.* 1990). Under these conditions the maintenance of the 'hedgerow network' may be necessary to allow the movement and dispersal of individuals between hedgerows and between hedgerows and woodland. Such movements may be necessary to ensure the long-term survival of local populations that may otherwise undergo extinction. The concepts of *metapopulations* (Hanski 1989) may be useful in understanding the spatial and temporal dynamics of arthropod groups that possess limited means of dispersal and which are confined to fragmented habitats (Soesbergen & Mabelis 1989, den Boer 1990).

Dispersal ability may largely be determined by the speed that an individual can traverse inhospitable habitats; speed will have direct bearing on (i) the length of time that an individual is vulnerable to predation in habitats that lack suitable cover, (ii) the degree of desiccation experienced while in habitats of unfavourable humidity, (iii) the ability of an individual to survive traversing a habitat that lacks suitable food items, and (iv) in arable habitats, the length of time individuals are exposed to toxic agrochemicals and mechanical disturbance by field operations. Of the soil macro-fauna, there is a general trend for the Diplopoda (millipedes) and Isopoda (woodlice) to be less mobile than, for instance, the Carabidae (ground beetles) and Chilopoda (centipedes), although precise rates of movement are not known for many species and there are wide variations between species of each group (Manton 1954, Sutton *et al.* 1984, Blower 1985, Soesbergen & Mabelis 1989). Nevertheless, woodlice and millipedes differ from ground beetles and centipedes in that they are predominantly saprophytic and as such do not rely on rapid predatory movements as a means to obtain food. The relatively slow locomotive ability of millipedes is largely a consequence of their adaptation to movement within the soil and leaf litter matrix as well as in sub-cortical habitats such as beneath the bark of trees. Millipedes have evolved '*low gear*' gaits that enable them to push and burrow rather than to run at high speeds (Manton 1954, Blower 1985).

Another factor that will influence greatly the ability to disperse through unfavourable habitats is that of physiological resistance to desiccation; whether this be the degree of lipid deposition in the epicuticle or the ability to reduce water loss from internal respiratory organs. Both millipedes and woodlice have evolved fewer physiological adaptations to reduce water loss than other terrestrial arthropods, particularly the Insecta and Arachnida (Barnes 1980, Cloudsley-Thompson 1988). Consequently, both groups are prone to rapid desiccation in dry air (Sutton 1980, Wieser 1984, Appel 1988).

5.2 Aims

Given that various physiological and behavioural characteristics of woodlice and millipedes are likely to limit their dispersal ability within arable farmland, the aim of the study was to investigate the distribution of these arthropod groups in a variety of hedgerows that differed in their relationship to adjacent landscape features. In particular, the influence of the degree of isolation from both other hedgerows and from woodland will be assessed, as will the influence of the density of other field boundary habitats and the area of woodland in the surrounding landscape. The intention, therefore, was to address millipede and woodlice communities at a 'landscape ecology' level (Forman 1981, Forman & Baudry 1984) and thus to examine the hypothesis that within the agricultural landscape the long-term survival of woodlice and millipede species may, at least partially, be dependent upon hedgerows. In this context, hedgerows may provide both a *permanent habitat* and a dispersal *corridor* or *network* through which individuals can move.

Over and above the hedges' connectance and wider landscape attributes, however, other variables may partially explain the distribution of these arthropod groups (Wheater & Read 1987) and so an additional objective was to assess this by recording a variety of other physical and biotic properties of the study hedgerows.

5.3 Methods

5.3.1 Selection of hedgerows

The hedgerows included in the survey were not selected randomly but were chosen as a subset of the hedgerows surveyed during the plant study of the previous year. This meant that certain botanical, physical and historical features of the hedgerows had already been obtained and, consequently, that more time could be spent directly surveying the soil fauna. The more southerly distribution of many of our woodlice and millipedes meant that only hedgerows from Oxfordshire were included in the study. It was hoped, therefore, that a larger number of species might be recorded than if the survey had been conducted in North Yorkshire.

Hedgerows can be classified into six broad 'connection types'; those that abut onto woodland, those that are isolated, and those that have either one, two, three or four connecting hedgerows (Figure 5.1). In the time available it was possible to sample approximately 30 hedgerows. Consequently, in order to assess woodlouse and millipede distributions in all the common hedgerow types, about five hedgerows in each of the six connection categories could be surveyed. Sampling was carried out in June and because it took place over a three week period it was necessary to eliminate any gross effect of time (and hence weather) on the study. Hedgerows from each category were, therefore, surveyed in rotation with one hedgerow of each connection type being sampled before another in the same category.

5.3.2 Millipede and woodlouse sampling procedure

The variations in surface activity of certain woodlouse and millipede species means that they are not adequately recorded by the use of pitfall traps (Sutton 1980, Blower 1985).

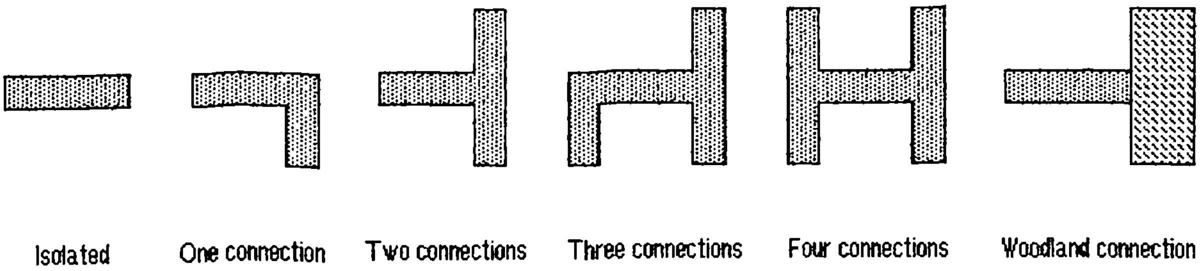

Figure 5.1 The six broad hedgerow connection categories.

Consequently, the collection of soil and surface litter samples and their subsequent hand sorting was chosen as a preferable sampling procedure. The area of the sampling quadrat was 1/25 m^2 (20 cm by 20 cm); this was chosen as being intermediary between the 1/50 m^2 quadrat size suggested by Sutton (1980) for the quantitative sampling of woodlice and that of 1/10 m^2 suggested by Blower (1985) for the sampling of millipedes. These authors gave no indication of the depth to which soil samples should be taken, and indeed this will depend on the season, the habitat and the particular species to be included in the survey. It was decided to excavate the soil within the quadrat to a depth of 5 cm because this depth was sufficient to allow the litter, fermentation and humus surface soil layers to be surveyed, as well as allowing soil to be collected from deeper eluvial horizons. Consequently, each sample consisted of approximately 2,000 cm^3 of soil. Photograph 5.1 illustrates the soil excavation quadrat *in situ*.

The need for replicating samples within a hedgerow was countered by the need to sample as many hedgerows as possible. In the time that was available, it was decided that six samples would be taken from each hedgerow; this provided a measure of replication while not requiring excessive amounts of time to be spent surveying an individual hedgerow.

Photograph 5.1 Soil excavation quadrat positioned in the interior of a hedgerow; also visible are the mallet used to drive the quadrat into the soil, the trowel used to excavate the soil and the collection bag of surface organic matter debris.

In order to collect unbiased samples along the entire length of each hedgerow a stratified random sampling technique was used. This involved two samples being chosen randomly from each third of the hedgerow. At each sample location the soil excavation quadrat was hammered into the earth as close to the central line of the hedge as possible. Where stones or large roots made this impossible the quadrat was repositioned 10 cm to the right. Having positioned the quadrat, the loose poorly decomposed organic matter, wood debris, leaf litter and stones were all collected into a polythene bag. The soil so exposed was then excavated with a trowel to the base of the quadrat, i.e. 5 cm, and collected in a second polythene bag.

5.3.3 Extraction and identification of individuals

For every hedge, each of the six samples was hand searched for 20 minutes in total; 10 minutes was spent examining the material collected from the soil surface and 10 minutes was spent on the soil itself (it was necessary to examine half of the collected soil at a time in order to make the sample more manageable and hence to increase extraction efficiency). In total, therefore, two hours were spent searching through the material collected from each hedgerow.

The searching procedure involved the contents of each polythene bag being emptied onto a large white sorting tray and then being carefully examined under strong illumination. Large pieces of wood debris and soil peds were broken to reveal hidden specimens. Individuals were collected in a pooter and preserved in 70% alcohol. Identification took place at a later date and was aided by the use of a binocular microscope with magnification of up to x 70 (this magnification was needed to discern the detailed characteristics of millipede genitalia). Information on the presence or absence and the frequency of occurrence of a given species is, therefore, available for each of the six samples from the surveyed hedgerows.

5.3.4 Measurement of hedgerow physical characteristics

The study was primarily concerned with assessing the importance of hedgerow connections in determining woodlice and millipede distribution patterns. A variety of other physical attributes, however, may also partially explain their distribution and, consequently, several other physical characteristics were also assessed. The environmental variables included in the survey are explained below.

(i) Number of hedgerow connections

Hedgerows were assigned to each connection category (Figure 5.1) in accordance with the following points: (a) an isolated hedge was taken to be one that was completely surrounded by cultivated land or one that was terminated at one or both ends by a wide and frequently used vehicle entry point characterised by compacted earth and sparse vegetation cover, (b) where the study hedge does in fact abut onto other hedgerows these criteria were also used to assess its degree of connectance, and (c) only hedgerows that abutted onto deciduous or mixed woodland were included, i.e. predominantly coniferous woodland was ignored.

(ii) Soil and surface-debris organic matter

The 'micro-organic' and 'macro-organic' matter content for each of the six samples from the surveyed hedgerows was estimated. The micro-organic matter of the soil was assessed by burning approximately 3 g of oven dried soil at 450°C for four hours (see Allen, 1974, for method). The estimated organic matter content was expressed as a percentage of the inorganic components of the soil. This 'loss on ignition' technique can not be equated directly to organic carbon because some mineral-bound water is lost at very high temperatures; the effects of this, however, have been lessened by burning the soils for longer at a lower temperature.

Macro-organic matter was assessed by sieving the surface material collected from each quadrat so that large items were retained (the sieve aperture was 8 mm by 8 mm). Large stones and soil peds were removed from this fraction. Consequently, the retained fraction consisted primarily of twigs, bark, leaves, dead vegetation and wood fragments. This macro-organic matter was then air dried at room temperature for 7 days before being weighed.

(iii) Solar radiation input

Millipedes and woodlice are relatively closely coupled with their immediate atmosphere and as such are prone to desiccation in dry air (Wieser 1984, Appel 1988, Cloudsley-Thompson 1988). In addition to the precipitation and air current characteristics of a given habitat, the amount of solar radiation reaching a habitat will largely determine its micro-hydrological characteristics. The solar radiation received by any given hedge will largely depend on its orientation to the course of the sun and the angle of its sides. An estimate of the potential radiation reaching the top and sides of the study hedges during the month of the survey (June) was made using an equation formulated to calculate the direct-beam solar flux on sloping habitats (Miller 1981). A mean radiation input per m^2 for each hedge was then calculated by averaging the potential radiation incident on each of the exposed hedge surfaces.

(iv) Hedgerow age

Hedgerow age was assessed by comparing the changes in field and hedge patterns as recorded by maps dating from different periods. The available sources of information were Parliamentary Enclosure maps, tithe land maps and private estate maps held by the Oxfordshire Local Studies Library and the Oxfordshire Archives's library. Further information on the dating of the study hedgerows is given in sub-section 3.3.5.

(v) Soil pH

Soil pH was measured at ten locations along the length of each hedge where the hedgerow verge met the side of the hedge crown; thus a mean pH of the soil under each hedge and a measure of its variability were obtained. The degree of variation in pH was expressed as the coefficient of variation calculated as the standard deviation of the ten pH measurements divided by the mean pH. More detailed methodology about the measurement of soil pH is given in sub-section 3.3.1.

(vi) Hedgerow dimensions

In order to calculate the area of land occupied by each hedgerow its length and mean width were measured. The hedgerow width was taken to be the distance between the outer edge of the two hedgerow verges. These measurements had been made in the previous summer and the full methodology is given in sub-section 3.3.1.

(vii) Adjacent boundary and woodland habitats

The amount of woodland and additional boundary habitats adjacent to each of the study hedgerows was estimated by making field observations within an 80 ha area centred on each hedgerow. These habitats were marked on a map and quantified at a later date using a digitising pad. The additional boundary habitats include other hedgerows, fencelines, stone dykes, roadside verges and woodland edges, while the adjacent woodland habitats in this study were defined as deciduous and mixed woodlands. More detailed methods for quantifying these surrounding habitats are given in sub-section 3.3.3.

5.3.5 Measurement of hedgerow floristic characteristics

Woodlice and millipedes are largely saprophytic and their quantitative and qualitative dietary preferences (Hassel & Rushton 1984, Wieser 1984) are, at least partially, likely to determine their distribution. To assess this factor the number of woody, herbaceous and grass species was recorded for each hedgerow by walking up both sides of the hedgerow while examining the hedgerow verge, hedge interior and hedge crown. Each species was recorded as being either present or absent.

5.3.6 Data Analysis

In order to assess adequately the influence of the recorded environmental variables on the woodlouse and millipede species distribution patterns a useful first step is to simplify the community data so that a summary of the community pattern is obtained (Gauch 1982). The ordination technique Twinspan (Hill 1979) was used to create a low-dimensional ordination space of the woodlouse and millipede community data. Twinspan generates a two-dimensional table that groups samples which have similar species composition and abundance closer together than those with dissimilar composition and abundance. Species that behave similarly across samples are also grouped closer together. Having obtained the ordination it is then possible to assess better the influence of particular environmental variables on the distribution of the species within the woodlouse and millipede communities. One way to do this is to conduct an analysis of variance using the ordination groupings as levels within a factor. This technique does not, however, indicate causality because a significant pattern between community structure and an environmental gradient may only be a correlative association. It does, however, allow hypotheses to be made and with further investigation it allows the causality of the observed associations to be assessed.

5.4 Results

5.4.1 General hedgerow and community characteristics

It was possible to study 31 hedgerows in total. These were distributed on eleven farms from Banbury to Reading; their Twinspan ordination code, farm, county parish and National Grid Reference are given in Appendix 5.1. The hedgerows studied were chosen primarily by virtue of their immediate connection attributes to other hedgerows and to woodland. These connection attributes, the other measured physical characteristics of the hedgerows, and the species richness of their plant, millipede and woodlouse communities are given in Appendix 5.2.

A total of 2,445 woodlouse and millipede individuals were collected from the study hedgerows and identified to species; 20% of these were millipedes. The species caught, their family, frequency of capture, the number of hedgerows from which each species was recorded and the Twinspan ordination code for each species are given in Table 5.1. It can be seen that the two woodlice *Porcellio scaber* and *Philoscia muscorum* were very numerous indeed, accounting for slightly over two-thirds of all individuals. Although *P. scaber* was the most numerous, only *P. muscorum* was recorded from all of the study hedgerows. *Polyxenus lagurus* was one of five millipedes to be caught only once and is distinctive because of its exotic rows of setae (trichomes) (Photograph 5.2).

Table 5.1 Frequency of capture of the millipede and woodlouse species recorded from the 31 study hedgerows, their ordination code, family and the number of hedgerows from which they were recorded.

Ordination code	Species	Family	Frequency of capture	No. of hedges where species was recorded
	Millipedes:			
21	*Tachypodoiulus niger* (Leach)	Julidae	163	17
13	*Glomeris marginata* (Villers)	Glomeridae	125	11
9	*Brachydesmus superus* (Latzel)	Polydesmidae	78	14
12	*Cylindroiulus punctatus* (Leach)	Julidae	54	11
18	*Polydesmus gallicus* (Latzel)	Polydesmidae	15	4
17	*P. angustus* (Latzel)	Polydesmidae	12	7
19	*P. inconstans* (Latzel)	Polydesmidae	10	1
16	*Ophyiulus pilosus* (Newport)	Julidae	9	4
14	*Nanogona polydesmoides* (Leach)	Craspedosomatidae	4	1
8	*Blaniulus guttulatus* (Fabricius)	Blaniulidae	3	1
7	*Archiboreoiulus pallidus* (Brade-Birks)	Blaniulidae	1	1
10	*C. caeruleocinctus* (Wood)	Julidae	1	1
11	*C. latestriatus* (Curtis)	Julidae	1	1
15	*Ophiodesmus albonanus* (Latzel)	Polydesmidae	1	1
20	*Polyxenus lagurus* (Linne)	Polyxenidae	1	1
	Woodlice:			
4	*Porcellio scaber* (Latreille)	Porcellionidae	865	30
3	*Philoscia muscorum* (Scopoli)	Philosciidae	788	31
5	*Trichoniscus pusillus* (Brandt)	Trichoniscidae	151	17
2	*Oniscus ascellus* (Linnaeus)	Oniscidae	130	24
1	*Armadillidium vulgare* (Latreille)	Armadillidiiae	32	11
6	*Trichoniscus pygmaeus* (Sars)	Trichoniscidae	1	1

The generally greater abundance of the relatively small number of woodlouse species is in contrast to the smaller catches of a more species rich millipede fauna. The full list of species recorded for each hedgerow are given in Appendix 5.3.

Photograph 5.2 The distinctive bristly millipede, *Polyxenus lagurus*, is nationally one of the rarest of the caught species (*c.* 3 mm).

5.4.2 Woodlouse and millipede ordination

The Twinspan analysis was conducted so that the ordination process made dichotomous divisions on the basis of the presence and absence of species while at the same time taking into consideration their rank abundance. This method, therefore, retains a degree of the quantitative nature of the data (in this case the number of individuals of each species recorded from each hedgerow) during the essentially qualitative ordination process. The result is that sites with similar species *and* similar abundances of these species are grouped closer together in the ordination table than sites with similar species but whose abundances are comparatively dissimilar. The default Twinspan rank abundance scale for this procedure is unsuitable for the present analysis because it has been devised to emphasise the salient features of percentage-abundance or presence and absence data. For the woodlouse and millipede data three new rank abundance classes were, therefore, selected to represent absent, scarcer and commoner species. Using the number of individuals of each species recorded from each hedgerow as a guide (Figure 5.2) these three abundance categories were defined as (i) absent - no individuals recorded, (ii) scarcer - one to ten individuals recorded and (iii) commoner - eleven or more individuals recorded. The "pseudospecies cut levels" (Hill 1979) used in the Twinspan ordination were, therefore, one and eleven.

