

THE IMPORTANCE OF FIELD MARGIN ATTRIBUTES TO BIRDS

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ABSTRACT

The research on the importance of field margin attributes to birds has particularly emphasised the importance of hedgerows. The current literature has been well reviewed and is outlined here. Also summarised here are some studies in progress. These have tended to emphasise the value of the structural dimensions of the different components of field margins to birds. Great care is required to make inferences from non-experimental field observations which might not be balanced over all covariates. The important topics of choice of sampling units, statistical independence and statistical modelling procedures are discussed.

INTRODUCTION

There is a considerable amount of literature on birds and field margins, particularly hedgerow, which suggests that on agricultural land field margins are important to birds (Moore *et al.*, 1967; Hooper, 1970a,b; Pollard *et al.*, 1974; Arnold, 1983; Osborne, 1984; O'Connor & Shrubbs, 1986; O'Connor, 1987; Lack 1987, 1992; Parish *et al.*, 1993a,b, in press).

Brown (1969) and Fretwell (1972) suggested that the bird population of hedgerows may also provide immigrants to woodland populations. However, Krebs (1971) found that hedgerow nesting Great Tits (mostly yearlings) had a lower reproductive success and tended to abandon hedgerow territories for experimentally created vacancies in nearby woodland habitat, suggesting that they used hedgerows only as an "overflow" habitat. Pollard *et al.* (1974) argued that hedges provided refuges for woodland birds enabling them to breed in otherwise unsuitable areas. Murton and Westwood (1974) claimed that the removal of hedgerows resulted in only small losses in overall bird populations; but this view has been challenged by Osborne (1982) and O'Connor (1984). Bernstein, Krebs and Kacelnik (1991) concluded that the evidence of relatively stable woodland populations compared with those of field boundaries provided by Krebs and Perrins (1977) supported the earlier view put forward by Brown (1969) and Fretwell (1972).

CURRENT LITERATURE

In many parts of intensive agricultural areas, field margins provide the major habitat for many bird species (O'Connor & Shrubbs, 1986). With considerable loss of hedgerows since 1945 (Pollard *et al.*, 1974; O'Connor & Shrubbs, 1986; Lack, 1992) and the rate of hedgerow loss not appearing to have slowed down (Barr *et al.*, 1993), much of the research on the value of field margins to birds has concentrated on hedgerows.

The *volume* of the hedge was thought to be of particular interest to

birds (Osborne, 1982; Arnold, 1983). Best & Stauffer (1980) showed that the volume of foliage around the nest site may reduce nest losses to avian predation. The ground layer cover promoted by tall and broad hedges may also protect against predation (Pollard *et al.*, 1974). Similarly, the number of herbs in a hedgerow base, and both the presence and variety of trees in a hedge had a positive association with the number of bird species and the number of individuals present in the hedge (Osborne, 1984, 1985; O'Connor, 1987). Shrub-rich hedges provide a greater variety of nesting locations as well as a greater variety of food (e.g. berries) for longer periods; and, different shrubs flower at different times, thus supporting a variety of invertebrates throughout the breeding season of the birds (da Prato & da Prato, 1977). Older hedges tended to be shrub-rich (Pollard *et al.*, 1974; Hooper, 1970b), and these may support a greater invertebrate fauna (O'Connor, 1987).

Field boundary features other than hedges have been studied less. Arnold (1983) found that in his sample plots of arable land in Cambridgeshire, plots containing ditches had twice as many bird species and nearly three times the density of birds, compared with the plots without ditches. He also found that, in winter, hedges with ditches alongside had nearly twice as many species (and if the ditch was large, there was a greater abundance of Blackbird, Song Thrush, Wren, Robin and Dunnock) compared with hedges without an adjoining ditch. A similar positive effect of ditches in the field margins was observed by da Prato (1985).

This paper is not intended to fully cover the literature on all field margin elements, but an important point is that the field margin components (field boundary, boundary strip and crop margin) provide further botanical and structural diversity enabling different species to co-exist (O'Connor, 1987). These components and their importance to game birds are reviewed in this volume (Aebischer *et al.*, 1994). O'Connor & Shrubbs (1986) gave a detailed account of studies on farm structure and bird habitats, and the effects of hedges and hedgerow loss on farmland birds. For birds occurring naturally in lowland farms, the literature has been well summarised by Lack (1992), with informative chapters on hedgerows, other field boundaries and field margins; these chapters also describe management practices which are thought likely to benefit birds.

#### STUDIES IN PROGRESS

Present research on field margins as habitats for birds include studies by staff at the Wildlife Conservation Research Unit (WCRU), Oxford University, at the Royal Society for the Protection of Birds (RSPB), and at the Institute of Terrestrial Ecology (ITE). Also, the British Trust for Ornithology (BTO) has two current projects: The winter hedgerow survey carried out in 1987/88 and The organic farming project, with preliminary reports in BTO News numbers 164, 178 and 185 (P. Lack *pers comm*).

