

Effect of increasing numbers of deer on bird populations in Wytham Woods, central England

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Summary

In Wytham Woods, the numbers of deer have increased markedly in recent years and they have had a major impact on the woodland vegetation, both the herb layer and the shrub layer (including the lower branches of trees); they also seriously affect the regeneration of forest trees and the regrowth of coppice. Over the same period, a number of woodland bird species have declined in numbers. The large declines seem to have occurred mainly in those species which nest in low vegetation, especially bramble (*Rubus fruticosus*). Bramble is an important element of the deer diet and its decline in the woods seems likely to be largely due to deer although canopy closure may also have reduced its abundance. Hence the declines in some bird species may be brought about by the increase in deer numbers. The relevance of this suggestion to other woods is discussed.

Wytham Woods

Wytham Woods were left to the University of Oxford in the 1950s. They comprise some 415 ha within a larger farmland estate. The Woods (Elton, 1966; Perrins, 1989) are primarily mixed deciduous woodland, but contain open areas, areas of scrub, small patches of marsh, etc. The Woods are now exceptional in lowland England because they encapsulate the range of habitats, both woodland and non-woodland, that were formerly common prior to agricultural intensification. They have been the site for many ecological studies including a long-term study of the populations of great tits (*Parus major*) and blue tits (*P. caeruleus*) started in 1947 and, since 1972, R. Overall has carried out a bird census on a 6.7 ha site near the top of the hill as part of the

British Trust for Ornithology's Common Birds Census (CBC). This census uses territory mapping to estimate numbers of territories of breeding birds (Marchant *et al.*, 1990). This study plot is covered mainly by large trees, partly oak (*Quercus* spp.) and partly beech (*Fagus sylvatica*), with open areas on two sides. The beech area has rather little ground cover, but formerly the oak area had much bramble understorey, though this has been reduced by browsing (see below). The open areas have, over time, become covered with scrub as a result of the reduction in rabbit (*Oryctolagus cuniculus*) grazing following the outbreak of myxomatosis in the late 1950s.

In this paper we examine the changes to the bird populations and try to see to what extent the deer may be responsible for these and compare these findings with those for other woodlands in

central England where there are CBC records available.

Deer

The information about deer numbers is mostly qualitative, rather than quantitative, owing to the difficulties of accurate counting; they have not been studied in Wytham. Three species are present. Roe deer (*Capreolus capreolus*) are scarce, probably numbering fewer than 10–20 individuals and are not considered further. The fallow deer (*Dama dama*) is a long-term resident. In the immediate post-war period and well into the 1960s, fallow deer were uncommon, with numbers probably seldom exceeding 20. In the very prolonged, cold winter of 1962/63, an attempt was made to count them from their prints in the snow. They mostly seemed to be in one small herd, made up of about 12 or 13 individuals. Small numbers were culled throughout this period. An increase in numbers was not readily apparent until the 1970s, when fallow deer were seen ever more frequently. By the 1980s, numbers were still increasing and they were becoming an increasing nuisance to the neighbouring farmers. At night, they left the woodland to feed in the fields. In winter and spring, winter wheat was a major food resource. In the winter of 1988/89, the main farmer on the south side of the Woods counted 198 fallow deer on his fields one night. Given that other animals would have still been in the Woods or feeding on other farms, this suggests that the population might have been of the order of 250 or more. As a result of pressure from farmers, the main part of the woodland was fenced off from the farms in 1987–1989 with 7 km of deer fence. Deer leaps, allowing deer outside the wood to enter, but not leave, were left open for some years after this.

Muntjac (*Muntiacus reevesi*) is a more recent arrival. It was not seen on a regular basis until the mid-1970s and even then it was some years before it was well-distributed throughout the Woods. Because they are secretive, solitary and small, muntjac are not easily counted, but they have clearly increased very greatly in the last 25 years. Wytham is a prime habitat; there might have been 100–200 animals in the 415 ha of Wytham in years prior to the major cull.

Table 1 gives the numbers of deer removed from the Woods by year. For a variety of reasons, the take has varied markedly from year to year, dropping to zero in the winter of 1997/98. With such a large population and no culling, it is not surprising that damage to the vegetation was very evident after this.

Table 1: Numbers (including both shot and live trapped) of deer removed from Wytham Woods 1990–2000

| | Numbers removed | |
|-----------|-----------------|---------|
| | Fallow | Muntjac |
| 1990–91 | 251 | 0 |
| 1991–92 | 178 | 33 |
| 1992–93 | 131 | 6 |
| 1993–94 | 73 | 21 |
| 1994–95 | 75 | 26 |
| 1995–96 | 46 | 62 |
| 1996–97 | 75 | 1 |
| 1997–98 | 0 | 0 |
| 1998–99 | 195 | 90 |
| 1999–2000 | 158 | 42 |

Vegetation changes

Deer damage was very obvious to the casual observer by the second half of the 1970s. A part of the Bean Wood, an outlying area of the wood, was coppiced in the late 1970s, but grew up abundantly, whereas another, almost adjacent, plot coppiced a few years later, showed almost no regeneration. One plot of 25 young oaks, planted in 1982 and fenced to protect them from deer, had to have the brambles and the young ash (*Fraxinus excelsior*), elder (*Sambucus nigra*), etc. cut from around them for the first few years to prevent them from being smothered, while outside the fence the area remained open.

