

Impacts of woodland deer on small mammal ecology

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Summary

The possible impacts of increased deer populations on small mammal ecology in British lowland woodlands are reviewed. These impacts occur mainly through two pathways. First, by the modification or removal of habitat which influences food supply, cover and the balance of competition between the species. Secondly, through direct competition for resources, particularly food supplies. Losses of woodland ground vegetation may provoke major changes in small mammal community structure which, in the extreme, may decrease from five to eight species, or more, to just wood mice (*Apodemus sylvaticus*). Reduction of understorey species such as hazel (*Corylus avellana*) or loss of shrub diversity, would be expected to lead to declines in yellow-necked mice (*Apodemus flavicollis*) and common dormice (*Muscardinus avellanarius*). Reduction of early succession mixed scrub and grassland may reduce colonization by shrews, harvest mice (*Micromys minutus*) and field voles (*Microtus agrestis*), although in woodland rides, field voles may benefit from preferential grazing of grasses by deer. Impacts on regeneration which may delay or inhibit canopy/understorey closure may encourage the ground and shrub vegetation and so favour species with a preference for ground cover such as the bank vole (*Clethrionomys glareolus*). Reductions in the availability of foods (e.g. mast crops) may reduce the potential for high population densities, particularly of bank voles, wood mice and yellow-necked mice, decrease the lengths of breeding seasons, and further affect community structure. If rodent densities are lowered, avian and terrestrial predators are likely to suffer reduced breeding success and tawny owls (*Strix aluco*) may prey more heavily on bank voles if their favoured ground cover is reduced. Studies at Wytham Woods, near Oxford, from 1949 to 1999, indicate that a significant reduction in bank vole, but not wood mouse, numbers has occurred; this is suggested to be the result of observed changes in the woodland vegetation, including a significant reduction in the ground cover of bramble (*Rubus fruticosus* agg.). Deer, as well as increased canopy shading, are probably the major factors causing this change in habitat and small mammal density.

Introduction

Small mammal population and community ecology in woodland have been well documented

for the common insectivores and especially for the rodents since the 1930s (Elton *et al.*, 1931; Southern, 1970; Flowerdew *et al.*, 1985; Corbet and Harris, 1991; Gurnell *et al.*, 1992; Wilson *et*

al., 1993; Mallorie and Flowerdew, 1994, 1996; Flowerdew and Trout, 1995). This has provided detailed information on population dynamics, regulation, habitat preferences and predation as well as changes with succession, coppice growth and other environmental impacts.

Increased densities of deer in lowland woodland in England (Chapman *et al.*, 1994; Cooke and Lakhani, 1996; Perrins and Overall, 2001) and the associated increase in grazing and browsing pressure may have far-reaching impacts on small mammal ecology and community composition. These impacts occur through two main pathways: (1) through the modification or removal of habitat, which influences food availability, cover (predation risk), and the balance of competition between the species, and (2) by direct competition for resources, particularly foods including herbs, seedlings, bramble (*Rubus fruticosus* agg.), fruits and mast crops (Jackson, 1980; Corbet and Harris, 1991; Chapman and Harris, 1996). The emphasis in this review will be primarily on the impacts of the main deer species present in lowland woodlands, Reeves' muntjac (*Muntiacus reevesi*), roe deer (*Capreolus capreolus*) and fallow deer (*Dama dama*) each of which feed in slightly different ways (Corbet and Harris, 1991; Chapman and Harris, 1996). All three deer species feed on bramble, climbing plants, herbs, shrubs, trees, ferns, fungi and grasses but fallow deer feed much more on grasses than either muntjac or roe deer. The latter two species have similar diets except that roe appear to feed more on conifers in winter than muntjac (Forde, 1989). We will discuss how these impacts, primarily the losses of cover and food supplies, may affect small mammal ecology and community dynamics, including species number, distribution in space and time, population density and possible effects on predators. The main species considered are the common and pygmy shrews (*Sorex araneus* and *S. minutus*), the bank vole (*Clethrionomys glareolus*), field vole (*Microtus agrestis*), harvest mouse (*Micromys minutus*), wood mouse (*Apodemus sylvaticus*), yellow-necked mouse (*A. flavicollis*) and the common dormouse (*Muscardinus avellanarius*). We end with associative evidence for long-term changes in woodland small mammal communities, possibly as a result of increased deer browsing since the 1950s.