(a) The WCRU work (David Macdonald *pers comm*) is based on studying the association of bird populations with the attributes of 266 hedgerows in Buckinghamshire farms. Both botanical and structural variables were used to explain the observed bird distribution. For each hedgerow, the botanical attributes were the abundance of nearly twenty woody species recorded as absent, present, abundant or dominant. The structural characteristics included mean hedgerow height, hedgerow width at summit and base, the



number of mature trees per m of hedgerow, the number of species of mature trees and of woody plants, and the proportion of length made up of gaps. Other categorised variables included ditches, gardens nearby, crop adjacent to the hedgerow, and presence/absence of trees, water and road. For each hedgerow, the birds were surveyed during April-July 1979, recording the nest locations and bird positions.

Multiple regression analysis relating bird variables to the botanical and structural variables showed that bird-rich hedges tended to be taller and had more species of shrub growing in them compared with hedgerows which had few bird species. Thus, the leading term in the final fitted model for total number of bird species was hedgerow height. The next important significant variable was the number of species of woody plant. Presence of dry ditches was also significant, as was the square of hedge height.

(b) The RSPB work (Green *et al.*, in press) is based on surveys of passerine birds during April-May and May-June 1988 and measurements of various attributes of hedgerows, field margin and adjacent land use. The study covered many types of farms in lowland England (46 farms), some with reduced spraying of herbicide and insecticide on the margin of cereal crops - Conservation Headlands. The study used 4760 sampling units of 50 m length of field margin.

For each 50 m section, the presence/absence of each bird species was recorded. The explanatory field margin variables included: number of trees, hedge height, hedge width, woody vegetation length, number of woody species, area of boundary strip, measures of geographical location and factors such as dominant shrub species, dominant plant growing under the hedge, dominant plant on the boundary strip, and adjacent land use.

Logistic regression models, based on those variables which significantly influenced the probability of occupancy of a 50 m section by the bird species, were developed for eighteen bird species. Most bird species preferred tall hedges with many trees, but Dunnock, Willow Warbler and Lesser Whitethroat preferred tall hedges with fewer trees; and, Linnet, Whitethroat and Yellowhammer preferred short hedges with few trees. The incidence of Robin, Song Thrush, Lesser Whitethroat, Whitethroat, Blue Tit and Yellowhammer was positively correlated with the number of woody species in the 50 m section; and the incidence of Lesser Whitethroat and Whitethroat was affected by the identity of the dominant woody plant species in the hedge. The adjacent land use (grass, tillage, roadside) had a significant effect on a number of bird species, with Willow Warbler, Blue Tit and Goldfinch preferring grass to tilled, but Greenfinch and Yellowhammer preferred tilled to grass. Both Goldfinch and Greenfinch preferred hedgerows bounded on one side by a road verge.

Most bird species occurred more often in hedges next to autumn than spring-sown cereals. Conservation Headlands appeared beneficial for bird occupancy in hedgerows adjacent to spring-sown cereals, but for hedgerows adjacent to autumn-sown cereals, the incidence of birds tended to be higher (particularly for Robin, Song Thrush and Greenfinch) when the spraying was not reduced. An explanation of such "negative" results might be along the lines suggested by Cracknell (1986) - dense weed growth in unsprayed areas hindering foraging activity and obscuring prey. Also, perhaps the Conservation Headlands need to be established for a longer time for its beneficial effects to be overriding and demonstrable.



(c) The ITE work (Parish *et al.*, 1993a,b, in press) covered winter and summer bird populations at two sites in East Anglia: Huntingdon (winters 1983, 1984; summer 1985) and Swavesey (winters 1985, 1986, 1991; summers 1986, 1987, 1991). At both sites the sampling units were 200 m long transects of field margin, extending 10 m into the crop each side.

The Huntingdon study was based on 79 transects for which the adjacent field type was small pasture (<20 ha), small arable or large arable. The Swavesey study used 131 transects in six sub-areas with a range of drainage regimes. The crop type was correlated with the drainage regimes; hence, the transects were categorised by the crop on either side: pasture/pasture, pasture/ley and ley/ley as "grass"; pasture/arable and ley/arable as "mixed", and the arable/arable transects as "arable".

The bird variables included various measures of species richness as well as the abundance of nearly thirty bird species. Further derived variables included the abundance of appropriate groups of similar species (FINCHES, WADERS, GAMEBIRDS, AQUATIC BIRDS, etc.) and also Simpson's index of diversity of birds.

The explanatory variables included, for each transect, the number and height of trees, hedge length (= 200 m, if there was no gap), hedge height, hedge crown width, hedge base width, verge width, ditch depth, ditch width. At Swavesey, the data included also the total number of woody, aquatic and herbaceous plant species, as well as the percentage of ground cover of woody, aquatic and herbaceous species and grass. Additional derived variables such as tree number x height, hedge length x height, hedge length x height x width (volume), ditch depth x width were also used.

Several hundred regression models were developed relating the bird variables to the field margin attributes and the adjacent land use. The factors LANDUSE (pasture, small arable, large arable) at Huntingdon and CROP (grass, mixed, arable) at Swavesey played a dominant part in the subsequent modelling. In the Huntingdon models, the significant terms were land use and the interaction of land use with variables reflecting the amount of "woody material" - the number and height of trees and the physical size of the hedge. The models explained a large proportion of the variation in winter, summer and breeding species richness variables at both sites. In the regression models for bird species abundance, land use and tree and hedgerow variables were significant for most woodland birds. Similarly, verge width was important for seed eating birds (most finches and buntings, Red-legged Partridge in summer, and for Carrion Crow in winter) and for insectivores e.g. Blue Tit. Some seed eaters (Linnet, Goldfinch, Reed Bunting) and insectivores (Blackbird, Great Tit, Skylark, Song Thrush and Wren) were associated positively with ditch dimensions; and, Kestrel and the groups RAPTORS, WADERS and AQUATICS with larger ditches. The number and height of hedgerow trees did not appear particularly beneficial to buntings, Skylark, Redwing, Goldfinch, Linnet and the groups GAMEBIRDS and WADERS. Most species favoured the field margins associated with pasture; but species such as Pheasant, Red-legged Partridge, Skylark, Carrion Crow and the group GAMEBIRDS showed greater abundance in field margins associated with large arable farms.