The vegetation changes have been monitored at 163 plots, each 10 × 10 m, since 1974 (Kirby and Thomas, 1999; Hall and Kirby, 2000) and are described elsewhere (Kirby, 2001; Morecroft *et al.*, 2001), so only the points relevant to this paper are mentioned here. The most marked changes are to the ground and shrub cover; the mean plot bramble cover has declined from 35 to 6 per cent since 1974. Declines in bramble cover occurred in 119/163 plots (15 plots registered an

increase). The number of plots ranked 5 (i.e. 76–100 per cent cover) fell from 27 to zero.

Qualitative changes in the bird populations

The woodland avifauna has changed markedly since the late 1960s. Species which have disappeared (approximate numbers of pairs/singing males in the early 1960s in brackets) are as follows: woodcock (*Scolopax rusticola*) (6–10), swallow (*Hirundo rustica*) (5), tree pipit (*Anthus trivialis*) (5), nightingale (*Luscinia megarhynchos*) (20–30), redstart (*Phoenicurus phoenicurus*) (20–30), spotted flycatcher (*Muscicapa striata*) (10), willow tit (*Parus montanus*) (6–10). Apart from the nightingale and redstart, the species listed above were not numerically abundant. However, many other species which are regarded as common British birds have also shown large declines in Wytham, but are still present in small numbers. These include the blackcap (*Sylvia atricapilla*), garden warbler (*S. borin*), willow warbler (*Phylloscopus trochilus*) and chiffchaff (*P. collybita*). Garcia (1981) gives densities for these four species in Wytham as: 0.5, 0.3–0.5, 1.0 and 1.2 territories ha⁻¹, respectively, although by the late 1980s, Gosler (1990) thought that willow warbler was more commonly to be found at densities of around 0.35–0.5 pairs ha⁻¹. Bullfinch (*Pyrrhula pyrrhula*) was also once a common species and the subject of an intensive study (Newton, 1964); such a study would no longer be possible since bullfinches are now very scarce.

Quantitative changes in the bird populations

Great and blue tits

We have data on the numbers of nesting pairs of great and blue tits in the Woods, dating back to 1947. The data shown in Figures 1a and 2 are for Marley Wood, the part of Wytham for which we have the longest run of data. There is no evidence for any long-term changes in great tit numbers (Figure 1a); some of the reasons for the year-to-year changes are known (Perrins, 1980). However, in the last 10 years or so, numbers have

risen slightly in other parts of Wytham (Figure 1b). Numbers of blue tits are slightly more difficult to interpret since they are subordinate to great tits when in competition for nesting-boxes. As a result, in years of high great tit numbers and/or in areas of low nest-box density, there may be insufficient boxes for all the birds and a varying proportion of the blue tits may be excluded. The excluded pairs are thought to nest in natural sites, but possibly not as successfully as they would have done in nest-boxes (East and Perrins, 1988). However, where there are high densities of nesting boxes, such as in Marley Wood, the blue tits show a highly significant increase in numbers with time (Figure 2).

Common Bird Census data

The CBC plot provides quantitative measures of changes even though most species were only present in small numbers. Figure 3a–j summarizes the declines. Two lines are shown in each part of the Figure. The line with triangles is the number of singing males in the CBC plot in each year and is plotted against the left-hand axis. For comparison, the line with the circles is an index for woodland plots in an area roughly centred on Wytham. These are based on data provided by the British Trust for Ornithology for woodland surveys in Oxfordshire and the six adjacent counties – Gloucestershire, Warwickshire, Northamptonshire, Buckinghamshire, Berkshire and Wiltshire – and are referred to as the ‘regional indices’. The figures for Wytham are therefore real numbers, albeit often rather small samples, while the regional indices are typically based on around 50 woodland plots; the reason that the axis varies in the different graphs is that the index for each species was fixed at 1.0 in 1970, but the graphs are based on one to five species. The indexing procedure used TRIM software to model bird counts with log-linear regression (Pannekoek and van Strien, 1996). The following briefly outlines the status of the various populations. Some species, which nest in similar sites have been lumped together to save space.

