

# The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research

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## *Summary*

Direct and indirect impacts of deer on invertebrates in lowland deciduous woodland are reviewed with particular reference to Britain. The evidence overwhelmingly indicates that deer grazing and browsing can have a very profound impact throughout the woodland ecosystem, including on invertebrates. Under certain circumstances, deer may be regarded as direct competitors with insect herbivores for plant biomass. However, more usually impacts will be indirect and mediated through changes in the structure, species composition and quality of the vegetation. The capacity of deer browsing activities to alter radically the species composition of the vegetation will have a major effect on the associated community of herbivorous insects. Whilst excessive deer densities will have detrimental effects on woodland biodiversity, including invertebrates, by inhibiting regeneration and removal of the understorey, some browsing will help to create and maintain open areas within woodland and arrest succession in rides and clearings. This will be beneficial for thermophilous insect species and those that require flowers for nectar and pollen. Evidence on how invertebrates respond to the regrowth foliage that is produced after deer damage remains equivocal but is an important question for future research. Deer also have a direct effect on the dung-associated invertebrate fauna that, in turn, provides an important food source at critical times of year for certain bird and bat species. Emphasis is placed on the importance of a multi-trophic approach in future studies of how deer interact with other components of the woodland ecosystem.

## **Introduction**

Herbivory by large vertebrates, including deer, has always been an important process in the ecology of lowland woodlands in Britain (Putman, 1996). Paradoxically, given the focus of this paper, they remove a far smaller proportion of the woodland annual primary productivity

than their invertebrate herbivore counterparts (Putman, 1986; Packham *et al.*, 1992). Nevertheless, evidence for considerable recent expansions in both population numbers and geographical range of several deer species in lowland Britain has drawn attention to the impact that they can have on various semi-natural habitats, especially mixed deciduous woodland (Putman and Moore,

1998). Their physical size and potential population density mean that the impact of deer on their food supply can be profound. The consequent changes in the vegetation would be expected to have knock-on effects throughout the woodland ecosystem. This review focuses primarily upon likely impacts on lowland mixed deciduous woodland in Britain; similar principles probably apply to other woodland types in Britain, although they have received rather less research attention.

There are four primary ways in which deer may affect invertebrates: (1) through direct competition with herbivorous invertebrates for plant food, (2) indirect effects brought about through changes in the species composition, biomass or quality of the vegetation, (3) indirect effects resulting from modifications to the physical structure of the habitat, and (4) direct effects on communities of deer commensals and parasites and on coprophagous invertebrates associated with deer dung. The precise nature and strength of all of these effects will depend upon the species of deer involved and their population density. Impacts on invertebrates may be detected as effects on population densities or changes in the structure (e.g. richness and diversity) or species composition of whole communities.

Invertebrates are an important, but somewhat neglected, component of the lowland woodland ecosystem. In terms of abundance, the group ranges from rare species that are of concern to conservationists, through species that are dominant components of the woodland community and are therefore important contributors to major woodland processes (e.g. herbivory and decomposition), to species that are considered pests by virtue of the damage that they can do to commercial forestry interests. This review concentrates on the potential impact of deer grazing and browsing on the non-pest species of invertebrate; this is not because impacts on pest invertebrate species are considered to be insignificant, but merely because this topic has received hardly any research attention.

Lowland mixed deciduous woodland is an important habitat for invertebrates, mainly because the structural complexity and species richness of the vegetation provides many niches for a large number of species; it is one of the most species-rich habitats for invertebrates in Britain

(Kirby, 1992a). A significant proportion of these species are rare, and in some cases endangered, having undergone widespread declines in both population numbers and range in the last 50–100 years (Warren and Key, 1991). These changes have resulted partly from the destruction and fragmentation of key sites, but also from the decline or abandonment of traditional woodland management practices such as coppicing. It is noticeable, and relevant to this review, that the rarest invertebrate species in woodlands tend to be associated with the opposite ends of the successional spectrum: open clearings and areas of comparatively bare ground within woodland, and mature or over-mature habitats, especially dead and decaying wood (Thomas and Morris, 1994).