## STATISTICAL CONSIDERATIONS

### Sampling design

A marked difference between some of the major studies in the published literature (Arnold, 1983; Osborne, 1984) and the studies in progress is in the choice of sampling units. To be able to make inferences about the importance of the structure of the different elements of the field margin to birds, the sampling design should include measurements (number, height, width, depth, etc. as appropriate of trees, hedges, ditches, banks, verges, vegetation) which can be related directly and meaningfully to the bird diversity and abundance.

The sample units used by Osborne (1984) were 42 hedges of variable length, but one hedge was almost ten times as long as another. It is possible for a longer hedge to have more bird species as well as a large area (hedge length x hedge width). Thus, the result that the variable logarithm of hedge area explained 40.7% of the variation in the observed number of species per hedge tells us little about the bird population's needs for tall or wide hedges. Arnold (1983) surveyed bird species in 37 sites in eastern England using quadrats of area equal to 5 ha as the sampling units. The sites ranged from arable land without ditches, hedges and trees, to arable land and grassland with up to 200 m of ditch and/or hedge of various sizes. With such a sampling scheme it was impossible to directly assess the importance of various field margin attributes to birds. In contrast, the sampling units used by Green *et al.* (in press) and Parish *et al.* (in press) were fixed length transects of hedges and field margins respectively, and they recorded a large number of botanical and structural attributes of the transects. This was important for understanding the requirements of different bird species as far as the field margin attributes were concerned.

### Statistical analysis and assumptions

Arnold (1983) found that, using data from those quadrats which contained hedges, the average number of species per plot clearly increased with the presence of increasingly larger hedgerows, but in his regression model the species numbers were significantly negatively correlated with hedge length. This is not surprising because it is difficult to obtain meaningful coefficients in modelling data from observational studies (James & McCulloch, 1990); and, this is particularly so if the choice of variables entering the model is based purely on statistical criteria (Parish *et al.*, in press). They found that the models for the same bird variable, based on data from successive years, might easily include different explanatory variables, by chance, particularly if the data were sparse. Such results conflict with ornithologically sensible expectation that the models for the same bird variable, in successive years, should contain the same or similar explanatory variables. They found that biologically consistent models were obtainable by relaxing the arbitrary significance level of  $p < 0.05$  to  $p < 0.1$  for a given explanatory variable in a particular year, if this variable was found to be highly significant in other years. An alternative approach is to pool the data of successive years. However, since birds are known to return to the same site year after year, the statistical requirement that the data from the different years should be independent will be violated for the pooled data.

The observations from the different sampling units should be statistically independent. This is not easy to achieve in practice because of the different territory size and mobility of different bird species. Care should nevertheless be taken to ensure that the sampling units are not contiguous, particularly if the units are small. However, in larger units the various structural variables (height, width etc.) might vary substantially, rendering the use of mean values (mean height, mean width etc.) unsatisfactory.

#### Interpretation of results

Most studies described here have been observational, and not experimental. In such studies, the different levels of the many factors of interest might not be represented in a balanced way in the data, requiring care in interpreting the results. For example, in Parish *et al.* (in press) the hedges in pasture fields tended to be larger than those in arable fields. Hence, though a simple plot of the total number of species against hedge height suggested a non-linear relationship, multiple regression analysis identified a combination of two linear relationships with a shallow slope for the data from arable transects, and a steeper slope for the data from pasture transects. Similarly, the significance of presence/absence of ditches might depend upon the species' daily need for water, its daily flight range and the distance to a water source, which might well be a ditch in a different sampling unit.

#### CONCLUSIONS

The synthesis of the large number of studies in the literature by O'Connor & Shrubbs (1986) and Lack (1992) helps enormously to focus attention on the main findings. However, most studies have been observational, and only in summer and the breeding season - the exceptions being Arnold (1983) and the current work by ITE and BTO. Also, field margins consist of complex collectives of field boundaries with variable botanical and structural properties, as well as banks, verges and other strips of a variety of dimensions and attributes, and indeed crop margins varying in time and space. The true functional relationships between the bird variables and the numerous habitat variables may involve also a large number of other variables and processes (e.g. abundance of invertebrates, number and distribution of predators at different stages of life, climatic factors, competition between species, Markovian effects of species richness and density in previous years). A considerable amount of further research, based on well-designed studies, is required for successful bird conservation in coming decades.