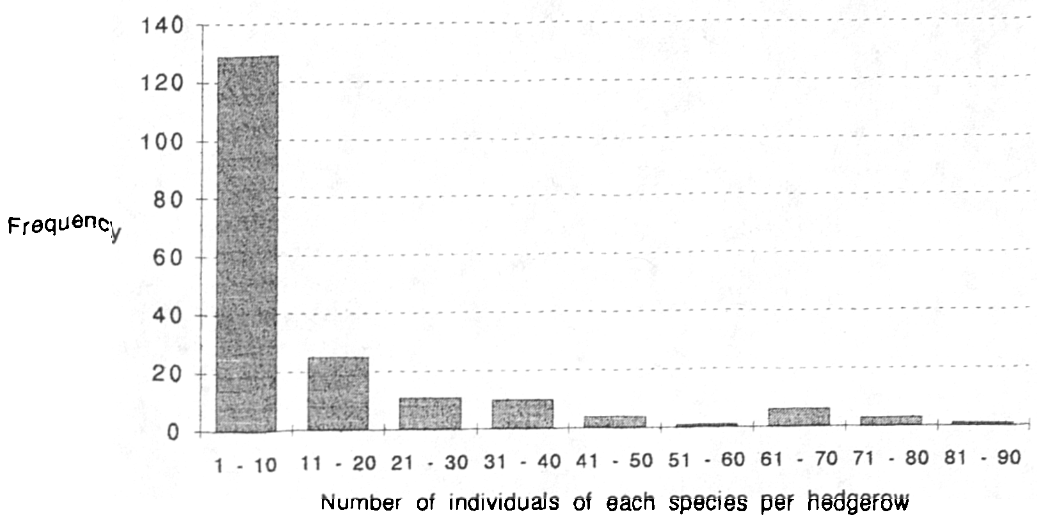

Figure 5.2 Frequency distribution of the number of times a species was represented by *n* individuals in each hedgerow.

The ordination table generated when using all the study hedgerows and species records is shown in Table 5.2. It can be seen that the primary hedgerow and species division has grouped a number of species in the upper left hand quadrant (ordination code 0 for both the hedgerow and species first level division) that are predominantly, if not exclusively, associated with this group of hedgerows. The preferential species that have greater than one occurrence in this group are *Ophyiulus pilosus*, *Cylindroiulus punctatus*, *Glomeris marginata* and *Tachypodoiulus niger* (all millipedes) and *Armadillidium vulgare* (a woodlouse). Indeed the "indicators" (Hill 1979) of this quadrant are identified by the analysis as *C. punctatus*, *A. vulgare* and *T. niger*; these *indicator species* are defined as those that are highly preferential to this group and as such are good indicators of this synecological community. Although *Brachydesmus superus* was preferential to the reciprocal group (ordination code 1 for both the first level divisions), only the

Table 5.2 Annotated Twinspan ordination table of hedgerow millipede and woodlouse faunas: vertical divisions emphasise the first four hedgerow groups identified (solid line - first level division; broken line - second level divisions); horizontal solid line emphasises the first two species groups; tabulated numbers represent rank abundance categories (i.e. '-', species not recorded; '1', species present with an abundance of 1 to 10 individuals; '2' species present with an abundance of greater than 11 individuals).

```
                          Species      22    1 111:1222|21123   1 222:113    Hedgerow
                     abbreviation      86357662494:7159|2418008931327:051    ordination code

                        Poly Inco      -----------:1---|-------------:---    0000
                        Arch Pall      ----------1:----|-------------:---    0001
                        Blan Gutt      ----------1:----|-------------:---    0001
                        Cyli Late      ----------1:----|-------------:---    0001
                        Ophy Pilo      1-----111--:----|-------------:---    0001
                        Cyli Caer      1----------:----|-------------:---    001
                        Cyli Punc      11111121112:----|-------------:---    001
                        Ophi Albo      1----------:----|-------------:---    001
                        Poly Lagu      ----1------:----|-------------:---    001
                        Arma Vulg      111--1-1111:1---|-----1-------:-1-    01
                        Glom Marg      121------1-:2112|---111-------:---    01
                        Tach Nige      11111221-22:-111|11-1-------1-:---    01
                       ----------------------------------------------------------------
                        Onis Asce      11111111111:1-12|1211121------:111    100
                        Poly Angu      --------111:-1--|--111--------:---    100
                        Poly Gall      1-1--------:----|-------------:11-    100
                        Phil Musc      12222222212:2111|2212222222121:222    101
                        Porc Scab      21212222212:2111|222122212221-:111    101
                        Tric Pusi      -1-----2111:----|22-211---1111:222    11
                        Tric Pygm      -----------:----|-1-----------:---    11
                        Brac Supe      --1---1--1-:2---|111111---1---:111    11
                        Nano Poly      -----------:----|-------------:-1-    11

                                       00000000000:0000|1111111111111:111    Dichotomous ordination
           Dichotomous ordination      00000000000:1111|0000000000000:111    coding for
                       coding for      00000011111:    |0000001111111:       species groups
                  hedgerow groups      01111100001:    |0011110000011:
                                        01111     :    |      00011   :
```

woodlouse *Trichoniscus pusillus* was identified as being an indicator species. In contrast to these preferential species, *Oniscus ascellus*, *Polydesmus angustus*, *Philoscia muscorum* and *Porcellio scaber* showed no tendency to be associated with either of the primary hedgerow groups.

The secondary hedgerow groups (00, 01, 10 and 11) identified by the ordination (dichotomies indicated by dashed-lines in Table 5.2) are less pronounced than the groups formed by the first level hedgerow division, and indeed only *C. punctatus* was identified as an indicator species of hedgerow group 00, while only *Polydesmus gallicus* was identified as an indicator species of the hedgerow group 11.

Of the four second level hedgerow groups, only groups 00 and 10 have been divided further by the analysis on account of the other two groups being composed of just four and three hedgerows each. A number of the member species are highly preferential to their respective groups; these indicator species are *P. gallicus* and *G. marginata* to group 000, *T. pusillus*, *P. angustus* and *O. pilosus* to group 001 and *O. ascellus* and *B. superus* to group 100. Subsequent divisions and their preferential species will not be considered further here on account of the small number of hedgerows classified into each group.

In summary, it can be said that the ordination has identified a number of hedgerow groups that are characterised by species with varying degrees of fidelity. In order to interpret in ecological terms the community structure identified by the analysis it is necessary to investigate the environmental parameters of the hedgerow groups.

5.4.3 Ecological interpretation of ordination

To determine whether or not synecological interpretation of the ordination groups is possible, analyses of variance were conducted on each of the environmental variables in turn for a number of the paired hedgerow groups. The significant differences between the ordination groups are considered below (starting with the first level division and followed by the divisions made at subsequent levels).

Comparison of the two hedgerow groups identified by the first level division (groups 0 and 1) reveals that hedgerows classified into group 0 have a significantly ($p \leq 0.05$) larger number of woody species in them than those hedgerows of group 1 ($F_{[1,29]}$=4.21), i.e. they have a mean of 9.2 woody species per hedgerow compared with 7.3 species. Of the physical hedgerows attributes recorded in the study, the soil pH characteristics also differ significantly between these groups. The mean pH of the hedgerows classified into group 0 is significantly ($p \leq 0.01$) greater than those hedgerows of group 1 by approximately one pH unit ($F_{[1,29]}$=10.40), i.e. 7.82 compared to 6.78. In addition, the soil pH along the length of the former hedgerow group was significantly ($p \leq 0.01$) less variable than hedgerows of the latter group ($F_{[1,29]}$=10.39). This is revealed by the mean coefficient of variation of this former group being approximately four times less, i.e. 2.85 compared to 11.27.

If the number of woody plant species in a hedge and its soil pH characteristics are indeed causal variables, and not just correlated ones, it appears that *O. pilosus*, *C. punctatus*, *A. vulgare*, *G. marginata* and *T. niger* may all prefer both higher and stabler soil pH conditions and hedgerows that are composed of a greater variety of woody plant species. All these species have either been predominantly, or exclusively, classified into the hedgerow group where these conditions prevail (group 0). Although *Polydesmus inconstans*, *Archiboreoiulus pallidus*, *Blaniulus guttulatus*, *Cylindroiulus latestriatus*, *Polyxenus lagurus*, *Cylindroiulus caeruleocinctus* and *Ophiodesmus albonanus* are also confined to this group they were only recorded from one hedgerow each and so little can be said about their fidelity and the parameters likely to influence their distribution.

Comparison of the physical parameters pertaining to the two hedgerow groups identified by the first level division also revealed that the *connectance* attributes of hedgerows may help to explain the community structure. Of the five hedgerows that abut onto woodland four of them (hedgerows coded 1, 9, 18 and 27) belong to group 1, and only one (hedgerow coded 19) belongs to the reciprocal group. Further comparison of the hedgerow groups formed after the subsequent second level division reveals, however, that this assessment is too coarse. It is apparent that all four 'woodland' hedgerows of group 1 do, in fact, belong to the second level hedgerow group 10. This may, however, reflect the fact that there are over four times as many hedgerows in group 10 than there are in group 11 (the split is 13:3).

The possible significance of hedgerow connections is also expressed elsewhere among the second level groups. In the case of the hedgerow groups 00 and 01 there appears to be a quantitative rather than a qualitative influence of hedgerow connectance on community patterns. The ten hedgerows of group 00 that abut to hedgerows have an average of 2.5 such connections (one hedgerow in this group, ordination code 19, abuts to woodland and is excluded from the analysis) compared to an average of 0.2 connections in the reciprocal group. This difference is significant at the 1% probability level ($F_{[1,12]}$=15.43, n=14). It is apparent, therefore, that species preferential to hedgerow group 00 (and in particular *C. punctatus* which is an indicator species) inhabit hedgerows with a greater degree of connectance.

The third level divisions also reveal that the age of a subset of the study hedgerows may influence species distribution. The dating of the hedgerows was hampered, however, by a lack of documentary evidence and as a result only 71% of the hedgerows could be dated with any degree of certainty. The large time span between the maps used to assess hedgerow age meant that the age of many of the hedgerows was imprecise, for example it is known that the study hedge coded 31 in the ordination was planted between 1773 and 1845 but a more accurate assessment of its age is not possible. It was decided, therefore, to group the hedgerows into three broad categories; these are (i) those planted before 1795, (ii) those planted after 1795, and (iii) those whose possible planting date spanned this 1795 division (i.e. it is not known if they are older or younger than 195 years old). The influence of age on community pattern is seen in that hedgerow group 000 is composed of six hedgerows which were all planted after 1795, while its reciprocal group (001) is composed of only one hedge in this age category, two which were planted before 1795 and two whose earliest possible planting date is unknown but which are at least 139 years old. Due both to the small size of these two hedgerow groups and the imprecise age data the significance of this finding is uncertain.

The degree of hedgerow connectance is again associated with the ordination groups when the third level divisions are considered. The mean number of hedgerow connections of group 100 is 3.4, while that of the reciprocal hedgerow group (101) is only 1.0. This difference is significant at the 0.1% probability level ($F_{[1,7]}$=28.0). The sample size in this instance is, however, only 9 hedgerows because four hedgerows included in group 10 abut to woodland and they were, therefore, excluded from the analysis. The possible influence of the surrounding landscape features on the community structure of these two hedgerow groups is also revealed when the quantity of neighbouring linear habitats (hedgerows, fences, stone dykes, roadside verges and woodland edges) is considered. An analysis of variance on the length of boundary habitats in an 80 ha area centred on the study hedgerows of both groups reveals that the former group (100) is characterised by hedgerows with a significantly ($p \leq 0.05$) greater length of neighbouring linear habitats than the latter group ($F_{[1,11]}=5.17$), i.e. 9637 m of adjacent boundary habitats compared to 6734 m. It would appear, therefore, that the occurrence of the preferential species in hedgerow group 100 (and in particular *O. ascellus* and *B. superus* which are its indicator species) may be partially determined by surrounding landscape features; these species appear to inhabit preferentially both relatively well connected hedgerows and those hedgerows surrounded by agricultural land with a comparatively high density of boundary habitats.

A summary of the major differences between the environmental parameters of the hedgerow groups is presented in Table 5.3. No significance testing was conducted on groups identified by the fourth and fifth level division of the ordination on account of the small size of these groups and hence the lack of replication.

5.4.4 Vegetation ordination

By studying the distribution of plant species in the study hedgerows it may be possible to assess further the factors influencing the distribution of the woodlouse and millipede faunas. Comparison of the two first level woodlouse and millipede ordination groups revealed that the hedgerows of group 0 have a significantly higher pH than those of hedgerow 1, i.e. a mean of 7.82 compared to 6.78 (sub-section 5.4.3). If the difference in soil pH between these two hedgerow groups is, indeed, an important one it might be expected that this influence would also be reflected in the flora of the hedgerows. It was hypothesised, therefore, that an ordination analysis of the vegetation data would identify two major hedgerow groups differing markedly in their pH characteristics. If the soil pH characteristics influence both the plant and the woodlouse and millipede faunas similarly it can also be expected that the hedgerow groups of each ordination would show considerable resemblance. Further more, it can be expected that plants with known specific pH requirements will be classified into the ordination groups characterised by those pH conditions.

Table 5.3 Major differences in botanical and physical characteristics of the hedgerow groups identified by the woodlouse and millipede ordination; *s*, standard deviation; *p*, probability.

Hedgerow variable	Hedgerow group ordination code	Mean	*s*	*p*
Number of woody species	0	9.2	2.8	≤0.05
	1	7.3	2.3	
Soil pH	0	7.82	0.68	≤0.01
	1	6.78	1.06	
pH coefficient of variation	0	2.85	5.48	≤0.01
	1	11.27	8.61	
Number of hedgerow connections	00	2.5	1.8	≤0.01
	01	0.2	0.5	
Number of hedgerow connections	100	3.4	0.6	≤0.001
	101	1.0	0.8	
Surrounding linear habitats (m)	100	9637	3274	≤0.05
	101	6734	849	

Hedgerow variable		Frequency
Hedges with woodland connections	10	4
	11	0
Approximate hedge age (years)	000	6 > 195
	001	1 > 195, 2 < 195, 2 unknown

An ordination was conducted on the presence and absence of all plant species recorded from the study hedgerows, except for those that occurred in less than 10% or greater than 90% of the hedgerows. These cut-off levels were chosen so that the very common and very rare plants were excluded from the analysis on the assumption that these species would be of comparatively little interpretive value. This selection process left 56 plant species in the ordination out of a total of 106 recorded in the vegetation survey.

The ordination table is shown in Table 5.4 and the full names of the plants abbreviated in the ordination table are given in Appendix 5.4.

An analysis of variance of the hedgerow soil pH characteristics reveals that there is, indeed, a significant ($p \leq 0.001$) difference between the hedgerow groups identified by the first level ordination division ($F_{[1,29]}=43.72$); the eighteen hedgerows classified into the left hand group (0) having a mean pH of 7.75 ($s=0.23$) compared to the thirteen hedgerows of the reciprocal group which have a mean pH of 6.36 ($s=0.99$). In addition, the hedgerows classified into the two first level groups of the plant species ordination correspond well with those classified into the corresponding groups by the woodlouse and millipede ordination, i.e. there is over 75% consistency between ordinations with only the hedgerows coded 2, 7, 11, 14, 29, 24 and 27 changing ordination groups.

Reference to the habitat preferences (Clapham, Tutin & Warburg 1985) of the plants recorded in the hedgerow survey reveals that those plants with a known preference for base rich and/or alkaline soils have indeed been classified into the ordination group characterised by hedgerows with significantly higher soil pH values than the reciprocal group. These species are *Acer campestre*, *Centaurea scabiosa*, *Clematis vitalba*, *Euonymus europaeus*, *Ligustrum vulgare* and *Rhamnus catharticus*. This division is further indicated by the presence of *Holcus mollis* (a species that commonly occurs on acid soils) in the hedgerow group characterised by soils with a comparatively low pH. The strong affiliation of some of these species to their respective groups is signified by the fact that the ordination identifies *A. campestre*, *E. europaeus*, *R. catharticus* and *H. mollis* to be indicator species of their respective hedgerow groups.

The ordination of the hedgerow flora appears to indicate, therefore, that the hedgerow plant distribution can be partially explained by the soil pH characteristics. The presence of calcicole and calcifuge plant species suggests that soil pH affects the calcium status of the hedgerow soils. The similarity between the first level hedgerow ordination groups generated by the ordination also appears to indicate that the distribution of woodlouse and millipede faunas may be partially explained by the soil pH of the study hedgerows.