### Evidence from experimental exclosures

Whilst there have been many attempts to demonstrate the effects on vegetation of relief from deer grazing and browsing using experimental exclosures, few such studies have included any examination of responses in the associated fauna. However, the following examples of where effects on invertebrates were examined are instructive.

The Denny Pens experiment in the New Forest, Hampshire, compared two 5.6 ha exclosures, one from which all large herbivores including deer were excluded and the other in which a small captive population of fallow deer (*Dama dama*) was maintained. The density of animals in the latter was excessively high (the equivalent of ~100 deer km<sup>-2</sup>), so that the remarkable differences in the vegetation and fauna between the two plots after 22 years (Putman *et al.*, 1989) illustrate responses to extreme grazing and browsing pressure rather than the norm. Nevertheless, results from this experiment are useful in providing clues to the type of impacts that deer will have.

The grazed plot was characterized by complete lack of tree regeneration, removal of most understorey species and a shift in the composition of the field layer towards light-demanding and unpalatable plant species. By contrast, relief from grazing in the adjacent plot allowed rapid regeneration and a succession to dense scrub. After 22 years, the exclosures had also developed contrasting communities of ground-dwelling invertebrates.

Amongst the ground beetles (Carabidae), *Pterostichus madidus* was significantly more numerous in pitfall trap catches in the grazed enclosure compared to the ungrazed one (a ratio of 192 : 125 individuals) and *Nebria brevicollis* was confined to the grazed enclosure (80 : 0). By contrast, *Abax parallelepipedus* and *Carabus violaceus* were significantly more numerous in the ungrazed enclosure (127 : 329 and 23 : 44, respectively) (R. How, unpublished data). These results reflect the basic ecologies of the species involved; all four are habitat generalists, but *Abax parallelepipedus* and *Carabus violaceus* are particularly associated with closed woodland and more dense ground cover (Greenslade, 1964; Thiele, 1977; Forsythe, 1987).

Where deer selectively eat one particular food plant, invertebrates associated with that species will inevitably suffer. Baines *et al.* (1994) found that grazing by red deer (*Cervus elaphus*) in Scottish native pinewoods decreased the ratio of heather (*Calluna vulgaris*) to grasses in the field layer and reduced both the height and biomass of bilberry (*Vaccinium myrtillus*) to half that in experimental enclosures. Numbers of invertebrates swept from bilberry were invariably higher inside grazing enclosures, a result that was consistent both across a range of taxonomic groups and across eight sites. The fact that lepidopterous larvae, which comprised 60 per cent of all invertebrates caught, were four times more numerous in the absence of deer grazing (i.e. far more than predicted simply by differences in plant biomass) may be explained by the selective removal of the growing tips of the bilberry by the deer; in this example, deer and herbivorous invertebrates could be said to be in competition for nutritious young growth on their shared food plant.

In the third example, comparisons of paired browsed and unbrowsed plots were used to assess the impact of moose (*Alces alces*) and reindeer (*Rangifer tarandus*) on boreal forests in Fennoscandia (Suominen, 1999; Suominen *et al.*, 1999a). At one site dominated by Scots pine (*Pinus sylvestris*) with bilberry field layer, it was shown that large herbivores effected the removal of most deciduous trees from the canopy with a consequent 90 per cent reduction in deciduous leaf-litter fall. The total abundance of ground-dwelling invertebrates was higher in the unbrowsed enclosure although diversity was

lower. In the invertebrate taxa showing any differences, there were usually more individuals in the unbrowsed enclosure compared with the browsed plot (Suominen *et al.*, 1999a). In a more wide-ranging survey of responses to herbivore removal at 23 sites, the abundance, species richness and diversity of gastropods all responded positively to relief from browsing either by moose or reindeer (Suominen, 1999). These findings were interpreted as resulting from the cooler and more humid microclimatic conditions and greater food resources in the deeper litter layer found in enclosures. Ground beetles, many of which require more open habitats for hunting, tended to be more numerous in plots grazed by reindeer, whereas phytophagous weevils (Curculionidae) were less abundant because the reindeer had reduced the biomass of their deciduous tree hosts (Suominen *et al.*, 1999b).

