

A Review of Damage by Mammals in North Temperate Forests: 1. Deer

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SUMMARY

The causes of browsing, bark stripping, and fraying damage by deer are examined by reviewing the available literature. Trees species differ in vulnerability and each form of damage occurs within certain age and size classes. Stem morphology has an important influence on bark stripping; lower branches and bark thickening tend to deter stripping in any one species. Site related factors such as hiding cover, snow and soil fertility also influence damage. The data relating deer population density to damage are imprecise and there is a need for improved density estimation methods to demonstrate the benefit of culling in different habitats. Vegetation affects both habitat and diet selection in deer, and can create both positive and negative relationships with damage. Computer models are proposed as an aid to damage prediction and forest protection decision making.

INTRODUCTION

The problems of deer are familiar enough to most foresters in Britain. Deer cause damage by browsing, stripping bark and fraying trees with antlers. Although methods of tree protection and deer control are well established to deal with the problem, there remains a need for prediction of possible losses, so that appropriate measures of protection and control can be taken.

Effective prediction of losses is only possible if the causes of deer damage are well enough understood. The purpose of this paper is to review the factors such as deer population density, tree characteristics and habitat that influence damage and to identify future research needs as well as to suggest improvements in methods of damage prediction.

Altogether five species of deer in Britain in sufficient numbers to cause damage (red deer *Cervus elaphus*, sika *C. nippon*, roe *Capreolus capreolus*, muntjac *Muntiacus reevesi* and fallow *Dama dama*). All, with the possible exception of fallow deer, have been increasing in range or numbers and are likely to continue to do so (Taylor, 1981; Ratcliffe, 1987, 1989; Gill, 1990).

The review addresses the problem of damage in British forests but draws heavily on investigations conducted in all north temperate forest ecosystems. Techniques of tree protection and deer control are not discussed. Collection of relevant published literature ceased after September 1991.

Two papers, covering other aspects of mammal damage, are due to be published; part two will review the causes of small mammal damage and part three will cover the responses of trees to damage, including the effects of browsing on tree regeneration, herbivore resistance and production losses due to both browsing and bark stripping.

The following definitions apply to this review:

Damage: Injury to trees in the form of tissue removal (leaves, bark, flowers, shoots, buds etc.). It does not necessarily imply economic loss.

Selection: Choice of a particular tree crop, individual tree or part of a tree for damage by an animal from those available.

Vulnerability or susceptibility: Likelihood or frequency of damage to a tree or tree crop of particular characteristics. It can only be recorded by observing selection by an animal and is therefore prone to all the factors that influence selection.

Incidence: Percentage of trees damaged in an area.

Intensity: Severity of damage to an individual tree, such as the proportion of shoots browsed, or the number or size of bark wounds.

Deer: Any member of the Cervidae.

BROWSING

The characteristics of browsing damage

Description

The term 'browsing', in the context of forest damage, refers to all forms of feeding damage other than bark stripping and therefore can involve the removal of twigs, shoots, leaves, needles, buds or flowers, from either young trees or coppice stools. Small seedlings can be uprooted. Deer are selective and the parts taken will depend very much on the species of tree and time of year. Some reports state that only the current year's growth is removed and a browsed shoot is unlikely to be re-browsed until new growth has formed (Holloway, 1967a; Severinghaus and Severinghaus, 1982), but this is likely to depend on browsing pressure.

Conifers are usually browsed in winter, often with increasing intensity as winter progresses, whereas broadleaves are more usually damaged in summer (Holloway, 1967a; König, 1976; Miller *et al.*, 1982; Cummins and Miller, 1982; Klein *et al.*, 1989; Maizeret and Ballon, 1990). Exceptions to this general pattern however do occur, for example a peak in browsing on spring-flush growth has been reported on Douglas fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*) in spring or early summer (Browning and Lauppe, 1964; Welch *et al.*, 1988a). Furthermore larch (*Larix* sp.) has been reported to be browsed more in summer than winter (Holloway, 1967a) and twigs of some broadleaved trees, particularly willow (*Salix* sp.) can form a significant component of the diet of red and roe deer in winter (Szmids, 1975; Jamroz, 1980).