Small mammals themselves, particularly the rodents, will also have modifying effects on woodland ecology, although probably at a lower level of severity than deer. Communities may be altered by them through seed dispersal and predation, seedling removal and even bark-stripping (Ashby, 1959; Gardner, 1977; Pigott, 1985; Gill, 1992b; Gill *et al.*, 1995), all of which could be further affected by changes in deer density.

Much of the following assessment of increased deer impact on woodland habitats and then on small mammals is speculative and will necessarily rely on what is currently known of deer and small mammal ecology in various woodland habitats. It is now vital that precise information should come from more experimental deer enclosure studies, as pioneered by Putman *et al.* (1989), using various combinations of deer species at a range of densities and incorporating research from a range of plant and animal disciplines.

Impacts of deer on lowland woodland habitats

This topic has been the subject of many reviews and detailed studies (e.g. Putman, 1986, 1988; Putman *et al.*, 1989; Gill, 1992a, c; McShea and Rappole, 1992; Gill *et al.*, 1995; Kirby *et al.*, 1996; Stromayer and Warren, 1997; Putman and Moore, 1998; Kirby and Thomas, 1999; Gill and Beardall, 2001). These authors emphasize that tree species differ in their susceptibility to damage and that each species is most vulnerable within particular age and size classes. In general, heavy browsing decreases plant species diversity, removes ground cover, and simplifies the vegetational structure. The main impacts are summarized below.

Deer favour immature woodland (Kay, 1993; Gill *et al.*, 1995). They may delay the succession to closed canopy (Peterken and Jones, 1989), and at high densities regeneration may be prevented (Putman *et al.*, 1989). Impacts are usually greater in broadleaved than in coniferous woodland. Many species of coppice may be severely damaged by muntjac, fallow or roe deer and occasionally regrowth is completely prevented (Ratcliffe, 1992; Kay, 1993; Putman, 1994; Cooke, 1999). Loss of the regrowth canopy, change in its species composition and even death

of the stools may result (Cooke, 1994; Cooke and Lakhani, 1996). Impacts on ground vegetation occur regardless of deer species or woodland type, reducing numbers and diversity of species of herbs and flowering plants and changing species composition compared with ungrazed areas (Kirby, 2001). Ground vegetation, shrub and understorey species such as bramble, honeysuckle (*Lonicera periclymenum*), wild rose (*Rosa arvensis*) and dog rose (*Rosa canina*) may be damaged, prevented from establishing, or lost altogether, and in new plantations grassland may be grazed. As a result, unpalatable or toxic species may increase (Gill *et al.*, 1995). In woodland rides the vegetational composition and structure of the edges are greatly affected by deer, changing grass species composition and reducing tree and shrub regeneration (Buckley *et al.*, 1997).

Deer impacts on small mammal communities through understorey reduction, modification of the field or shrub layer and food supply

Small mammal communities are essentially transient in time, being determined by the stage in the vegetational succession and the potential for colonization (Ferns, 1979a, b; Gurnell, 1985; Flowerdew, 1993; Flowerdew and Trout, 1995). In general, the succession from clear-felled woodland or grassland to mature broadleaved woodland will show a shift from a community dominated by field voles, to a community dominated by wood mice and bank voles. The early stages of succession may also support wood mice, shrews and possibly harvest mice, while mature woodland may also support yellow-necked mice and common dormice. The climax community would be modified if the woodland was coniferous, where yellow-necked mice and dormice are less likely to occur (Bright and Morris, 1992a; Marsh and Harris, 2000). In coppice, the small mammal community varies with tree species, but in mixed coppice with standards from cutting to complete regrowth, the species mimic the change from grassland to woodland but with field voles less evident at the start (Gurnell *et al.*, 1992).