These three sets of experiments were conducted in very different woodland ecosystems and with different cervid herbivore species, but they all leave no doubt that grazing and browsing by large mammalian herbivores can have definite and profound effects on woodland invertebrate populations and community composition. In most cases, invertebrate responses were brought about through changes in the vegetation, although changes in the abiotic environment induced by deer may be important as well.

### Effects mediated through changes in the vegetation

Woodland vegetation provides a habitat, and in many cases a food supply, for a considerable diversity of invertebrate species. Many use its physical structure as a refuge from natural enemies or adverse weather conditions and the variety of microhabitats that it provides are important for critical life history events such as oviposition and hibernation. Any changes induced by deer in either the species composition, physical structure or productivity of the vegetation will therefore have major impacts on the associated invertebrates. In addition, deer browsing may induce qualitative physiological and biochemical changes in plants which change their suitability as food for invertebrate herbivores. Of course, all impacts on herbivorous insects will

have implications for the community of associated invertebrate predators and parasites. Excepting results from enclosure experiments (above), most conclusions about vegetation-mediated effects on invertebrates have to be deduced from a combination of what is known about (1) the effects of deer on vegetation and (2) the relationship between invertebrates and various aspects of vegetation composition, structure and quality.

#### *Effects of changes in species composition of the vegetation*

Since most insect herbivores are monophagous or narrowly oligophagous (Strong *et al.*, 1984), their diversity in woodlands will be heavily dependent upon the species composition of the vegetation. Predatory invertebrates are generally considered to be more generalist in feeding preferences and therefore, as is the case with spiders, more dependent upon habitat structure. Any simplification of either the structure or the species composition of the vegetation by deer browsing will therefore result in a reduced diversity of associated invertebrates.

The invertebrate fauna, especially herbivorous insects, associated with British trees is particularly well catalogued (Kennedy and Southwood, 1984). This shows that there is very considerable variation in the number of species associated with different tree species. Likewise, deer show definite browse preferences between tree species. However, results from a range of studies demonstrate that browse preferences vary considerably between deer species, across the seasons, in different geographical areas and in relation to the availability of alternative forage (Mitchell *et al.*, 1977; Gill, 1992; Kay, 1993; Cooke and Lakhani, 1996; Putman and Moore, 1998; Moore *et al.*, 1999; Gill and Beardall, 2001). Nevertheless, preferred browse species such as oaks (*Quercus* spp.), willows (*Salix* spp.) and aspen (*Populus tremula*) also support some of the richest insect herbivore communities, while trees that are generally avoided by deer, e.g. yew (*Taxus baccata*) and holly (*Ilex aquifolium*), are very depauperate in associated insects. In between, however, there are examples of tree species that support a rich invertebrate fauna but tend to be avoided by deer (alder *Alnus glutinosa*) and others that attract deer browsing but have

comparatively few associated insects (ash *Fraxinus excelsior*). In any event, heavy deer browsing on particular trees, perhaps to the point of suppressing regeneration or even removal of the species from the community, will have detrimental consequences for the associated insect community.

In fact, the effect of deer on the upper canopy invertebrates is likely to be minimal, except where long-term regeneration is suppressed, because browsing is generally confined to herbaceous plants, shrubs and tree foliage within 2 m of the ground. A far greater impact will result from changes to the composition of the shrub and field layers. A number of rare insect species are dependent upon common components of these layers. For example, bramble (*Rubus fruticosus*) is preferentially browsed by deer, especially early in the season (Putman, 1986). Dead and snapped-off bramble stems provide important breeding sites for rare solitary bees (e.g. in the genera *Osmia* and *Hylaeus*) and the flowers provide an important food source for a considerable list of insects that require nectar for energy and pollen as a protein source for maturation of eggs. In addition to the well-known attraction of butterflies to bramble blossom, it is also important for the adults of many uncommon saproxylic beetles (e.g. *Strangalia* spp.) and hoverflies (e.g. *Criorhina* spp.) whose larvae live in, and feed on, dead wood. These comprise some of the rarest and most vulnerable woodland insects that, because of their limited dispersal ability, are dependent upon the juxtaposition of their dead wood larval habitat with open flowery rides and clearings for the adults (Warren and Key, 1991; Kirby, 1992a). Other important sources of nectar along woodland rides and in clearings include blackthorn (*Prunus spinosa*) and hawthorn (*Crataegus monogyna*), both of which are eaten by deer (Putman, 1986), as well as elder (*Sambucus nigra*) and various members of the Umbelliferae and Compositae.