Trends in hole-nesters are summarized in Figure 3a and b. The split between the two graphs is artificial, but the five species which have not declined (Figure 3a) now form the dominant part

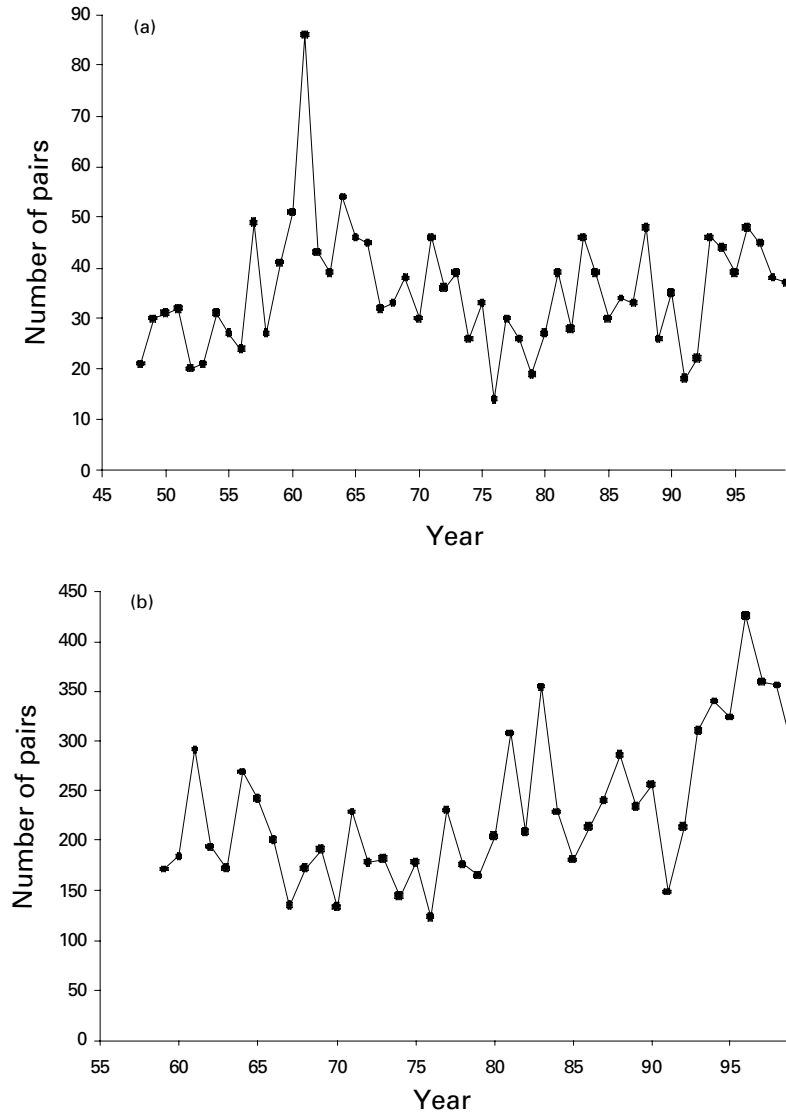


Figure 1. (a) The numbers of breeding pairs of great tits in Marley Wood, part of Wytham Woods, 1947–1998. (b) Numbers of breeding pairs of great tits in the rest of Wytham Woods.

of the passerine avifauna. Blue and great tits have not declined, nor have three other hole-nesting species, coal tit (*Parus ater*), nuthatch (*Sitta europaea*) and treecreeper (*Certhia familiaris*). However, three other hole-nesters, marsh tit (*Parus palustris*), willow tit and redstart, have shown marked declines (Figure 3b). In Wytham, marsh tits have declined from two or three pairs

to one, while the regional indices indicate a similar decrease of some 75 per cent. The willow tit has disappeared from Wytham (the whole of the Woods, not just the plot) and has decreased by >90 per cent in the regional indices. Redstart has disappeared from both Wytham (not just the plot) and the regional indices.

Robin (*Erithacus rubecula*) and wren

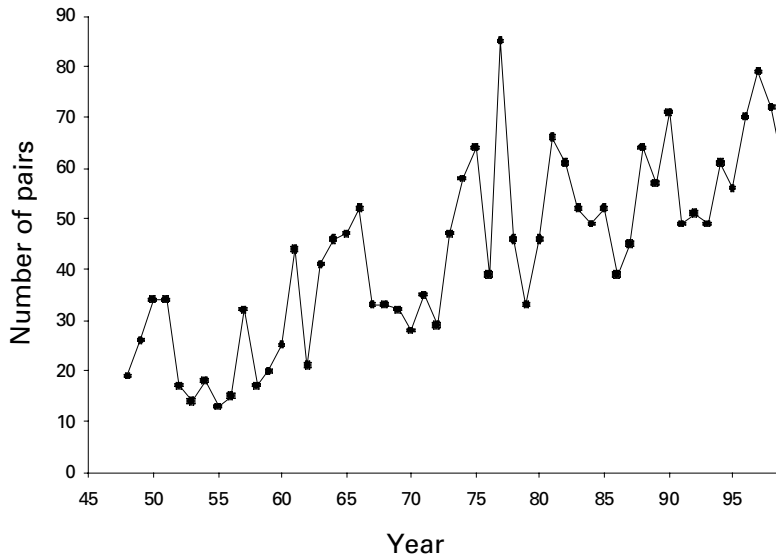


Figure 2. The numbers of breeding pairs of blue tits in Marley Wood, part of Wytham Woods, 1947–1998.