Reduced height and density of shrubs and climbers as a result of deer grazing and browsing may have varied effects on small mammals

according to the species. The yellow-necked mouse is localized and southerly in its distribution and favours mature deciduous woodland with good canopy cover and hard seed/fruit diversity, especially if hazel (*Corylus avellana*) is in the understorey and there is fallen dead wood (Marsh and Harris, 2000). The similarly localized common dormouse requires less high level canopy so that the understorey (responsible for a diversity of fruit production) is less shaded (Bright and Morris, 1992a). Hence, if deer impacts reduce understorey species such as hazel, yellow-necked mice may suffer and, common dormouse density may be reduced, especially if shrub/understorey diversity declines. A lack of connecting habitats and trampling (hibernation may be at ground level), may also have negative impacts on dormice (Bright and Morris, 1992b). Deer population expansion may even cause local extinctions if impacts from deer exacerbate current problems; these localized species may already be at risk due to habitat loss from changing woodland management or from climatic limitation at the edge of their distributions (Bright, 1993; Morris, 1993).

The prevention of woodland regeneration and the extension in time of canopy openings by deer may be beneficial to some small mammal species depending on the impacts to the field and shrub layers. Bank voles favour good ground cover in woodland habitats (Southern and Lowe, 1968; Fitzgibbon, 1997) and so they may increase if ground and shrub cover is promoted while there is a more open canopy. Shrews and field voles may also benefit if some grassland is maintained. It follows that any reduction of woodland ground or shrub cover, and changes to its species composition by deer, are likely to make woodland less suitable for bank voles. Just how important ground cover, and increased possibilities for predation (see later), are to the small mammal community have been demonstrated by comparisons of captures outside and inside deer exclosures over 2 years in the New Forest, where there was heavy grazing pressure (1 ha^{-1}) by fallow deer (Putman *et al.*, 1989). Wood mice, bank voles, and common shrews (with occasional yellow-necked mice and pygmy shrews) occurred inside the exclosure but only reduced numbers of wood mice were caught in the neighbouring grazed area.

Tall grassland and early succession mixed grass–scrub favours harvest mice, field voles and the shrews, as well as wood mice (Wolk and Wolk, 1982; Gurnell, 1985; Mayle and Gurnell, 1991; Gurnell *et al.*, 1992). These species may be reduced in density or excluded by heavy browsing and grazing. Similarly, in woodland rides, where grassland and ground vegetational structure is reduced, colonization by field voles and possibly bank voles may be inhibited if the turf is short. However, the structure may be altered by invading grass species unpalatable to deer. Here the feeding preferences of the small mammals and other grazers would determine the suitability of the habitat. For example, *Brachypodium sylvaticum* is a preferred food species for field voles (Evans, 1973) and it is unpalatable to deer (Buckley *et al.*, 1997).

Variations in habitat requirements within small mammal species make predictions about the likely impacts of deer even more uncertain. In Northern Ireland, woodland cover over 5 m and seed availability are important determinants of wood mouse spatial distribution (Montgomery *et al.*, 1991). However, in English farmland copses, understorey cover (<3 m from the ground) is important in wood mouse distribution in autumn (Fitzgibbon, 1997). In Gloucestershire, the abundance of breeding male wood mice in woodland was mainly influenced by the height of the herb layer in spring and autumn and by the height of the understorey (0–1.8 m) only in autumn (Marsh and Harris, 2000). Thus, possible impacts on small mammal distribution within woodland may vary with geographical location.

