Ecological impacts of increasing numbers of deer in British woodland

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Summary

In recent decades, serious impacts on woodland regeneration have become widespread in Britain as a consequence of increasing numbers of deer. Concern has also been growing about possible effects of deer on the wider ecology of woodland. In April 2000, the Forest Ecology Group of the British Ecological Society held a meeting on 'Ecological Impacts of Deer in Lowland Woods'. This paper summarizes the main issues that emerged from papers presented at that meeting, several of which are published in this special issue of *Forestry*. The probable causes of the increases in deer populations and the problems posed for deer management are briefly considered. There are convincing reasons to believe that for a wide range of taxa, abundances of particular species and overall community composition can be strongly modified by increasing numbers of deer. Such ecological changes are probably well advanced in many British woods as a result of recent intensified grazing. The general effect of sustained heavy grazing and browsing is a reduction in the richness of biological communities. There are, however, considerable differences among species in their responses and heavy grazing is not detrimental to all species. Responses of many species will be non-linear, with intermediate levels of deer pressure being beneficial in many cases. Ecologists have an important role to play in gaining a better understanding of these effects; this is essential if informed decisions are to be made about deer management at both local and regional levels. However, such research presents many methodological challenges.

Introduction

Increasing populations of deer have become one of the major forces of ecological change in British woodland. The problems of deer damage are well known to foresters (Gill, 1992), but the issue has received remarkably little attention from woodland ecologists. The pioneering studies by Arnie Cooke at Monks Wood, summarized by Cooke and Farrell (2001), stand out as a notable exception. Awareness of the potentially wide implications for biodiversity has been further enhanced by several reviews (Mitchell and Kirby, 1990; Putman, 1994, 1998; Putman and Moore, 1998; Gill, 2000). By the end of the 1990s, grazing and browsing by deer was widely recognized as a serious constraint on conservation management in British woodland. The time was right to take stock of what was known of the ecological impacts and of where future ecological research should focus. In April 2000, the Forest Ecology Group of the British Ecological Society held a 2-day meeting at the University of East Anglia, Norwich, UK, on the subject of 'Ecological Impacts of Deer in Lowland Woods'. This special issue of *Forestry* is devoted to several of the papers presented at that meeting.

The conference did not address issues of deer management directly; the primary purpose was to assess the evidence for deer-related impacts on the ecology of woodland. Nonetheless, as a background to the papers that follow, we start by giving an account of the patterns and causes of change in deer populations, and a brief discussion of the problems created for deer management. We then summarize several key messages from the papers published in this issue.

Why have deer populations increased?

On the basis of historical accounts, it is clear that deer populations have been increasing in Britain for ~200 years (Ritchie, 1920; Staines *et al.*, 1998). This situation is not unique to the UK: deer have also been increasing in Europe, Russia and North America during the last 100–200 years (Syroechkovskiy and Rogacheva, 1974; McCabe and McCabe, 1984; Stubbe and Passarge, 1979; Gill, 1990). There are similar reasons for the changes in numbers of deer in each continent and the increase in the UK should be seen as part of a wider and more general phenomenon.

Besides the deliberate and accidental releases of deer into the wild, there are at least six factors which have brought about the increase, although the same factors have not been influencing deer populations at all times and places. (1) The area of forest and woodland has been increasing, mainly through planting but also as a result of the neglect of marginal land (Hart, 1968; Surber *et al.,* 1975; Locke, 1987; Williams, 1989). (2) Some changes in agriculture have clearly been beneficial. Winter cereals are now grown more extensively, providing an important winter food source for deer. (3) There has been a reduction in extensive livestock husbandry, especially in lowland woodlands (Ahlén, 1975; Williams, 1989). Livestock grazing reduces understorey vegetation in woodlands, reducing both food and hiding cover for deer (Peterken and Tubbs, 1965; Loft *et al.,* 1987). (4) In the last 100–150 years, hunting of deer has been subjected to more controls and management. These controls have been effective at both reducing the scale of hunting as well as reducing its impact on the population, e.g. by focusing on males in preference to females (McCabe and McCabe, 1984; Gill, 1990). (5) The climate has been in a warming trend during the last 200 years (Lamb, 1982). Warmer winter and spring weather has been correlated with increased recruitment and overwinter survival of deer, particularly in populations at higher latitudes and altitudes (Albon *et al.,* 1983). (6) Large predators have been virtually eliminated from much of the region, resulting in the removal of a major mortality factor (Gasaway *et al.*, 1983; Nelson and Mech, 1986).

