Biodiversity in the New Forest

Edited by Adrian C. Newton





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Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset, United Kingdom



Newbury, Berkshire

Dedicated to the memory of Muriel Eliza Newton (1929–2009), who loved the New Forest, especially the donkeys.

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The maps in this book are for illustrative purposes only, and do not represent the legal definition of National Park boundaries or any other feature

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Contributors

Keith Alexander, 59 Sweetbrier Lane, Heavitree, Exeter, Devon EX1 3AQ.

Patrick D. Armitage, Freshwater Biological Association, Moor House, Field Station, Garrigill, Alston, Cumberland DL12 0HQ.

Andrew J. Barker, 13 Ashdown Close, Chandler's Ford, Eastleigh, Hampshire SO53 5QF.

Ian Barker, New Forest National Park Authority, South Efford House, Milford Road, Everton, Lymington, Hampshire SO41 0JD.

Samantha Broadmeadow, Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH.

Libby Burke, Forestry Commission, The Queen's House, Lyndhurst, Hampshire SO43 7NH.

Elena Cantarello, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Clive Chatters, c/o Hampshire and Isle of Wight Wildlife Trust, Beechcroft, Vicarage Lane, Curdridge, Hampshire SO32 2DP.

Greg Conway, British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU.

John Davy-Bowker, Centre for Ecology and Hydrology, c/o Freshwater Biological Association, East Stoke, Wareham, Dorset BH20 6BB.

Sarah Douglas, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Maxine Elliott, Environment Agency, Solent and South Downs Office, Colvedene Court, Colden Common, Hampshire SO21 1WP.

Naomi C. Ewald, Department of Biology and Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG.

David Green, Butterfly Conservation, The Cottage, West Blagdon, Cranborne, Dorset BH21 5RY.

Rachel Green, Natural England, 1 Southampton Road, Lyndhurst, Hampshire SO43 7BU.

Sue E. Hartley, Department of Biology and Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG. **Timothy Holzer**, Environment Agency, Solent and South Downs Office, Colvedene Court, Colden Common, Hampshire SO21 1WP.

John G. Jones, Centre for Environmental Sciences, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton, Hampshire SO17 1BJ.

Terry Langford, Centre for Environmental Sciences, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton, Hampshire SO17 1BJ.

Colleen Mainstone, Hampshire Bat Group, 42 Saxon Way, Halterworth, Romsey, Hampshire SO51 5QY.

Gillian Myers, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Adrian C. Newton, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Martin Noble, New Forest Ecological Consultants, Keepers Cottage, Holmsley, Burley, Ringwood, Hampshire BH24 4HY.

Andrew Page, Forestry Commission, The Queen's House, Lyndhurst, Hampshire SO43 7NH.

Bryan J. Pinchen, 7 Brookland Close, Pennington, Lymington, Hampshire SO41 8JE.

Rory Putman, Keil House, Ardgour by Fort William, Inverness-shire PH33 7AH.

Martin Rand, South Hampshire Vice-county Recorder, Botanical Society of the British Isles, email: vc11recorder@hantsplants.org.uk.

Neil A. Sanderson, Botanical Survey and Assessment, 3 Green Close, Woodlands, Southampton, Hampshire SO40 7HU.

Peter Shaw, Centre for Environmental Sciences, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton, Hampshire SO17 1BJ.

Jane Smith, Forestry Commission, The Queen's House, Lyndhurst, Hampshire SO43 7NH.

Rod Stern, British Bryological Society, 15 Selham Close, Chichester, West Sussex PO19 5BZ.

Alan J. A. Stewart, Department of Biology & Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG.

Natalia Tejedor, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

David J. Thompson, School of Biological Sciences, University of Liverpool, Crown Street, Liverpool, Lancashire L69 7ZB.

Stephen Trotter, New Forest National Park Authority, South Efford House, Milford Road, Everton, Lymington, Hampshire SO41 0JD. Lena K. Ward, 53 Miles Avenue, Sandford, Wareham, Dorset BH20 7AS.

Phillip C. Watts, School of Biological Sciences, University of Liverpool, Crown Street, Liverpool, Lancashire L69 7ZB.

Diana Westerhoff, Natural England, 1 Southampton Road, Lyndhurst, Hampshire SO43 7BU.

Simon Wotton, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL

14 The effects of grazing on the ecological structure and dynamics of the New Forest

Rory Putman

Introduction

While other chapters in this volume focus on particular habitats, species or species groups, and highlight their especial character, or value, one of the recurring themes in all such analyses is the unique character of the Forest; or, put another way, its essential oddness.

This, to me, is one of the main characteristics of the Forest (and one of its major interests to an ecologist): that the composition and dynamics of the woodlands are not quite like those of other, more 'normal' woodlands; the same might also be said of other habitats, such as heathlands and grasslands.

Aspects of this unique character include the following.