While wood mice and possibly common dormice are less sensitive than bank voles to the loss of ground cover in mature woodland (Southern and Lowe, 1968; Putman *et al.* 1989; Bright and Morris, 1992a), they are all likely to be reduced in numbers through decreases in fruit, mast and herb food supplies (Flowerdew, 1985; Bright and Morris, 1991). The knock-on impacts to small mammal distribution and community structure in woodland through possible competition for these or alternative foods and for habitat are uncertain. The only results come from the enclosure experiment of Putman *et al.* (1989), detailed above, where the results of two extremes of deer impacts (heavy grazing or no grazing) on small mammals are presented. The possible

impacts of reductions of food supplies on population dynamics are discussed below.

Population dynamics and persistence

Bank voles, wood mice and yellow-necked mice all show strong relationships between population densities and/or survival and autumn/winter fruit-fall in a range of woodland types (Watts, 1969; Flowerdew and Gardner, 1978; Jensen, 1982; Flowerdew, 1985; Mallorie and Flowerdew, 1994). Under poorer feeding conditions, which may be the case where pressure from deer is high, the peaks in densities and survival may be reduced (Louarn and Schmitt, 1972; Flowerdew, 1976). This impact has already been recorded in western Virginia, USA, where the exclusion of deer grazing influenced both white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*). After low mast years, increases in the numbers of these rodents often occurred on the deer exclusion sites but not on the control sites (McShea, 2000).

The occurrence of breeding over winter and the associated changes in the times of the start and end of the breeding season in spring and autumn in bank voles and wood mice are also influenced by the abundance of overwinter food supplies (Smyth, 1966; Watts, 1970; Flowerdew, 1973) and so could be modified by the removal of mast by deer. There is already indirect evidence of competition for food between the two *Apodemus* species. Yellow-necked mice breed earlier when the presumed feeding competition of wood mice is removed and vice versa (Montgomery, 1981) and higher proportions of male wood mice are in breeding condition in habitats without yellow-necked mice (Marsh, 1999).

Woodland community impacts – invertebrates and their predators

Though the information available is limited, the impacts of deer on invertebrates are potentially far-reaching (Stewart, 2001). All the shrew species include in their diets one or more of the invertebrate groups possibly affected by deer grazing and browsing (Corbet and Harris, 1991; Stewart, 2001) but how significant any losses

might be is uncertain. Species such as the wood mouse, and probably the yellow-necked mouse, often depend heavily on insect food in the early spring when seeds and fruits are in short supply (Watts, 1968; Hansson, 1985) and the significance of these possible preferences is again uncertain. There is, however, a possible beneficial impact under conditions of high deer density; the increased deposition of deer faecal material may affect soil fertility and also provide additional habitats for dung-associated invertebrates. The relationships between species in North American woodland communities undergoing density variations in mast, deer, small mammals and invertebrate populations are complex (Elkington *et al.*, 1996; Ostfield *et al.*, 1996) but such interactions have not been studied in European woodlands.

Effects of changes in small mammal ecology on predators and vice versa

Terrestrial predators of small mammals include the specialist weasel (*Mustela nivalis*), the more generalist stoat (*M. erminea*) and red fox (*Vulpes vulpes*) (Macdonald, 1977; King 1980, 1985, 1989; Corbet and Harris, 1991). All are likely to show strong reactions to changes in the densities of small mammals, especially the rodents, affecting numbers, breeding success and local distribution. This has already been demonstrated following the loss of rabbit (*Oryctolagus cuniculus*) prey and the later related loss of field vole (prey) habitat in Britain after the outbreak of myxomatosis in the 1950s (Sumption and Flowerdew, 1986). Similar effects may also occur in woodland as predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) significantly increases when small mammal numbers are low (Dunn, 1977).