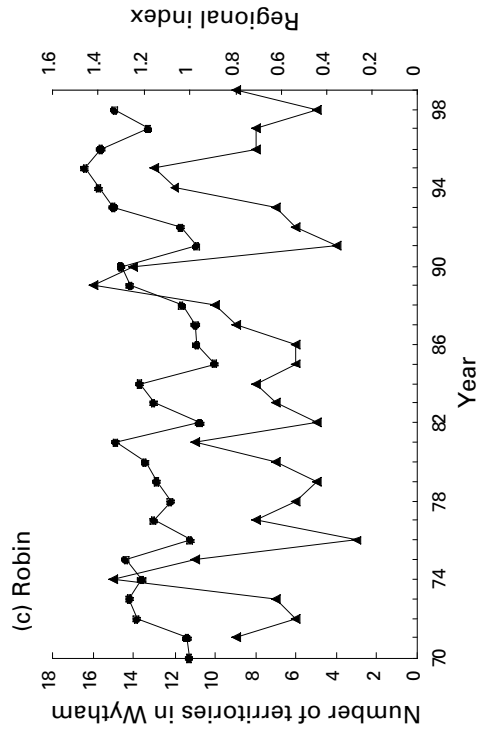
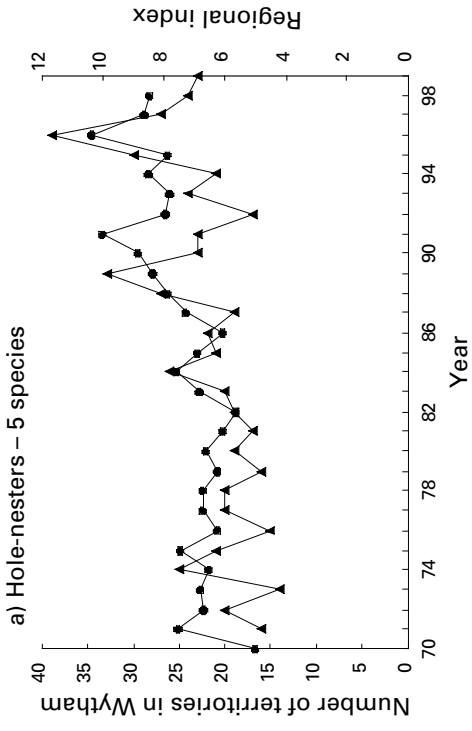
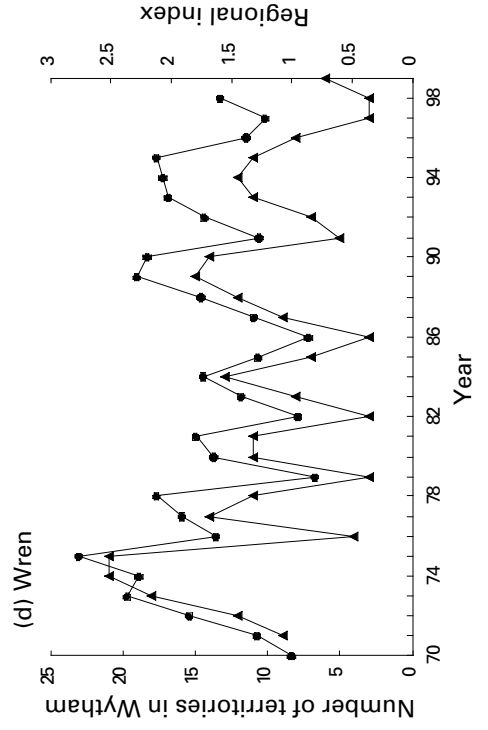
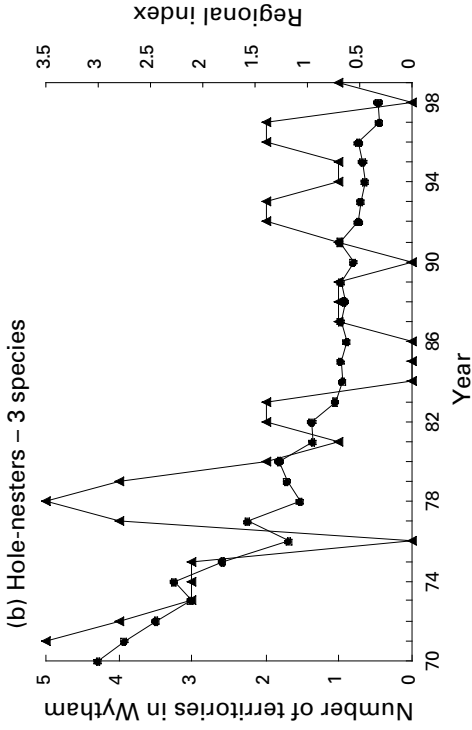
(*Troglodytes troglodytes*) (Figure 3c and d) might also be classed as hole-nesters; they tend to nest low down, but the robin's nest is placed in the ground while the wren's domed nest tends to be built into a split in a tree, against the trunk or on a steep bank or similar position. Neither species show any long-term trends, though there is some tendency for the wren to fluctuate in parallel in both data sets. It is well known that this species is susceptible to hard winters.