- The vegetation structure is unusual (both in terms of its physical three-dimensional structure and its age-structure).
- The age-structure of the trees in the ancient woodlands is bizarre. Instead of what might more normally be expected in a woodland, namely a continuous age-profile of trees of a whole range of ages, the Forest woodlands have a curiously discontinuous age-structure, consisting of trees that established in the 1750s, some from the late 1850s, some from the 1930s, and some more recently from the late 1980s (Peterken and Tubbs 1965, Putman 1986, 1996; see Chapter 13).
- Much of the Forest is nutrient-poor, but this is grossly distorted in most communities by nutrient dislocation and translocation (*sensu* Spedding 1971).
- Whether in woodlands or more open communities, there are virtually *no* small mammals at all, and a remarkable scarcity of resident predatory birds and mammals in terms of both number of species and density. Roe deer, until very recently, were declining sharply in numbers at a time when roe populations were expanding dramatically throughout the rest of southern England.

However, in adoption of the old philosophical device of taking an argument to extremes in order to expose weaknesses, or flaws of logic not apparent within more 'normal' boundaries, it is sometimes instructive to study such 'atypical' situations in more detail, for the insights they may offer into the underlying ecological processes. Therein lies a great deal of the Forest's interest (and charm!). For, in the case of the New Forest, its rather off-beat ecology is a reflection of some 950 years of heavy grazing by large mammalian herbivores – at levels that I believe are unique and probably higher than anywhere else in Europe. In this chapter, therefore, I want to take a somewhat wider perspective than have many of the other contributions to this book, and explore what have been the effects of this unbroken history of heavy grazing pressure on the wider ecology of the New Forest. In a sense, this chapter uses the Forest as a case-study to exemplify the effects of grazing and browsing by large herbivores on communities more generally. This review draws heavily on work undertaken by myself and my colleagues and students from the University of Southampton through the late 1970s and the 1980s, and summarises work already published elsewhere (e.g. Pratt *et al.* 1986, Putman 1986, 1996; Putman *et al.* 1987, Langbein and Putman 1999).

The vegetation of the New Forest

Perhaps only the English, with their unwitting natural irony, could have retained the name New Forest for an area that is neither new (it is one of the oldest seminatural areas of woodland in Great Britain, as well as one of the largest), nor what most would regard as a forest. It was 'New' only when it was first created as the latest in a series of 'Royal Forests' in the 11th century, and it is also a 'forest' only in the medieval sense of an area set aside as a Royal hunting preserve (and thus coming under Forest rather than Common law). In practice this 'New Forest' comprises a diverse mix of vegetational communities: only some 10,000 hectares (of a total administrative area at the current time of approximately 37,500 ha) are actually forested in the sense of covered with trees; the remaining area is a complex mixture of wet and dry heathlands, grasslands and bog (see Chapter 12), all patchworked together into an intimate mosaic.

Heavily leached and base-poor plateau gravels are widespread, particularly to the north, and support a Calluna-dominated dry-heath community. At lower altitudes, and where the plateau gravel has been eroded, more fertile clays and loams support mixed deciduous woodland. These are predominantly of beech and oak, with an understorey of holly; common bent Agrostis capillaris colonises the woodland floors in openings and glades. Many of the more fertile woodland sites have been enclosed over the past 100 years and now support commercial plantations, which are largely coniferous (see Chapter 13). Also common on these more fertile soils are a range of natural acid-grassland communities, dominated by the coarse bristle bent Agrostis curtisii and to a lesser extent by the purple moor-grass Molinia caerulea, usually also colonised to a greater or lesser extent by bracken Pteridium aquilinum and often by extensive brakes of gorse Ulex europaeus.

Where drainage is impeded on the lower slopes, domination of the heathland community by *Calluna* is reduced and the species diversity of the whole heathland increases. A clear gradation is observed from the dry-heath association through humid and wet heath, with increasing abundance of cross-leaved heath *Erica tetralix* and purple moor-grass and the appearance of true wetland plants such as bog asphodel *Narthecium ossifragum* and *Juncus* species. This progression frequently ends in the development of a bog community.

The valley bogs offer some of the richest communities in the New Forest in terms of plant diversity, and are one of the formations unique to this area. The species composition varies considerably in relation to the degree of eutrophication and several distinct communities may be recognised. Perhaps the most widespread in base-poor water is that dominated by tussocks of purple moor-grass with common cottongrass Eriophorum angustifolium and Sphagnum mosses abundant between the tussocks. In many heathland catchments, carr woodland communities develop in the valley bottoms where drainage waters have a definite axis of flow. These carrs are composed of willows, alder buckthorn Frangula alnus, alder Alnus glutinosus and other tree species, and have a diverse herb layer including the greater tussock-sedge Carex paniculata.

In areas that are well drained by one of the many small streams that dissect the Forest, the bogs are replaced, and the heathland progression terminates abruptly at the edge of alluvial strips bordering the streams. These alluvial deposits are covered by grassland, often dominated by velvet bent *Agrostis canina*, interrupted with patches of riverine woodland. These streamside lawns are particularly nutrient-rich because of regular annual flooding from the rivers they border, which carry base-rich compounds from north of the Forest area.