Table 5.4 Twinspan ordination table of plant species occurring in greater than 10% and less than 90% of the study hedgerows: vertical and horizontal lines emphasise the first level hedgerow and species divisions respectively; hedgerow codes are given in Appendix 5.1, plant species abbreviations in Appendix 5.4; tabulated figures represent absence ('-') and presence ('1') of each species; species annotated with '*' or '#' represent those that are cited to be particularly common on calcareous or on acid soils respectively.

```
                 2122212  12 12  12112 1133   12
                 0915877266932645140521480187933

• 44 Clem vita   1-11----------1----------------   00000
  45 Cory avel   111-1--1-1---------------------   00000
  10 Gali moll   -1111-11---1--1--1-------------   00001
• 42 Acer camp   11111--111-11-111---1----------   00001
• 46 Euon euro   1-11111--11--1---1-------------   00001
  18 Papa rhoe   -1--1---1----1--1-----1--------   0001
  49 Ilex aqui   --111--------1----------1------   0001
  11 Gera robe   -------1--11-11----------------   0010
•  5 Cent scab   --1----1111--11-11-------1-----   001100
• 56 Rham cath   --1-11-11-1111--1-----------1--   001100
   8 Cirs vulg   -----1------1-11---------1-----   001101
  14 Knau arve   ---11----1111-1-11--1----1-----   001101
  25 Sile vulg   --1--------11-1-1--1-----------   001101
  31 Gera diss   --1------11111-11111-----------   001101
  40 Loli pere   --1---1-1--1--1111---1---------   001101
  35 Elym cani   1-1------1-111-1-----------11--   00111
  17 Myos arve   ------1-1--1-------------1-----   0100
  29 Tara offi   ---------------111--------1----   0100
  27 Sonc aspe   1-1--11-----1-1-1111-----1-----   01010
  51 Malu sylv   1-------1---111---11-----------   01010
   4 Bryo dioi   111-11111111111111-111-1-111---   01011
  24 Sile alba   --11-1--1-1--11--1----1--11----   01011
  37 Fest rubr   --111--11--111--1-11----1--1---   01011
• 50 Ligu vulg   1-1--1-----1-1---1--1-1--------   01011
   1 Alli peti   111111-111-11111--1-1--1-1-1111   0110
  16 Laps comm   -11-11----1-111--111------1-11-   0110
  52 Prun spin   11111-111-11111-1-1-1--1---1111   0110
  12 Geum urba   ----1--1--1---11-----------11--   01110
  19 Pote rept   ----1---------11-----------1---   01110
  22 Rume cris   -11-----111---11-----------1111   01110
  32 Agro stol   ---1-----1-11111111-1------1111   01110
• 30 Viol odor   ---------1-1-1-------------11--   01111
  41 Poa  triv   11111-1-1-1111-11111111-11-111-   1000
  47 Frax exce   11111-1-11-1-1-1-1111-11----111   1000
   9 Conv arve   1111111111111111-11-111111-1---   1001
  36 Elym repe   111111111111111-1111111111---11   1001
  48 Hede heli   111111-111-1111--111111111-1--1   1001
  54 Rosa cani   1--111111111-11111-111-111-1111   1001
  55 Ulmu proc   1----------1-11--1-1-------1-11   101000
  13 Glec hede   -11----111111111111111111--11-1   101001
  21 Rubu frut   -1-11-111-111111111111111111111   101001
  28 Tamu comm   1111--11111111-111111-11111111-   101001
  34 Dact glom   11----11111111-11111111111-1111   101001
   3 Arum macu   -----------1--1--------1-1-----   10101
   2 Arct lapp   1----------------1---1------1--   1011
   6 Chae temu   --1-1-----1---1-1-----1--11--1-   1011
   7 Cirs arve   -111111-1-11-111111111111111111   1011
  15 Lami albu   11111----------1----11-111----1   110
  33 Alop myos   ------------11-------11--------   110
  26 Sola dulc   -----1111-11---1--11-111-111--1   11100
  43 Acer pseu   --1-------1--1----1---11--1----   11100
  20 Ranu repe   ----------------1----1--11111-1   11101
  38 Holc lana   -------------------1111-1---1-1   11101
# 39 Holc moll   ---------------------11-11---11   11101
  23 Rume obtu   -1-------------1-1-11--11111--1   1111
  53 Quer rubu   -11---------------111-1--1-----   1111

                 0000000000000000001111111111111
                 0000011111111111110000000001111
                 011110000000001111000111111
                      001111111       000001
                        0000111       00001
```

5.4.5 Characteristics of hedgerows inhabited by millipedes

No millipedes were recorded from the five study hedgerows coded 8, 9, 13, 23 and 27 in the ordination (Appendix 5.1). To assess whether or not these hedgerows were characterised by physical and/or biotic properties that differed significantly from the other hedgerows an analysis of variance was conducted using the two hedgerow groups (those with and those without millipede communities) as levels within a factor.

The properties that differ significantly are shown in Table 5.5. It can be seen that the hedgerows in the group that lacked an observed millipede fauna had an average area approximately half that of the hedgerow group from which millipedes were recorded. In addition, and as with the ordination of the combined millipede and woodlouse data, it again appears that soil pH characteristics have an explanatory nature for the hedgerows in this latter group are also characterised by more alkaline soils, i.e. their mean pH is approximately 1.3 units greater than the group of hedgerows that lack an observed millipede fauna.

Table 5.5 Hedgerow characteristics that differ significantly between those study hedgerows where millipedes were recorded (+ millipede) and those where no millipedes were recorded (- Millipedes); *s*, standard deviation; *p*, probability;, d.f., degrees of freedom.

		Mean	*s*	*p*	*F*-ratio	d.f.
Hedgerow Area	+ Millipedes	692 m^2	304	<0.05	6.45	1, 29
	- Millipedes	330 m^2	193			
Average soil pH	+ Millipedes	7.50	0.87	<0.01	8.27	1, 29
	- Millipedes	6.20	1.18			

5.4.6 Distribution of *Cylindroiulus punctatus*

The ultimate aim of the ordination of community data is to allow an ecological interpretation of the distribution of species. Twinspan ordination starts with a complex assemblage of species and groups the species and their sample sites by virtue of the whole suite of abundance data. An alternative approach to this grouping procedure, however, is to construct the groups on the presence or absence of a single species. This approach is of interest when a given species is known, on an *a priori* basis, to have a strong habitat requirement. Under these circumstances the groups so constructed can be compared to see if this habitat variable can indeed offer an explanation to the distribution of this species. This approach, therefore, differs from Twinspan ordination in that it starts with a specific *a priori* hypothesis and groups the data on the basis of the presence and absence of a single species. This approach is considered below for *Cylindroiulus punctatus*, a common Julid millipede.

C. punctatus has a particularly strong habitat preference in that it has been noted to be the commonest British species to be found in association with dead wood as well as being found in the leaf litter (and its humus) of the less palatable species of deciduous trees (Blower 1985). The hypothesis that *C. punctatus* would tend to be found in hedgerows with soils characterised by well developed L and H horizons was tested by comparing the macro-organic matter content of the hedgerows grouped on account of the presence or absence of this species. When this is done, it appears that the macro-organic matter content of the hedgerows from which *C. punctatus* was recorded is indeed greater (2468 compared to 2393 g/m^2), however, this difference is not significant at the 5% probability level ($t_{[29]}=0.64$). It is likely, therefore, that the amount of dead wood and organic matter debris does not greatly influence the distribution of *C. punctatus* in these hedgerows.

5.5 Discussion

5.5.1 Species richness and national comparisons

The 15 species of millipedes recorded from the Oxfordshire study hedgerows represent 29% of the total British complement (52 species). In contrast, the hedgerows studied appear to be a relatively poor habitat for woodlice because only 17% of the native and naturalised British species were recorded (6 of 35 species). Comparing the recorded hedgerow millipede fauna with census data collated by the British Myriapod Survey (Fairhurst & Armitage 1979, Blower 1985) it is evident that 13 (56%) of our commoner species but only 2 (7%) of our rarer species were recorded during the hedgerow survey. Of the nationally common species that were absent, *Ommatoiulus sabulosus* is of most note because it is both the ninth most common British species and is generally considered to have a vagile behaviour. One possible explanation is that *O. sabulosus* generally prefers sandier soil types which were not encountered during the survey.

As with the recorded millipede species, the hedgerow woodlouse fauna is also composed of our commoner species as censused by the Isopod Survey Scheme (Harding and Sutton 1985). In fact, the nationally most common six species nearly account for all the hedgerow species recorded, with only the coastal species *Ligia oceanica* naturally going unrecorded. The observed species richness of the hedgerow woodlouse fauna falls considerably short of the 16 species that have been observed inhabiting hedgerows since the inception of the Isopod Survey Scheme in 1968. As might be expected, however, the six species recorded in the present study are indeed the commonest of the species observed to inhabit hedgerows by the national survey.

5.5.2 Influence of surrounding landscape features

The motivation behind studying woodlouse and millipede distributions in hedgerows was primarily one of studying a group of species that have relatively poor dispersal abilities compared both to the vertebrate fauna of hedgerows and to certain other invertebrate groups (such as insects which commonly disperse independently of directional features (Morris & Webb 1987)). Such a group was chosen because it was felt that a survey of their distribution and abundance may better assess the role that both hedgerows and woodland within the surrounding landscape have in influencing the fauna of hedgerows. Thus, their function as source habitats and dispersal routes can be addressed. This is the case because soil and soil-surface living organisms with no means of flight and with comparatively slow rates of movement are likely to rely more on continuous and relatively undisturbed habitats (such as hedgerows) in order to disperse. In contrast to hedgerows, the arable field environment represents a disturbed matrix habitat with poorly developed L and H soil horizons. Consequently, arable fields afford only limited protection to millipede and woodlice fauna against desiccation and predation while at the same time offering an impoverished food resource in terms of quantity and variety of organic matter. In addition to these indirect factors, the arable field environment also presents direct hazards in the form of the application of toxic agrochemicals and mechanical disturbance from ploughing and tillage. Consequently, the arable field habitat is likely to be a poor habitat for both woodlice (Sutton 1980, Harding & Sutton 1985) and millipedes (RIN 1987) and as such may constitute a barrier to dispersal.

The influence of adjacent landscape features was assessed in this study by (i) recording the immediate non-agricultural habitat connections to the study hedgerows (i.e. the number of other hedgerows or the connection to woodland) and (ii) estimating the area of deciduous and mixed woodland and the length of linear habitats in the surrounding 80 ha of land. The observed influence of these features is discussed in the next two sub-sections.

5.5.3 Hedgerow connectance

This was measured both in *quantitative* terms (the number of connecting hedgerows) and *qualitative* terms (whether or not hedgerows abut onto woodland). Taking the latter measurement first, it is apparent that the ordination identified species assemblages that are characteristic of hedgerows that abut onto woodland (hedgerow group 10) and by those that have no woodland connections (hedgerow group 11) (Table 5.3). Comparison of the species composition of those hedgerows that actually abut onto woodland (i.e. hedges coded 1, 9, 18 and 27 in the ordination and not just those which are classified into this general woodland hedgerow group) reveals, however, that they are not consistently inhabited by a specific species. It appears, therefore, that either the influence of adjacent woodland is diffuse or that the association is spurious and that these woodlands do not influence the millipede and woodlouse faunas of connecting hedgerows in a substantial or consistent manner.

Addressing hedgerow connectance in terms of the *number* of hedgerow connections, at two levels the ordination identified species assemblages that characterised hedgerow groups that differed significantly in their degree of connectance. Species preferential to hedgerow groups 00 and 100 may require a greater degree of hedgerow connectance than other members of these two soil fauna groups under the prevailing environmental conditions (Table 5.3). One important theoretical explanation as to why these species appear to be absent from, or scarcer in, more isolated hedgerows is considered below.

There is a general trend for woodlice and millipedes to have slower rates of locomotion than a variety of other ground living arthropods (e.g. the carabids and centipedes) on account of (i) the biomechanics of leg design, (ii) the gregarious nature of woodlouse and millipede populations, and (iii) their saprophytic feeding behaviour. It is likely, however, that there will also be considerable variation in the locomotion speed of individual species within these groups. This may, therefore, exclude poorly dispersing species from (i) newly created hedgerows whose soils are not already inhabited by millipedes and woodlice, and (ii) hedgerows that have lost their populations through local extinction events. The implications of this latter point are discussed at the landscape level in sub-section 5.5.9. It is possible that the species preferential to the comparatively well connected hedgerow groups are poorer dispersers than the species of the reciprocal group and that they are, therefore, less able to reach the more isolated farmland habitats.

Although the variety of morphologies, sizes and habits of the different woodlouse and millipede species do indeed suggest marked differences in locomotion speed and dispersal ability, there is little systematic information actually known about these abilities. At best, dispersal ability can be inferred from their walking speed although even this information has only been recorded for a few species. Manton (1954) gave walking speeds for a variety of millipedes and made general comments about the speed of locomotion of the various orders. These observations and others relating both to millipedes and woodlice are given in Table 5.6.

Taking the most preferential species of the two hedgerow groups characterised by well connected hedgerows (*C. punctatus* in the case of group 00 and *O. ascellus* and *B. superus* in the case of group 100) as examples, the incomplete knowledge about the dispersal abilities of woodlice and millipedes is illustrated. It can be seen that only *O. ascellus* is mentioned explicitly although no rate of movement is documented for this species. This woodlouse is, however, noted to cling tightly to surfaces (Harding and Sutton 1985) with its first behavioural defence against disturbance being to fasten itself to its substrate in order to avoid removal or dislodgement. Hence it does not rely on speed as its strategy for survival and, on the assumption that speed is positively correlated to dispersal ability, there is an indication that this species may be comparatively poorly dispersing. Consequently, its highly preferential occurrence in a relatively well connected group of hedgerows may be partially explained.

Table 5.6 Locomotion rates, movement characteristics or habits of millipedes and woodlice.

Species/order	Speed and/or comment	Source
Millipedes:		
Cylindroiulus spp.	8 mm per second	Manton 1954
C. caeruleocinctus	4-5 mm per second	Manton 1954
Glomeris marginata	3.5 mm per second	Manton 1954
Polydesmus angustus	11-22 mm per second	Manton 1954
Tachypodoiulus niger	13 mm per second	Manton 1954
T. niger	Fastest julid millipede	Blower 1985
T. niger	Ranges far and wide	Blower 1969
T. niger	Highly vagile behaviour	Fairhurst 1970
Polydesmida	Highly vagile behaviour	Fairhurst 1970
Chordeumatida	Faster than Polydesmida	Manton 1954
Polydesmida	Faster than Julida	Manton 1954
Julida	Slower than Polydesmida	Manton 1954
Woodlice:		
Armadillidium vulgare	13 m in 12 hours (summer)	Warburg *et al.* 1984
A. vulgare	10 m in 6 days (winter)	Warburg *et al.* 1984
A. vulgare	"Roller" ecological strategy	Schmalfuss 1984
Oniscus ascellus	Clinging habit	Harding & Sutton 1985
O. ascellus	Clinging habit	Hopkin 1987a
Philoscia muscorum	"Runner" ecological strategy	Schmalfuss 1984
Porcellio spp.	"Creeper" ecological strategy	Schmalfuss 1984
Trichoniscus pusillus	"Creeper" ecological strategy	Schmalfuss 1984
T. pusillus	Fast moving	Hopkin 1987a
Woodlouse (unspecified)	13 m in one night	Sutton 1980

Without additional evidence, however, the causal nature of this association is speculative because this species is both very widely spread (Hardy & Sutton 1985) and being a large species, the adults are approximately 16 mm in length (Sutton 1980), its movements are relatively rapid (personal observation). The complicated nature of this relationship is further exemplified by the classification of *O. ascellus* into the hedgerow group with *fewer* hedgerow connections at the subsequent ordination level, i.e. it is classified as a preferential species of hedgerow group 01 (with a mean number of 0.2 hedgerow connections) and not to group 00 (with a mean number of 2.5 connections). It seems, therefore, that the number of hedgerow connections does not explain the distribution of *O. ascellus* in a consistent manner and that other environmental variables have considerable influence.

The second highly preferential species of hedgerow group 100 is *B. superus*. This millipede species is a member of the Polydesmida and as seen in Table 5.6 this family is less mobile than the Chordeumatida but more mobile than the Julida (these three orders make up 90% of the British species). Again no rate of movement is available for this species. The Polydesmida, however, are generally faster moving than the Julida because of their habit of burrowing in leaf litter, in relatively uncompacted soils and in sub-cortical habitats. These habitats offer less resistance to lateral projections and the Polydesmida have consequently evolved relatively long legs. On the assumption that dispersal power increases with greater mobility it might not, therefore, be expected that this relatively mobile species would be an indicator species of a hedgerow group that is characterised by being well connected to others. This is particularly so because *B. superus* is noted to occur in arable fields (Blower 1985) and so is unlikely to find cultivated ground as inhospitable a habitat, and as great a barrier to dispersal, as some soil arthropods. Consequently, a reliance on hedgerows for dispersal routes seems less likely.

C. punctatus is highly preferential to hedgerow group 00 and is again not mentioned explicitly although Manton (1954) noted *Cylindroiulus* species to move approximately 8 mm per second and considered the Julida (of which *C. punctatus* is a member) to be comprised of slower moving species than both the Chordeumatida and Polydesmida. This rate of movement is slower than certain species such as *P. angustus* and *T. niger* but faster than *C. caeruleocinctus* and *G. marginata*.

In summary, it appears that the degree of hedgerow connectance influences the distribution of many species in an inconsistent manner and is likely to be dependent on other additional features of the hedgerows. One such feature is the wider connectance attributes of the hedgerow. The degree of connectance calculated for each of the study hedgerows measures the *immediate* connections with adjacent hedgerow and woodland habitats. This measurement may, however, not adequately reflect their true connectance attributes. It is possible that the connection characteristics of these directly connecting habitats may, in turn, be important in determining community distribution patterns. This possibility could be assessed by calculating the *hedgerow accessibility* of the study hedgerows in a similar manner to that used in Chapter 3 when estimating the connectance attributes of the hedgerows whose flora was surveyed by the complete sampling technique (sub-section 3.3.4).

This approach has not been adopted here because even a hedgerow's wider connection attributes may not, however, adequately reflect the degree of isolation perceived by ground dwelling arthropods. An assumption that has been made is that arable fields act as barriers to the movement of most woodlice and millipede species. Among the millipedes there are at least two known exceptions, however, for both *B. guttulatus* and *B. superus* are commonly found in association with crop roots and potato tubers (Blower 1985). The woodlouse *P. muscorum* is also likely to be less impeded by arable fields because this species is very fleet of foot (Harding & Sutton 1985) and is included in the "runner" category of the eco-morphological classification of Schmalfuss (1984). This species achieves its comparatively fast rate of locomotion because of its long legs and raised posture (Photograph 5.3). It is of note that this species was the only one found in every hedgerow surveyed in this study and that it has been found to occur in farm woodland independently of area and isolation parameters (Soesbergen & Mabelis 1989). The ease with which cryptozoic fauna can traverse fields will, presumably, ultimately depend on the fields' past and present crop and soil management regimes and the stage of crop growth at any given time. It is the case, therefore, that the actual degree of functional isolation (as apposed to physical isolation) is unknown. In the nomenclature of landscape ecology (Baudry & Merriam 1988), the degree of *connectedness* (physical connectance) may poorly represent the degree of *connectivity* (functional connectance).