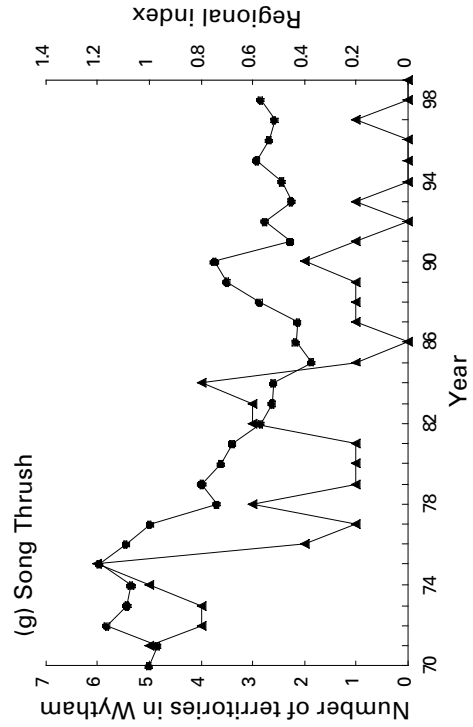
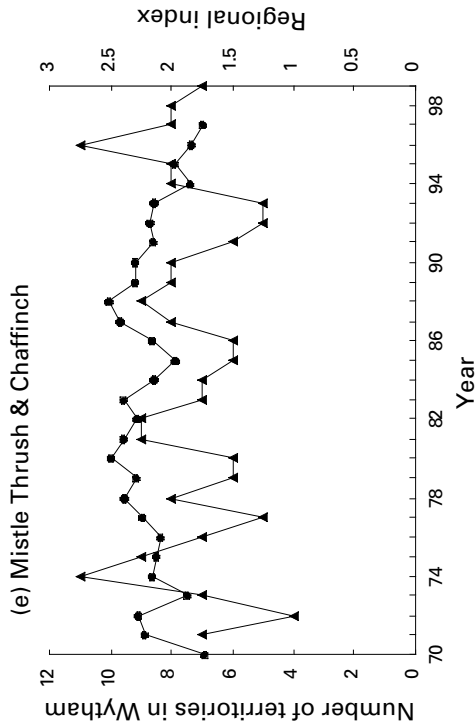
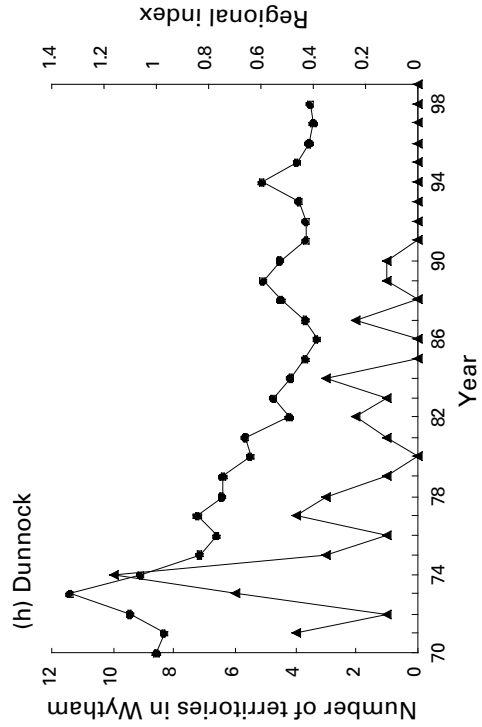
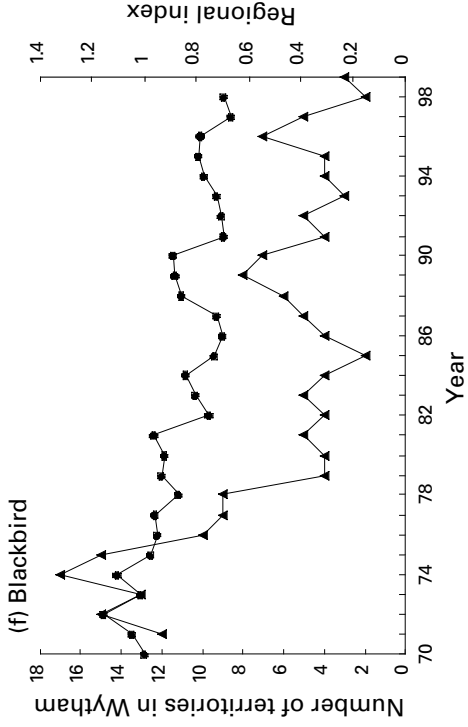
We have included two species together (Figure 3e), the mistle thrush (*Turdus viscivorus*) and the chaffinch (*Fringilla coelebs*), because both tend to nest high in trees. Neither species shows any long-term trend in either data set. Other species which also nest high, but in small numbers, include the corvids; these have not declined, indeed jackdaw (*Corvus monedula*) and magpie (*Pica pica*) have increased in numbers. Blackbird (*Turdus merula*; Figure 3f) is one of the most common woodland birds. The regional index provides some evidence of a decline of perhaps one-third during the course of the study. The decline in Wytham is more marked, perhaps two-thirds.