Very little of the New Forest vegetation can be considered as entirely natural, and most areas have at various times been subjected to management by people. Heathland communities, for example, were created originally by extensive livestock grazing, but nowadays are maintained in a programme of regular cutting or controlled burning, so that any extensive area of heath contains a patchwork of sub-communities from 0 to 15 years of maturity. Woodlands, even ancient deciduous blocks, are commonly of artificial structure and origin, planted initially by people for timber production, even if subsequently left more to processes of natural regeneration and decay. The 8,000-odd hectares of commercial coniferous forest established mostly in the past 100 years are clearly also of entirely artificial origin.

In addition there are other distinct communitytypes of anthropogenic origin. A number of areas of the natural acid grassland of the Forest were fenced during the Second World War, ploughed, fertilised and cropped for potatoes or oats. At the end of the War, these areas were reseeded with a commercial ley, and after the grassland had become established, the fences were removed to return these reseeded areas to the Forest grazing. In the late 1960s and early 1970s a number of other attempts were made to improve the Forest grazing, by clearing bracken from other areas of acid grassland and liming them. These improved areas once again form a distinct and characteristic plant community.

The Forest's large herbivores and their management

At least 2,500 wild deer currently have access to the entire New Forest (Table 34).

Of the four main deer species present on the Forest today, red deer *Cervus elaphus* and sika deer *Cervus nippon* populations are of relatively recent origin and are essentially local in distribution. Populations of these species are restricted to relatively limited areas of the Forest, although both are currently expanding their range. Roe deer *Capreolus capreolus* are distributed more widely, but the distribution is patchy and they are everywhere uncommon. Fallow deer *Dama dama* are both widespread and abundant. Reeves muntjac *Muntiacus reevesi* are also more regularly reported, but numbers are thought to be low and as yet they have had no pronounced impact upon the Forest vegetation.

Fallow deer have long been the dominant deer species within the Forest; indeed William I's declaration of the area as a Royal Forest was chiefly to conserve hunting interests for this species. It is difficult to assess what numbers may have occurred on the Forest at that time. The earliest complete 'census' is that of 1670, when the Knights Regarder charged with administration of the Forest returned an estimate of 7.593 fallow deer and 357 red deer within the Forest boundaries. (Painfully aware myself of the difficulties of assessing population sizes of any deer species in a huge area of difficult terrain, and the lengthy debates in the literature about the accuracy and application of alternative survey methods, I cannot help but marvel at the delightful precision of these figures, and take them with a pinch of salt!).

A government report of 1789 gave a more global estimate of the average number of fallow deer present as 5,900 and numbers seem to have remained at roughly

Table 34

Current numbers of different deer species in the New Forest, in relation to recommended sustainable population size.

| Species | Recommended sustainable population size (after Putman & Langbein 1999) | Estimated current numbers (2004/5) in the Crown lands (after Forestry Commission 2007) |
|-------------|--|--|
| Fallow deer | 1,200 | 1,728 |
| Red deer | 100 | 183 |
| Sika deer | 100 | <100 |
| Roe deer | Up to 400 | 468 |
| Muntjac | Prevent population establishment | Not censused, but numbers appear to be increasing |

this same level until the 1850s. In 1851, the New Forest Deer Removal Act, in relinquishing the Crown's rights to an exclusive hunting reserve, provided for the 'removal' of all deer from the Forest within three years of the enactment. Total extermination of such a large population of animals, scattered over so large an area, was of course as impracticable as a precise count, but numbers were certainly dramatically reduced and population estimates in 1900 gave a figure of 200 head (Lascelles 1915). Since that time the population has gradually expanded and is now maintained by culling at a level that has been estimated at about 2000 animals (Putman and Sharma 1987, Putman and Langbein 1999; Table 34).

Red deer were also established in the New Forest at the time of the Conqueror, but numbers were always substantially lower than those of fallow, and the population throughout seems to have been barely selfsustaining. Populations have indeed continuously been 'subsidised' by introductions, not merely in an attempt to improve the perceived 'quality', but also simply to bolster numbers. Both James I and Charles II introduced fresh blood from France, Charles II importing no fewer than 375 red deer that were released near Brockenhurst in the south of the Forest. Further introductions continued throughout the 19th century and even into the early 20th century.

Census records are patchy. During Henry VII's reign there were several records of red deer being killed within the Forest; the Regarders' survey of 1679 estimated numbers at 357, with 103 male and 254 female deer. By the late 18th century, however, the Forest's red deer population was almost certainly extinct; certainly returns of 1828–1830 of deer in Royal Forests omit any mention of red deer within the New Forest. References to sightings in the 19th century probably relate to escapes from nearby deer parks, and in the past 200 years numbers have probably never exceeded 80–100 animals. Current populations derive in the main from reintroductions to two distinct areas of the Forest in the 1960s.