Incidence and intensity

Browsing damage is not regularly surveyed in Britain and it is therefore not easy to make statements about the severity of damage in different regions, years or among tree species. Nevertheless, the incidence of browsing is clearly very variable and quite often every tree in a stand is affected (Staines and Welch, 1989). Rates of average leader loss close to 50 per cent per year have been reported in Sitka spruce crops, with replaced leaders also suffering damage (Welch *et al.*, 1991).

Browsing is rarely evenly distributed through a stand and several reports state that it is usually clumped, (Zai, 1964; Welch *et al.*, 1988a), or that it is more severe near crop edges (Thirgood and Staines 1989). Previously browsed trees have also been found to be preferentially selected (Löyttyniemi and Piisilä, 1983; Löyttyniemi, 1985; Danell *et al.*, 1985; Welch *et al.*, 1991), a feature which probably compounds the uneven impact. It is often assumed that patches of damage are reflections of differences in plant quality, but they may be created simply by feeding behaviour (Crawley, 1983).

Differences between tree species and variety

Deer show marked preferences for particular tree species. These are most apparent in mixed species stands, where the level of damage on each species is usually distinctly different (e.g. Horton, 1964). The susceptibility of each of the common tree species to red and roe deer browsing in Europe have been summarized in Table 1. In general, willows, aspen (*Populus tremula*) and silver fir (*Abies alba*) are most preferred whereas Sitka spruce, Scots pine (*Pinus sylvestris*) and Corsican pine (*P. nigra*) are usually least preferred.

There are also however many discrepancies: lodgepole pine (*P. contorta*) for example has been reported to have both high and low relative preference. As discussed later, preferences can depend on the vegetation composition, so they cannot be expected to be consistent.

In common with between species differences in palatability, there are also reports of within species variation. The susceptibility of Douglas fir to black-tailed deer (*Odocoileus hemionus*) browsing has been found to be a heritable characteristic, passed from parent to known progeny trees (Dimock *et al.*, 1976; Silen and Dimock 1978). In Finland moose (*Alces alces*) have been reported to prefer browsing some clones of Scots pine more than others (Haukioja *et al.*, 1983; Danell *et al.*, 1990), and also show a preference for varieties of southern rather than northern origin (Niemela *et al.*, 1989). It is not yet clear however whether these origin differences are more related to the levels of secondary compounds or to phenological development.

The influence of size and age

Most browsing by deer usually occurs at an intermediate level between ground and full reach resulting in smaller and larger trees being relatively protected (Holloway, 1967a; Löyttyniemi and Piisilä, 1983). In Sitka spruce