The problems of interpreting hedgerow isolation and landscape scale result from an incomplete knowledge about the dispersal abilities of the various woodlouse and millipede species. Dispersal information such as that collected by Mader (1984) for carabids in an agricultural landscape is therefore needed for woodlice and millipedes before the significance of hedgerow for these comparatively poorly dispersing soil fauna groups can be assessed. Two additional factors that may hinder the interpretation of hedgerow connectance are that (i) the history of the hedgerow configuration may influence the present faunal composition, and that (ii) the effective area of the study hedgerows may be positively correlated with the degree of connectance. These factors are considered in sub-sections 5.5.7 and 5.5.8 respectively.

Photograph 5.3 *Philoscia muscorum* (*c.* 10 mm)

5.5.4 Adjacent woodland and boundary habitats

Assessment of the influence of non-cultivated habitats in the surrounding landscape revealed that the area of deciduous and mixed woodland in the eighty hectares around each hedgerow did not appear to influence the species composition of the study hedgerows. The amount of source habitats in itself, therefore, does not appear to be of a major consideration.

The length of additional boundary habitats in the surrounding landscape does, however, appear to influence the species composition of a subset (group 10) of the hedgerows

(Table 5.3). It may, therefore, be that the preferential species of the hedgerow group with a significantly greater density of surrounding linear habitats (group 100) require a greater number of hedgerows in the neighbouring landscape than the reciprocal group (101). These preferential species are *G. marginata*, *P. angustus*. *T. niger* and, in particular, *O. ascellus* and *B. superus* which are the indicator species. The surrounding hedgerows may act both as source habitats and movement corridors. It is of note that hedgerow group 100 also has a significantly greater number of immediate hedgerow connections (Table 5.3). It is possible, therefore, that both these properties make the hedgerows of this group more accessible to certain millipede and woodlouse species. Hence these properties may partially explain the affiliation of the preferential species to this hedgerow group.

These findings have a number of implications for the persistence of millipede and woodlouse populations in landscapes that vary in both their degree of hedgerow connectance and their density of linear habitats. Before these are considered, however, there are several other characteristics of the study hedgerows that the ordination identified as being of additional interpretive value; not least of these is soil pH which differed significantly between the two major hedgerow groups identified by the first level ordination division. The hedgerow soil pH characteristics along with the other physical properties of the hedgerows that may have interpretive value are discussed below.

5.5.5 Soil pH and calcium status

As already seen from the woodlouse and millipede ordination and the subsequent analysis of variance, there appears to be an influence of soil pH on the distribution of certain species. Ignoring species recorded from single hedgerows, it is evident that *O. pilosus*, *C. punctatus*, *A. vulgare*, *G. marginata* and *T. niger* all occur with some fidelity in hedgerow group 0 which is characterised by hedgerows that have a significantly higher pH than the hedgerows of the reciprocal group (Table 5.3). This influence may be an indirect one for correlated high soil calcium levels are indicated by the plant ordination, i.e. there are several calcicole species associated with the more alkaline hedgerow groups. The saprophytic feeding behaviour of the majority of woodlice and millipedes means that their occurrence will be strongly influenced by the nutrient status of the plants in their environment. It seems likely, therefore, that the millipede and woodlouse assemblages are influenced by soil pH in an indirect manner through the calcium status of the hedgerow plants.

Examining the ecological information known about the woodlouse and millipede species preferential to the more alkaline hedgerow group, there is some evidence to suggest that these species do in fact prefer habitats with more base rich soils. Taking the woodlouse species (*A. vulgare*) first, it is of note that the national Isopod Survey Scheme records this pill woodlouse as occurring within calcareous habitats on 80% of the occasions that it was encountered by those participating in the survey (Harding & Sutton 1985). In addition, Hopkin (1987b) and Sutton (1985) also noted that this species has a preference for calcareous soils. A possible explanation for this preference is that this species has a particularly heavy exoskeleton and as such requires calcium in relatively high concentrations in order to manufacture calcium carbonate which is a major constituent its chitinous endocuticle (Sutton 1980).

Of the millipede species *O. pilosus*, *G. marginata* and *T. niger* are also noted to be more numerous on base rich habitats (Blower 1985). It is possible that this distribution may again be related to a requirement for increased deposition of calcium in the skeletal plates of the exoskeleton. Alternatively it is possible that the efficiency of extraction or utilisation of the available calcium is less in these species. The one species with a known behaviour that does not, however, suggest it should be confined to this 'calcicole' group is *C. punctatus*. This millipede is both the commonest in Britain and is noted by Blower (1985) as "*extending its range into quite acid conditions*".

If pH is either directly or indirectly influential in determining the distribution of some millipede and woodlouse species in hedgerows it is important to know what causes the pH to differ between hedgerows. The most obvious and likely explanation is the base content of the underlying soil and rock. With the use of 1:50,000 solid geology and drift maps produced by the Geological Survey it was possible to compare the soil and rock types found on the eleven farms included in the survey. There are, however, no clear trends because hedgerows overlying Oxford Clay and Great Oolite Limestone are classified within the same ordination group. The implication of this is that some other factors, such as the management of the hedgerows and the adjacent fields or the presence of certain plant species, may be additionally influencing soil pH. A comparison between the pH of the hedgerow and adjacent field soils reveals that 84% of the study hedgerow soils differed significantly ($p \leq 0.05$) from the soil of the adjacent fields (67% of the hedgerows were more alkaline and 17% were more acidic). This indicates that direct or indirect management can alter the pH of field soils relative to adjacent hedgerows. What influence this field management has on the hedgerows themselves is unknown, but with hedgerows being relatively narrow habitats with little buffering from adjacent agricultural operations it is likely that in some circumstances the hedgerow soil pH will be perturbed by agricultural operations.

5.5.6 Surface-debris organic matter

Looking at the effects of organic matter, the *a priori* hypothesis that hedgerows where *Cylindroiulus punctatus* was present would have a significantly higher macro-organic matter content than those where it was absent did not gain support from the data. This is despite the fact that this species both feeds and oviposits on dead wood (Blower 1969 & 1985). Four possible explanations for this are that (i) the general trend for *C. punctatus* to be found in association with dead wood and accumulated organic matter debris does not hold true for the hedgerow habitat, (ii) the influence of macro-organic matter is modified and/or weakened by other environmental variables, (iii) the survey techniques used to sample the hedgerows did not adequately record the distribution of *C. punctuates* and/or the dead surface wood and leaf litter content of the hedgerows, and (iv) an artefact of the national myriapod sampling procedure may have placed too great an emphasis on the explanatory power of macro-organic matter debris to account for the distribution of *C. punctatus* (this is the case because many casual surveys of millipedes are directed specifically to rotting wood, sub-cortical wood crevices and the under-side of fallen logs and branches, so that if *C. punctatus* is more common in these habitats this association will be emphasised).

It is not possible to say which of these explanations is correct, and indeed a combination is likely. The first explanation is possible if *C. punctatus* has a preferred wood type for it is possible that hedgerows may neither provide the correct quantity or quality of wood debris. For example if *C. punctatus* requires large sections of wood then only those hedgerows with mature hedge shrubs or hedgerow trees would provide the right habitat. The number of mature trees in the 31 study hedgerows included in this analysis varied widely (a range of 0-8 was recorded). The alternative hypothesis, that hedgerows where *C. punctatus* was recorded would be characterised by more mature trees, was however not substantiated ($t_{[29]}$=0.31, p=0.62; one-tailed t-test using pooled standard deviation). Even where trees are present, however, the use of a quadrat to survey the millipede fauna may be insensitive to the presence of *C. punctatus* and may partially preclude it from being recorded on account of large fragments of wood debris not being sampled. Despite the possibility of these two 'null' hypotheses, it remains likely that the distribution of *C. punctatus* is not determined solely by the macro-organic matter of the hedgerow soils and that other environmental variables will influence its distribution.

Although the ordination of the woodlouse and millipede data did not reveal any group of species that were characteristic of hedgerows that differed significantly in their macro-organic matter content, the ecological effects of litter debris has been noted elsewhere. Petto (1990) considered that the amount of litter debris may influence the distribution of hygrophilous epigeic arthropods through its role in determining microclimate humidity. In a study of the spider *Coelotes terrestris* inhabiting hedgerows in West Germany, he found a greater abundance of this species in hedgerows with well developed litter layers and considered this to be due to ameliorated moisture conditions. Assuming a correlation between the quantity of litter and air humidity at the soil surface, a possible influence of humidity was not demonstrated here despite the fact that the woodlouse and millipede survey was conducted during a particularly dry and hot period when certain species may have been experiencing water stress.

5.5.7 History of hedgerow configuration

The interpretation of woodlouse and millipede distributions in hedgerows by a 'static' study such as this is complicated by the possibility that the extant communities may, in fact, be *relic* communities that do not reflect present day connectance and area attributes. These relic communities may arise because the response time of the hedgerow populations to changes in hedgerow configuration my be slow enough to allow community characteristics to persist for many years. MacArthur & Wilson (1967) formulated the equilibrium theory of island biogeography which predicts both that smaller islands undergo more frequent population extinction than larger ones and that more isolated islands experience a lower immigration rate of species than less isolated ones. Both increased isolation and decreased area are, therefore, predicted to lower the species richness of a habitat island. The actual number of species inhabiting an island of a given area and degree of isolation is envisaged to depend upon the equilibrium reached between those extinction and immigration processes. Consequently, should either the area or the degree of physical connectance of a hedgerow be reduced (processes that have much been in evidence in recent years (MAFF 1985, Allison 1989, Barr *et al.* 1991)) the theory predicts that its species composition will undergo a relaxation until a new equilibrium number of species is reached.

If this relaxation phenomenon does occur it is entirely unknown how long the process will take given the degree of initial hedgerow perturbation. However, den Boer (1990) estimated that the survival times of localised populations of the more mobile carabids were between several decades to a few centuries depending on the species, while Reh & Seitz (1990) observed significant changes in the genotype of frog populations isolated by roads after a period of approximately 30 years. From map records dating back to 1685, it is apparent that the hedgerow landscape of each of the study farms has altered to varying degrees and that these changes have occurred at different times. If the time taken for the woodlouse and millipede faunas of hedgerows to adjust to new area and isolation conditions is in the order of tens or hundreds of years then many of the study hedgerows will be undergoing a change in their equilibrium number of species. At present there is no way of judging how far this relaxation process has progressed and thus to what degree the extant species distributions reflect a past landscape configuration.

There is an indication that hedgerow age may be an important factor influencing at least a subset of the hedgerow soil fauna community. This is indicated by the fact that all six of the hedgerows classified by the ordination into hedge group 000 are younger than 195 years old (i.e. planted after 1795) while only one of the five hedgerows in the reciprocal group is known to date from this period (Table 5.3). Of the 31 hedgerows included in the soil fauna study, 4 could be identified as having been planted before 1795 and 18 to have been planted after 1795. A comparison between the combined species richness of the millipede and woodlouse communities of each of the two hedgerow groups reveals that the mean number of species in the group of older hedgerows was slightly greater than that of the younger group (6.8 species compared to 5.8). This difference was, however, not significant ($t_{[20]}$=0.68, p=0.25; one-tailed *t*-test using pooled standard deviations).

A species-age relationship that is stronger than the non-significant relationship observed here has been observed in another poorly dispersing invertebrate animal group inhabiting hedgerows. Cameron *et al.* (1980) observed that the snail fauna of hedgerows less than 30 years old was impoverished compared to older hedgerows. It was observed, however, that no species-age relationship was apparent in hedgerows greater than 100 years old and presumably, therefore, there is an indication that many of the snails could reach the hedgerows included in this study after a period of 30-100 years. Working with woody plants Hooper (1970, 1971, 1974) also observed that older hedgerows were generally more species rich than younger ones and that this relationship appeared to be a linear one. In the present study, however, until a more accurate assessment of hedgerow age is possible the precise influence of hedgerow age on the millipede and woodlouse faunas remains unknown in terms of how it affects both species composition and species richness. It can be predicted, however, that younger hedgerows will both have a comparatively impoverished fauna and that this fauna will be composed of species that are better able to disperse and establish themselves.

Although the contribution of both relic communities and species relaxation are unknown variables in the present analysis, under controlled circumstances they may be of an explanatory nature. There remains the possibility that the long-term monitoring of hedgerows that have had their extinction and immigration rates altered may help to test the validity of the hypothesis that hedgerows are perceived as isolates by poorly dispersing organisms. Such a study may, therefore, aid in the assessment of the importance of maintaining the hedgerow network.

5.5.8 Hedgerow area

The area measurement used in this study did not indicate an influence of hedgerow area on the species assemblages of the ordination groups. There was, however, a significant difference in area when those hedgerows that lacked an observed millipede fauna were compared to those from which millipedes were recorded (the mean area of the hedgerows of the former group is approximately half that of the latter group; Table 5.5).

The equilibrium theory of island biogeography (MacArthur & Wilson 1967) predicts that as the area of an island decreases the likelihood of species extinction increases. This is the case because smaller populations are less resilient to severe disturbance, predation, disease and severe weather conditions. It is not possible to say whether or not the group of hedgerows that lack millipedes do so because they are subject to increased extinction pressures. The situation is, however, likely to be very complex because of at least two additional considerations; these are considered below.

First, four of these small hedgerows abut onto non-cultivated habitats (two connect with another hedgerow and two connect with a woodland) and so the effective area of the hedgerow may be larger than the value included in the analysis of variance. The area measurement used in the analysis reflects a single length of hedgerow terminated by a vehicle entry point, cultivated land or adjoining hedgerows or other uncropped habitats. Defining a length of hedgerow as such avoids complications of grouping hedgerows together that may differ in their age, past and present management, aspect, and the soil type they occur on (hedgerows were often planted to delimit changes in soil type). The consequence of such a definition is that the influence of physically connected habitats has not been quantitatively assessed here in terms of area, although it has been assessed in terms of the number of immediate hedgerow connections to the study hedgerow and whether or not the study hedgerow abuts onto woodland.

5.5.9 Woodlice and millipede communities as metapopulations

The analysis has indicated that subordinate to the broad influence of soil pH on the millipede and woodlouse communities, the connection attributes of the study hedgerow may offer a partial explanation for the distribution of certain species. It may be, therefore, that under the prevailing environmental conditions certain species such as *C. punctatus*, *O. ascellus* and *B. superus* perceive the arable landscape as a series of habitat patches and movement corridors. The theory of metapopulations (Levins 1970, Hanski 1989) has arisen to help explain the survival of species which do indeed perceive their environment as a series of fragmented habitats, with each habitat being functionally connected by emigration and immigration events that have a lower probability of occurrence than movement within the same habitat patch. The survival of the species at a landscape level is ensured even if local populations within habitat patches undergo extinction provided that recolonisation of these patches occurs at a greater rate than the overall rate of patch extinction (Mader 1990). The concept of metapopulations has arisen, therefore, to help explain the distribution of sub-populations of one species on many habitat patches/islands. By contrast, the equilibrium theory of island biogeography (MacArthur & Wilson 1967) is concerned with a large number of populations of different species on a single habitat patch/island.

Given the assumption that hedgerow connectance may be important in aiding the movement and dispersal of relatively immobile groups (such as woodlice and millipedes, or certain member species), metapopulation theory predicts that the survival of such species at a landscape level will depend on their ability to recolonise hedgerows whose local sub-population has gone extinct. In addition to the direct effects of disturbance by agricultural operations, factors that may induce extinction in millipede and woodlouse populations are severe weather conditions (Paris 1963), predation (Sunderland & Sutton 1980) and disease (Federici 1984). The successful recolonisation of hedgerow habitats may partially be dependent upon the maintenance of hedgerow connections within the agricultural landscape. The importance of habitat connectance in the agricultural landscape for poorly dispersing invertebrate species is further illustrated by the work of Hurin & den Boer (1988) on carabids and Soesbergen & Mabelis (1989) on the invertebrates of farm woodlands. These authors found that poorly dispersing species tended to be absent from the most fragmented habitats.

The interpretation of the ordination analysis has, however, been hindered by three major considerations. Consequently, the ability of the metapopulation concept to help explain the distribution of millipede and woodlice, or certain member species, in the arable landscape is as yet undetermined. These major areas of uncertainty are (i) an insufficient knowledge of the dispersal ability of different woodlouse and millipede species, (ii) the response time of hedgerow millipede and woodlouse populations to changes in the hedgerow configuration (i.e. the influence of relic faunas is undetermined), and (iii) the interpretation of isolation features and scale factors and how these are perceived by cryptozoic groups such as the millipedes and woodlice. In particular, the assumed poor dispersal ability of woodlice and millipedes must be addressed because both large scale and long distance movements have been recorded in other countries. For instance dispersing individuals of *Hemilepistus reaumuri* (a desert species) were recorded 247-458 m from their burrows (Warburg *et al.* 1984) and in 1878 a Hungarian train was stopped on its tracks by an enormous mass of migrating millipedes (Cloudsley-Thompson 1988). Indeed a concluding remark of Hopkin (1987b) when referring to the aforementioned desert species is that "*the speed at which woodlice can spread should not be underestimated*"; the relevance of this comment for British species is yet to be determined.

Until the above influences are adequately assessed, little can be concluded about the survival of woodlouse or millipede species at the landscape level. Consequently, the reliance of these organisms on a series of interacting local populations inhabiting hedgerows and other uncropped habitats is as yet undetermined. The metapopulation theory predicts that functional connections are necessary to maintain species survival. At present there is an indication that under certain circumstances this connectivity is achieved through physically connecting hedgerows. The consequences of this relationship and the conditions under which it prevails are yet to be fully discerned. The occurrence of poorly dispersing cryptozoic species in the arable landscape may, however, be understood better once the relationship is investigated further.