Roe may also be presumed to have been native in the New Forest area, but by medieval law, red deer were beasts of the Forest (reserved for Royalty), whereas fallow and roe, the lesser beasts of the 'Chase', were generally less jealously protected. During the Middle Ages roe deer became virtually extinct throughout England and much of Scotland. As with the red deer, modern populations of roe in southern England have resulted from reintroductions of animals into several areas during the 19th and 20th centuries (Prior 1973). Roe recolonised the New Forest from 1870 onwards, spreading across from Dorset (Jackson 1980). Census figures suggested a population of perhaps 400–500 animals in the early 1970s; for a period thereafter numbers declined substantially to really very low values (estimated in 1990 at between 250 and 350 animals across the whole of the Forest). Populations are now showing some recovery but are still somewhat patchily distributed within the Forest.

Sika deer are a much more recent and completely exotic introduction to the New Forest. Sika were first

introduced to Great Britain in the 1860s and to the New Forest in the early 1900s. Current populations are descended from animals that escaped from a collection in the nearby Manor of Beaulieu. For many years they were restricted to a small area in the south of the Forest. an area seemingly bounded to the north by a major railway line, by the sea to the south, and to the east and west by the waters of the Beaulieu and Lymington Rivers. These boundaries were hardly impassable, at least those to the north and west. Populations were contained until perhaps the late 1970s or early 1980s, but by the late 1980s, increasing reports were made of sika spreading beyond this initial localised area. By the late 1980s numbers were assessed as in excess of 200-300 animals, and while still restricted to the southern part of the Forest, sika were recorded over a far more extensive range. Numbers were reduced by heavy culling in the late 1980s and are now held at approximately 100.

As an aside here, we may note that recent DNA analysis of samples of both sika and red deer taken from the New Forest confirmed that current populations of red deer were of fairly mongrel origin (as would be expected for a population derived from introductions from various sources), but offered no evidence for recent hybridisation with sika deer (Diaz et al. 2006). Further analysis (using STRUCTURE, a procedure that calculates the proportion of the DNA profile that is sika and red deer DNA) detected low-level hybridisation, with presence of at least some red deer genetic 'markers' in 12.5% of sika deer from the Purbeck region of Dorset, while only 3.7% of New Forest sika contained any red deer markers (Diaz et al. 2006). These small, but perhaps important, genetic differences between the populations support the earlier deduction based on cranial morphometrics (Putman and Hunt 1994) that New Forest sika may be more pure genetically than other populations of feral sika in Britain.

Domestic animals (chiefly cattle and ponies) have of course also been depastured on the Forest alongside the deer, ever since its designation as a Royal Forest, and probably considerably before that time. One of the concessions granted to the local populace after the declaration of the area as a Royal Hunting Forest, was the right of Common Grazing. On the payment of an appropriate 'marking fee', local cottagers and farmers could turn out cattle and horses to exploit the rough grazing of the Forest lands. These rights are still honoured and large numbers of cattle and ponies are regularly pastured at free range upon the Forest grazings. Ancient rights of 'pannage' also provide for the turning out of pigs into the Forest's woodlands for a restricted period in the autumn, to feed upon the rich crop of tree-fruit: acorns and beechmast. Small numbers of sheep and donkeys are also pastured under Common Rights in small areas of the Forest.

The numbers and relative importance of all these herbivores have fluctuated over the years (Tubbs 1986). However, in the past numbers of domestic livestock were probably much lower than at present, and in addition a far larger area of land was unenclosed and available for common grazing (Putman 1986, 1996). As a result, the impact of the common stock was historically probably secondary to that of the deer. Throughout this time, the deer would have been predominantly fallow, with at most a few hundred red deer. At the end of the 19th century, however, the area was 'disafforested'; with the passing of the Deer Removal Act in 1851, deer populations were decimated and have only recently recovered to their present numbers. With the reduction of numbers of deer and simultaneous increased effective density of domestic stock, cattle and ponies emerged as the major grazing influence on the Open Forest and have remained so to this day.

The impacts of grazing on the fauna and flora

Some seven species of large ungulate co-occur within the boundaries of the New Forest, giving it not only an unusually high biomass of grazing herbivores, but also a remarkably high diversity of species. Whether by deer or domestic stock, the New Forest area has always sustained a tremendous grazing pressure from large herbivores. At present, 20,000 ha of some of the poorest possible grazing (current land-use survey maps class the majority of the area as grade 5, or non-agricultural land) support a total large herbivore biomass in excess of 2,500 tonnes (Putman 1996), and it is clear that equivalent grazing pressure must have existed over the centuries.

This history of continued grazing has stamped its mark on the Forest vegetation, and indeed the current ecology of the open ground outside the Forest enclosures can in my view *only* be correctly interpreted in relation to the various effects of past and present grazing. Any attempt to explain the ecology of the Forest – in accounting for the curious lack of diversity of many of the vegetational systems, the low numbers and diversity of small mammals, curious behaviour of birds of prey and other predators – forces the attention back to the dominating effect of grazing in the shaping of this ecosystem.

The effects of grazers and grazing upon vegetational systems in general are far-reaching. Grazing may directly affect the species composition, diversity, productivity, and even physical architecture of the plant community. Patterns of foraging, trampling and elimination may affect nutrient dynamics and patterns of nutrient flow, with further implications for plant species composition, distribution and productivity. In addition, effects of grazing are not limited to an influence on vegetational structure and dynamics. Through their impact on the composition and productivity of the vegetation, herbivores immediately have a secondary and equally significant influence upon all other animals dependent on that same shared vegetation, affecting the composition and dynamics of the entire community.