Song thrush (*Turdus philomelos*; Figure 3g) has undergone a national decline of as much as 65 per cent during the period 1975–1993 (Thomson *et*

al., 1997). The decline in the regional index does not seem to be quite as marked, reaching perhaps ~50 per cent. However, the decline in Wytham, albeit based on a small sample, has been greater, from about four or five pairs in the early 1970s to zero for most years since 1992. Dunnock (*Prunella modularis*) and bullfinch (Figure 3h and i) show similar patterns. In the regional indices both show declines, the dunnock of >50 per cent and the bullfinch rather more. The Wytham declines are much more marked; although based on small samples, both species ceased to breed regularly in the study plot in the late 1980s. Both species nested largely in bramble.

Figure 3j shows four species of warbler: the garden warbler, blackcap, willow warbler and chiffchaff. The first two species nest mainly in bramble, while the latter two nest on or close to the forest floor in thick, low vegetation. The decline in these species is the most marked of all, from around 30 singing males at the beginning of the study to just one to three in recent years. The combined regional indices for these four species show no decline, though at the species level blackcap has increased, as has chiffchaff to a lesser extent, but these increases are balanced by a decline in willow warbler.





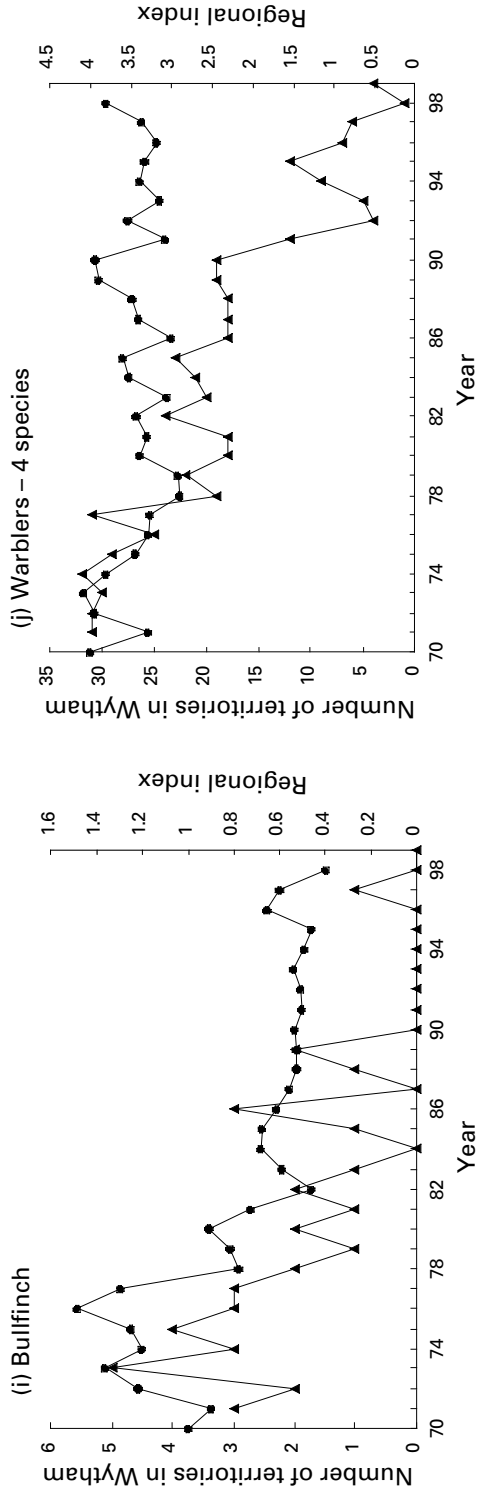


Figure 3. The numbers of territories of a variety of species in a census plot in Wytham Woods compared with regional population indices for CBC plots in central England (see text for further details). Two lines are shown in each of the figures. The line with triangles is the estimated number of territories in the Wytham plot in each year and is plotted against the left-hand axis. The line with the circles, plotted against the right-hand axis, is the regional index for woodland plots in an area roughly centred on Wytham, namely for the seven counties of Oxfordshire and all those contiguous to it: Gloucestershire, Warwickshire, Northamptonshire, Buckinghamshire, Berkshire and Wiltshire. (a) hole-nesters – great tit, blue tit, coal tit, nuthatch and treecreeper; (b) hole-nesters – marsh tit, willow tit and redstart; (c) robin; (d) wren; (e) mistle thrush and chaffinch; (f) blackbird; (g) song thrush; (h) dunnoek; (i) bullfinch; (j) warblers – garden warbler, blackcap, willow warbler and chiffchaff.

Discussion

The decline in woodland birds

Considerable publicity has been given to the state of Britain's farmland birds, many of which have declined markedly in the last 25 years (Fuller *et al.*, 1995; Krebs *et al.*, 1999). Declines in woodland birds have received less attention. The declines shown here (Figure 3) are as large as, or larger than, those in many of the farmland species. However, compared with the regional indices, the Wytham declines appear to be more extreme. The data have not been analysed statistically, partly because the Wytham samples have often been very small.