TABLE 1: *The relative susceptibility of trees to deer browsing*

Deer species	Most susceptible		Least susceptible	S/W*	Author (Area)
Red deer	<i>Fraxinus</i> <i>Salix</i> <i>Frangula alnus</i>	<i>Betula</i>	<i>Alnus</i>		Ahlén, 1965 (Sweden)
	<i>Populus tremula</i> <i>Quercus</i> <i>Abies alba</i> <i>Acer platanoides</i> <i>Fraxinus</i>	<i>Pinus sylvestris</i> <i>Picea abies</i> <i>Fagus</i> <i>Pseudotsuga</i> <i>Larix</i>	<i>Picea sitchensis</i> <i>Alnus</i> <i>Betula</i>		Ueckermann, 1960 (W. Germany)
	<i>Juniperus</i> <i>Quercus</i> <i>Pinus contorta</i> <i>Picea abies</i>	<i>Larix</i> <i>Acer pseudoplatanus</i> <i>Pinus sylvestris</i> <i>Betula</i>	<i>Picea sitchensis</i> <i>Fagus sylvatica</i> <i>Alnus glutinosa</i>		Chard, 1966 (England)
	<i>Quercus</i> <i>Salix caprea</i> <i>Sorbus aucuparia</i> <i>Corvulus</i>	<i>Acer platanoides</i> <i>Carpinus</i> <i>Prunus serotina</i> <i>Frangula alnus</i>	<i>Pinus sylvestris</i> <i>Juniperus</i>		Dzięciolowski, 1970 (Poland)
	<i>Salix</i> <i>Juniperus</i> <i>Pinus sylvestris</i> <i>Acer pseudoplatanus</i>	<i>Abies alba</i> <i>Corylus avellana</i> <i>Sambucus</i>	<i>Fagus</i> <i>Picea abies</i>	W	Jamroz, 1980 (Poland)
	<i>Salix</i> <i>Populus tremula</i> <i>Fraxinus</i> <i>Quercus</i>	<i>Sorbus aucuparia</i> <i>Betula</i>	<i>Tilia</i> <i>Carpinus</i>		Sablina, 1959 (USSR)
	<i>Sorbus aucuparia</i> <i>Pinus sylvestris</i>	<i>Betula</i>	<i>Pinus sylvestris</i> <i>Betula</i> <i>Sorbus aucuparia</i>	S W	Cummins and Miller, 1982 (Scotland)
	<i>Picea sitchensis</i> <i>Pinus sylvestris</i>		<i>Pinus contorta</i>		Mitchell and McCowan 1986 (Scotland)
	<i>Salix</i> <i>Sorbus aucuparia</i>	<i>Betula</i> <i>Alnus</i>	<i>Pinus sylvestris</i>		Mitchell <i>et al.</i> 1982 (Scotland)
	Roe deer	<i>Quercus</i> <i>Sorbus aucuparia</i> <i>Salix</i>	<i>Alnus glutinosa</i> <i>Betula</i> <i>Populus tremula</i> <i>Fagus sylvatica</i> <i>Tilia cordata</i>	<i>Abies alba</i> <i>Picea abies</i> <i>Pinus sylvestris</i> <i>Sambucus nigra</i>	S
<i>Fagus sylvatica</i> <i>Sorbus aucuparia</i>		<i>Carpinus</i> <i>Quercus</i> <i>Salix</i> <i>Picea abies</i> <i>Abies alba</i> <i>Pinus sylvestris</i>	<i>Betula</i> <i>Tilia cordata</i>	W	
<i>Picea abies</i> <i>Pinus contorta</i>		<i>Pinus sylvestris</i>	<i>Picea sitchensis</i> <i>Pinus nigra</i>		Rowe, 1982 (GB)

*S/W Summer or winter browsing

crops, the most vulnerable height range has been reported to be 40–55 cm for leader removal and 30–60 cm for browsing in general, with very little damage occurring above 85 cm (Staines and Welch, 1984; Welch *et al.*, 1988a and

1991). Broadleaved saplings can be browsed by red deer up to a height of 2.5 m if they bend the main stem (Mitchell *et al.*, 1982), but conifers are apparently not treated in this way, presumably because the stems are less pliable and the shoots less palatable. The susceptibility of shorter trees depends on their height relative to other plants. Small seedlings can be browsed if growing on bare ground, but otherwise they may not be damaged until they have grown above the surrounding vegetation (Miller *et al.*, 1982).

The browsing height preferences of deer in Sitka spruce stands have been found to result in the tallest trees being selected for leader damage in short stands and conversely, shorter trees selected in taller stands (Staines and Welch, 1984). Among similar sizes trees in the most susceptible height range, damage in autumn occurred on smaller than average trees and in spring on larger than average (Welch *et al.*, 1991).

Snow can exert a considerable influence on browsing by concealing seedlings or forcing deer to browse on trees when other vegetation is buried (Holloway, 1967a). When hard packed, it can raise an animal's reach, creating a new browse line (Ahlén, 1965).