Deer bring about changes to the species composition of the field layer vegetation, partly through selective grazing on susceptible species and avoidance of unpalatable ones (Cooke *et al.*, 1995; Cooke, 1997), but also through stimulation of shade-intolerant species by opening up or removing the woodland layers above. Host-specific insect herbivores that are dependent upon

common components of the field layer vegetation include the negro bug (*Thyreocoris scarabaeoides*) on violets (*Viola* spp.), the stilt bug (*Metatropis rufescens*) on enchanter's nightshade (*Circaea lutetiana*) and the weevil (*Barynotus moerens*) on dog's mercury (*Mercurialis perennis*). Additionally, many insect herbivores associated with field layer species require host plants in a particular physiological condition (nutrient status, stature, flowering status, etc.) and microclimate. Thus, a selection of rare Heteroptera require their host plants to be in sheltered sunny rides and woodland clearings: *Tingis reticulata* on bugle (*Ajuga reptans*), *Eurydema dominulus* on cuckooflower (*Cardamine pratensis*) and *Dicranocephalus medius* on wood spurge (*Euphorbia amygdaloides*) (Kirby, 1992b). The fortunes of all these insects will be contingent upon the impact of deer on the field layer vegetation. Under extreme deer pressure, the host plants and other field layer species such as bramble are likely to be replaced by unpalatable grasses and bracken (*Pteridium aquilinum*), with a net loss of invertebrate richness.

#### *Effects of changes in woodland structure*

The impressive species richness of invertebrate communities in woodlands is mainly due to the structural diversity of the habitat (Southwood *et al.*, 1979). It follows that any simplification of the habitat structure is likely to result in a reduction in invertebrate diversity. At very high densities, large mammal herbivores including deer will remove virtually all green foliage up to a height of ~2 m, producing the familiar 'browse-line' on the underside of the tree canopy. This leaves a vacant understorey which would otherwise be occupied by shrubs and small saplings. Heavy grazing can also eliminate all but the most unpalatable and strongly defended components of the herbaceous field layer. This has a number of consequences for invertebrates. First, as described above, it removes a whole suite of plant species that provide important sources of food and shelter for invertebrates. Secondly, plants that can escape serious browsing damage by growing tall will nevertheless have their three-dimensional structure greatly modified. This can affect associated invertebrates, since many are reliant on very particular parts of the plant, e.g. leaves growing in rather precise

microclimatic conditions. The white admiral butterfly (*Ladoga camilla*) lays its eggs on the lower leaves of its food plant, honeysuckle (*Lonicera periclymenum*), normally between 0.5 and 1.5 m above the ground, or on the trailing strands that hang down from higher branches. Pollard and Cooke (1994) have shown that heavy browsing by muntjac deer (*Muntiacus reevesi*) in Monks Wood removed honeysuckle leaves within this critical height range. Although butterfly monitoring data were unable to demonstrate any effect of the deer on the population of white admiral adults in the wood, the mean height of eggs increased significantly over the 20-year period in which muntjac numbers built up. It is very likely that this type of subtle change in behaviour, in response to habitat modification by deer, is widespread amongst other invertebrate species.