Almost all of these effects may be registered within the various communities of the New Forest. None of these effects is of course unique to the New Forest: equivalent examples of the effects of grazing upon the structure and species composition of vegetation are legion, and are extensively reviewed elsewhere (e.g. Putman 1994, Gill and Beardall 2001). 'Knock-on' effects of such changes upon other herbivores or their predators are also increasingly commonly reported (e.g. Petty and Avery 1990, Stewart 2001, Feber *et al.* 2001, Flowerdew and Ellwood 2001, Fuller 2001). But what is perhaps unusual is that in the New Forest, all of these various changes are clearly documented within a single system. Analysis of the ecological dynamics of this one site allows us to clearly illustrate all of the potential effects of heavy grazing within the one area.

Changes in species composition

Clear changes in species composition in response to grazing, with selective elimination of species particularly sensitive to defoliation, or others more tolerant but heavily preferred, are apparent in most of the Forest communities. This is accompanied by a gross shift in community structure towards those species that are in some way more resistant to, or tolerant of grazing impact. Such changes may be recorded quite quickly, as in the grassland areas ploughed and reseeded ('reseeded lawns') after the Second World War and only opened to the Common grazing in the early 1960s (Pickering 1968, Putman et al. 1981, Putman 1986). Significant changes were already apparent in the species composition of the sward by the mid 1960s, and certainly by the end of the 1980s. This resulted in the establishment at equilibrium of communities dominated by stoloniferous grasses (such as common bent) and prostrate or rosette-forming herbs such as daisies Bellis perennis, cat's-ear Hypochaeris radicata or ribwort plantain Plantago lanceolata, which by their growth form are more able to withstand or escape grazing (Table 35).

Species composition and horizontal patterns of distribution within these same grassland communities are also affected by clear 'dislocation' of nutrient

Table 35

Percentage cover of Long Slade reseeded lawn in 1963 and 1979, by comparison to the proportional composition of the seed mixture applied in 1958. Data for 1958 and 1963 from Pickering (1968); data for 1979 from Putman *et al.* (1981). This table presents only a summary; more detail is presented as Table 7.13 in Putman (1986).

| | | 1958 | 1963 | 1979 |
|-----------------------------|----------------------|------|------|------|
| Grasses Agrostis capillaris | | - | 47.8 | 51.0 |
| | Dactylis glomerata | 58 | 6.8 | 2.4 |
| | Festuca rubra | - | - | 2.9 |
| | Lolium perenne | - | 2.0 | 2.5 |
| | Vulpia bromoides | - | 5.3 | 0.1 |
| | Other grass species | - | 5.5 | 4.3 |
| Forbs | Bellis perennis | - | 4.7 | 6.3 |
| | Hypochoeris radicata | - | 3.2 | 3.8 |
| | Leontodon autumnalis | - | 3.7 | 1.8 |
| | Plantago lanceolata | - | 0.3 | 7.4 |
| | Trifolium pratense | 10 | 0.6 | 0 |
| | Trifolium repens | 32 | 12.8 | 3.2 |
| | Other forbs | - | 5.9 | 6.0 |
| | | | | |

Figure 64

A schematic representation of the mosaic of grazing and latrine areas on a reseeded lawn (redrawn after Edwards and Hollis 1982). Areas grazed by ponies (with grass usually too short to be grazed by cattle) extend to 38% of the total area (illustrated in black), while pony latrines (areas also grazed by cattle) cover 62% of the area (illustrated in white).

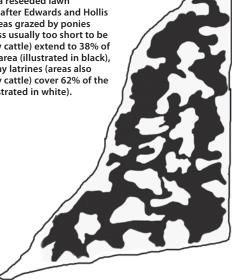


Table 36

Differences in the species composition of pony-grazed and latrine areas in reseeded lawns (from Putman et al. (1981) and Putman (1986)).

| Status | Species | % age cover in latrines | % age cover in grazed areas |
|------------------------------------|--|-------------------------------|--------------------------------------|
| Confined to latrines | Cirsium arvense Cirsium vulgare Senecio jacobaea | | - - - |
| More abundant in latrine areas | Hypochoeris radicata | 7.7 | 4.8 |
| | Lolium perenne | 2.2 | 0.3 |
| | Trifolium repens | 5.3 | 1.3 |
| More abundant in pony-grazed areas | Poa compressa | 1.8 | 2.8 |
| | Sagina procumbens | 1.2 | 2.2 |

Table 37

Species composition of trees and shrubs in two woodland enclosures: one grazed, one ungrazed (from Mann 1978). Data shown as number of trees or saplings per 10 m-radius circular plot.