The causes of browsing damage

Deer population density

The incidence and intensity of browsing are widely accepted to be positively associated with deer population density (Roy, 1960; Westman, 1958; Holloway, 1967a; Lavsund, 1981; Alverson *et al.*, 1988; Conover, 1989; Maizeret and Ballon, 1990; Welch *et al.*, 1991) It is not however easy to estimate deer numbers in a forest habitat (Andersen, 1953; Staines and Ratcliffe 1987; Gill, 1990), nor to control for it in studies of damage, and therefore many of these reports contain imprecise data or report a weak correlation, leaving doubt about the contribution of density in relation to other factors.

Perhaps the clearest example has been provided by Tilghman (1989), who kept white-tailed deer (*Odocoileus virginianus*) in five enclosures at fixed densities (0–31 km⁻²) for 5 years. At the end of the period, seedling heights at the highest density were 50 per cent of those in plots without deer. Furthermore, the abundance of browse-sensitive species and seedling diversity declined with increasing density, resulting in dominance by one or two browse resistant species. Many of the vegetation responses observed by Tilghman (1989) appeared to be curvilinear; very little effect was apparent until densities reached 15.5 km⁻².

The existence of this threshold confirms what is stated later, namely that trees, particularly the less palatable species, are often not the most important food item of deer and that browsing may not be significant if more preferred food plants are present. It is also clear from other studies that damage can vary as much between sites, or with vegetation, than with density (Welch *et al.*, 1991), or that the correlation with density is better in some habitats or tree crops than others (Mitchell and McCowan, 1986; Maizeret and Ballon, 1990).

The strength of the association between damage and density therefore depends both on density itself as well as on habitat or tree related factors.

Feeding and ranging behaviour

Deer are all selective browsers or browser/grazers and will choose both communities within their home range as well as plants and plant parts on which to feed (Hofmann, 1985). In view of the constraints imposed on digestion by a smaller gut, smaller bodied species are forced to be more selective than larger species, but the latter have larger home ranges (Bunnell and Gillingham, 1985). Selective feeding therefore creates a number of relationships between browsing damage and forest vegetation that differ between species of deer.

The main food plants of deer include herbs, shrubs and grasses. Although trees are taken they usually form a minor component of the diet (Grigorov, 1976 and 1987; Mitchell *et al.*, 1977; Hosey, 1981; Hearney and Jennings, 1983; Maizeret and Tran Manh Sung, 1984; Maillard and Picard, 1987; Mann and Putman, 1989). As a consequence, there are many examples, particularly among the most selective deer species, of damage to trees being inversely related to the abundance of other food plants. Browsing by red and roe deer on Sitka spruce, particularly in winter, has been found to be related to the cover of ericoid shrubs and trees tall enough to provide lateral shoots to browse (Welch *et al.*, 1991). Similarly, damage to some conifer crops by deer in the USA is dependent on the amount of other browse available (Roy, 1960; Furrh and Ezell, 1982).

Weed control methods can reduce the availability of food plants and in Norway spruce (*Picea abies*) stands it has been found to increase browsing damage by roe deer, resulting in situations where the best growth per unit establishment cost may be achieved without either weeding or fencing (Huss and Olberg-Kalfass, 1982). Direct seeding of native herbs into Douglas fir plantations has also been found to reduce browsing damage by black-tailed deer (Campbell and Evans, 1978).

In a tree species mixture, damage can be influenced by relative palatability. Browsing by roe deer on silver fir has been found to be reduced where more palatable species like ash (*Fraxinus excelsior*), rowan (*Sorbus aucuparia*) and sycamore (*Acer pseudoplatanus*) were present, but increased where less palatable species like beech (*Fagus sylvatica*) and Norway spruce are abundant (Eiberle and Bucher 1989). The influence of other plants will also depend on vegetation phenology. Cummins and Miller (1982) found that browsing by red deer on Scots pine in summer was less where more birch (*Betula* sp.) and rowan were present, but in winter this was not the case.