Finally, removal of the understorey profoundly alters the microclimate of the lower layers of the woodland, in particular allowing an increase in the amount of light reaching the field layer and a consequential increase in temperature, as well as greater wind speed and reduced humidity. Such changes will affect different invertebrate groups in contrasting ways. As long as suitable larval food-plants and adult nectar sources remain, greater insolation will be beneficial to many woodland butterflies. However, many of the rarer woodland Diptera (including members of the Lauxaniidae, Tipulidae and Sciomyzidae) are dependent upon the moist and shaded conditions provided by a dense canopy or shrub layer and lush field layer vegetation (Fry and Lonsdale, 1991; S. Falk, personal communication). At Gait Barrows in Lancashire, the rare whorl snail *Vertigo angustior* is found on cool and moist moss-covered limestone pavement underneath overhanging trees (Killeen, 1997). Petley-Jones (1995) has expressed the concern that removal of low branches, especially those of yew, by deer will have changed the microclimate and adversely affected the snail. Dead wood is most suitable for colonization by saproxylic species when situated in partial shade (Kirby, 1992a), e.g. under bramble. Removal of the sheltering effect of overgrowing vegetation and exposure of the microhabitat to full sun will increase the range of temperatures experienced, which will restrict the number of saproxylic species that are able to exploit the resource.

In spite of its obvious effect of reducing the architectural complexity of woodland, the removal of a shrub layer may not be unequivocally deleterious for invertebrates. It is noticeable that some of the best sites in Britain for saproxylic insects, such as Windsor Great Park, Moccas Park and Knole Park (Harding and Alexander, 1994), are essentially wood-pastures that are maintained predominantly by deer grazing and that generally lack a shrub layer. Such sites are entomologically rich across a range of groups, although this may reflect more the importance of a long history of habitat continuity and the quality of the dead-wood habitat that they contain.

Many characteristic woodland invertebrates are actually species of woodland edges and glades (Kirby, 1992a). This applies not only to several woodland butterflies (Feber *et al.*, 2001) but also to many other thermophilous insects that require the shelter and warmth provided by open south-facing rides, glades and clearings (Fry and Lonsdale, 1991). The ideal cross-sectional profile for these open areas within woodland is one of a gradual transition in height from bare ground and grasses to tall herbaceous plants to scrub and finally to the tree canopy. Light to moderate herbivore pressure, perhaps with rabbits grazing the short vegetation and deer browsing the young trees, can maintain this ideal structure. The size and shape of clearings is critical, since many deer tend to occupy the ecotone between woodland and grassland and avoid large open areas away from suitable cover (Moore *et al.*, 1999). If deer can help to create and maintain such clearings (Putman, 1994), they will greatly enhance the diversity of invertebrates, as long as they do not also remove the flowering species that provide a source of nectar.

Very high grazing intensities may generate open areas with bare ground. Such patches within woodland rides and clearings provide important ground nesting sites for solitary bees and wasps, as well as sun-basking and foraging areas for other groups. Predatory species often require small-scale open territory for hunting. Wood ants (*Formica rufa*) responded positively to the heavy grazing pressure in the Denny Pens experiment (114 individuals in the grazed enclosure and 15 in the ungrazed plot), mirroring a similar response to the more open structured habitat created by coppicing (Welch, 1978).

The habitat requirements of each of the insect life history stages (egg, larva, pupa, adult) are often radically different. However, the restricted dispersal ability that is characteristic of many woodland insects (Warren and Key, 1991) means that these disparate habitat requirements have to be met within a comparatively small area. In this context, small-scale habitat heterogeneity is critical, with patches of woodland, scrub and grassland in an intimate mosaic. Deer may help to create and maintain this pattern through their browsing activities on young trees and shrubs in a way that other large mammalian herbivores cannot. Likewise, deer may remove nutrients from one area (through feeding) and deposit them in another (through dung, urine and carcasses), forming local pockets of enrichment. Although this effect will be less pronounced and at a smaller scale compared to herbivores such as rabbits that exhibit distinct latrine behaviour, the capacity of deer to redistribute nutrients and thereby create heterogeneity in the vegetation may be important (Putman, 1994).

Deer may also create other minor habitat features that are relevant to particular invertebrate groups. Muddy margins around drinking holes and bare wet patches of soil created by deer trampling provide a microhabitat for various fly groups (including Syrphidae, Sepsidae and Dolichopodidae). Bark rubbing and stripping on mature trees, 'fraying' of young saplings and other types of antler-inflicted damage will create access points for secondary fungal infections, with the resultant decaying wood being colonized by wood-boring and saproxylic insects. Excessive wounding may induce 'sap runs' which attract their own particular fauna (Kirby, 1992a).