Avian predators such as the tawny owl (*Strix aluco*) take large numbers of wood mice and bank voles (Southern, 1954, 1970). In mixed deciduous woodland, Southern found that mice and voles make up a mean of 50 per cent of the annual owl diet (expressed as prey units equivalent to one small rodent) and even field voles make up 10 per cent in territories *within* woodland. The highest predation on small rodents occurs during the tawny owl breeding season (January–April) when mice and all voles reach ~70 per cent of the owls'

vertebrate prey (expressed as prey units). Owl predation success is to some extent dependent on habitat type, so that more wood mice are caught in areas with open ground cover and predation is much less successful in areas with dense ground cover such as bracken (*Pteridium aquilinum*) and bramble (Southern and Lowe, 1968). Bank voles are caught in all cover types, in proportion to their densities (more in the most dense cover), but the precise location of captures indicates that even those voles caught in the dense areas were caught on a boundary with a less dense cover type, indicating that the owls find it easier to hunt just outside the most dense areas. A large amount of dense cover in a territory is usually a distinct disadvantage for the owls (Southern and Lowe, 1968). It follows that under increased deer impact, wood mice are likely to be caught more easily by owls in the more open habitats produced, and bank voles would be caught more easily if the edges of dense cover habitats were broken up and extended. This may affect bank voles more than wood mice, as their numbers would already be reduced by the lack of dense cover.

Overall, losses of habitat and increased predation would make the reduction of bank vole density the most likely occurrence with a smaller reduction in wood mouse densities as more are caught in the increasing areas of open ground. This would culminate in the extreme situation of the absence of bank voles and reduced presence of wood mice as found by Putman *et al.* (1989).

Tawny owl breeding is largely dependent on woodland mice and voles (e.g. Southern, 1970; Wendland, 1984). The owls show marked reductions in breeding success in years with low rodent densities and at exceptionally low rodent densities they fail to lay eggs at all (Southern, 1970). Increasing deer impact in woodland is likely to make breeding failure more common, but short-term population effects are unlikely as the annual recruitment of fledglings to breed is usually very low and the survival of breeding owls (territory holders) is usually high (Southern, 1970). However, an eventual population effect on tawny owls seems quite probable in areas where deer pressure is constantly high over substantial areas and, as a consequence, there is a sustained reduction in small mammal densities. The effect would appear to depend on whether small mammals are

reduced over a sufficiently long period and also on the spatial scale of the 'overgrazing' by deer.

Long term changes in woodland vegetation and small mammal communities – Wytham Woods as a case study

A test of the hypothesis that reduced ground cover (possibly as a result of increased deer impact) in woodland would lead to reduced densities of bank voles compared with wood mice may be carried out as a desk exercise using data from standard 6-monthly live trappings at Wytham Woods, near Oxford, England. These give population indices of wood mice and bank vole numbers since 1949 (Southern, 1970; Southern and Lowe, 1982; Flowerdew, 1985) which may be compared with data on long-term changes in the vegetation (Kirby *et al.*, 1996; Kirby and Thomas, 1999).

The ratio of bank voles to wood mice in Wytham has changed steadily since 1949. Table 1 shows marked changes in the ratios of the two species caught in the decades of the 1960s and the 1980s, indicating a reversal in their relative abundance in both May/June and December with sig-

nificant reductions in bank vole mean catches in the 1980s compared with the 1960s. There were also significantly higher mean catches of bank voles compared with wood mice in the 1960s but not in the 1980s (all paired *t* tests assuming unequal variances).

The trend of December bank vole numbers (Figure 1a) shows, as predicted, a highly significant downward slope from 1949 to 1999. (This is also shown without the exceptionally high figures of 1954 and 1959.) However, wood mouse numbers (Figure 1b) show no significant change. December figures are taken as the most reliable because they do not vary according to the timing of the start of the breeding season and the consequent number of juveniles caught (Watts, 1969; Flowerdew and Gardner, 1978).