Alternative food sources have also been found to have an opposing effect on browsing damage, namely that it is *positively* associated with the abundance of preferred food plants (Holloway, 1967a, 1967b; Mitchell and McCowan, 1986). In this case, damage can occur even to relatively unpalatable trees because the effort of moving to another site to find better

food plants may outweigh any benefit (Crawley, 1983). Holloway (1967a) concluded that with red deer in Scotland, damage was more usually positively correlated with good feeding sites because these attracted deer, rather than deflected browsing.

In other countries ranging behaviour has been successfully exploited by providing a food source well away from a vulnerable tree or agricultural crop (Stenin, 1970; Dasmann *et al.*, 1967; Brown and Mandery, 1962; Long, 1989). It is worth noting that three of these examples are for red deer or wapiti (*Cervus elaphus*) which have large home ranges, whereas there are none for roe, which in Britain have small home ranges and are unlikely to be drawn a significant distance.

The influence of preferred food plants may of course both attract deer and deflect feeding, resulting in a negligible overall effect. This is often the case with moose browsing in Scots pine stands (Löyttyniemi and Piisilä, 1983; Lääperi and Löyttyniemi, 1988), although both positive (Lavsund, 1987) and negative (Kuznetsov, 1987) associations have also been reported.

The effect of vegetation is unfortunately complicated by the complexities of foraging behaviour. Both the pattern and abundance of other plants as well as an animals state of satiety can alter preference (Crawley, 1983). Preference reversal in response to changes in tree species abundance have been reported for moose feeding on birch (Danell and Ericson, 1986). Furthermore, browse availability, and therefore preference can be difficult to assess in the field (Rutherford, 1979). It is therefore dangerous to assume that a preference identified in one habitat will apply in another.

Nevertheless, where preferences are strong, damage to a relatively unpalatable tree species will depend on the on the abundance of more preferred species (Crawley, 1983). The examples cited above suggest that this may be a common occurrence for the most selective species of deer, and some assessment of the more preferred plants may therefore be necessary to adequately predict the severity of damage.

Plant and site quality

There is plenty of evidence that elevated levels of nitrogen in foliage or soil will increase a tree's susceptibility to browsing. Roe deer can apparently detect differences in protein and starch content of as little as 3 per cent (Rusterholz and Turner, 1978), and moose can select individual Scots pine trees with a higher nitrogen content (Niemela and Danell, 1988). Repetitive browsing on individual trees appears to occur because regrowing shoots have higher nutrient and lower monoterpenes levels (Löyttyniemi, 1985). Deer have also been found to browse Douglas fir and Scots pine stands more heavily after the application of nitrogen fertilizer (Carpenter, 1972; Laine and Mannerkoski, 1980), although the effect can vary between sites (Löyttyniemi, 1981).

Sites with higher natural fertility can also attract more browsing pressure (Jacobson, 1983; Danell, 1989) although some authors investigating this

effect have found no clear relationship (Löyttyniemi and Piisilä 1983), or the reverse (Lavsund, 1987; Maizeret and Ballon, 1990). Poor sites may suffer more damage either because the ground flora is poorer providing less alternative food, or because the trees remain within browsing reach longer.

Using relatively simple rules of diet selection based on minimum nutrient content and plant size, Belovsky (1981) was able to make quite accurate predictions of the amount of browsing by moose on some tree species, but on other species the model failed because of the (supposed) influence of secondary compounds. There is increasing evidence that these compounds influence diet choice and that they can be produced by plants in response to damage or low nutrient availability (Bryant and Kuropat, 1980). Some monoterpene alcohols have been found to inhibit deer rumen microbe activity (Oh *et al.*, 1967) and browsing damage on varieties of juniper (*Juniperus* sp.) has been found to relate to their volatile oil content (Schwartz *et al.* 1980a and 1980b). Tannins and phenols bind to protein and reduce availability and since these compounds occur naturally in different concentrations between plant species and habitats they may affect diet or habitat selection (Robbins *et al.*, 1987; Happe *et al.*, 1990).