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FIELD MARGINS AND SMALL MAMMALS

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ABSTRACT

Britain's small mammal species have colonised the agricultural ecosystem with varying degrees of success. The most adaptable species is the wood mouse which is found on open farmland throughout the year. However, the suitability of arable fields for small mammals is seasonally variable and hedgerows are valuable resources for wood mice through the winter, providing both food and cover, although the open field is still exploited by sections of the population. As the cover and food abundance in the fields increase during spring and summer, mice move out into the fields - nesting, mating and foraging entirely within the crop. Selective pesticide application onto field headlands significantly increases food availability for the small mammals. Harvesting drives most of the arable population back into the hedgerows, temporarily at least, in autumn.

Other small mammal species, such as the shrews and voles, are less adapted than wood mice to the arable ecosystem and live there almost entirely in the hedgerows and field margins. Bank voles were never recorded away from the field margins until May, when the high crop allowed them sufficient cover to venture into the fields. Similarly, the shrews, although common in hedgerows, rarely ventured into the field.

INTRODUCTION

The majority of Britain's small mammal species evolved in woodland and are most frequently, and abundantly, found there to this day. However, as with many other indigenous plant and animal species, small mammals have, in historical times, succeeded also in taking advantage of the opportunities afforded by the agricultural ecosystem.

Despite the more recent (post-war) 'intensification' of farming systems, which has almost certainly reduced its suitability for many species, small mammals still inhabit the agricultural ecosystem. This paper examines the importance of one facet of that ecosystem - the field margin (taken here to include hedgerow, boundary strip and field headland). The question asked was: What is the importance of field margins to small mammals, does it vary between species and/or seasonally, and can it be improved by management? As a useful paradigm for mammals on farmland (Macdonald *et al.* 1993), the wood mouse, *Apodemus sylvaticus* was the main study animal.

The importance of the hedgerow was also investigated, using both live-trapping and radio-tracking techniques. Radio-tracking was also used to determine the effects of 'conservation headlands' (Sotherton 1988) on small mammals. Since wood mice eat many of the species (Pelz 1989) that are known to increase in abundance on conservation headlands (Sotherton *et al.* 1989), it was hypothesized that the selective reduction of agricultural herbicides onto headlands of winter wheat fields would create localised food-rich patches for the wood mice. For convenience, conservation headlands and hedgerow use are considered separately below.

## METHODS

Fieldwork was carried out on arable farmland adjacent to deciduous woodland at the Oxford University Farm, Wytham, Oxfordshire (OS Ref. SP4609) and on arable farmland at Sescut Farm, Woodeaton (OS Ref. SP5210), between May 1986 and October 1992.

### Conservation headlands

The application of herbicides onto headlands of winter wheat fields was experimentally manipulated in 1986 and 1987 at Wytham, and in 1988 at Sescut. The application of all other chemicals (insecticides, fungicides, growth regulators, fertilisers) throughout this time was consistent both between plots and between plots and the rest of the field. During 1986 experimental plots, either normally sprayed ('sprayed') or completely unsprayed ('unsprayed') alternated along the field headland; each plot was 20m long and extended 10m into the field. During 1987 a pattern of 'sprayed', 'conservation' and 'unsprayed' plots (20m x 10m) alternated along the field headland. During 1988 the entire field was sprayed normally, receiving broad-spectrum herbicides in autumn 1987 and spring 1988, to provide a control to the previous two years. Both botanical and invertebrate sampling was conducted in each of the three years to determine the effects of the experimental spraying regimes on the floral and invertebrate communities. Full experimental details are given in Tew *et al.* (1992). Once the experimental plots were in place, resident wood mice were live-trapped (see below for methods) and radio-tracked (see below). Analysis of the radio-tracking data was either by calculation of a normalised index of preference (Duncan 1983) followed by a bootstrapping correction (Efron 1979), or by non-parametric multiple comparison analysis.

### Hedgerow use - live trapping

Live-trapping data to investigate the use of hedgerows by small mammals was collected at Wytham between May 1990 and October 1992. Small mammals were captured in aluminium Longworth live traps which were deployed in two ways. Firstly, a regular grid was set across two adjacent cereal fields; 292 traps were used, with each trap separated from its neighbours by 24m; the trapping grid covered approximately 15 ha. Secondly, traps were set along approximately 1.2km of hedgerow, at 24m intervals, and set in the base of the hedgerow as far as possible. In this way, all the hedgerows surrounding the two cereal fields were trapped.

Traps were stocked with clean dry hay for bedding and were provisioned with whole grain winter wheat. Bedding and grain were replenished as necessary. Traps were checked thrice daily around the clock, to minimise trap mortality, for four consecutive days each month. Wood mice were weighed, sexed and individually marked with numbered metal ear tags. Other species were recorded and were weighed and sexed but not marked. Other species caught were harvest mouse, *Micromys minutus*, house mouse, *Mus domesticus*, bank vole, *Clethrionomys glareolus*, field vole, *Microtus agrestis*, common shrew, *Sorex araneus*, pygmy shrew, *Sorex minutus* and water shrew, *Neomys fodiens*. Of these, only wood mice, bank voles and common shrews were commonly trapped.