| Species | Grazed | Ungrazed | |
|--------------------|--------|----------|--|
| Fagus sylvatica | 2.5 | 22.4 | |
| Quercus sp. | 1.8 | 12.9 | |
| Pinus sylvestris | 1.0 | 43.3 | |
| Betula sp. | 0.3 | 65.3 | |
| Salix sp. | 0 | 23.8 | |
| llex aquifolium | 0 | 17.1 | |
| Ulex europaeus | 0 | 19.7 | |
| Crataegus monogyna | 0 | 1.0 | |
| Prunus spinosa | 0 | 0.6 | |

return, whereby feeding patterns of the various large herbivores result in a very patchy and discontinuous return to the system of abstracted nutrients. Animals that forage over a relatively wide area but defaecate in a smaller area can have a substantial impact on local nutrient availability. Sheep, for example, graze widely over a pasture during daylight hours but congregate in camps at night or for shade. In consequence 35% of their faeces are deposited on less than 5% of the grazing area, resulting in a gradual impoverishment of the wider grazing range but continued enrichment of small areas within it (Spedding 1971). These patterns of grazing and elimination result in the development of a fine-scale heterogeneity of species associations within swards grazed by sheep (Bakker et al. 1983 a,b).

Such 'nutrient dislocation' has also been recorded for horses (Archer 1973, Edwards and Hollis 1982), which establish distinct and fixed grazing and latrine areas in different parts of their foraging range. Edwards and Hollis (1982) showed that free-ranging ponies of the New Forest, like their more domesticated counterparts in fields, established within their grazing grounds distinct and traditional sites for grazing and for elimination. The animals cropped swards close in areas selected for grazing, and undertook specific and purposeful movements away from these areas to defaecate and urinate in traditional latrine sites, within which they did not graze except in occasional periods when other forage was extremely scarce.

These traditional latrine sites were fixed and persisted in the same areas for year after year (Figure 64), establishing a clearly non-random pattern of return of nutrients within the community that was not masked or reversed by the activities of other grazers. Although cattle and deer also utilised these Forest grasslands, their feeding was restricted to the pony latrines. With incisors in both upper and lower jaw, the ponies can crop the sward in grazing areas so close that ruminants such as cattle or deer cannot themselves utilise those patches. Neither cattle nor deer establish distinct latrine and grazing sites. Both dung wherever they happen to be at the time, and since they spend most of their time grazing within the pony latrines, their dung, too, accumulates in these latrine sites.

Over time this dislocation in nutrient return even within a single community leads to continued impoverishment of pony-grazing areas and continuous nutrient enrichment of latrines. Already, in grasslands ploughed and reseeded after the War, consistent differences are recorded in the potassium and phosphorus content of soils, with nutrient concentrations being higher in the latrine areas by a factor of about 1.2 (phosphorus) to 1.7 (potassium) (Putman et al. 1981). Organic matter content of latrine areas is also consistently a little higher. Differences between latrine and non-latrine patches reflect both the nutrient status and grazing regime experienced (given that plants growing in pony grazing areas are subjected to a closer cropping than those in latrine areas foraged only by cattle or deer). Such factors have led to significant differences in species composition, producing a fine-scale mosaic in species associations

across the sward. Species such as ragwort *Senecio jacobaea*, spear thistle *Cirsium vulgare* and creeping thistle *Cirsium arvense* occur only in latrine areas, and other species are more or less abundant in latrine or heavily grazed patches (Putman 1986, Ekins 1989) (Table 36), although it is hard to be certain that this is solely the result of differences in soil nutrient status rather than in some part to differences in the grazing regime experienced.

Within the Forest woodlands, the effects of grazing are even more apparent. There are differences in the species composition of the ground flora of grazed areas equivalent to those observed in open, grassland communities, with a similar shift towards species of prostrate growth form in heavily-grazed areas (Putman 1986, Putman et al. 1989) (Table 37). The most dramatic and obvious effects of the heavy grazing pressure can be seen within the shrub layer (see Chapter 13). Within unfenced woodlands, there is a stark absence of understorey species such as hazel *Corylus avellana*, birch *Betula* sp., blackthorn *Prunus* spinosa, hawthorn Crataegus monogyna, bramble Rubus agg. or dog-rose Rosa canina. These are shrub-layer species that would be expected and that indeed form a dense understorey in woodlands just beyond the proverbial Forest Fence, where grazing pressure is more moderate. The shrub layer in effect is represented only by the unusually abundant hollies *Ilex aquifolium*, which provide a classic illustration of the separate phenomenon of competitive release. This refers to the situation under intense grazing pressure, where palatable species will ultimately be eliminated, causing a release from competition for those species that are very tolerant of defoliation, permitting an expansion in range and abundance of species that have specific defences against herbivory.

Such changes in species composition and growth form, as well as the continued imposition of grazing, have clear effects on the physical structure of these same communities. New Forest grasslands boast little vegetational material higher than a few millimetres, even in the height of summer, for taller vegetation is immediately cropped. Such grasslands clearly lack many of the possible structural layers of mature, ungrazed grasslands. On heathlands, too, the effects of grazing are very clear in this reduction of structural diversity. Heathlands in southern Hampshire generally support dense stands of purple moor-grass among the Calluna and Erica heaths. Outside the Forest boundary, the flower spikes of purple moor-grass tower above the canopy of the heather plants and provide a whole additional structural element within the vegetation. Inside the Forest, this whole stratum is missing. Purple moor-grass is just as abundant within the heathlands, but it is an important component of pony diet and the plants are always heavily grazed - and kept well below the heather canopy.