Other elements, including calcium, phosphorus, sodium and selenium have all been found to influence diet choice in deer when either naturally deficient or available in excess (Robbins, 1983; Bazely, 1989), but so far, none have been found to be related to browsing damage.

Habitat and silviculture

Several silvicultural practices appear to influence browsing damage. Some authors report relatively more damage in smaller compartments than larger ones (Westman, 1958; Zai, 1964; Rowe, 1982), although other investigations report no effect (Löyttyniemi and Piisilä, 1983), or even the reverse (Reimoser, 1986; Lääperi and Löyttyniemi, 1988). Reimoser (1986) found browsing damage by roe deer to increase progressively with coupe size; shelterwood and selection forests were affected less than plantation forests. Unfortunately, comparisons of compartment area are invariably confounded with other factors and so generalizations are difficult. Small coupes would however increase the edge:area ratio this would be expected to improve the habitat for deer, increasing the likelihood of damage.

The presence of adjacent cover can increase damage by making a site more attractive to deer. Browsing damage has been found to be worse where a nearby mature conifer canopy provided protection from snow for roe deer (Zai, 1964). Damage has also been found to be more severe adjacent to a thicket edge (Thirgood and Staines, 1989) and less severe near roads, where disturbance is more frequent (Repo and Löyttyniemi, 1985).

Some authors have found browsing damage to be more severe in planted than in naturally seeded stands (Jamrozy *et al.*, 1981; Strandgaard, 1983). It is not always clear whether this is a result of differences in plant quality, or simply that seeded stands are so dense that browsing leaves sufficient intact

survivors, as noticed in places by Chard (1966). Seedlings in clusters may benefit from mutual physical protection, in a similar way to the protection provided by slash (Grisez, 1960). Browsing damage has however been reported to increase following respacing of naturally seeded balsam fir (*Abies balsamea*) stands apparently because of improvements in tree vigour (Thompson, 1988).

BARK STRIPPING

The characteristics of bark stripping by deer

Description

Among the species of deer present in Britain, red, sika and fallow are known to remove bark, usually in winter, when it is gnawed off with the aid of the lower incisors and eaten (Kaji *et al.*, 1984; Springthorpe and Myhill, 1985; Welch *et al.*, 1987). In spring and summer bark can be more easily removed (Wästerlund, 1985) and deer can then pull it away from the stem, sometimes leaving loose strands on the tree (Springthorpe and Myhill, 1985).

Bark is usually taken from the main stem at a height of 50–100 cm above ground, although it can also be removed from the root buttresses. Wounds tend to be larger on larger girthed trees (Welch *et al.*, 1988b; Girompaire, 1990). Complete girdling is relatively scarce but is likely to arise more frequently on the most susceptible trees or species. Kinnaird *et al.* (1979) found as many as 72 per cent of the rowan trees in one wood were completely girdled after a serious outbreak of stripping by cattle.

Although in general bark stripping occurs in winter, there are areas (for example in Holland) where it is more common in summer (Van der Veen, 1973; Reijnders and Van der Veen, 1974). Some species (e.g. beech) are usually only stripped in summer. Bark stripping on beech has been found to be positively correlated to rainfall which was thought to make the bark easier to remove (De Crombrughe, 1965).

Incidence and intensity

The occurrence and severity of bark stripping is extremely variable. It can occur at a relatively constant rate of a few trees a year or in sudden and serious outbreaks (Kinnaird *et al.*, 1979; Welch *et al.*, 1987). Like most other forms of damage, variables expressing the incidence and intensity of bark stripping invariably have a skewed frequency distribution, with the least severe attacks being the most common. This pattern applies to damage expressed in terms of the number of trees in a stand (Holloway, 1968; Welch *et al.*, 1987), the number of wounds per tree (Welch *et al.*, 1987; Girompaire, 1990), or the size of each wound (Welch *et al.*, 1988b). Damage does not usually occur uniformly or randomly throughout a stand, but is normally clustered (Hildebrandt, 1959; McIntyre, 1975; Welch *et al.*, 1987). Other examples reflecting these distribution patterns have been reported, for

example the mean number of wounds per tree increases with the incidence of damage in the stand (McIntyre, 1975), and a damaged tree is more likely to be damaged again (Staines and Welch, 1984). In spite of the skewed frequency of damage incidence, every tree in a stand can occasionally be damaged.