The declines in the species which were scarce on the plot are, however, not easily explained away as atypical. While only one pair of nightingales and two pairs of redstarts were ever present on the CBC site, their disappearance there mirrors what has happened over the whole wood. However, the declines of these two species seem unlikely to be related to the changes in Wytham; both have shown major changes of range within Britain, the nightingale retreating south-eastwards, while the redstart has deserted many of its former fastnesses in the south-east (Gibbons *et al.*, 1993). Similarly, the declines in marsh and willow tits are mirrored by national declines. While there is no reason to blame woodland changes brought about by deer, all four species are heavily dependent on the shrub layer of woodland.

The species which have shown the most marked declines on the CBC plot, namely black-bird, song thrush, dunnock and bullfinch, plus the four warblers, are generally typical of this sort of woodland, and their decline/disappearance requires an explanation. Although the four warblers are migrants, the other four species are largely resident. The single feature which all these eight species have in common and which contrasts with the species which have not declined, is that they most commonly nest in low vegetation such as brambles.

Great tit

Some of the species which have not declined, e.g. the great tit and the chaffinch, feed a great deal on the ground at certain times of year, especially

in the winter. The changes to the vegetation may have affected the great tits in subtle ways. A study by Hunt (1999) showed that both clutch size and fledging weight of great tit chicks seem to decrease with increasing bramble cover. However, only clutch size was consistently (negatively) correlated with bramble in all analyses. The situation is complicated because clutch size is also (positively) correlated with canopy cover and the amount of canopy cover and brambles are inversely correlated (Morecroft *et al.*, 2001).

There could be simple explanations for the declines in both clutch size and fledging weight with increasing bramble cover (though the correlation between fledging weight and bramble cover is weak and requires confirmation). Great tit clutch size is correlated with caterpillar numbers, suggesting that the birds adjust their clutch size in relation to the food supply (Perrins, 1990). Great tits feed on the ground quite a lot in early spring and bramble cover would limit their opportunity to do this. Similarly, a major component of the diet of great tits is the winter moth (*Operophtera brumata*), a common caterpillar on oaks. When fully grown, the caterpillar drops to the ground, and buries itself before pupating. The caterpillars must be particularly vulnerable to predation when they are dropping onto the ground, but bramble cover would make it much more difficult for the tits to get them then.

The cause of the increase in deer numbers

The management of the woodlands has not changed in any way likely to have led to the increase in numbers of deer. The most noticeable changes have occurred in the surrounding farmland. For most of the post-war period until about 1970, this land was planted with spring-sown cereals; throughout the winter the fields around the woods were bare, ploughed soil. In the 1970s, as elsewhere, farmers switched increasingly to winter-sown cereals. The effect of this was that the surrounding fields were green and, as described above, many of the deer made conspicuous use of this new food. It seems very likely that this increase in winter food supply played an important role in the success of the deer and in their increase.

Against this argument, the erection of the deer fence did not reverse the process. There was

concern at the time that the animals might suffer a serious food shortage in winter and contingencies were put in hand to feed the deer if they seemed to be short of food. There is some grazing land within the fence, so the deer were not completely deprived of winter graze by the erection of the fence. However, despite their large numbers, the deer do not seem ever to have been in poor condition as a result of being denied access to the farmland.

Are the deer responsible for the declines in bird numbers?

The impact of the deer on the vegetation in Wytham probably has had a deleterious effect on the bird populations. However, the deer may not be the only cause of all the changes observed. There are two reasons for this. First, as shown above, the national declines in central England, while mostly of the same species, have not been as great as those in Wytham; therefore either Wytham has been more seriously damaged by deer than the average central English woodland or there is another explanation. It seems possible that Wytham has indeed been more seriously affected by deer than other woodlands, but we lack comparative data. Secondly, some declines, such as that of the nightingale, seem to be part of a more general picture of a 'retreat' from many areas which it inhabited formerly as it becomes more strongly located only in south-eastern England (Gibbons *et al.*, 1993). While this could also be the result of changes in the habitat brought about by deer there is no evidence that deer damage is greater outside this area than in it, so habitat damage by deer seems at best an incomplete explanation for such changes.

Nevertheless, we suggest that the loss of brambles has been one of the driving forces in the decline in bird numbers. Also, the reasons for the loss of brambles are complex. Undoubtedly deer grazing has played a major part, but the effect of other changes, such as closure of the canopy cover, is also likely to have played a part (Morecroft *et al.*, 2001).