#### *Effects of changes in plant biomass and quality*

Deer browsing will have an impact on the numerical abundance of invertebrate herbivores through the removal of plant biomass. The effects of selective browsing will depend upon how invertebrate population densities vary between plant species and between foliage in different stages of growth. There have been few attempts to quantify this, although the available data suggest that both abundance and biomass of invertebrates vary considerably between different species and growth stages of tree (Moran and

Southwood, 1982; Southwood *et al.*, 1982; Hill *et al.*, 1990). Additionally, if selective browsing or grazing is concentrated upon particular parts of the plant that are also favoured by herbivorous insects, the effect on the invertebrate population may be disproportionate in relation to the amount of plant biomass actually removed (Baines *et al.*, 1994). Whilst heavy grazing may suppress plant productivity, lighter grazing may actually stimulate plant growth and biomass production, so generalizations about likely effects on invertebrates have to be made with caution.

Deer-induced changes to the vegetation will have effects on the quantity and composition of leaf litter and its rate of decay. Mammalian herbivores such as deer selectively browse tree species that tend to grow fast and produce a greater biomass of litter that also decomposes faster. Intense browsing may therefore shift the species balance towards less palatable and slow growing species, which produce less litter that decays more slowly. Such changes will have effects on the soil and litter fauna, such as spring-tails (Collembola), mites (Acari) and earthworms (Lumbricidae) as well as on rates of energy and nutrient flow through the system (Pastor *et al.*, 1993).

Many plants respond to herbivory by mobilizing secondary chemical defences, usually close to the damaged tissue but sometimes throughout the plant. These 'induced responses' have been widely reported and can affect the palatability of regrowth foliage to other herbivores or change their performance (growth rate, survival, etc.) when eating affected leaves (Karban and Baldwin, 1997). In most cases, experimentally inflicted damage or early-season insect herbivory has resulted in strong negative effects on invertebrate herbivores appearing later in the season (Haukioja and Niemelä, 1979; West, 1985; Edwards *et al.*, 1986; Fowler and MacGarvin 1986; Hartley and Lawton, 1987; Hunter, 1987; Neuvonen *et al.*, 1988). Curiously, where the damage has been inflicted by mammalian herbivores, insects feeding subsequently on the same tree have been found to respond positively (Danell and Huss-Danell, 1985; Roininen *et al.*, 1997; Martinsen *et al.*, 1998). Other studies have shown complex interactions between both vertebrate and invertebrate herbivores, all mediated through the host plant (Strauss, 1991). It would

be surprising if heavy deer browsing did not induce significant changes in plant leaf chemistry, although the question of whether these would prompt herbivorous insects to respond positively or negatively remains unanswered.

Young leaves are generally more nutritious than older leaves for herbivorous insects because they contain more available nitrogen and lower levels of digestibility-reducing substances such as tannins (Feeny, 1976; Rhoades and Cates, 1976). However, at least one study has shown that higher population densities of some insect species on young foliage are offset by greater species diversity on older leaf material (Godfray, 1985). Regrowth foliage that is produced after deer browsing may be chemically similar to that which grows after coppicing. Greatorex-Davies and Marrs (1992) list several scarce herbivorous species that may be dependent upon regrowth foliage. For example, leaf beetles (Chrysomelidae) in the genus *Cryptocephalus* tend to be associated with the young foliage of birches, hazel, aspen and other deciduous trees growing at the interface between grassland and woody scrub (Hodge and Williams, 1997). Deer browsing may encourage such insects both by ensuring a supply of young foliage and by keeping open a matrix of woodland clearings.