The incidence of annual damage in any stand is likely to rise and then fall in relation to its age (see '*The influence of tree age and morphology*') but marked yearly fluctuations are likely to be superimposed on this general trend (Holloway, 1968).

Differences between tree species and variety

At least 21 species have been reported to have been bark stripped by red deer in Europe (Holloway, 1968; Mitchell *et al.*, 1977; Jamrozy, 1980). Differences in susceptibility between species are distinct and appear, if anything, to be more consistent than those due to browsing (see Table 2). Norway spruce, lodgepole pine and ash are typically reported as vulnerable and Sitka spruce avoided. Some discrepancies in relative vulnerabilities are however apparent, for example silver fir is reported as seldom affected by Ueckermann (1960) but often attacked by Jamrozy (1980) and rowan has been reported to be approximately equal in susceptibility to Scots pine in central Europe but this is clearly not the case in Britain. Differences in susceptibility can also occur between provenances, for example Lodgepole pines of coastal origin are less susceptible than inland provenances (Melville, 1980).

The influence of tree age and morphology

Susceptibility to bark stripping is strongly age and size dependent. Damage can begin when the main stem becomes rigid and accessible and ends when the bark is too coarse, thick or difficult to remove.

The period of vulnerability varies considerably between species, for example Norway and Sitka spruce have been reported to be vulnerable between 5 and 50 years (Welch *et al.*, 1987), beech for up to 70 years (Schultz, 1960), Douglas fir between 12 and 44 years (Reijnders and Van der Veen, 1974), and Scots and lodgepole pine for between 5 and 16 years (Rijcken, 1965; Lavsund, 1974; McIntyre, 1975). Some workers suggest rather shorter vulnerable age periods, for example 18–38 and 10–45 years have been quoted for Norway spruce by Holloway (1968) and Lenz (1964) respectively. These differences may be a reflection of different stem sample sizes, growth rates or indeed any of the other factors which affect damage.

Specific morphological characteristics such as bark thickness, bark roughness, stem branchiness and the ease of bark removal have all been suggested or reported to be important determinants of damage (Ueckermann, 1960; Pellew, 1968; McIntyre, 1975; Papageorgiou and Neophytou, 1981), but since many of these characteristics develop together as a stand ages it is difficult to isolate which of them are the most important. Bark roughness does not appear to have been objectively evaluated, but is

TABLE 2: *The relative susceptibility of trees to red deer bark stripping*

Most susceptible		Least susceptible	Author (Area)
<i>Salix</i> <i>Fraxinus</i>	<i>Alnus incana</i> <i>Sorbus aucuparia</i> <i>Quercus</i> <i>Pinus sylvestris</i> <i>Picea abies</i> <i>Betula</i>	<i>Tilia</i> <i>Carpinus</i>	Sablina, 1959 (USSR)
<i>Picea abies</i> <i>Fraxinus</i> <i>Salix</i> <i>Populus</i>	<i>Pseudotsuga</i> <i>Tilia</i> <i>Pinus sylvestris</i> <i>Fagus</i> <i>Larix</i> <i>Sorbus aucuparia</i> <i>Acer pseudoplatanus</i>	<i>Abies</i> <i>Quercus</i> <i>Alnus</i> <i>Betula</i>	Ueckermann, 1956 and 1960 (W. Germany)
<i>Picea abies</i> <i>Pinus contorta</i> <i>Pinus mugo</i>	<i>Larix</i> <i>Pseudotsuga menziesii</i> <i>Picea sitchensis</i> <i>Abies</i>		Strandgaard, 1967 (Denmark)
<i>Pinus contorta</i> <i>Pinus sylvestris</i>	<i>Larix</i> <i>Picea abies</i>	<i>Picea sitchensis</i>	McIntyre, 1975 (Scotland)
<i>Salix</i> <i>Sorbus aucuparia</i>	<i>Alnus</i>	<i>Pinus sylvestris</i>	Mitchell <i>et al.</i> , 1982 (Scotland)
<i>Pinus contorta</i> <i>Pinus sylvestris</i> <i>Picea abies</i>	<i>Pseudotsuga menziesii</i> <i>Larix</i>	<i>Picea sitchensis</i>	Pellew, 1968 (England)
<i>Salix</i> <i>Fraxinus</i> <i>Corylus avelana</i> <i>Acer pseudoplatanus</i> <i>Populus tremula</i> <i>Sorbus aucuparia</i>	<i>Pinus sylvestris</i> <i>Abies alba</i>	<i>Larix</i> <i>Fagus</i> <i>Betula</i>	Jamrozy, 1980 (Poland)
<i>Pinus heldreichii</i>	<i>Abies borisii-regis</i>	<i>Pinus nigra</i>	Papagiorgiou and Neophytou, 1981 (Greece)