### Hedgerow use - radio-tracking

Data on habitat use by individuals were collected by radio-tracking. Previous studies (Wolton 1985, Tew 1989) had demonstrated that wood mice were amenable to radio-tracking techniques and, where appropriate, wood mice were radio-collared. The radio-tags (SS1 transmitters: Biotrack U.K. Ltd., Wareham, Dorset, U.K.) weighed < 2g and were attached only to mice which weighed > 19g (Wolton 1985, Pouliquen *et al.* 1990). The transmitters were attached to the mice as radio-collars, using nylon cable-ties with a self-locking ratchet. Radio-collars were attached while the animals were lightly anaesthetised, for approximately one minute, with either pure diethyl-ether or methoxy fluorane ('Metofane'). The radio-collared mice were returned to the trap, allowed to recover full



locomotor activity, and released at its site of capture. The mice were retrapped, usually after one month, and the radio-collars removed, also under light anaesthesia.

The mice were tracked on foot and could generally be located from 30m, using a Mariner receiver (Model M57: Mariner Radio, Lowestoft, Suffolk, UK.) and hand-held three-element Yagi aerial. Locational radio-fixes were taken continuously every 10 minutes throughout the night, from first to last activity, to an accuracy of 5m. Individual mice were radio-tracked for a minimum of three complete nights. The mice habituated quickly to the radio-trackers' presence and could be approached to within 5m. To facilitate accurate data collection a 50m grid was marked out across the study sites using fibre-glass canes marked with coloured reflective tape.

Habitat utilisation was analysed using the compositional analysis technique described by Aebischer *et al.* (1993). To facilitate this, the study site was divided up into 5m x 5m grid cells and each grid cell was assigned one of four habitat variables - wheat, barley, rape and hedge. Since crop characteristics are highly seasonal, and are likely to affect habitat utilisation in a highly seasonal manner, analysis of the data was divided into two broad time periods - winter and summer.

For each animal's home range the proportion of each of the four habitats - wheat, barley, rape and hedge - contained within it was calculated (the 'available' habitat). Following this, the location of every radio-fix was assigned to a habitat type and the proportions of each habitat calculated (the 'utilised' habitat). Following Aebischer *et al.* (1993), one of the habitats was chosen arbitrarily (in this case wheat) and ratios calculated for each of the other habitats by dividing its proportion by the proportion of wheat and then calculating the logarithm of this value, resulting in a logratio. These values were calculated for each habitat for both the available and utilised habitats. If there is no preference for a particular habitat, then the logratios for available and utilised habitat will not differ significantly from zero. A matrix is constructed first to test for an overall non-random use of habitats, followed by a final ranking of the habitats and analysis of significant differences between pairs of habitats.

## RESULTS

### Conservation headlands

#### Floral census

In 1986 unsprayed headland plots contained significantly ( $P < 0.001$ ) more weeds than did sprayed headland plots for all three species sampled (blackgrass, *Alopecurus myosuroides*, sterile brome, *Bromus sterilis*, and wild oats, *Avena sp.*). In 1987 33 weed species were recorded from the headlands (with a maximum of fifteen from any one headland plot); the abundance of three species was significantly (single factor ANOVA -  $P < 0.001$ ) influenced by the spray treatments and a Student-Newman-Keuls multiple range test indicated that black-grass and wild oats were more abundant ( $P < 0.05$ ) in the unsprayed plots, whilst field forget-me-not was more abundant in the conservation plots ( $P < 0.05$ ). In 1988 there were no significant differences in the abundance of any weed species between areas sampled 1, 5 and 8m from the hedge, except for cleavers, *Galium aparine*, and sterile brome, which were absent from the 5m and 8m quadrats. Neither was there any significant variation in the abundance of weeds within the field headland nor between headland and mid-field for any species.

#### Invertebrate census

In 1986 15 Orders of invertebrate were identified from the samples. There were significant ( $P < 0.05$ ) differences in abundance between the sprayed and unsprayed treatments for four of the fifteen orders (Collembola, Hemiptera, Diptera and Parasitica). In 1987 8 Orders of invertebrate were identified (all of which also appeared in the 1986 sample); there were no significant differences in the abundance of any of the eight orders of invertebrate between the three spray treatments.

### Spatial Use of the home-range by wood mice

In 1986 871 radio-fixes were recorded from two males and one female tracked over the experimentally sprayed areas. Preliminary analysis employing a normalized index of preference (PI) (Duncan 1983), indicated that the mice appeared to be selecting the unsprayed plots (Figure 1a).

Further analysis, to determine if this preference was significant for each of the mice, applied the bootstrap method (Efron 1979) to mean nightly values of PI to circumvent the problems caused by non-independence (*sensu* Swihart & Slade 1985) of radio-fixes. A value of PI = 0.3 indicates no habitat preference, so a percentile interval that does not include this value indicates preference (>0.3) or avoidance (<0.3). Full details are given in Tew *et al.* (1992). The results (Figure 1b) show a significant preference for the unsprayed plots for two of the three mice.