During the early 19th century, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Britain were largely confined to the Scottish Highlands, and fallow deer (*Dama dama*) were mainly restricted to their original release sites in parks or private estates (Ritchie, 1920). Populations of these three species, as well as sika (*Cervus nippon*) and muntjac (*Muntiacus reevesi*), became more widespread during the 19th and 20th centuries following both intentional and accidental releases of captive animals back into the wild (Ratcliffe, 1987; Chapman *et al.,* 1994). Currently, deer occur in most of Britain, although there are still areas with few or no deer. These include parts of Wales, the Midlands, Kent, Cornwall, the Isle of Man and the Isle of Wight (Staines *et al.,* 1998). In contrast, there are areas where densities above 40 km^{-2} have been recorded, or where three or four species co-exist (Gill *et al.,* 1996, 1997; Mayle *et al.,* 1996). The situation is therefore very varied and the potential for further increases in distribution and density is clear.

The problems posed for deer management

It is important to consider why shooting has not been more effective at preventing the increase in deer populations. The development of firearms has certainly made this possible. However, hunting organizations were developed at a time when deer were scarcer, and therefore they adopted a very conservative approach to shooting. Population densities have proved very difficult to estimate in woodland environments. As a result, stalkers have typically underestimated numbers and have not shot sufficient to limit the increase (Andersen, 1953). Furthermore, in some areas hunting is not permitted, nor is it safe and practical everywhere, and it is very difficult to shoot sufficient numbers to prevent dispersal. Deer have therefore been able to continue to spread and exploit new areas. If shooting is ever to be an effective means of managing deer, there is a need to gain more acceptance of the scale of the problem from landowners, stalkers and, perhaps, from the public. The need to manage deer to reduce impacts on vegetation, rather than yielding trophies, is still a relatively novel concept to some stalkers, and one which may offer the prospect of a lower financial return to landowners.

As a result of both human and environmental factors, deer have become abundant throughout most of the north temperate region. Within largely wooded landscapes, there are reasons for thinking that the densities of deer are as high or higher than they were before human agricultural activities began to affect the landscape (Rooney, 2001). In contrast to relatively pristine conditions, many forests today are cut on a regular cycle, creating ideal habitat conditions following re-stocking. Deer densities are typically higher in young forest stands than in mature forest with a closed overstorey (Pucek *et al.,* 1975; Staines and Welch, 1984; Gill *et al.,* 1996).

What is likely to happen in the future? Many of the conditions which permitted deer to recover so dramatically are still present today. The area of woodland cover continues to increase, the use of winter cereals continues and the re-establishment of large predators is unlikely in the near future. Further, climatic trends look set to favour the continued increase in deer populations. Warmer weather will benefit deer directly (see above), and an increase in stormy weather could increase the frequency of windthrow damage, thus creating more pockets of suitable habitat. Unless sufficient control is levied, deer populations are likely to continue increasing in both distribution and density in the foreseeable future. (Interestingly, the outbreak of Foot and Mouth Disease in the United Kingdom in February 2001 has drawn attention to the potential risk of the wild deer population acting as a reservoir for the virus and this could be seen as an additional reason for increased control of deer.)