These changes in small mammal numbers have occurred while deer populations have been increasing in Wytham (Perrins and Overall, 2001). At the same time (1974–1991) the vegetation of the whole estate has shown a significant decrease in mean canopy cover (>2.5 m), mid-cover (0.5–2.5 m) and of bramble cover and significant losses of dog's mercury (*Mercurialis perennis*), bracken and bramble, attributed to increased shade from canopy growth in the

Table 1: Mean numbers and mean proportions of bank voles and wood mice live-trapped on 1.6 ha of Wytham Great Wood, Oxford, in the 1960s and 1980s in (a) May/June and (b) December

	1960–69		1980–89	
	Bank voles	Wood mice	Bank voles	Wood mice
(a) May/June catches				
Mean \pm SE ($n = 10$)	85.9 \pm 13.6	17.8 \pm 5.0	20.2 \pm 2.9	33.1 \pm 5.7
Mean (%)	82.8	17.2	37.9	62.1
Mean bank voles 1960–69 vs. mean wood mice 1960–69, $t = 4.69$, $P < 0.001$				
Mean bank voles 1980–89 vs. mean wood mice 1980–89, $t = 2.01$, $P < 0.06$ (n.s.)				
Mean bank voles 1960–69 vs. mean bank voles 1980–89, $t = 4.72$, $P < 0.001$				
Mean wood mice 1960–69 vs. mean wood mice 1980–89, $t = 2.01$, $P < 0.06$ (n.s.)				
(b) December catches				
Mean \pm SE ($n = 10$)	68.7 \pm 6.6	39.7 \pm 3.9	27.8 \pm 5.2	33.9 \pm 2.6
Mean (%)	63.3	36.7	45.1	54.9
Mean bank voles 1960–69 vs. mean wood mice 1960–69, $t = 3.76$, $P < 0.002$				
Mean bank voles 1980–89 vs. mean wood mice 1980–89, $t = 1.05$, $P < 0.32$ (n.s.)				
Mean bank voles 1960–69 vs. mean bank voles 1980–89, $t = 4.84$, $P < 0.0002$				
Mean wood mice 1960–69 vs. mean wood mice 1980–89, $t = 1.23$, $P < 0.23$ (n.s.)				

Data from Southern (1970), K. Marsland, J. Lloyd and P. Taylor (all personal communication)

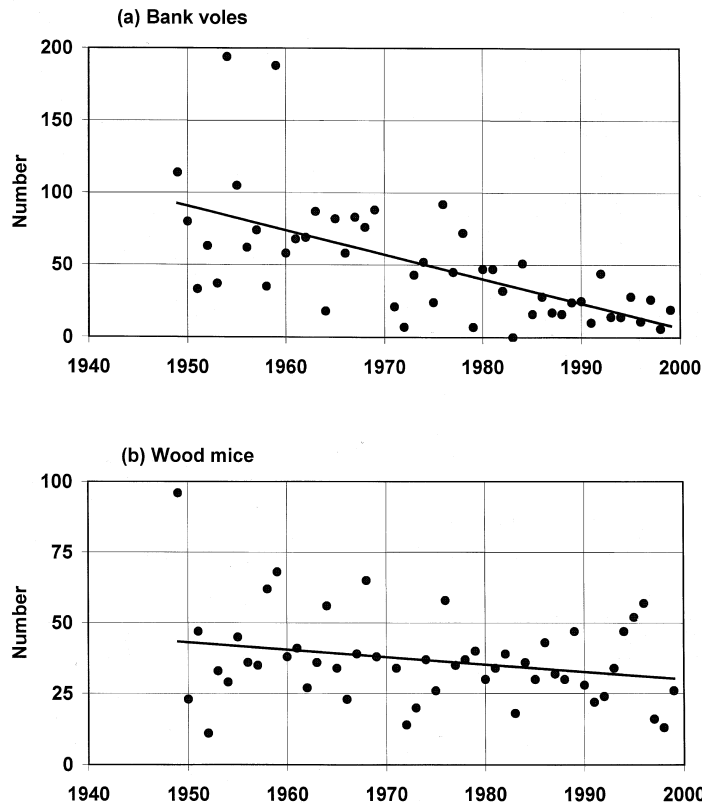


Figure 1. Scatter plots and regression lines for (a) bank voles and (b) wood mice live-trapped in December on 1.6 ha of Wytham Great Wood, Oxford, from 1949 to 1999 (omitting 1970). Bank voles: $y = 33.99 - 1.696x$, ($n = 50$), $r^2 = 0.386$, P (slope) < 0.0001 . Wood mice $y = 558.9 - 0.264x$, ($n = 50$), $r^2 = 0.065$, P (slope) < 0.075 (n.s.). Data from Southern (1970), Southern and Lowe (1982), K. Marsland, J. Lloyd and P. Taylor (all personal communication). Trapping methods are described in Southern (1970).