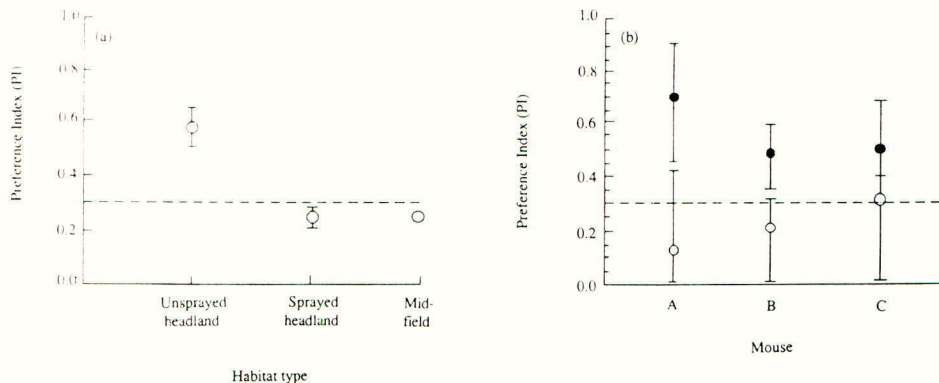


Figure 1. Radio-tracking data from Wytham 1986. a) Normalised preference indices (mean  $\pm$  SE of the mean) for different habitat types. Values  $>$  0.3 indicate selection, values  $<$  0.3 indicate avoidance. b) Bootstrap distribution, with percentile confidence limits, of the normalised preference indices for each of the mice in the two experimental treatments. Closed circles - unsprayed plots, open circles - sprayed plots. Bars represent 95% confidence limits.

The unsprayed plots, which the mice preferred, were characterised by abundant grass weeds and observation by torchlight revealed the mice to be feeding on these. Typically, the mouse was seen eating blackgrass seeds, having detached the seed head from the stem. Individual seed husks were ejected from the mouth and these, together with fallen seeds, left characteristic piles of debris on the ground. Thus, it was often possible to retrace the movements of the previous night's radio-tracking to find small piles of weed debris from the mouse's feeding activity.

In 1987 the home-ranges of twelve radio-tracked mice encompassed the experimentally-produced sprayed, conservation and unsprayed plots and 6427 radio-fixes were recorded; once again the mice appeared to select the headland plots that received reduced herbicide application. A Friedman two-



way analysis of variance by ranks rejected the Null Hypothesis that the radio-fixes were equally distributed throughout the habitat types ( $X^2 = 23.65$ ,  $P < 0.001$ ); and non-parametric multiple comparison analysis revealed that the radio-fixes were more abundant in the unsprayed (1) and conservation headlands (2) than in the sprayed headlands (3) and mid-field areas (4) (S.E. = 4.47,  $Q_{0.05,40,4} = 3.63$ ; 1 vs. 2:  $Q = 0.45$ , N.S.; 1 vs. 3:  $Q = 4.03$ ,  $P < 0.05$ ; 1 vs. 4:  $Q = 5.59$ ,  $P < 0.05$ ; 2 vs. 3:  $Q = 4.47$ ,  $P < 0.05$ ; 2 vs. 4:  $Q = 6.04$ ,  $P < 0.05$ ; 3 vs. 4:  $Q = 1.57$ , N.S.).

In 1988 17 mice were radio-tracked to test the null hypothesis that the mice would not prefer conventionally sprayed field headlands over mid-field areas. Of these, only 5 (29%) were ever observed to enter the field headland and, in fact, the mice showed a significant overall preference for the mid-field (Mann-Whitney one-tailed test,  $P < 0.05$ ). Data from the five mice that did use both mid-field and headland showed no significant preference for either.

#### Hedgerow use - Live-trapping

##### Shrews and voles

Both common and pygmy shrews were caught entirely in the hedgerows during the winter months, but as crop cover increased over the summer were occasionally also caught in the cereal field itself (Figure 2). Bank voles showed a similar seasonal distribution and were only ever trapped (with one exception) away from the hedgerow during the summer (Figure 2).

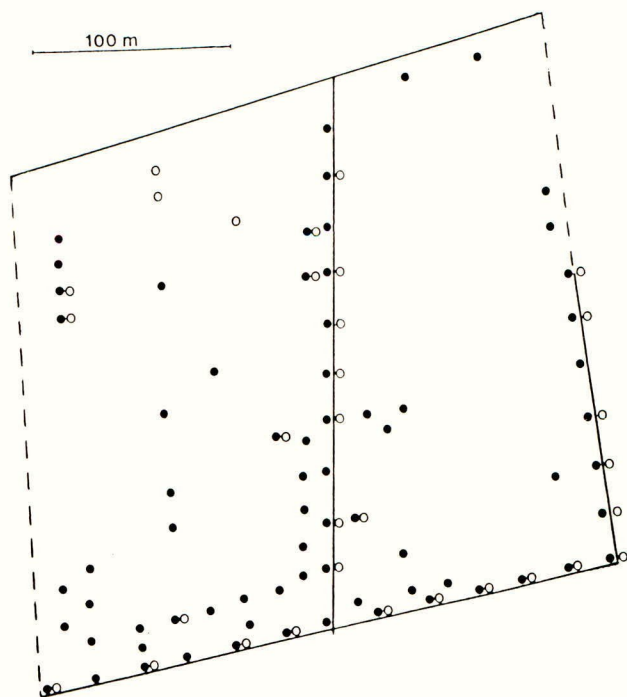


Figure 2. Diagrammatic map showing the capture points of bank voles (closed circles) and common shrews (open circles) between April and October 1991. Solid lines indicate hedgerows, broken lines indicate a field boundary other than a hedgerow. The left field was sown with winter wheat, that on the right with spring barley.

Because the bank voles were not individually marked it is not possible to say how many different individuals were captured. However, between May to August inclusively there were on average approximately 40 bank vole captures per monthly trapping round in the cereal fields, compared to zero for the period October to April inclusively. There was also a corresponding decrease in the number of bank vole captures in the hedgerow over the summer period.