Without sufficient control, deer populations can rise to densities where damage to trees and changes in the structure and composition of the understorey vegetation are very likely (Kay, 1993; Gill, 2000; Cooke and Farrell, 2001; Gill and Beardall, 2001) and widespread impacts are to be expected on flora and fauna (see below). In Britain, the most biologically rich woodlands are often ancient semi-natural woodlands, which are typically small in size. Almost 70% of ancient semi-natural woodlands in England and Wales are <50 ha in area (Spencer and Kirby, 1992). In view of the fact that the larger deer species (red, sika and fallow deer) can have home ranges of up to 1000 ha, and young roe and muntjac deer disperse over distances of >10 km (Staines *et al.,* 1998), it is impossible to control deer populations in these small woodlands in isolation. Although efforts are being made in Britain and elsewhere to foster co-operation between landowners, it is clear that more information is needed on the ecological consequences of high deer densities to determine whether a more extensive approach to deer management is justified.

The implications of increasing numbers of deer for woodland ecosystems

To examine what is known about the wider effects of deer on woodland ecosystems, many of the papers include reviews focusing on the mechanisms by which increasing pressure by deer may affect different taxa: trees and shrubs (Gill and Beardall, 2001), ground flora (Kirby, 2001; Watkinson *et al*., 2001), invertebrates (Feber *et al*., 2001; Stewart, 2001), small mammals (Flowerdew and Ellwood, 2001) and birds (Fuller, 2001). For each of these taxa there are convincing reasons to believe that abundances of particular species and overall community composition can be modified substantially by increasing numbers of deer. Other taxa may also be sensitive to habitat modification by deer. For example, lichens and bryophytes may be affected by changes in microclimate as understorey structure is altered. Shifts in species composition in the biological communities of many lowland ancient semi-natural woods in Britain and elsewhere in western Europe are probably already well advanced as a result of intensified grazing in recent decades. The studies at Monks Wood (Cooke and Farrell, 2001) and Wytham Wood (Morecroft *et al.,* 2001; Perrins and Overall, 2001) strongly suggest that this is the case. With few exceptions, however, the reviews of taxa were unable to identify quantitative studies of these probable impacts; in nearly all cases, predictions of species responses have to be based on detailed knowledge of species requirements rather than on empirical evidence. Quantifying relationships between community composition for a range of taxa and deer abundance is essential if the real impacts of deer on biodiversity are to be understood. Documentation of effects on species abundances and distributions is a minimum requirement; demographic approaches are also highly desirable (Watkinson *et al*., 2001).

Europe can learn useful lessons from North America, where dramatic, and relatively thoroughly researched, increases in numbers of white-tailed deer (*Odocoileus virginianus*) have affected the status of a wide range of forest species (Rooney, 2001). The North American experience also shows that ecological effects of intense grazing by deer can extend throughout woodland food webs (Waller and Alverson, 1997). For example, under some circumstances deer can potentially modify interactions between mast availability, small mammals, birds and insects (Ostfeld *et al*., 1996; McShea, 2000). It should not be assumed that these ecological linkages will be the same in European forests. Masting is generally a more pronounced phenomenon in eastern North America than in Europe, and just one species of deer is involved, whereas several species of deer coexist in many European forests. Nonetheless, the effects of deer grazing are expected to ripple across trophic levels in all forests; some of the possibilities are explored by Stewart (2001) who advocates a multi-trophic approach to future research on deer impacts. At a minimum, such a multi-trophic approach should encompass work at the same sites on shrub and tree composition, ground flora, lichens and bryophytes, a range of invertebrates, small mammals and birds.