plantations and generally to increased browsing by deer (Kirby *et al.*, 1996; Kirby and Thomas, 1999; Morecroft *et al.*, 2001). Other causes of vegetation change include storm damage and woodland management. General changes which could have led to the decline in small mammals should also be considered. A reduction in the mast crops available, because of increased competition with deer and other mast predators, climatic factors affecting flowering and/or seed setting or even an increase in the infection of acorns by Knopper galls, caused by the cynipid wasp, *Andricus quercuscalicis* (mainly found on the edge of the wood (P. Taylor, personal communication)) could all have reduced winter food

supplies, but the extent of any of these factors is unknown.

Some habitat changes have been monitored directly on the small mammal trapping areas. In autumn 1954 rabbits declined in numbers with myxomatosis (Southern, 1970). The reduced grazing pressure led to a dense regrowth of ash (*Fraxinus excelsior*) and sycamore (*Acer pseudo-platanus*) which was recorded on part of one area (Grid A) in 1968 (Paviour-Smith and Elbourn, 1993). At that time there was still substantially more ground cover, including bramble, than is currently present (photographic evidence provided by K. Paviour-Smith and authors' personal observations). Before 1983, the trapping areas

had dense high canopy with poor ground cover but clearance in that year allowed dense ground cover (including bramble) to grow; this had started to revert to poor ground cover (reduced bramble) by 1993 and the lower numbers of bank voles on Grid A at that time were attributed to this (J. Lloyd, personal communication). Clearly, deer browsing must be involved in the loss of ground cover and subsequent changes in small mammal populations but they have probably interacted with both management and with increased shade from growing saplings. Whatever the cause, this loss of cover is likely to be the major factor driving the decline in bank vole densities. Whether deer are the major player will only be resolved by experiment. Replicated enclosure studies (cf. Morecroft *et al.*, 2001) in a range of woodland types with varied deer densities on a long term basis would allow a better understanding of the mechanisms involved in deer impacts on small mammals.

Conclusions

Lowland woodland deer are potentially capable of having strong impacts on most small mammal species, especially when densities of deer are high and this, in turn, may have further effects on the woodland community. At lower grazing pressures, there are a few positive effects such as the possible maintenance of grassland in rides and other areas. The effects of increased faecal deposition by deer on soil fertility and on insect populations (habitat diversity) are uncertain. However, if the ground flora is lost or the grassland degraded to a short turf then the small mammals characteristic of these habitats would be lost because of loss of cover, food supplies and possibly also through trampling. Species of particular conservation concern such as the harvest mouse, yellow-necked mouse and common dormouse may all encounter negative influences, perhaps local extinctions, as a result of deer impacts in woodland and even the common rodents and shrews may lose habitat and food supplies, and be increasingly exposed to predation. In addition, the 'knock-on' effects to predators of reductions in the densities of small mammals, especially on their breeding success and alternative prey could also be serious. It is worth emphasizing, however,

that the presence of deer may help maintain the earlier successional stages of woodlands and small mammal communities associated with them before the trees are above browsing height. Not all deer impacts on small mammal communities should be interpreted as negative; the presence of some deer is a good thing, too many deer and too few are not.

Acknowledgements

We are grateful to the late Dr H.N. Southern, Ken Marsland, Judith Lloyd and Philip Taylor for the provision of the small mammal trapping data and/or information about Wytham Woods, and to Professor C.M. Perrins, Dr Kitty Paviour-Smith and Cliff Elbourn for information on, and photographic evidence of, its past vegetation. We are also grateful to M.J. Toms for many constructive comments on an earlier draft.

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