### Direct effects

The presence of deer will have a direct effect on certain invertebrate groups that are intimately associated with them. As with most large herbivores, deer harbour a small community of commensals and parasites. They are host to various fly parasites including the deer ked (*Lipoptena cervi*) and the deer bot-fly (*Cephenomya auribarbis*), both specific to deer (Hutson, 1984). Deer are also one of the more important hosts for the 'sheep tick' (*Ixodes ricinus*) which is responsible for transmitting the spirochaete *Borrelia burgdorferi* that causes Lyme disease. The inevitable presence of dead animals will attract carrion-feeding invertebrates, such as sexton beetles (Silphidae) and rove beetles (Staphylinidae) as well as assorted flies (Calliphoridae, Sarcophagidae, Sphaeroceridae, etc.). Most of these tend to be neither habitat- nor host-specific, although several are known to occur predominantly in

woodlands and are nationally rare (Falk, 1991; Hyman and Parsons, 1992a, b).

#### *Invertebrate communities associated with dung*

The copious quantities of faeces produced by deer will attract a diverse community of dung-associated invertebrates. The most obvious of these will be dung beetles (Geotrupidae) and scarab beetles (Scarabaeidae), although most species are rather unspecific in terms of the animal species whose dung they use. However, two nationally scarce woodland species are reported to be associated primarily with deer dung: *Aphodius nemoralis* in northern coniferous woods and *A. zenkeri* in more southern woodlands and deer parks (Hyman and Parsons, 1992a). Other common dung-specialists in woodland include dor beetles (in the genus *Geotrupes*), a distinctive fly fauna (Chandler, 1978) and certain rove beetles (Staphylinidae) that feed upon the plentiful supply of insect larvae in dung (Cooter, 1991). Putman *et al.* (1989) found distinct differences in abundance of rove beetles between the Denny Pens: *Philonthus cognatus* was significantly more numerous in the grazed enclosure compared to the ungrazed plot (67 : 15 individuals), while *Staphylinus olens* was confined to the grazed plot (35 : 0).

In many woodlands, deer will represent the only large vertebrate herbivores producing significant quantities of dung which is suitable for colonization by invertebrate decomposers. Furthermore, the widespread prophylactic use of avermectins to treat intestinal parasites in grazing livestock probably means that much cattle, horse and sheep dung is deficient in associated invertebrates (Wall and Strong, 1987; Strong *et al.*, 1996). Consequently, it is possible that deer dung may be an important refuge for dung-associated invertebrates in woodlands as well as in other habitats.

#### *Potential knock-on effects at higher trophic levels*

Dung-associated invertebrates are an important source of food for some predatory animals, at least at certain critical times of year. Hiron (1984) showed that dor beetles (*Geotrupes* and *Typhoeus* spp.) comprised >50 per cent of prey

items within the winter diet of tawny owls (*Strix aluco*) in the New Forest. This was at least partly due to the relative scarcity of the small rodents that are normally the owls' preferred prey, low densities of which were in turn another consequence of the effects of heavy grazing by deer and domestic stock (Putman *et al.*, 1989).

Dung beetles and scarab beetles may also be important prey items in the diets of certain woodland bats, again at critical stages in their life cycle. Analysis of the diet of greater horseshoe bats (*Rhinolophus ferrumequinum*), a species that is seriously threatened within the UK, shows that juveniles take advantage of the abundance of *Aphodius* spp. (especially *A. rufipes*) between July and October. This period also corresponds with the later stages of lactation, when adult female bats are often under severe physiological stress. Under these circumstances, dung beetles provide an important alternative food source if there is a shortage of the adults' preferred prey, moths and crane flies (Ransome, 1996). Although a high proportion of these *Aphodius* will be taken from cattle dung in open pasture, greater horseshoe bats also hunt extensively in woodlands, where the main source of coprophagous insects will be deer dung. Similarly, recent studies have shown that adult greater horseshoe bats emerging briefly from hibernation during winter months feed primarily on dor beetles; such insects may be equally vital to the bats at a time when very few other prey species are available.

Similar associations may apply to several other woodland bat species. Half of the winter diet of lesser horseshoe bats (*R. hipposideros*) is known to be composed of dung flies (McAney and Fairley, 1989). Other woodland species where diet analyses have shown a significant reliance on dung-associated insects include Natterer's bat (*Myotis nattereri*), noctule (*Nyctalus noctula*), whiskered bat (*M. mystacinus*) and both common and grey long-eared bats (*Plecotus auritus* and *P. austriacus*) (Shiel *et al.*, 1991; Swift, 1997).