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Appendix 5.1 Ordination code, hedgerow code, National Grid Reference, farm and parish of the Oxfordshire hedgerows included in the millipede and woodlice survey.

Hedgerow ordination code	Hedgerow code	National Grid Reference	Farm	County parish
1	404	SP420003	Manor Farm	Fyfield & Tubney
2	416	SP306225	Uppercourt Farm	Chadlington
3	417	SP308224	Uppercourt Farm	Chadlington
4	422	SP312218	Blaythorne Farm	Chadlington
5	424	SP315216	Blaythorne Farm	Chadlington
6	426	SP314215	Blaythorne Farm	Chadlington
7	434	SP315217	Blaythorne Farm	Chadlington
8	441	SP445275	Downhill Farm	Westcot Barton
9	443	SP447277	Downhill Farm	Westcot Barton
10	445	SP448273	Downhill Farm	Westcot/Steeple Barton boundary
11	446	SP447273	Downhill Farm	Westcot/Steeple Barton boundary
12	448	SP445269	Downhill Farm	Steeple Barton
13	452	SP440277	Downhill Farm	Westcot Barton
14	453	SP438276	Downhill Farm	Westcot Barton
15	454	SP438270	Downhill Farm	Westcot Barton
16	455	SP438266	Downhill Farm	Steeple Barton
17	462	SU631865	Hammonds Farm	Crowmarsh
18	471	SP413223	Kiddington Estate	Kiddington with Asterleigh
19	472	SP415219	Kiddington Estate	Kiddington with Asterleigh
20	473	SP418228	Kiddington Estate	Kiddington with Asterleigh
21	480	SP410215	Kiddington Estate	Kiddington with Asterleigh
22	481	SP468284	Coldharbour Farm	North Aston
23	483	SP473292	Coldharbour Farm	North Aston
24	491	SP289011	Friars Court	Clanfield
25	503	SP364216	Ditchley Estate	Spelsbury
26	504	SP364223	Ditchley Estate	Spelsbury
27	505	SP374222	Ditchley Estate	Spelsbury
28	507	SP351227	Ditchley Estate	Spelsbury
29	508	SP399231	Ditchley Estate	Enstone
30	521	SP650933	Grove Farm	Brightwell Baldwin
31	536	SP417392	Broughton Castle	Broughton

Appendix 5.2 The Twinspan ordination codes and the physical and biotic characteristics of the Oxfordshire study hedgerows included in the woodlouse and millipede survey (age category codes: 0, hedge planted before 1795; 1, hedge planted after 1795; 2, initial planting date unknown; 3, planting date spans 1795).

Ordination code	Hedgerow code	Number of woodlice and millipede species	Number of woodlice species	Number of millipede species	Number of hedge connections	Total number of plant species	Number of woody species	Hedgerow length (m)	Hedgerow area (m^2)	Area of deciduous and mixed woodland in surrounding 80 ha	Length of boundary habitats in surrounding 80 ha	Age category	Mean radiation input (W/m^2)	Micro-organic matter (%)	Macro-organic matter (g)	Mean pH	CV pH
1	404	4	3	1	5	27	4	477	1418.3	48889	5133	1	366.3	11.8	87	7.37	6.18
2	416	6	4	2	3	31	8	107	299.6	92705	10573	1	361.7	15.4	83	7.62	2.90
3	417	9	4	5	4	43	11	349	872.5	76911	10378	1	366.3	14.4	90	7.80	2.93
4	422	11	5	6	2	44	9	243	558.9	0	7857	2	511.0	11.4	89	8.06	1.04
5	424	5	3	2	3	33	5	80	208.0	5251	8437	1	511.0	9.2	102	8.13	1.55
6	426	7	3	4	4	35	9	159	349.8	3538	7769	1	347.3	11.1	110	8.12	1.22
7	434	6	3	3	3	32	6	73	189.8	11652	3492	1	511.0	11.8	103	7.86	1.01
8	441	3	3	0	0	34	5	100	304.0	14026	6191	1	512.0	14.4	102	5.98	24.26
9	443	2	2	0	5	32	7	40	180.0	32298	7614	1	490.0	13.5	92	5.23	7.46
10	445	6	4	2	4	33	9	203	588.7	31795	8580	0	380.3	8.7	97	6.33	11.50
11	446	5	3	2	4	36	6	309	741.6	15621	14423	0	480.7	16.1	110	7.71	3.67
12	448	8	5	3	3	36	8	278	722.8	630	7933	0	490.0	14.2	110	7.73	0.92
13	452	2	2	0	1	28	7	195	663.0	31755	7123	1	480.7	21.9	119	6.19	10.50
14	453	8	5	3	1	32	7	300	870.0	148547	12527	0	380.3	15.7	111	5.48	22.52
15	454	8	5	3	0	31	9	300	600.0	0	7831	1	498.0	11.7	96	6.66	15.05
16	455	6	4	2	1	30	8	122	512.4	0	7187	1	415.7	17.1	100	7.94	1.45
17	462	6	4	2	1	25	9	277	803.3	0	6601	1	372.0	10.3	88	7.57	1.73
18	471	8	4	4	5	28	7	243	680.4	47523	9783	1	402.3	16.5	97	8.04	19.16
19	472	10	5	5	5	31	9	282	789.6	162244	6374	2	508.3	14.1	97	7.88	1.32
20	473	7	4	3	3	31	14	228	798.0	28107	11138	2	375.3	16.3	98	8.01	2.60
21	480	5	2	3	0	46	15	350	1295.0	215632	9133	2	490.0	14.0	77	7.95	0.66
22	481	4	3	1	2	31	9	87	669.9	0	7465	2	362.7	10.3	79	7.25	18.23
23	483	3	3	0	1	27	6	55	291.5	68926	6829	2	470.0	14.4	02	5.42	12.48
24	491	7	5	2	3	40	8	386	926.4	10484	6398	1	372.0	10.1	114	7.62	2.35
25	503	5	3	2	0	29	9	74	222.0	0	6543	1	480.7	11.6	76	8.28	1.60
26	504	8	5	3	2	42	14	318	890.4	1155	7849	1	402.3	12.0	88	8.27	1.23
27	505	2	2	0	5	31	7	111	210.9	81594	6781	1	415.7	9.6	88	8.19	1.24
28	507	11	4	7	2	42	12	206	473.8	50665	8004	1	364.0	13.5	86	8.08	2.75
29	508	5	3	2	0	33	7	274	630.2	26653	7463	2	430.3	13.0	110	8.22	0.86
30	521	7	5	2	4	37	5	260	1014.0	16629	5509	2	402.3	9.1	125	5.62	31.07
31	536	5	4	1	4	29	6	195	858.0	1100	10190	3	366.3	13.8	84	5.32	11.71

Appendix 5.3 Species list and frequency of capture *(f)* of the millipede and woodlouse faunas recorded from each study hedgerow ("Code" is of hedgerow number and farm initials).

Code	*f*	Species	Code	*f*	Species
404MF	66	*Philoscia muscorum*	462HF	4	*Armadillidium vulgare*
	32	*Porcellio scaber*		1	*Oniscus asellus*
	10	*Trichoniscus pusillus*		35	*Philoscia muscorum*
	3	*Brachydesmus superus*		79	*Porcellio scaber*
				47	*Brachydesmus superus*
416UC	2	*Oniscus asellus*		53	*Glomeris marginata*
	23	*Philoscia muscorum*		10	*Polydesmus inconstans*
	13	*Porcellio scaber*			
	18	*Trichoniscus pusillus*	471KE	2	*Oniscus asellus*
	1	*Brachydesmus superus*		18	*Philoscia muscorum*
	4	*Tachypodoiulus niger*		6	*Porcellio scaber*
				16	*Trichoniscus pusillus*
417UC	3	*Armadillidium vulgare*		1	*Brachydesmus superus*
	2	*Oniscus asellus*		6	*Glomeris marginata*
	19	*Philoscia muscorum*		1	*Polydesmus angustus*
	23	*Porcellio scaber*		10	*Tachypodoiulus niger*
	6	*Brachydesmus superus*			
	1	*Cylindroiulus punctatus*	472KE	1	*Armadillidium vulgare*
	6	*Glomeris marginata*		1	*Oniscus asellus*
	10	*Polydesmus gallicus*		4	*Philoscia muscorum*
	2	*Tachypodoiulus niger*		7	*Porcellio scaber*
				2	*Trichoniscus pusillus*
422BT	5	*Armadillidium vulgare*		1	*Brachydesmus superus*
	7	*Oniscus asellus*		1	*Cylindroiulus punctatus*
	70	*Philoscia muscorum*		5	*Glomeris marginata*
	50	*Porcellio scaber*		1	*Polydesmus angustus*
	5	*Trichoniscus pusillus*		16	*Tachypodoiulus niger*
	1	*Archiboreoiulus pallidus*			
	1	*Cylindroiulus latestriatus*	473KE	5	*Oniscus asellus*
	11	*Cylindroiulus punctatus*		12	*Philoscia muscorum*
	2	*Polydesmus angustus*		34	*Porcellio scaber*
	28	*Tachypodoiulus niger*		7	*Trichoniscus pusillus*
	3	*Blaniulus guttulatus*		2	*Brachydesmus superus*
				6	*Glomeris marginata*
424BT	3	*Oniscus asellus*		1	*Polydesmus angustus*
	23	*Philoscia muscorum*		9	*Philoscia muscorum*
	4	*Porcellio scaber*		2	*Porcellio scaber*
	1	*Cylindroiulus punctatus*		2	*Glomeris marginata*
	3	*Tachypodoiulus niger*		1	*Polydesmus angustus*
				6	*Tachypodoiulus niger*
426BT	5	*Oniscus asellus*			
	61	*Philoscia muscorum*	481CF	14	*Philoscia muscorum*
	64	*Porcellio scaber*		9	*Porcellio scaber*
	1	*Brachydesmus superus*		3	*Trichoniscus pusillus*
	13	*Cylindroiulus punctatus*		9	*Tachypodoiulus niger*
	2	*Ophyiulus pilosus*			
	50	*Tachypodoiulus niger*	483CF	4	*Philoscia muscorum*
				39	*Porcellio scaber*
434BT	7	*Oniscus asellus*		1	*Trichoniscus pusillus*
	47	*Philoscia muscorum*			
	29	*Porcellio scaber*	491FC	14	*Oniscus asellus*
	4	*Cylindroiulus punctatus*		28	*Philoscia muscorum*
	1	*Polyxenus lagurus*		38	*Porcellio scaber*
	3	*Tachypodoiulus niger*		22	*Trichoniscus pusillus*
				1	*Trichoniscus pygmaeus*
441DH	3	*Oniscus asellus*		1	*Brachydesmus superus*
	23	*Philoscia muscorum*		1	*Tachypodoiulus niger*
	11	*Porcellio scaber*			

Continued overleaf...

Appendix 5.3 *Continued from overleaf*

Code	*f*	Species	Code	*f*	Species
443DH	16	*Philoscia muscorum*	503DE	1	*Oniscus ascellus*
	4	*Porcellio scaber*		10	*Philoscia muscorum*
				4	*Porcellio scaber*
445DH	4	*Oniscus ascellus*		1	*Glomeris marginata*
	33	*Philoscia muscorum*		2	*Tachypodoiulus niger*
	8	*Porcellio scaber*			
	17	*Trichoniscus pusillus*	504DE	2	*Armadillidium vulgare*
	5	*Brachydesmus superus*		1	*Oniscus ascellus*
	2	*Polydesmus gallicus*		33	*Philoscia muscorum*
				6	*Porcellio scaber*
446DH	4	*Oniscus ascellus*		3	*Trichoniscus pusillus*
	7	*Philoscia muscorum*		7	*Cylindroiulus punctatus*
	28	*Porcellio scaber*		13	*Glomeris marginata*
	4	*Brachydesmus superus*		3	*Tachypodoiulus niger*
	3	*Polydesmus angustus*		3	*Philoscia muscorum*
				4	*Trichoniscus pusillus*
448DH	2	*Armadillidium vulgare*			
	8	*Oniscus ascellus*	507DE	2	*Armadillidium vulgare*
	40	*Philoscia muscorum*		5	*Oniscus ascellus*
	75	*Porcellio scaber*		6	*Philoscia muscorum*
	11	*Trichoniscus pusillus*		17	*Porcellio scaber*
	3	*Cylindroiulus punctatus*		6	*Cylindroiulus punctatus*
	5	*Ophyiulus pilosus*		1	*C. caeruleocinctus*
	2	*Tachypodoiulus niger*		7	*Glomeris marginata*
				1	*Ophiodesmus albonanus*
452DH	13	*Philoscia muscorum*		1	*Ophyiulus pilosus*
	64	*Porcellio scaber*		1	*Polydesmus gallicus*
				4	*Tachypodoiulus niger*
453DH	1	*Armadillidium vulgare*			
	9	*Oniscus ascellus*	508DE	11	*Oniscus ascellus*
	20	*Philoscia muscorum*		9	*Philoscia muscorum*
	64	*Porcellio scaber*		6	*Porcellio scaber*
	3	*Trichoniscus pusillus*		20	Glomeris marginata
	5	*Cylindroiulus punctatus*		6	*Tachypodoiulus niger*
	1	*Ophyiulus pilosus*			
	2	*Polydesmus angustus*	521GF	5	*Armadillidium vulgare*
				25	*Oniscus ascellus*
454DH	3	*Armadillidium vulgare*		74	*Philoscia muscorum*
	4	*Oniscus ascellus*		90	*Porcellio scaber*
	32	*Philoscia muscorum*		2	*Trichoniscus pusillus*
	10	*Porcellio scaber*		2	*Brachydesmus superus*
	16	*Trichoniscus pusillus*		6	*Glomeris marginata*
	2	*Brachydesmus superus*			
	2	*Polydesmus gallicus*	536BC	5	*Oniscus ascellus*
	4	*Nanogona polydesmoides*		23	*Philoscia muscorum*
				9	*Porcellio scaber*
455DH	4	*Armadillidium vulgare*		11	*Trichoniscus pusillus*
	1	*Oniscus ascellus*		2	*Brachydesmus superus*
	13	*Philoscia muscorum*			
	38	*Porcellio scaber*	480KE	9	*Philoscia muscorum*
	1	*Cylindroiulus punctatus*		2	*Porcellio scaber*
	14	*Tachypodoiulus niger*		2	*Glomeris marginata*
				1	*Polydesmus angustus*
505DE	3	*Philoscia muscorum*		6	*Tachypodoiulus niger*
	4	*Trichoniscus pusillus*			

Appendix 5.4 Names of the plant species abbreviated in the Twinspan ordination (Table 5.4) of those hedgerows included in the woodlice and millipede survey.

Abbreviation	Name	Abbreviation	Name
Acer camp	*Acer campestre*	Holc moll	*H. mollis*
Acer pseu	*A. pseudoplatanus*	Ilex aqui	*Ilex aquifolium*
Agro stol	*Agrostis stolonifera*	Knau arve	*Knautia arvensis*
Alli peti	*Alliaria petiolata*	Lami albu	*Lamium album*
Alop myos	*Alopecurus myosuroides*	Laps comm	*Lapsana communis*
Arct lapp	*Arctium lappa*	Ligu vulg	*Ligustrum vulgare*
Arum macu	*Arum maculatum*	Loni peri	*Lonicera periclymenum*
Bryo dioi	*Bryonia dioica*	Malu sylv	*Malus sylvestris*
Cent scab	*Centaurea scabiosa*	Myos arve	*Myosotis arvensis*
Chae temu	*Chaerophyllum temulentum*	Papa rhoe	*Papaver rhoeas*
Clem vita	*Clemetis vitalba*	Poa triv	*Poa trivialis*
Cirs arve	*Cirsium arvense*	Pote rept	*Potentilla reptans*
Cirs vulg	*C. vulgare*	Prun spin	*Prunus spinosa*
Conv arve	*Convolvulus arvensis*	Quer robu	*Quercus robur*
Cory avel	*Corylus avellana*	Ranu repe	*Ranunculus repens*
Dact glom	*Dactylis glomeratus*	Rham cath	*Rhamnus catharticus*
Elym cani	*Elymus caninus*	Rosa cani	*Rosa canina*
Elym repe	*E. repens*	Rubu frut	*Rubus fruticosus*
Euon euro	*Euonymus europaeus*	Rume cris	*Rumex crispus*
Frax exce	*Fraxinus excelsior*	Rume obtu	*R. obtusifolius*
Fest rubr	*Festuca rubra*	Sile alba	*Silene alba*
Gali moll	*Galium mollugo*	Sile vulg	*S. vulgaris*
Gera diss	*Geranium dissectum*	Sola dulc	*Solanum dulcamara*
Gera robe	*G. robertianum*	Sonc aspe	*Sonchus asper*
Glec hede	*Glecoma hederacea*	Tara offi	*Taraxacum officinale*
Geum urba	*Geum urbanum*	Tamm comm	*Tamus communis*
Hede heli	*Hedera helix*	Ulmu proc	*Ulmus procera*
Holc lana	*Holcus lanatus*	Viol odor	*Viola odorata*

Chapter 6

General Discussion

Contents

> *"Any person breaking a hedge or stealing wood be put next sunday*
> *or holyday in the stocks for two hours at the least, and the wood*
> *be placed before them signifying the cause of their punishment."*
>
> A 1597 decree, Felsted, Essex.

6.1 Conservation in the agricultural landscape

In many areas the pressures of agriculture, urbanisation, transportation and recreation necessitate that the factors that govern biotic diversity and species distributions are understood. It is with the translation of this knowledge into judicious habitat management that the survival of species of conservation value many be facilitated. Two contrasting approaches to wildlife conservation can be identified (Schreiber 1988, Mader 1990), although in reality they are simply two extremes on a continuum. The first approach, the *segregation model*, involves the partitioning of specific areas for nature conservation with the surrounding land matrix being farmed as, or more, intensively as previously. The alternative approach, the *integration model*, entails a general decrease in the intensity of agricultural operations across the landscape with a concurrent promotion of an integrated system of habitats and corridors to create a *biotope network* (Schreiber 1988). The practical purpose of much ecological enquiry is to allow the construction and subsequent validation of such models and so to enable predictions to be made about present and future population and community characteristics. The present research has sought to contribute to the understanding of the distribution of vascular plants, small mammals and two soil arthropod groups in hedgerows with the use of static, dynamic and manipulative survey approaches. It is by addressing and answering the questions that relate to species distributions and community characteristics that may ultimately enable the conservation of species and species groups within the intensively farmed agricultural landscape.