Important questions and research approaches

The overwhelming message from studies in both North America and Europe is that the effect of sustained heavy grazing and browsing pressure is a reduction in the richness of biological communities. It appears that uniformly high grazing and browsing pressure reduces habitat quality for many woodland species and would probably eventually lead to widespread local extinctions. There are, however, considerable differences among species in their responses. Not all species decline with increasing deer pressure. Feber *et al.* (2001) give the example of how grazing by red deer helps to maintain habitat quality for the pearl-bordered fritillary butterfly (*Boloria euphrosyne*). Some birds, such as redstarts (*Phoenicurus phoenicurus*) and wood warblers (*Phylloscopus sibilatrix*), prefer habitat structures that develop under conditions of heavy grazing (Fuller, 2001). In western Britain, lichens and bryophytes may benefit from the microclimates created by heavy grazing. Equally, there are probably many species that benefit from intermediate levels of grazing and the highest levels of species diversity within some taxa may develop under conditions of moderate grazing (Fuller, 2001; Kirby, 2001; Stewart, 2001). In all probability, different communities of woodland plants and animals will characterize the habitat structures created by different grazing regimes. In terms of maximizing regional biodiversity, it can be argued that a diversity of woodland structures and, hence, of management systems and grazing pressures, is highly desirable (Fuller and Warren, 1995; Kerr, 1999). The role of future applied research should be to define how the abundances of individual species and the structure of communities are affected by spatial and temporal variations in grazing and browsing. This knowledge is essential for making informed decisions about deer management at both local and regional levels.

The numerical responses of many woodland species to deer pressure will be non-linear (Gill and Beardall, 2001; Fuller, 2001; Stewart, 2001; Watkinson *et al.,* 2001). Studies examining ecological impacts across gradients of deer density are a fundamental requirement for understanding how ecosystems are affected by increasing deer populations. However, the methodology of studying ecological impacts at different densities of deer is problematic.

Research has often relied on exclosures, which have frequently demonstrated dramatic effects of heavy grazing and browsing on vegetation (e.g. Putman *et al*., 1989; Cooke and Farrell, 2001; Morecroft *et al*., 2001). Exclosures will remain a valuable tool for studying ecological impacts, especially where used in rigorous experimental designs, but they have their limitations (Watkinson *et al.,* 2001). It is relatively easy to exclude deer, but it is more difficult to investigate responses to variations in deer density. Several studies in North America have stocked deer at different densities within enclosures (Tilghman, 1989; deCalesta, 1994) but to be truly successful, enclosures need to be sufficiently large not to interfere with the social behaviour of the deer and also to allow herbivore-induced spatial patterns to develop in the vegetation. To meet these requirements, they may need to be in excess of several hundred hectares. There are also severe practical difficulties in maintaining deer at a target density in a woodland, because shooting may alter the amount of migration (McIntosh *et al.,* 1995). It is clear that new approaches are needed, possibly combining experiments at a variety of scales with data derived from field observation of woodlands carrying different densities of deer.

The papers presented here reveal little about the comparative impacts of different deer species or combinations of deer species on biodiversity. This is potentially an important aspect because there is considerable local and regional variation in the composition of the deer fauna in British woodland. For example, in many parts of East Anglia, roe and muntjac are now virtually ubiquitous, but in some woods these species are supplemented by red or fallow deer. Extremely high grazing and browsing pressure by any of these deer species will substantially diminish the quantity of understorey foliage. However, different combinations of species are likely to alter patterns of niche width and segregation among deer, perhaps resulting in differences in vegetation composition and structure.

It would be entirely misleading to ascribe all recent changes in woodland environments to increases in deer. Other factors may be changing simultaneously which could induce ecological changes similar to those predicted to occur in response to rising numbers of deer. The influence of canopy closure reducing bramble (*Rubus fruticosus*) is one example (Morecroft *et al*., 2001). Increasing soil nitrogen appears to be a major cause of vegetation change in many lowland areas (McCollin *et al*., 2000). The effects of other mammalian herbivores, especially rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*), may be equally important as those of deer. Climate change also needs to be considered. Future work seeking to quantify impacts of deer must somehow control for as many of these additional agents of change as possible.

Ecologists face difficult challenges in seeking to gain a better understanding of the impacts of increasing numbers of deer in woodland. Nonetheless, the changing patterns of grazing within our woods offer many opportunities to address absorbing ecological questions and to provide vital information that will help land managers tackle one of the major contemporary conservation issues.

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