#### Wood mice

Wood mice, on the other hand, were frequently caught away from the hedgerow throughout the year. Immediately following harvest there was a marked reduction in the number of captures on the open ploughed field, but this was temporary in nature and over the winter months mice were again caught away from the field margin (Figure 3).

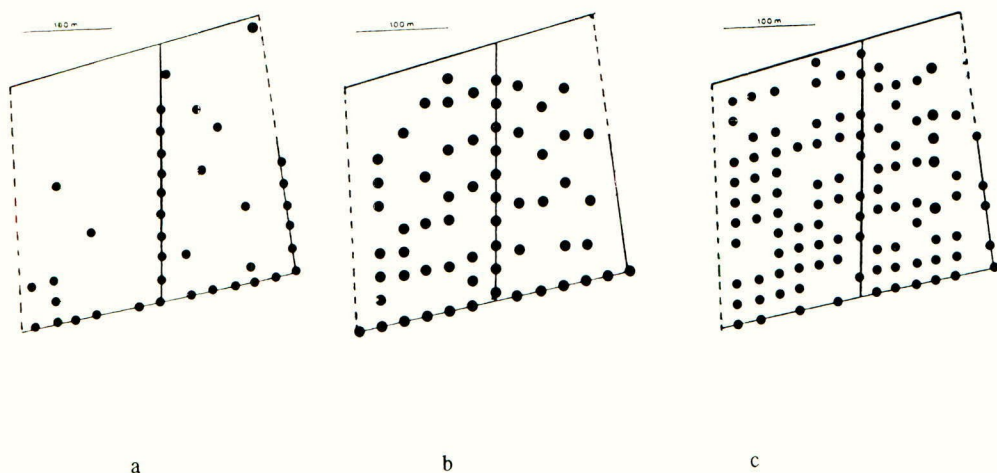


Figure 3. Diagrammatic representation of wood mouse capture locations during:

a - September, ground bare following harvest and ploughing

b - January, wheat 12cm high, barley 5cm high

c - June, wheat and barley full grown.

Symbols as for figure 2. Note the lack of foraging activity on the open field following harvest, followed by a move back out into the fields as crop cover increases.

As with the other species, the hedgerows were an important part of the arable ecosystem for the wood mice throughout the winter months. Between October and April up to 70% of the mice caught in the open field were also caught in the hedgerow, but between October and February only 30% of the mice caught in the hedgerow were also caught in the field. From May onwards, there was no interchange between the field and hedgerow and the two 'populations' were discrete.



### Hedgerow use - radio-tracking.

#### Wood mice - Winter

During the winter wood mice occupied small home ranges that predominantly included hedgerows, although they were also observed to forage on the field surface (Figure 4). Ten animals provided data for at least three of the four habitats analysed during the winter period (November - March). The compositional analysis indicated that overall there was a significant deviation from random use of the habitats ( $X^2=15.36$ ,  $v=3$ ,  $P<0.01$ ). The ranking of habitat use was hedgerow > rape > wheat > barley.

#### Wood mice - Summer

During the summer mouse home-ranges increased dramatically and were largely, and very often exclusively, in the field (Figure 4). However, nineteen animals provided data on at least three of the four habitats during the summer period prior to harvest (June - August). Overall, there was no significant deviation from random use ( $X^2=5.23$ ,  $v=3$ , NS), although the ranking once again showed that hedgerows were the most preferred habitat type (hedgerow > rape > barley > wheat).

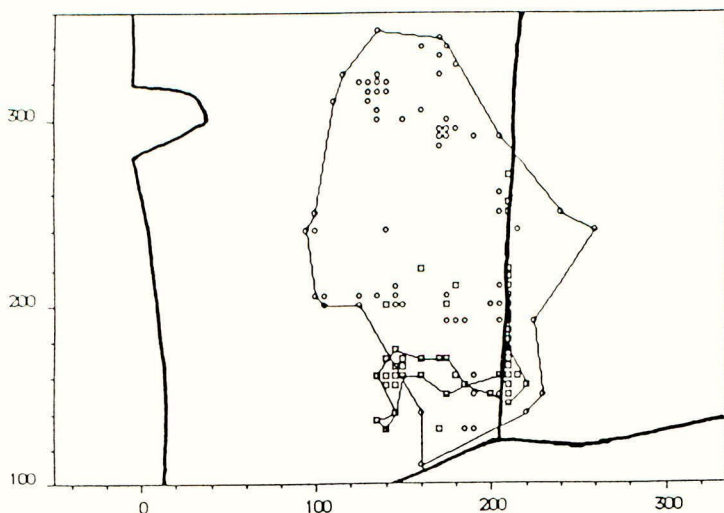


Figure 4. Diagrammatic representation, as an example, of an animal's radio-locations and home-range (calculated using a restricted polygon technique) over winter (open squares) and summer (open circles). Over winter the animal is largely dependant on the hedgerow, over summer the same animal nests and forages largely in the field. Bold lines denote hedgerows. Cropping as in figure 2. Axes scale in metres.