In order to assess the merits of conservation models, such as the segregation/integration model, it is necessary to determine how species perceive the landscape both in terms of the suitability of isolates for inhabitation and in terms of the role that landscape features play in promoting dispersal and thus the maintenance of viable populations (Mader 1990). As is commonly recognised, linear habitats may be particularly important as features that facilitate the movement and dispersal of species (e.g. Baird & Tarrant 1972, Dendy 1987, Sullivan 1989). As such, they may promote the continued existence of species within the landscape by allowing a relocation of individuals and/or the transfer of genes (Hobbs *et al.* 1989). The extent to which these phenomena hold true will, for instance, swing the balance in favour of either the segregation model or the integration model depending upon the aims of the conservation policy. Depending upon these goals, it may be possible to create a landscape by design and management that is of the desired *ecological infrastructure* (Selm 1988). If the intention is to create a landscape tailored to the needs of a species with known ecological requirements then the aim will be to create a landscape with a *specific ecological infrastructure.* As is commonly the case, however, the detailed autecological requirements of species are often unknown. In such circumstances it may be desirable to incorporate the less well known needs of many species into a landscape with a *broader ecological infrastructure* (Selm 1988). This second approach has been adopted in France during the process of agricultural land consolidation (*remembrement*) (Burel 1984, Baudry & Burel 1984). Here, broad ecological concepts have been successfully employed to lessen the detrimental effects of land reorganisation.

6.2 Hedgerows as habitats

Provided that management does not cause severe disturbance, the value of hedgerows as *habitats* is great for many species that are reliant (at least for part of their life cycle) upon the shelter or food provided by comparatively undisturbed strips of land with associated woody vegetation. In terms of land area, the value of hedgerows should not be assessed on a comparative basis to 'two dimensional habitats' such as woodland or meadow, but to other field boundaries or to open agricultural land because it is these habitats that would exist if hedgerows were removed. While well established fencelines and walls do indeed have their own ecological value (e.g. Middleton & Merriam 1981, Darlington 1981) the living nature of the barrier component of the hedged field boundary means that their wildlife value exceeds both fencelines (which are often narrow and less permanent) and stonewalls (which are comparatively homogeneous habitats).

The value of hedgerows as habitats is illustrated by the present research. In the study, 120 plant species were recorded from the North Yorkshire hedgerows and 136 in hedgerows from Oxfordshire (Appendix 3.1). Of these only about a quarter can be said to have a greater association with disturbed habitats, such as arable fields, than with hedgerows or other semi-permanent habitats. Of the six species of woodlice and fifteen species of millipedes recorded from Oxfordshire (Table 5.1) perhaps less than one-fifth of these are able successfully to inhabit arable cropland. In North Yorkshire, five of the seven species of small mammal caught in or adjacent to the hedgerow complex (Table 4.3) were predominantly, or exclusively, caught within the body of the hedge itself.

The factors that contribute to the value of hedgerows as habitats are poorly understood, not least because they are likely to differ from species to species or taxon to taxon. The present study has revealed that no one overall factor is a major or consistent determinant of species richness. It has, however, indicated that the species richness and composition of hedgerows are partially explained by a diverse array of influences that can be summarised into the formula

$$S = f\,(\text{area, isolation, age, habitat diversity, landscape diversity,}\\ \text{management and disturbance, location, season})$$

where S is species richness and f denotes a function. The importance of any one parameter may be dependent upon the magnitude of another (e.g. the species composition of a hedge may bear little relation to its age if the disturbance regime is high). Obviously the species richness of any habitat patch, hedgerows included, is a reflection of the number of populations inhabiting that patch. In order to interpret species richness, therefore, it is necessary to understand the factors that determine the survival and physical range of individual populations in patchy habitats. The survival of small fragmented populations, whether they are populations within hedgerows themselves or populations inhabiting adjoining habitats, may be crucially dependent upon their interaction with neighbouring populations. Small populations are prone to extinction from environmental, biotic and man induced perturbations (Frankel & Soulé 1981) and unless either (i) a 'mainland' source population exists, or (ii) extinctions are asynchronous and locally based events that can be countered by subsequent immigration from donor patches, then successive extinction events may see the loss of a species from the landscape unit. In both the former 'mainland-island' situation and the latter 'patch-patch' (or metapopulation) situation an understanding of the interactions between populations is central to the interpretation of species distributions. Structural connectance between hedgerows provides an obvious means by which such interactions may be facilitated. Where these connections exist, hedgerows should not, therefore, be viewed in isolation but rather as interconnecting habitats.

6.3 Hedgerows as corridors

Interactions between sub-populations require a functional connectivity between respective habitats. More than any other discipline, and where the traditional application of island biogeography has failed, landscape ecology has sought to address the implications of the physical connectivity between habitat patches. The contention is that the physical connections between habitat patches may offer an insight into the functional connections between sub-populations. The conceptual framework of landscape ecology has, however, outgrown the empirical data upon which it is based for although graph theory offers indices of connectance, e.g. the *gamma* index (measuring connectivity) and the *alpha* index (measuring circuitry), rarely have they been employed to assess landscape pattern (but see Braekevelt 1988) and no instance was found where they have been used to interpret species distributions. Nevertheless, as advocated by Forman & Godron (1984) these indices may be instructive. The present study found no evidence, however, that landscape connectivity as measured by *gamma* and *alpha* were deterministic for plant species richness or composition; either the indices are insensitive or physical connectance is unimportant or subordinate to other factors determining species distributions.

With the development of a third connectance index, *hedgerow accessibility*, an attempt was made to measure the degree of linkage that a hedgerow has to all other hedgerows on a network. Developed here from its corollary used in transportation theory (nodal accessibility), this index proved to offer only limited additional insight into the distribution of hedgerow plants. Clearly then, while connectance indices may offer a means to describe the *structural connectance* attributes of a network (Taaffe & Gaulthier 1973) they do not necessarily relate directly to *functional connectance* (i.e. connectance as perceived by the species in question). It is this relationship between structural connectance (*connectedness*) and functional connectance (*connectivity*) (Baudry & Merriam 1988) that needs to be assessed further before such indices can be used to estimate the isolation of sub-populations in hedgerows and habitat patches in general (Forman & Godron 1984). The enumeration of functional connectance rather than structural connectance attributes is only possible with detailed autecological information which is unavailable for many species. This lack of detailed ecological and behavioural information hinders the interpretation of 'snap-shot' distribution patterns such as those described in Chapter 3 for plants and in Chapter 5 for woodlice and millipedes.

Ultimately, the role of hedgerows as corridors (and thus their importance as habitats facilitating interactions between resident or adjacent sub-populations) will be dependent upon the functional mobility of the species. As a general rule, it may be the case that for slow moving species (such as certain plant species and flightless invertebrates) any corridor function that hedgerows might have will largely be determined by their suitability as a habitat. For species of intermediate mobility any value of hedgerows as corridors may depend upon their structure and quality (e.g. their width or density). At a higher hierarchical level, and for both these species types, any role of hedgerows in linking up the landscape by forming a network of linear habitats will depend upon the degree of connectance between individual corridors. For highly mobile species such as birds and flying insects there may, however, be no reliance upon hedges as movement corridors, although preferred movement patterns may remain. The particular case of habitat islands on farmland and the differing habitat and dispersal requirements of species, led Duelli (1990) to conclude "*while it appears that the concept of island biogeography is of limited value for interpretation of the faunal composition in cultivated areas it may be applicable to extremely specialised and rather sedentary species, for which their habitat patch is a 'true island in an otherwise hostile sea'*".

6.4 Relic communities and population dynamics

A common problem with 'static' studies, where no monitoring or manipulation is involved, is the unknown degree to which the present inhabitant species reflect current environmental conditions. If the response time of populations and communities is longer than the time that has elapsed between the change in environmental circumstance (e.g. the removal of three out of four hedges around a field) and the execution of the survey, then species will be recorded that reflect the inertia of the system rather than current ecological conditions. The impracticality of studying the dynamics of many ecological systems (Usher 1985, Opdam 1988) means that 'snap-shot' surveying is often the approach that is selected by default. This approach is valuable in providing an initial insight into questions concerning equilibrium island biogeography and landscape ecology. However, both the fact that the former concept is built upon the dynamic and opposing processes of immigration and extinction and that the latter concept stresses the landscape-wide dynamics of interacting populations mean that static approaches fall short of an ideal. The small mammal study goes some way to addressing the dynamics of patch to patch, patch to matrix and matrix to patch movements. It is clear from this study that the species under investigation is a major consideration and that generalisations about the influence of landscape structure may be few and far between.

The dynamics of plant dispersal are obviously more difficult to study than many animal species because individual plants can not move their location. Although not presented in this thesis, the study of hedgerow verge flora dynamics introduced in Chapter 2 sought to address questions concerning the turnover of species by surveying over three summers the vegetation falling within ten fixed quadrats positioned in the verges of ten hedgerows. At this early stage, what is clear from this study is that mechanical and chemical disturbances from adjacent field operations can cause a dramatic change in the species composition of hedgerow verge communities. It was repeatedly observed that such disturbances prompted the occurrence of opportunistic weed species with the loss of biennials and perennials (see also Marshall & Smith 1987 and Marshall 1988). Depending on the intensity of disturbance, or the width of the hedgerow, these disturbances are also likely to influence the floral composition of the hedge interior and the hedge itself. Indeed, it may be these influences of external, man induced forces that mitigate against the application of many island biogeographic principles to the hedgerow habitat. This is the case because edge effects are poorly addressed by island biogeographic theory (Laurance & Yensen 1991) and yet, at least in this country where hedgerows are comparatively narrow, hedgerows can in effect be viewed as two edge habitats back to back. As such they are highly susceptible to disturbances impinging upon them from the matrix of agricultural land within which they are set. Consequently, the dynamics of many hedgerow populations may largely be determined by extraneous, man induced and environmental influences that override internal and traditional 'island biogeographic' influences.

The study of the dynamics of hedgerow flora may provide insights into which species are consistently found inhabiting a hedge over the course of several years and which ones are occasional inhabitants of hedgerow verges. What is evident at this stage is that because there is a local turnover of species, the actual species richness of hedgerows can not be gauged from one point survey alone. This is illustrated by the four year study of hedgerows by Usher (1987) who noted that only in the order of 65% of the species recorded during the entire survey were present in any one year. Depending upon which species actually exhibit this dynamic behaviour, the true conservation value of hedgerows may be better assessed over a period of several years.

Trends in species richness and species representation are also of great interest because a central prediction of the equilibrium theory of island biogeography is that, when rates of immigration and extinction are in balance, species turnover will occur with species richness remaining essentially constant. Again, however, the correct interpretation of such dynamic studies will rely upon both a knowledge of the precise disturbance and management history of the habitat and upon the response time of the inhabitant populations. Since this information is often lacking for hedgerows, the most informative approach to the study of the dynamics of hedgerow vegetation may be to perform manipulative studies involving the modification of factors considered to be influential in determining species richness or composition (such as area, isolation, habitat diversity); although the time scales involved here may also necessitate long-term studies. Nevertheless, it is important to address the question of community dynamics of habitat patches in a manipulative manner because future habitats are likely to become increasingly fragmented and to occupy smaller land areas. It is the case that the problems of sampling and study design are many; indeed Merriam (1988) comprehensively concluded that "*to understand dynamics in farmland, landscape ecologists must solve the problems of sampling spatially and temporally heterogeneous dynamic systems and the problem of multiple scaling in hierarchical systems*".

6.5 Implications for population genetics

Depending upon the hierarchical level considered, the presence or absence of hedgerows has a number of implications for population genetics. These implications relate to both the genetic characteristics of a population or sub-population and to the gross effects of genetic loss due to the local extinction of populations within habitat patches. These qualitative and quantitative aspects may, however, be related because small populations are not only prone to local extinction due to biotic, environmental and man induced processes *per se* (Frankel & Soulé 1981). They are also susceptible to increased homozygosity that may itself increase the chance of local extinction by reducing a population's resilience to perturbation. Increased homozygosity results as a consequence of intra-population breeding between relatively small numbers of individuals. If small populations are confined within either structurally and/or functionally isolated hedgerows then individuals are likely to share a common or similar ancestry. The mating between genetically related individuals (*inbreeding*) results in homozygosity and a shift towards the phenotypic expression of recessive genes. This is the case because the offspring of successive generations are increasingly likely to inherit the same gene from each parent. Recessive genes, therefore, find phenotypic expression because dominant alleles can no longer mask those that are recessive. Under such circumstances there is a reduction in the population's fitness because a disproportionately large number of maladaptive genes are recessive (Crow & Kimura 1970).

Homozygosity can also result from *genetic drift*. As a result of population *bottlenecks* (the collapse in population size that may, for instance, follow a cyclic pattern in relation to seasonal resources or predator-prey interactions) only a fraction of *qualitative* (specific genes) and *quantitative* (the amount of variability in the genotype of a specific characteristic) information will be retained within the population. The consequence is that alleles are lost at specific loci and gene fixation may result (Crow & Kimura 1970). The effects of genetic isolation due to roads on populations of common frog (*Rana temporaria*) were studied by Reh (1989) and Reh & Seitz (1990). They found that populations isolated by heavily used roads showed reduced heterozygosity and they considered such populations to be affected both by inbreeding and genetic drift phenomena and to be prone to extinction because of reduced immigration.

A related concern is that the effective population size of a species inhabiting a patch may be considerably smaller than the numeric population size (Hedrick 1983). Three important reasons for this are (i) that not all individuals will be sexually mature, (ii) that the ratio of sexually active individuals may be sub optimal, and (iii) females may be polygamous. A hedgerow population that consists of a large proportion of males, juveniles or polygamous females is likely, therefore, to have a lower fitness and a greater risk of extinction.

With both increased heterozygosity, and hence a greater flexibility in response to disturbance, and with larger effective population sizes, the fitness of a hedgerow population is likely to increase. The physical connections between two or more hedgerows and between a hedgerow and other species rich habitats (particularly woodland) may act to increase both heterozygosity and the effective population size of certain species. If this is the case, the retention of hedgerows may become important at a landscape level in order to maintain genetic diversity by allowing the movement of individuals between sub-populations. Species that are not reproductively isolated by the agricultural field matrix may, however, maintain heterozygosity regardless of any proposed corridor function of hedgerows. Under these circumstances, hedgerows may be used as a series of *stepping-stones* rather than isolated habitat patches or corridors. Such non-isolated populations may be more resilient to both (i) locally intense disturbance events because their populations extend and interact beyond the disturbance foci ,and to (ii) more diffuse disturbance because they have greater flexibility in response to changing conditions due to greater genetic variability.

The extension of genetic enquiry into the field of wildlife conservation in fragmented habitats may be of great value. Techniques such as genetic fingerprinting may allow both a better understanding of present distribution patterns and a means to predict future distributions. With modern machinery facilitating the rapid modification of landscape characteristics and the possibility of climate change, the ability to model the distribution and the characteristics of farmland wildlife populations may enable more informed policy making.

6.6 Island biogeography and beyond

MacArthur and Wilson's (1967) theory of equilibrium island biogeography may have been accepted as the predominant working model for many years because of its appealing simplicity (McCollin *et al.* 1988, Williamson 1989). The possibility exists, however, that habitat and environmental diversity may be the major underlying cause of the species-area relationship. In many studies, this has not been investigated fully because it is a very complex parameter to evaluate and hence it runs counter to the simplicity of the equilibrium theory of island biogeography (Williamson 1989). However, in the case of many habitats, including hedgerows, the equilibrium theory itself may no longer deal with simply derived and estimated parameters such as area, isolation and age. For example, the hedgerow area measurement is confounded by edge effects and the undetermined and temporally variable extent to which inhabitant species may extend their ranges into adjacent habitats. The isolation measurement of hedgerows no longer remains a simple measure of Euclidean distance but may need to become a species specific index that enumerates both structural connectance and functional connectivity as modified by temporally variable corridor and matrix quality. Habitat age becomes a complex parameter in that the age of the hedgerow, and the time that has elapsed since the removal or planting of adjacent or neighbouring hedgerows, is often difficult to ascertain. Consequently, the lengths of time that immigration and extinction processes have been in operation become uncertain and the possibility of relic communities confound ecological interpretation. It is apparent that for the equilibrium theory of island biogeography to transfer successfully to linear inter-connecting habitats in heterogeneous landscapes its parameters, and the processes they model, can no longer be viewed in simplistic terms.

Landscape ecology, and the self-contained theory of metapopulations, may offer a better framework within which to investigate the species richness and composition of hedgerow communities. To this end, the further development of indices derived form graph theory may be valuable. This may particularly be so regarding the enumeration of accessibility measures that record *qualitative* as well as *quantitative* information about habitat isolation. In conjunction with this, there are a number of other areas where knowledge is currently incomplete; perhaps the most important of these are:

(i) the autecology of individual species and hence how their dispersal and habitat requirements effect their distribution,

(ii) the effects of habitat quality and diversity on species richness and composition,

(iii) the response time of isolate populations to environmental change,

(iv) information about the *zonation* of habitat patches as determined by both man-induced disturbances and environmental processes, and

(v) the genetic characteristics of hedgerow populations.

A greater understanding of these areas may be informative and as such they should be earmarked for further research.

At least with the spatially and temporally variable agricultural landscape, the first step in the understanding of species richness should be a modest one, e.g. an understanding of the distribution of individual species or species groups. Based on sound autecological information, the concept of the metapopulation may be a powerful interpretive tool (Opdam 1988). Extending this to the concept of the '*metacommunity*' (Hanski & Gilpin 1991) and by incorporating the holistic and landscape-wide approaches of landscape ecology, it may be possible to address the species-richness question of MacArthur and Wilson. When dealing with hedgerow communities, I am in agreement with Hanski & Gilpin (1991) who comment that the "*fusion of metapopulations and landscape ecology should make for an exciting scientific synthesis*". Ultimately, it is the application and extension of island biogeographic principles into these developing fields that will promote a more complete understanding of the processes that determine the distributions of species in hedgerows.