#### **Conclusions and priorities for future research**

There is some direct, and much anecdotal, evidence that impacts of deer on invertebrates will normally be mediated through the changes that



deer generate in the structure and species composition of the vegetation. This model invites comparison with the impact of rabbit grazing on grasslands and the changes in both vegetation and associated invertebrates that occur when such grazing is removed (Morris, 1989). Viewed in this way, deer could justifiably be described as 'key-stone herbivores' (Mills *et al.*, 1993), having a disproportionate impact on the woodland ecosystem in relation to their population density and biomass. Similarly, deer apparently perform the function of allogenic physical ecosystem engineers (*sensu* Jones *et al.*, 1994), in that they also have non-trophic impacts on the woodland community through their modification of the physical environment. For example, removal of the woodland understorey by intensive deer browsing has effects on the microclimate, the provision of microhabitats and rates of litter decomposition, all of which have important implications for invertebrate communities.

The degree of invertebrate response will depend primarily upon deer population density, although the details of the relationship need to be explored further. Without vertebrate herbivores, woodland succession will proceed more quickly to climax high forest that, although not without its invertebrate interest, will tend to have a lower overall diversity. At the other extreme, excessive browsing and grazing pressure will lead to removal of the shrub layer, prevention of regeneration and a consequent reduction in overall plant and animal diversity, as shown by the extreme example of the Denny Pens experiment (Putman *et al.*, 1989). Different invertebrate species will respond uniquely to the changes brought about by increases in deer densities; there will be 'winners' and 'losers'. However, maximal invertebrate diversity is likely to occur under moderate grazing pressure, reflecting the hump-backed relationship in most grazing systems between grazer density and the species richness of other animals (van Wieren, 1998). This conclusion is consistent with the prediction of the 'intermediate disturbance hypothesis' (Connell, 1978; Fox, 1979), where grazing and browsing is considered to be a type of disturbance. However, the objective of promoting maximal diversity may conflict with that of preserving the rare invertebrate species which tend to occur in either the very early or very late stages of woodland succession.

Woodland management strategies, including the management of deer, should therefore seek to create and maintain a mosaic of habitat types.

Significant benefits would accrue to thermophilous invertebrates from the preservation of open habitats within woodland, such as rides, glades and clearings. Many of the rarer species are at the northern edge of their range in Britain and are therefore dependent upon the warm temperatures provided by sheltered areas with high insolation. Much of the potential benefit of deer would depend upon their ability to create and maintain such features. More research is needed on the circumstances that promote this, in particular the extent to which positive interactions exist between the grazing effects of deer and rabbits. Deer also help to create spatial and temporal heterogeneity in the system by moving nutrients around, albeit on a local scale, through grazing in one area and dunging in another. The small-scale patchiness in the vegetation that this produces is vital to many rare invertebrate species whose contrasting habitat requirements in different life history stages have to be met within a restricted area due to their poor powers of dispersal.

Information about how insect herbivores respond to damage inflicted on their food plants (by vertebrate browsing, mechanical damage or other insect herbivores) is contradictory. Post-browse regrowth foliage may provide an important nutritious resource for some species, whilst induced plant defences may strongly inhibit others. This is an active area of research (Karban and Baldwin, 1997) and one which is amenable to simple but rigorous experimentation. Important questions need addressing, such as the spatial and temporal extent of insect responses and whether there are interactions with invertebrate natural enemy complexes.

It is clear that the grazing and browsing activities of deer have the potential for far-reaching impacts throughout the woodland ecosystem, including on invertebrates. This review has drawn attention to possible impacts on two other groups at higher trophic levels: predatory birds and bats. One would expect to find further examples of complex multi-trophic interactions affecting other taxa, as well as effects on the flow of nutrients and energy through the system. Recent studies on boreal forests show how subtle these

interactions can be (Suominen *et al.*, 1999a). Future research on the impact of deer on lowland mixed deciduous woodland in Britain should adopt a similar multi-trophic approach.

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