### DISCUSSION

Shrews are widespread wherever there is ground cover and are frequently live-trapped in hedgerows. As cover in the cereal fields increases from May onwards, common shrews are also

occasionally caught away from the hedgerow, although it is likely that most of these captures will be of animals nesting in the hedgerow but foraging in the field. Shrews take a wide variety of invertebrate prey (Churchfield 1991), many of which are seasonally available in the lowland cereal fields of southern England (Aebischer 1991). The restricted distribution of shrews away from hedgerows in the summer may be limited by their poor burrowing abilities (Churchfield 1991).

For bank voles, as with shrews, ground cover is an important habitat requirement (Gurnell 1985) and their distribution on arable land is severely restricted. However, whilst previous trapping studies on arable land have suggested that the bank vole is never caught away from hedgerows (Pollard & Relton 1970, Loman 1991, Greig-Smith 1991), in this study, as the cover afforded by the crop increased throughout the summer, the bank voles frequently foraged into the field. Food availability is likely to be low in the crop, since the preferred foods of bank voles are fleshy fruits and seeds and the leaves of woody plants (Watts 1968, Hansson 1985), but it is possible that the invertebrate fauna of the cereal field represents an alternative to the pre-fruiting hedgerow.

Many arable wood mouse populations are self-sustaining and do not require seasonal immigration from other habitats to maintain numbers (Green 1979, Tew 1989, Loman 1991). However, through either emigration or predation arable mouse numbers drop markedly at harvest (Greig-Smith 1991, Tew & Macdonald 1993) producing population dynamics different to those of woodland, in which animal numbers continue to rise into early winter (Flowerdew 1985). However, not all mice leave the arable fields during the winter and a proportion over-winter on arable land, even where woodland is close by. In this study, wood mice continued to be trapped on the open fields throughout the year, in accordance with previous work (Pollard & Relton 1970, Green 1979, Greig-Smith 1991, Loman 1991), and it seems likely that there is sufficient food available (waste grain, invertebrates) to sustain them away from the hedgerows (Green 1979). Indeed, many animals appeared never to visit hedgerows (Tew 1989).

Thus, as with other species, hedgerows are an important part of the arable habitat for wood mice during the winter, and are significantly preferentially utilised. Throughout the winter it appears that a large section of the population uses the hedgerow only, without recourse to the field, whilst fewer are able to use the field without recourse to the hedgerow. In winter, the fruits, berries and invertebrate supply of the hedgerows are likely to be an increasingly important food source for the arable mice. From May onwards there is no interchange between the hedgerow and field and the two populations are discrete (Tew, in press). Clearly, at this time of year the cereal fields can provide all the resources necessary and the field population of mice, in contrast to that of the hedgerow, increases markedly.

Further confirmation of these population processes are provided by the study of movement patterns of individual mice. Often, mice lived largely in the hedgerows over the winter, with occasional forays onto the open field, expanding their range and moving out into the cereal field in the summer as the crop grows. The social system of arable mice during the summer is one of female defence polygyny (Tew 1989, Tew & Macdonald, in press), with females defending small (0.4 ha) territories intra-sexually and males occupying large (1.5 ha) home-ranges that overlap both inter- and intra-sexually (Tew 1992). Seasonal territoriality by females may explain the seasonal nature of the interchange between the hedgerow and field populations.

For arable-dwelling wood mice cereal grains, weed seeds and arthropods are preferred food items in the summer (Green 1979; Pelz 1989; Plesner Jensen 1993). The floral and entomological data from this study and other related studies (e.g. Sotherton 1988), show that the reduced input of certain herbicides onto cereal headlands creates areas of high weed and insect abundance. Given the food preferences and diet of wood mice, we conclude that reduced herbicide input increased food availability. Small mammals in general, and wood mice in particular (Don 1979; Angelstam *et al.* 1987), are well able to recognise and exploit resources that are highly variable in both space and time. This study demonstrates that wood mice are able to recognise, and take advantage of, the localised conditions of high food abundance produced by the experimental spraying regimes. Wood



mice spent significantly more time in the conservation and unsprayed headland plots, where food availability was high, than would be expected from the relative abundance of such plots within their home-range. Furthermore, direct observations suggested that the time spent in the food-rich patches was largely spent feeding. These conclusions are strengthened further by the inter-annual comparison since in the absence of experimentally-created areas of high food abundance, the mice showed no preference for the field headlands. This suggests that the mice were indeed reacting to the high food abundance in the earlier experiments and were not preferring the cereal field headlands for other reasons such as richer seed banks or increased cover from predators.

The analyses presented here have differentiated the hedgerow, headland and the body of the field. A finer level of resolution has considered the grassy margin between hedge and crop, which conservationists have viewed as a sanctuary for wildlife but which farmers have often viewed as a reservoir for weeds. Another experiment at Oxford University's farm at Wytham sought to discover whether grassy margins could be managed in ways which optimised the integration of nature conservation and farming. Ten management regimes were imposed on 2m margins in a complete randomised block design replicated eight times around arable fields (Smith & Macdonald 1989). Plesner Jensen examined the effects of eight of the management regimes on farmland rodents (Plesner Jensen 1993, Smith *et al.* 1993). Although wood mice preferred taller vegetation, margin management regimes were less important to small mammals than was the presence of boundary features such as hedges and ditches. Boundaries with hedgerows had relatively high numbers of wood mice, bank voles and common shrews, whereas bank voles were more numerous in margins with ditches than in those without.

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