Stability of nature reserves

Wytham is a biological reserve, managed both for amenity and its flora and fauna. Yet, over the

almost 50 years that the University has owned it, it has not been a stable community, because of things which have happened 'outside' the Woods. Before it became a reserve, the grey squirrel (*Sciurus carolinensis*) spread from its sites of introduction; it causes serious damage to certain tree species, e.g. beech, which makes it almost impossible to plant young specimens which will survive to replace the large trees planted in the early 1800s. Since Wytham became a reserve in the late 1940s/early 1950s, other large changes have happened. In 1956 myxomatosis almost completely destroyed the rabbit population and this had a major impact on the flora and probably also on some of its main predators, the weasel (*Mustela nivalis*) and the stoat (*M. erminea*) and probably through these on to some of the birds (Perrins, 1979). Dutch elm disease has virtually eliminated elms (*Ulmus* spp.) from the wood. The sparrowhawk (*Accipiter nisus*) disappeared from the wood towards the end of 1959 as a result of the use of organo-chlorine pesticides (outside the woods) and only slowly re-appeared in the mid-1970s when restrictions on these pesticides were introduced (Newton, 1986). Knopper galls, caused by the hymenopteran (*Andricus quercuscalicis*) (Hails and Crawley, 1991; Gurnell, 1993) are starting to affect the production of acorns by the oaks and sycamores (*Acer pseudoplatanus*) are increasingly suffering from tar spot fungus (*Rhytisma acerinum*) (Peace, 1962).

Hence the deer are merely the most recent in a series of ecologically destabilizing events, but the problem of deer damage is not one which will go away; deer will need continual culling if the vegetation is to flourish. Although Wytham seems to have been particularly hard hit by the effects of deer, the deer may pose one of the greatest threats to the diversity of lowland British woodlands at the present time.

Acknowledgements

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References

- East, M.L. and Perrins, C.M. 1988 The effect of nest-boxes on a breeding population of birds in broad-leaved temperate woodland. *Ibis* 130, 393–401.
- Elton, C.S. 1966 *The Pattern of Animal Communities*. Methuen, London.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. and Carter, N. 1995 Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* 9, 1425–1441.
- Garcia, E.F. 1981 *An experimental and observational study of interspecific territoriality between the Blackcap Sylvia atricapilla (Linnaeus) and the Garden Warbler Sylvia borin (Boddaert)*. D.Phil. thesis, University of Oxford.
- Gibbons, D.W., Reid, J.B. and Chapman, R.A. (eds) 1993 *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. T. and A.D. Poyser, London.
- Gosler, A.G. 1990 The birds of Wytham – an historical survey. *Fritillary* 1, 29–74.
- Gurnell, J. 1993 Tree seed production and food conditions for rodents in an oak wood in southern England. *Forestry* 66, 291–315.
- Hails, R.S. and Crawley, M.J. 1991 The population dynamics of an alien insect: *Andricus quercuscalicis* (Hymenoptera: cynipidae). *J. Anim. Ecol.* 60, 545–562.
- Hall, J.E. and Kirby, K.J. 2000 *Trends in Vegetation Cover and Species in Wytham Woods: 1974–1999*. *English Nature Research Reports* 363. English Nature, Peterborough
- Hunt, M. 1999 *Spatial variation of changes in great tit Parus major breeding parameters – a response to deer-related habitat degradation? A study of ecosystem interactions and a possible warning for woodland management*. M.Sc. thesis, University of Oxford.
- Kirby, K.J. 2001 The impact of deer on the ground flora of British broadleaved woodland. *Forestry* 74, 219–229.
- Kirby, K.J. and Thomas, R.C. 1999 *Changes in the Ground Flora of Wytham Woods, Southern England, 1974–1991, and their Implications for Nature Conservation*. *English Nature Research Reports* 320. English Nature, Peterborough
- Krebs, J.R., Wilson, J.D., Bradbury, R.B. and Siriwardena, G.M. 1999 The second Silent Spring? *Nature* 400, 611–612.
- Marchant, J.H., Hudson, R., Carter, S.P. and Whittington, P. 1990 *Population Trends in British Breeding Birds*. British Trust for Ornithology, Tring.
- Morecroft, M.D., Taylor, M.E., Ellwood, S.A. and Quinn, S.A. 2001 Impacts of deer herbivory on ground vegetation at Wytham Woods, central England. *Forestry* 74, 251–257.
- Newton, I. 1964 *The ecology and moult of the bullfinch*. D.Phil. thesis, University of Oxford.
- Newton, I. 1986 *The Sparrowhawk*. T. and A.D. Poyser, Calton.
- Pannekoek, J. and van Strien, A.J. 1996 *TRIM (Trend and Indices for Monitoring Data)*. Statistics Netherlands, Voorburg.
- Peace, T.R. 1962 *Pathology of Trees and Shrubs*. Clarendon Press, Oxford.
- Perrins, C.M. 1979 *British Tits*. Collins, London.
- Perrins, C.M. 1980 The great tit *Parus major*. *Biologist* 27, 73–80.
- Perrins, C.M. 1989 Wytham Wood. *Biologist* 36, 5–9.
- Perrins, C.M. 1990 Factors affecting clutch-size in great and blue tits. In *Population Biology of Passerine Birds: An Integrated Approach*. NATO ASI Series 9, Vol. 24. J. Blondel, A.G. Gosler, J.-D. Lebreton and R.H. McCleery (eds). Springer-Verlag, Berlin, pp. 121–130.
- Thomson, D.L., Baillie, S.R. and Peach, W.J. 1997 The demography and age-specific annual survival of song thrushes during periods of population stability and decline. *J. Anim. Ecol.* 66, 414–424.