Once again the change in species composition, and the continued effects of browsing, are strikingly obvious in the three-dimensional structure of the Forest's open woodlands. The effects of centuries of heavy browsing pressure are so marked that New Forest

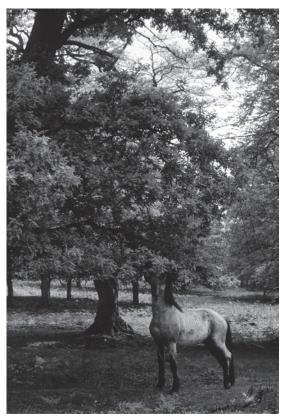


Plate 8

Heavy browsing pressure, especially by cattle and ponies, eliminates most of the understorey in woodlands and establishes a clear browse line at around 1.8 metres.

woodlands virtually lack *any* ground, field or shrub layer; and indeed the whole structural 'layer' between ground level and the clear browse horizon at 1.8 m is almost completely missing (Plate 8).

With this obvious change in woodland architecture comes another effect, which is less apparent. Under centuries of heavy grazing pressure, not only have many species of the field and shrub layers been eliminated, there has also been a virtual lack or regeneration of any of the canopy tree species in unfenced woodlands (but see Chapter 13). With pigs turned out to help the deer clear up the mast, and deer and ponies to graze upon such tree seedlings as do germinate, few trees tend to survive beyond the seedling stage. In what has become a classic analysis, George Peterken and Colin Tubbs (1965) noted that in consequence, the Forest woodlands present a most peculiar age-structure, composed largely of trees established in particular periods where, for one reason or another, browsing pressure was reduced (see Chapter 13).

Effects of grazing on the Forest fauna

All of these various effects upon the vegetation, upon species composition, productivity and physical

architecture, clearly affect the resources offered to other animals dependent on that same vegetation for food, shelter or cover from predators. The diversity and species composition of invertebrates in any community has been shown to have a strong correlation with diversity of vertical structure within the vegetation as well as spatial heterogeneity (Southwood *et al.* 1979). Clear responses to a change in grazing regime have been recorded in the invertebrate fauna characteristic of particular communities, particularly among beetles and butterflies (eg. Putman *et al.* 1989, Stewart 2001, Feber *et al.* 2001; see also Chapter 7).

Similar effects are recorded in other animal groups. The New Forest again offers excellent example of the knock-on effects of the vegetational changes resulting from centuries of heavy grazing on populations of mice, voles and shrews. Work undertaken in the early 1980s, by Steve Hill as part of his PhD research, compared the species diversity and population sizes of these small mammals within the Forest with those recorded in equivalent vegetation types in areas outside the Forest boundary (grazed by deer but not by domestic livestock). This revealed striking and consistent differences (Hill 1985, Putman 1986, Putman et al. 1989). All ungrazed woodland areas studied supported substantial populations of woodmice Apodemus sylvaticus and bank voles Clethrionomys glareolus, with lower densities recorded of yellow-necked mice Apodemus flavicollis, and both common and pygmy shrew Sorex araneus, S. minutus. Rodent communities of grazed woodlands within the Forest were characterised by healthy populations of woodmice, but all other species were rare or absent (Hill 1985). What is interesting however is that those species that do occur (Apodemus in woodlands) seem to manage to maintain density and dynamics equivalent to those recorded in ungrazed sites (see also Flowerdew and Ellwood 2001).

Forest heathlands and grasslands are equally profoundly affected by grazing; the physical structure of these open vegetation types displays, as we have already noted, marked contrast with heathland or acidgrassland sites not subject to heavy grazing. The reduced structural 'depth' provides scant cover from predation. While heathland plots beyond the Forest boundary supported large, permanent populations of woodmice and harvest mice *Micromys minutus*, and grasslands in turn supported strong populations of woodmice and field voles *Microtus agrestis*, small mammals were virtually completely absent from open communities within the Forest itself (Hill 1985).

Responses to grazing of this kind illustrate very clearly that an increase in grazing intensity in any ecological system will have implications far beyond the immediate consequences for the vegetation itself or upon direct competitors. Indeed, these 'knock-on' effects have repercussions throughout the entire community. The effects of grazing may be seen to have consequential effects on the abundance and behaviour of higher order predators, neither directly linked to the dominant herbivores, nor themselves directly affected by the changes in the vegetation, but influenced by secondary changes in the abundance of prey or competitors. Within the New Forest, the reduced diversity and overall abundance of small mammals in the heavily grazed woodlands and open 'wastes', have been shown in their turn to have had an effect on the species composition and foraging behaviour of the Forest's predators (see Chapter 1).