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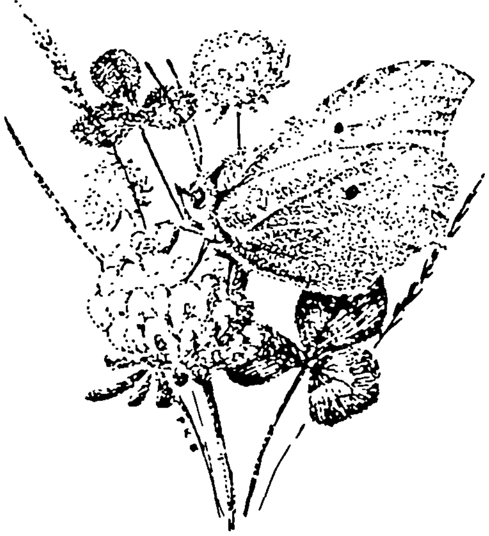
Appendix 6.1

HABITAT CONSERVATION FOR INSECTS - A NEGLECTED GREEN ISSUE



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Photographs by senior authour; Plate 20a omitted.

CHAPTER 6

HEDGEROWS AND ARABLE FIELD MARGINS

HABITAT CHANGES IN RECENT YEARS

by Stephen Jones, Reg Fry and David Lonsdale

In Chapter 5 we considered the history of grassland habitats, during which many insect species are believed to have benefited from human land-use over many centuries, only to suffer marked declines due to recent agricultural intensification.

A similar pattern of habitat extension followed by reversal has occurred in arable areas. When man began to cultivate land for crop production, a range of grassland and woodland species were able to take advantage of the rather unstable habitats which were created in the process. Some species existed within crop fields, while others flourished in the surrounding banks, ditches and hedgerows or dry stone walls. Insects in these habitats have also suffered in recent times either as a direct result of neglect, removal of the habitat, or from the direct application of pesticide and herbicide sprays, or indirectly through spray drift from nearby crops.

Until recently, the government policy of intensification provided capital incentives for the improvement of agricultural land and the cultivation of previously unproductive areas. Under the European Economic Community's Common Agricultural Policy, guaranteed prices were offered for certain agricultural products and as a result various foodstuffs saturated their markets and stockpiles grew. The high costs entailed in their storage and subsequent destruction forced a change in policy and in recent years a number of financial incentives for increased production have been removed. Indeed, in the case of hedgerows, the grants that were available for their removal up until 1974 have recently been replaced by grants for replanting. Unfortunately, this does not yet seem to have encouraged any significant planting of new hedgerows.

The major long term problems with hedgerows arise both from their removal from agricultural land and, in recent years in particular, increasingly harmful methods of maintenance, including cutting at the 'wrong' time of year. There is considerable scope for improvement, particularly in conjunction with conservation headlands on farms.

As far as arable areas are concerned, there are large tracts of land which have become an ecological desert, as a result of 'intensive farming' and grassland 'improvement'. However, recent studies by the Game Conservancy have shown that there is considerable scope to increase insect populations (some of which are beneficial predators of crop pests) by adopting conservation headlands (Sotherton *et al*, 1989) whilst maintaining high levels of production; these are outlined at the end of this chapter.

HEDGEROWS

by Stephen Jones

HEDGEROW LOSS

It was at a landscape level that people first appreciated the effects of hedgerow removal. The mosaic pattern of hedgerow and field is seen by many to be the hallmark of the English countryside and when this is no longer in evidence a sense of aesthetic satisfaction is lost. From a distance it is perhaps the variety afforded to the eye by hedge and hedgerow tree that is their greatest asset, while close at hand it is the sights, sounds and smells of the inhabitant plants and animals that has endeared them to the naturalist and general public at large.

Estimated rates of hedgerow removal vary greatly, to some extent because of the different methods that have been used to quantify it but also because the degree of removal, its rate and its time of onset have varied from place to place. Extensive hedgerow removal first occurred after the Second World War and estimated rates of removal in England and Wales from that time up until the 1970s vary from 5,600 to 8,000 km per year, with a peak of 16,000 km per year in the 1960s. More recent rates of removal have been estimated by MAFF (Ministry of Agriculture Fisheries & Food) to be about 1,600 km per year which appears to indicate a dramatic reduction. This presumably reflects the facts that a large proportion of farmers have long since removed those hedgerows that they deemed to offer the greatest hindrance to the effective use of modern machinery, and that grants for hedgerow removal are no longer available.

Despite this recent decrease in hedgerow removal and an estimated 500,000 km of hedgerow which remains in England and Wales, a very large proportion of this is likely to be suffering from unsympathetic management or neglect, both of which have a deleterious effect on a hedge's scenic and wildlife value. It is apparent that such damage has become widespread and is increasing. Roadside hedgerows are among those that have suffered most in many areas. Whilst it is appreciated that some hedges must be severely cut back to avoid hazards for passing traffic, it is often common practice in cutting operations to 'savage' everything in sight, which is not only harmful to wildlife but also a waste of money. There is also the intentional application of herbicides and insecticides. In addition to this direct damage, there are also incidental adverse effects caused by farming practices in adjoining fields, such as close ploughing and drift of agrochemicals.

VALUE OF HEDGEROWS FOR INSECT CONSERVATION

Unlike plant species and a variety of other animal groups, the insects that inhabit or are associated with hedgerows have not been fully listed. The number of species in Britain probably runs to several thousand and it is probably the task of identifying so many to species level - except in the case of a few popular groups - that has so far prevented their accurate enumeration. Of the herbivorous species, some of the more notable taxa include the Lepidoptera (butterflies and moths), Hymenoptera (particularly bees, wasps and sawflies), Psyllidae (jumping plant lice), Miridae (mirid bugs), Pentatomidae (shield bugs) and the Chrysomelidae (leaf beetles). Predatory species are also well represented, the Carabidae (tiger and ground beetles) and Coccinellidae (ladybirds) being two of the better-known groups.

The value of hedgerows for insects lies partly in their varied structural components and partly in the diversity of plant species that they support. The structural diversity of hedgerows can be divided into the following four components (Figure 13):-

(1) Hedge body - consisting of a more or less continuous line of shrubs and bushes which can sometimes be of considerable width and so offer an 'interior' as well an 'edge' habitat to many insects. The bottom of the hedgerow and any associated banks are important as nesting sites for bees and wasps.

(2) Hedgerow trees.

(3) Hedgerow verge - the strip of land either side of a hedge relatively undisturbed by agricultural activities (where there is grazing by stock the hedgerow verge may be reduced substantially).

(4) Ditches - in low lying areas ditches may provide either permanent or ephemeral habitats for aquatic or semi-aquatic insects, e.g. the Odonata (dragonflies), Ephemeroptera (mayflies), Plecoptera (stoneflies) and Heteroptera (true bugs).

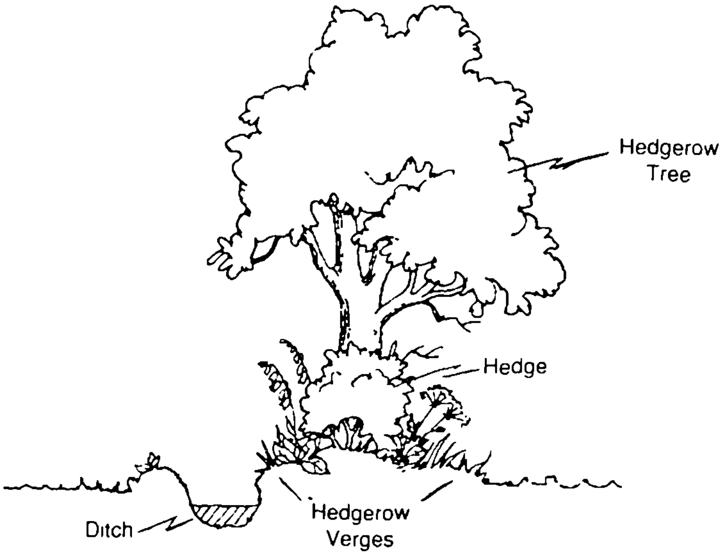

FIGURE 13. STRUCTURAL COMPONENTS OF A HEDGEROW

In short, there are a variety of habitats distributed both vertically and horizontally within the hedgerow complex. In the agricultural setting the margins or headlands of arable crop fields are also important both as sources of food and as overwintering sites for many important species of insects. Many of these prey on crop pests such as aphids and are therefore of economic importance to the farmer. This is discussed in greater detail in the section on conservation headlands, at the end of this chapter.

The shrubs and bushes most usually planted for the body of the hedge include Blackthorn, Beech, Hazel and hawthorns, but it is also important to include or allow the growth of woody species, including those which will normally form sizeable trees. Species such as sallows, Aspen and Wild Privet, which can be cut as part of the hedge should be allowed to grow sufficiently large to flower, and this necessitates rotational cutting on a two or three year cycle or even longer as will be discussed later. Among the several species which are important as hedgerow trees are oaks, Crab-apple and limes. Elm species are also important and, with the tragic loss of so many trees in recent years to disease it is important to retain the few that are left. There are several insect species dependent on elms such as the White-letter Hairstreak butterfly (*Strymonidia w-album*) and whilst this has always been regarded as requiring large mature trees, there is evidence that small colonies can survive on suckers remaining from diseased trees, particularly those at the edges of small woods and clearings and therefore these should be retained.

In addition to the woody plants making up the main body of the hedgerow, there are many smaller ones, including grasses and other herbaceous species, which provide habitats for a wide variety of insects. Altogether, approximately 1,000 plant species have been recorded from the hedgerow habitat and of these about 250 are closely associated with it. Some of these plants attract insect species whose foodplant requirements are specific, such as the Peacock (*Inachis io*) and the Small Tortoiseshell (*Aglais urticae*) butterflies whose larvae feed on nettles (*Urtica* spp.), while other plants (e.g. the Compositae) are utilised by generalist insect species.

Insects from a wide variety of larval habitats depend on pollen or nectar in their adult stages and these food sources are provided virtually year-round by the wide variety of hedgerow plants with their different flowering seasons. An additional sugar source for some insects is honeydew excreted by aphids. The flowers of hedgerow shrubs such as Blackthorn (Plate 19b) and sallows attract a profusion of insects early in the year, while the combined flowering of the various members of the Umbelliferae, such as Cow Parsley (*Anthriscus sylvestris*), Upright Hedge-parsley (*Torilis japonica*), Rough Chervil (*Chaerophyllum temulentum*) and Hogweed (*Heracleum sphondylium*), means that pollen and nectar are available from March through to November. These members of the Umbelliferae are particularly attractive to Syrphidae (hoverflies), Cerambycidae (longhorn beetles), e.g. the Wasp Beetle (*Clytus arietis*) and small parasitic Hymenoptera.

For some insects it is not sufficient simply to maintain a hedge with the right foodplants; the details of management are also important. This can be illustrated by reference to some examples from among the better known hedgerow insects such as the butterflies, of which 25 or so visit hedgerows either for food, shelter, or for breeding and overwintering sites.

The relatively scarce Brown Hairstreak butterfly (*Thecla betulae*) is a good example of an insect which needs special care of the hedgerow if it is to survive. For the reasons explained in Chapter 2, annual trimming could be a disaster for a colony of this insect, as any eggs laid would be effectively destroyed each year, thus severely reducing the population and perhaps wiping it out. In areas where this butterfly occurs, some method of selective annual pruning should be adopted as outlined later in this chapter. The same remarks also apply to the rarer Black Hairstreak (*Strymonidia pruni*) although this favours tall mature Blackthorns on the borders of woods, rides and clearings, and hence these should be left with plenty of top growth (see also Chapter 4).

Amongst the wide range of moths associated with hedgerows are the delicate White Plume moth (*Pterophorus pentadactyla*) whose larvae feed on Hedge Bindweed (*Calystegia sepium*) and several members of the family Lasiocampidae such as the Small Eggar (*Eriogaster lanestris*) which overwinters in an oval shaped cocoon spun on twigs (and is therefore another species that is vulnerable to winter pruning). Another very notable species is the Lappet (*Gastropacha quercifolia*) which flies up and down hedgerows rapidly at night in June and July. When at rest the moth, which has serrated wings, looks very much like a withered bramble leaf. It has a fine large larva which also has a very good disguise when at rest on the stem of a shrub, but when disturbed flashes two blue stripes between its second and third body segments. A hawkmoth which is closely associated with garden hedgerows is the Privet Hawk (*Sphinx ligustri*), which is one of our largest moths and flies at night in June and July. Its larvae, which grow to about 3 inches (75 mm) long, feed principally on privets (which need to be left uncut to attract this insect) and Lilac and it is commonest in the south of England, becoming scarcer in the Midlands and northwards.

The ground beetles (Carabidae) and the rove beetles (Staphylinidae) provide further examples of the importance of hedgerows for insect conservation. Hedgerows and their grassy verges and raised banks fulfil a variety of functions for many of these beetles and, for example, have been found to be important overwintering sites for 24 of the 35 carabid species found in the agricultural setting. Examples of these include *Agonum dorsale* and *Bembidion guttula*. Some species visit hedgerows in search of prey, while others live entirely within them or their vicinity; these latter include *Abax parallelopipedus*, *Trechus obtusus* and *Leistus ferrugineus* .

Hedgerows that may be of particular value for carabids are those that are raised on a bank. This is presumably because drainage is better and the likelihood of freezing during the winter months is reduced. There is also some indication that hedgerows cut on a regular basis are beneficial to ground beetles. This may be because frequent trimming produces a mat of cut material that will provide an insulation layer for overwintering individuals.

The role of hedgerows in the dispersal of insects

Recently, the idea that hedgerows act as 'corridors' for the dispersal of plants and animals through the otherwise hostile agricultural landscape has been the subject of much debate. Few patterns have emerged, however, and there are as many instances where the so-called 'corridor effect' have been discredited as there are instances where it has been verified. The idea that hedgerows act as paths for movement and dispersal is intuitively appealing. Indeed, if it is tenable, the role of hedgerows in facilitating the recolonisation of other adjoining habitats that have lost species through local extinction events may be of considerable importance.

Habitats that are most likely to receive dispersing individuals are woodland edge and woodland interior habitats as well as other hedges on the hedgerow network. Island biogeographical theory predicts that the smaller and the more isolated a habitat the more likely local extinctions will occur. Recent trends in agriculture have indeed increased the fragmentation of suitable farmland habitat, including hedgerows, and at the same time have reduced the area that they cover. Consequently, the likelihood of local extinction of insect species through chance effects such as over-predation, disease, severe weather conditions, or disturbance by agricultural activities is increased.

The role of hedges in facilitating movement of species may largely depend on the precise configuration of the hedgerow network and on the mobility and behaviour of the species concerned. It may be that highly mobile insect species, such as the Painted Lady (*Cynthia cardui*), a migratory butterfly, are not impeded by agricultural fields and so have little reliance on the continuous and relatively undisturbed habitat of the hedgerow for their dispersal. The opposite may, however, hold for more sedentary or ground-living insects since these will be unable to traverse fields before ploughing and insecticide application and are unlikely to survive such farming operations.

Hedgerows may, however, also inhibit the movement of certain insects in that they are effective windbreaks and as such may act as barriers to the aerial movement of weakly flying insects. The reduced wind velocity on the leeward side of hedgerows causes a concentration of insects as they 'drop out' of the air stream. This barrier to the passage of airborne insect populations may, therefore, have a significant enriching effect on hedgerow insect communities. In this manner hedgerows may act as 'stepping stones' rather than 'corridors' for the dispersal of certain insects.

ADVANTAGES AND DISADVANTAGES OF HEDGEROWS FOR MAN

In a book dealing primarily with insects, it would not be appropriate to discuss all the agricultural merits and demerits of hedgerows. However, the view is sometimes expressed that hedges harbour pests. Although some pest species can be found in hedges, most available evidence points to the nett benefit of hedges as sources of the natural enemies of pests, including carabid beetles, ladybirds and parasitic wasps.

A word of caution is worth adding at this stage about the larvae of the relatively common Yellow-tail moth (*Euproctis similis*) which live in a communal web which they spin when young but can frequently be seen feeding separately on hawthorns and other shrubs in April and May. The larva is easy to recognise as it is fairly hairy and has a bright vermilion stripe with a black central line running down the middle of its back. The hairs of this larva penetrate the skin very easily, are highly irritating, and can very quickly find their way over the whole body creating a very unpleasant rash which can look like shingles. There are several moth species with hairy larvae which can have this effect and some people are more sensitive than others. The most notorious of these, although less widely-distributed than the Yellow-tail, is the Brown-tail (*Euproctis chrysorrhoea*). The larvae of this moth are fairly similar to those of the Yellow-tail, but they stay in and around their webs rather later in the season. These webs are very conspicuous and may be seen on single bushes of a wide range of shrubs as well as on hedgerows. Great care must be taken when handling these larvae and most people find it essential to use gloves and even a face mask. Even then the hairs blow around very easily in the wind and it is not unusual for people living near colonies of Brown-tails to suffer rashes without closely approaching the hedgerows.

CONVENTIONAL MANAGEMENT TECHNIQUES AND THEIR IMPLICATIONS FOR INSECT CONSERVATION

Hedgerow management involves much more than decisions on the cutting implements to be used to check the growth of shrubs and trees; whether this be by flail, saw or billhook. Not only is the timing and frequency of such operations critical but the management of the adjoining hedgerow verges is equally of concern. All these aspects of management of hedgerows, along with the incidental management of adjoining fields, will influence their wildlife value. Not least is the value of this habitat for insects.

As already discussed, the unsympathetic management and neglect of hedgerows is now widespread. The culmination of this process may be the eventual loss of a hedgerow either through grubbing out when it no longer fulfils any agricultural function or when all that remains is a series of isolated remnant shrubs. Long before this stage, however, much of the wildlife that it supports will be lost.