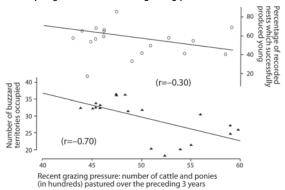
Two independent studies of the diets of foxes *Vulpes vulpes* within the New Forest (Senior, unpublished data quoted in Putman 1986; Farley 1986) reveal that while New Forest animals did consume small rodents when available, the frequency and relative proportion in the diet was lower than that recorded in other areas. Few birds were taken and the foxes clearly relied heavily on invertebrate material (particularly earthworms and beetles), carrion and autumn fruit. Perhaps in response to scarcity of prey, the overall density of foxes within the Forest is also unusually low, estimated as only 2 per km², with an adult density of 0.75 per km² (Insley 1977).

Avian predators are also affected by the low rodent abundance (see Chapter 1). Colin Tubbs (1974) first noted that there seemed to be a close correlation between the breeding success of buzzards Buteo buteo in the New Forest and population density of grazing cattle and ponies. Tubbs noted that in the New Forest, as in other parts of England where rabbits are not readily available, buzzards appear to rely very heavily upon rodent prey and breeding success is directly related to the abundance of such rodent prey. Although he had no direct data on the changing abundance of small mammals within the Forest over the years, he nonetheless showed a clear correlation between the number of buzzard pairs attempting to breed in any year and the numbers of domestic stock grazed on the Forest over the preceding three years (Tubbs and Tubbs 1985) (Figure 65).

Similar effects have been demonstrated by Graham Hirons, who examined diet and breeding success of

Figure 65

Relationship between grazing pressure on the New Forest and breeding success of buzzards (based on data from Tubbs and Tubbs 1985). Note that while success of nests, once a breeding attempt has started, shows no significant effect of grazing pressure, the actual number of buzzard pairs attempting to nest declines as grazing pressure increases.



other raptors within the Forest whose diets would normally be expected to contain high numbers of rodents. Tawny owls Strix aluco are very much woodland predators (and it is within the woodlands of the Forest, of course, that changes in rodent abundance are least extreme). New Forest owls continued to maintain a high proportion of rodent prey within the diet, although this was almost exclusively woodmice (Hirons 1984). This contributed only 42% of all prey taken, however (as against 60%-70% recorded from studies elsewhere). New Forest owls compensated with increased reliance on invertebrate prey, particularly dor beetles (Geotrupes and Typhoeus species), which contributed a surprisingly high proportion of the prey taken, especially over winter when they accounted for some 60% (by mass) of the total diet. In response to the comparative scarcity of rodent prey, Hirons noted a significant reduction in density of owls overall and a reduction also in the proportion of pairs breeding in any year (25% in the Forest as against 65% of pairs in areas outside; Hirons 1984).

Kestrels Falco tinnunculus also characteristically take a significant amount of mammalian prey. Bank voles and field voles together made up 73% of all vertebrate prev taken by kestrels in the population in the Lake District studied by Yalden and Warburton (1979). By contrast, mammalian prey only contributes 30.5% by mass of vertebrate prey taken by New Forest kestrels, with the shortfall made up by greater reliance on birds and, unusually, by extensive predation on common lizards Zootoca vivipara (Hirons 1984). Once again, shortage of high quality rodent prey has implications for population density and productivity; in 1982 and 1983 densities of kestrels within the New Forest were one pair per 16 km² or less, compared to a figure of one pair on average per 4 km² in farmland outside the Forest boundary (Hirons 1984).

Conclusion

The aim of this chapter is, specifically, to review the effects of grazing and browsing animals on the overall ecology of the New Forest. As already noted, none of these effects of grazing is unique to the Forest and a more general review of the 'effects of grazing and browsing by large herbivores on ecological systems in general' would of course make far wider reference to other comparable studies (e.g. Putman 1986, 1994, Gill and Beardall 2001, Petty and Avery 1990, Stewart 2001, Feber *et al.* 2001, Flowerdew and Ellwood 2001, Fuller 2001). But what is unusual is that in the New Forest all of these potential impacts and reactions are so clearly documented within a single system, and that the effects of its long history of heavy grazing do so profoundly affect all aspects of the Forest's ecology.

Through a combination of social and economic reasons, the numbers of cattle and ponies turned out onto the Open Forest have varied somewhat in recent years and the particular geographic areas subjected to greater or lesser commoning activity have also tended to fluctuate. The Forestry Commission's New Forest

Management Plan (see Chapters 19 and 20) includes proposals for conversion of many former (fenced) plantation areas back to open heath, a process which has already been embarked upon in a number of areas. The Plan also provides for the restructuring of other areas of planted coniferous forest to native broadleaved woodland. These changes will undoubtedly have a marked effect on the proportional availability of different habitats in different parts of the Forest, and the relative disposition of those habitats in relationship to one another. In turn this is likely to have a significant effect on the distribution of both deer and commoners' livestock across the Forest, with the implication that some areas may see a gross reduction in usage (and correspondingly, impact), while other areas may see some increase. In addition, since 2000, the Forestry Commission have made concerted efforts to reduce numbers of deer (particularly fallow) in the forestry enclosures, to try and reduce impacts on the ground flora and shrub layer. Given how much the wildlife and the ecology of the Forest has been influenced by the heavy grazing of the past, it will be interesting to see how that wildlife now responds.

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