The farm activities that can determine the value of hedgerows for insects include:

(1) The method, frequency and timing of hedge and bank cutting;

(2) Management of hedgerow trees;

(3) The way in which pesticides and herbicides are used in the vicinity of hedgerows and the hedgerow verge

(4) The proximity of ploughing to the hedge body i.e. the width of the hedgerow verges

(5) Disposal of field residues; i.e. the choice whether to burn and if so, how to control the burning.

These activities are discussed below.

Cutting of hedges

There are three main implements used to check the growth of hedgerows by cutting: (a) the flail, (b) circular saw and (c) billhook and axe used in hedge laying. Hedgerows today are almost exclusively cut using a flail mounted on a tractor. Hedges that have grown particularly tall or those that are to be coppiced, however, are cut using a saw (again mounted to a tractor). The traditional craft of hedge laying (or layering) is practised less and less; it cannot be performed mechanically and so is time consuming and hence expensive in the short term.

The use of machinery tends to encourage the cutting of a high percentage of the hedgerow length at any one time and this can detrimentally effect insect populations that are at a sensitive stage of their life cycle. This is unlike traditional hedge laying which was carried out in rotation and thus gave invertebrate populations a chance to recover by providing them with safe refuges from which they could recolonise the cut sections.

Although flail cutting can initially encourage the growth of young shoots at the cut surface, repeated cutting at the same height eventually produces a mass of scar tissue and dead branch ends that support few healthy shoots. Frequently the flail cut is taken back to the main upright trunk of hedges, resulting in bark being torn off. The timing of cutting can also be damaging to hedgerow insect communities. If cutting is carried out during the growing season, insects can lose their food supply (whether it be foliage, flowers or fruits), or be directly killed in the cutting operation. Plate 18a illustrates a hedgerow that has been savagely cut in mid-September.

Management of hedgerow trees

It has been estimated that the loss of hedgerow trees is proportionately greater than the loss of the hedgerows themselves. The loss of these trees is due to death caused by (i) old age, (ii) disease (especially affecting elms), (iii) selective removal and (iv) decline in health due to agricultural practices in adjoining fields. A recent report calculated that, by the year 2000, there would be one-third fewer hedgerow trees than there were in the late 1980s. Management practices that have prevented the replacement of felled or dying hedgerow trees include the decline in the number of saplings planted and the stunting of those naturally regenerating in the hedge by the yearly cutting with mechanised flails. The loss of oak species from hedgerows is particularly deleterious to insect conservation because of the very large number of insect species associated with them.

Application of agrochemicals to hedgerows

Agricultural chemicals finding their way into the bottoms of hedgerows can lead to a decrease in insect abundance. Insecticides obviously have a direct effect on insects while herbicides and fertilisers have a mainly indirect effect, although some have been shown to cause direct injury or toxic effects. Herbicides kill plants and hence deprive insects of their primary food source, while fertilisers cause eutrophication of the soil and so encourage the growth of a few vigorous plants that will smother the more species-rich plant community that existed before.

Some arable farmers purposely spray their hedgerow verges to eradicate weed species. This activity, however, also kills perennial species that are of little threat to the crop and hence the opportunity exists for further weed species to invade the hedgerow in the following year. This procedure is therefore both harmful to insect conservation and counter-productive. The majority of sprays that reach the hedgerow habitat, however, do so through accidental drift during field spraying operations (Plate 18b). Such events are even more likely when land has been ploughed right up to the hedge side so that there is little to buffer the hedgerow from the management practices in adjoining fields. Plate 19a shows an example in which herbicide spray drift has damaged both the hedge and its verge.

Control of hedgerow verge width

A common practice in recent years has been to minimise the verge width as illustrated by Plate 19b. In addition to increasing the exposure of hedgerow habitats to agrochemicals and to fire damage, this decreases the area of undisturbed land available for insect habitation. It is generally found that as the area of habitat increases so does the number of species found within that habitat - the 'species-area effect'. If this phenomenon holds true for insects of the hedgerow, then reducing the area of hedgerow verge will lower the number of insect species associated with the hedgerow.

Burning of field residues

The practice of burning field crop residues has come under strict guidelines introduced by the National Farmers' Union and the incidence of fires burning out of control has consequently decreased. Nevertheless, fires that burn or scorch adjacent hedgerows still occur and obviously have a devastating impact on their wildlife communities.

MANAGEMENT RECOMMENDATIONS

In view of the hazards outlined above, several recommendations can be made to conserve the hedgerow habitat as one suitable to support a diverse community of insects.

Hedgerow cutting techniques

(1) **Cutting implements**: Flails should only be used to cut small and medium sized material so that the excessive splintering of cut branches is reduced. The use of the circular saw for heavy hedge cutting work is to be recommended so that branches are cut with a clean finish so that die-back and fungal infection are lessened. The traditional craft of hedge laying is a valuable technique to employ when a hedge develops gaps both along its length and at its base. Hedge laying involves partially cutting the hedge shrub trunks at their bases and laying these shrubs (the pleachers) laterally. The advantage of this technique is that new growth is stimulated from below the cut surface and the hedge grows with new vigour from its base, although the pleaches themselves will eventually die. Gaps in the base of the hedge will soon become occupied by new woody growth. The advantages of this technique for insect conservation are that it prolongs the life of the hedge and encourages the growth of new shoots that are of greater nutritional value because they contain fewer secondary metabolites (substances which may be toxic to insects or which inhibit feeding or digestion). Hedge laying needs to be repeated every fifteen years or so and between times flail cutting can be used to check growth.

(2) **Frequency**: Hedgerows should be cut every two to three years, which will allow strong growth while not presenting the flail operator with large branches that are poorly cut by a flail. Yearly cutting or cutting with a flail after five or more years of unchecked growth should be avoided.

(3) **Extent**: Only a proportion of the total hedgerow length in any given area should be cut in any single year, to ensure that species overwintering on the branches are not completely eliminated. A three-year rotational plan should meet the needs of most insects. A procedure that is little practised at present (except in the case of boundary hedgerows that are managed independently by the neighbouring land owners) is that of trimming only one side of the hedge at a time, and so allowing insects from the untrimmed side to recolonise the other.

(4) **Timing**: The timing of cutting should be outside times when the hedge is in foliage, flower or when large quantities of fruits still remain attached. The Agricultural Development and Advisory Service recommends farmers to cut hedgerows in late winter. Cutting during very severe frost is inadvisable; nevertheless, cutting while the ground is frozen allows for the easy passage of tractor wheels.

(5) **Shape:** The best shape of the hedge for insects is unknown but is likely to be that which encourages a rich ground flora. Therefore although the 'A' shape is the most economical to cut, and allows for the easier avoidance of emerging hedgerow trees during cutting, it encourages a thick hedge base that may smother the hedgerow verge flora. Provided that a wide enough hedgerow verge is left, however, all the benefits described above can be obtained.

Little work has been carried out to assess the precise significance of hedgerow cutting regimes and techniques for insect conservation and consequently the best advice that can be offered is to manage hedgerows in rotations and to employ a variety of cutting techniques. It is recommended that those hedges that are required to be stock-proof, or have a great visual significance, should be periodically laid. Hedges running north to south or whose north side is associated with a track can be allowed to grow tall without major problems of crop shading being encountered.

Establishment and maintenance of hedgerow trees

The most cost-effective way of establishing hedgerow trees is simply to select straight and vigorous saplings of the preferred species that have naturally colonised a hedgerow and to avoid cutting these 'hedgelings' during trimming activities. This can be done by tying tags to them before cutting commences. Hedges cut to an 'A'-shaped profile lend themselves to this. Where shade is a problem, hedgerow trees should be established or preferentially retained at the corners of fields (where crop production is low) or in hedges bounded by a road on the north side, or those that run north to south. Trees in field corners or near wide road verges may have a higher chance of remaining healthy into maturity than those which grow between adjacent field margins, since the latter may show a serious decline due to disturbance associated with tillage and other agricultural work.

Avoidance of agrochemicals reaching hedgerows

The spraying and drift of agricultural chemicals into the hedge bottom has dire consequences for hedgerow insects and steps should be taken to prevent this happening (see Boatman *et al*, 1989). The Ministry of Agriculture now advises farmers against deliberately spraying hedgerow verges to control weeds because this activity is often counter-productive. Steps that can be taken to eliminate spray drift include the following.

(1) Leaving a sufficiently wide hedgerow verge to reduce the likelihood of the spray reaching the hedge bottom, although this on its own may not be effective enough to avoid some damage (Dover & Cuthbertson, 1989).

(2) Leaving an 'expanded field margin' to act as a buffer zone (such as that shown in Plate 20a) between the species-rich hedgerow and the intensively farmed field. (Such margins may take the form of wildlife fallow margins, grass margins or conservation headlands as discussed in a later section in this chapter. All of these are intended to help establish particular plant and animal communities in the margin and also result in a reduction of agrochemical inputs in the area adjacent to the hedgerow).

(3) Turning off the outer half of the spray boom when spraying next to the hedgerow on the downwind side of the field.

(4) Not starting the flow of the chemical into the spray boom at the field edge because the initial rush of the spray can carry further than necessary.

(5) Spraying when the wind is light in order to minimise spray drift.

Retention of wide hedgerow verges

By leaving a wide hedgerow verge a greater area is available for habitation by insects. This area should be as undisturbed as possible and, to this end, mechanical disturbance by tractor wheels, plough blades and chemical inputs should be kept to a minimum, although there may be some scope for the use of selective herbicides in the early stages to discourage domination by Cleavers (*Galium aparine*) and Barren Brome (*Bromus sterilis*) (Boatman, 1989). With time a community of biennial and perennial herbs and grasses should develop that will attract a variety of insects other than those early successional species that are associated with the disturbed hedgerow habitat and the crops themselves.

Avoidance of fire damage

To minimise the risk of stubble fires spreading to the hedgerow the guidelines set out by the National Union of Farmers should be strictly adhered to, pending legal restrictions being planned at the time of writing.

CREATION OF HEDGEROWS

As pointed out earlier in this section hedgerow loss has been widespread and extensive, and indeed up to one quarter of all our hedgerows were lost between the 1940s and the late 1980s, with much of the remainder becoming seriously depleted of their value for insect conservation. Thus to help redress the loss, it is very desirable for new, sensitively planned, hedgerows to be created. An added incentive at the time of writing is that the Ministry of Agriculture now offers a 30% grant (60% in Environmentally Sensitive Areas) to establish new hedges.

There are a number of steps that should be followed to plant and maintain new hedgerows successfully and to maximise their value to insects. Some of the more salient of these include:

(a) **The location of new hedges**. This requires careful planning since their location should not be at the expense of existing herb-rich margins. The provision of ditches also needs some care, since although these may be of value for aquatic species, they could easily drain existing valuable damp or marshy areas of meadow etc. - see the section on freshwater marshes, fens and bogs in Chapter 8 for further details.

(b) **Hedgerow width**. As wide an area as practicable should be given over to the body of the hedge and its verges so as to provide a large area for the establishment of plant species and hence their associated insect communities.

(c) **The use of native shrub and tree species that attract a large number of insect species.** The choice of species should be based mainly on those which are natural or traditional components of the local landscape. These may include Blackthorn, Hazel, Crab-apple, hawthorns, limes, poplars, Ash, oaks, elms and sallows, although the latter should not form a large proportion of a hedge in which bushy growth is required as a barrier to livestock. Elm is unlikely to form large trees unless suitable disease-resistant strains become available, although suckers sprouting from around dead stems are well worth retaining. Note particularly the value of allowing shrubs and trees to flower. Trees should be tagged to avoid subsequent cutting.

(d) **The use of locally-grown saplings and saplings from a diverse genetic source.** This will ensure slight differences in the leafing, flowering and fruiting times of individuals within a species and so offer food to insects for longer periods of time.

(e) **Planting technique**. Saplings should be planted in two parallel and staggered rows to create a dense hedge.

(f) **Weed control**. The use of broad-spectrum herbicides to control weed growth should be avoided and alternative methods such as mulching around the young shrubs should be considered.

(g) **Protection**. The young hedgerow may need to be fenced on either side for the first few years if grazing stock or rabbits are likely to be a serious enough problem for the expense to be justified.

(h) **Provision of a raised bank to increase the suitability of the hedge bottom for overwintering carabid beetles.** If it has a sunny aspect and is kept free of shade such a bank may also be of value for solitary bees and wasps.

(i) **Ditch construction.** Excavation of an associated ditch where drainage is essential so that insects, such as the water bugs, that require bodies of still or slow-moving water are accommodated. Note, however, that the ditch will be of little value to aquatic insects unless it has shallow margins. Thus it should be neither excessively deep, nor have very steep sides.

(j) **Establishment of expanded field margins.** This should be considered so that a buffer zone is established between the hedgerow and the cropped field; such a zone will support populations of some insects in its own right. This theme is discussed further in the next section.

OTHER HABITATS IN FIELD BOUNDARIES

Although hedgerows have attracted more attention from conservationists than other features of field boundaries, important habitats may also exist in banks, ditches and walls. Banks and ditches are discussed together with hedgerows above, and ditches are also mentioned in Chapter 8. Morris & Webb (1987) have pointed out that dry stone walls are particularly valuable as habitats and refuges because of the many spaces between the stones. They have also raised the interesting possibility that the lichens growing on such walls, especially in areas of low atmospheric pollution, may provide a background on which many cryptic insects (particularly moths) can rest, or possibly a food source for certain specialised insects. This could be important in areas where trees are scarce.

Mismanagement or neglect of walls does not seriously reduce their habitat value, in contrast to the situation with hedgerows, and they have been less subject to total removal of the habitat they provide. However, spray drift and atmospheric pollution can harm the lichens and other plants growing on walls as well as affecting insects directly.

THE MANAGEMENT OF ARABLE FIELDS

by Reg Fry

In principle many insects and other arthropods such as centipedes, spiders, mites etc. can inhabit arable farmland, but significant declines have been reported, particularly in cereal fields. In 1984 the Game Conservancy set up the 'Cereals and Gamebirds Research Project' to investigate the problems associated with wild gamebird losses and they found that the most likely reason was a reduction in availability of insects as food for the young chicks. These insect reductions have been shown to result from the use of herbicides (Sotherton, 1982,; Rands & Sotherton 1986), insecticides (Vickerman and Sunderland, 1977) and possibly fungicides (Sotherton and Moreby, 1984).

As discussed in the section above on hedgerows, most of the insects affected by agrochemicals are non-target species and include the larvae of many species of butterflies, moths and sawflies, a wide range of beetles, and many heteropteran bugs. Many useful predators of cereal aphids also overwinter in field margins including the carabid beetles *Agonum dorsale, Bembidion lampros* and *Demetrias atricapillus* ; the staphylinids (rove beetles) *Tachyporus chrysomelinus* and *T. hypnorum* ; the dermapteran *Forficula auricularia* (Sotherton and Rands, 1987) and the syrphids (hoverflies) *Episyrphus balteatus* and *Metasyrphus corollae* (Cowgill, 1989). Whilst both insecticides and insect-toxic fungicides can affect all these species, it is now thought that the most important single contributory factor is the use of herbicides, because of their ability to destroy the foodplants of either the larval or adult stages of these insects.

In response to this realisation, various studies have been carried out to try to devise practical and costed management options whereby farmers can continue to farm profitably but at the same time ameliorate some of the detrimental effects of chemicals on game and other wildlife. Most of this work has been done under the 'conservation headlands' experiment conducted by the Game Conservancy.

CONSERVATION HEADLANDS

The conservation headlands concept is that of reducing the spraying of field margins by being very selective in the pesticides used or not spraying them at all. In this system the outermost section of the spray boom (usually the outermost six metres) is either switched off when spraying around these headlands, to avoid applying certain chemicals at crucial times of the year, or the headlands are sprayed with more selective compounds. Most of the field is fully sprayed with the usual combination of pesticides, and only the outermost crop margin (usually found to be something of the order of 6% of the total field area) receives lower pesticide inputs.

The current guidelines resulting from the Cereal and Gamebirds Research Project are given in Table 8. These guidelines have been shown to increase the average brood sizes of the Grey Partridge (*Perdix perdix*) and Pheasant (*Phasianus colchicus*) (Sotherton *et al*, 1989) and also butterfly populations (Dover, in press), but it may be desirable to avoid spraying with insecticides in headlands altogether if all insects are to benefit. The instructions allow for the removal of pernicious and unacceptable weeds such as Black-grass (*Alopecurus myosuroides*), Wild Oat (*Avena fatua*) and Cleavers (*Galium aparine*). This has been achieved by field screening of herbicides for their spectrum of activity against these target weeds and the broadleaved species we wish to encourage in cereal headlands (Boatman, 1987).

The results of introducing conservation headlands are very encouraging with significant increases in populations of butterflies, bumblebees and other insects - compared with many intensive farming areas which are ecological deserts. Although conservation headlands were developed initially for purposes of game conservation, the net result has been to provide nature conservation on the farm with a powerful tool for reducing the impact of intensive agriculture on the remaining farmland wildlife habitats.

TABLE 8. A SUMMARY OF THE GUIDELINES FOR SELECTIVE PESTICIDE USE IN CONSERVATION HEADLANDS

	AUTUMN SPRAYING	SPRING SPRAYING
INSECTICIDES	YES (Avoiding drift into hedgerows)	NO
FUNGICIDES	YES	YES (Except compounds containing pyrazophos)
GROWTH REGULATORS	YES	YES
HERBICIDES		
(a) Grass weeds	YES (But only those compounds approved for use. i.e. avoid broad spectrum residual products)	
(b) Broadleaved weeds	NO (Except those compounds approved for use against specific problem weeds e.g. cleavers)	

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18a. A savagely cut hedgerow — all too common nowadays

18b. Spraying operations with a potentially high level of drift

PLATE 18

19a. Hedgerow with damage from spray drift

19b. Hedgerow in blossom — but with no verge

PLATE 19

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"I will but look upon the hedge and follow you."

William Shakespeare