probably closely correlated with bark thickness in any one species. Bark thickens with age and girth more rapidly in Scots and lodgepole pine than in Norway and Sitka spruce (Pellew, 1968; McIntyre, 1975), which probably explains why pines are vulnerable for a much shorter period. McIntyre (1975) found damage more frequent on lodgepole pines with thinner bark, and damage to Scots pine and larch was found to stop when bark thickness exceeded 3.8 and 5.1 mm respectively (Pellew, 1968). Provenances of lodgepole pine with thicker bark are the least susceptible (Melville, 1980). Wästerlund (1985) found that bark cohesion began to decrease once bark

thickness exceeded 2.5 mm in Scots pine, and that thickness was least and cohesion greatest for suppressed trees rather than dominants. Because suppressed trees in pole-stage stands are more susceptible than dominants (see below), it therefore appears to be bark thickness or roughness, rather than ease of removal, that determines the upper age limit of bark stripping in this species and probably others also.

Bark thickness alone does not however explain the differences in susceptibility *between* each species. The relative susceptibilities of Sitka spruce, lodgepole pine and larch for example do not correspond with average bark thickness (McIntyre, 1975). Neither is it very clear why Sitka spruce is less vulnerable than Norway spruce, although the latter does have a smoother bark. Differences in damage levels between species and stem diameters have been found to relate clearly to bark adhesion in winter in three coniferous species in Greece (King Boris fir *Abies borisii-regis*, Austrian pine *Pinus nigra* and Heldreich pine *P. heldreichii*; Papageorgiou and Neophytou, 1981), but these authors did not unfortunately investigate bark thickness.

Lower branches provide physical protection for the stem and the timing of lower branch senescence appears to coincide with the onset of bark stripping in Norway spruce and possibly other species (Holloway, 1968). Close canopy Norway spruce trees have been found to be more susceptible than open grown trees because branch death occurs earlier (Ahlén, 1965). Furthermore, brushing is widely reported to increase the risk of damage (Szederjei, 1957; Strandgaard, 1967; Chard, 1966; Holloway, 1968). Pines typically have more open lower branches than spruces, but McIntyre (1975) none the less found that lodgepole pine trees with short internodes were unlikely to be damaged.

The age related changes in bark and branch form have clear implications for the distribution of damage. Several investigators have found that deer select larger stems in very young stands and smaller stems in older stands (Hildebrandt, 1959; McIntyre, 1975; Welch *et al.*, 1987), or that suppressed trees are more vulnerable than dominants in pole stage crops (Reijnders and Van der Veen, 1974). The size at which the change in selection from larger to smaller takes place has been reported to be 10 cm d.b.h. for lodgepole pine (McIntyre, 1975) and about 20 cm d.b.h. for Sitka spruce (Welch *et al.*, 1987).

Since bark on suppressed trees is thinner than dominants and the thickening of bark clearly restricts stripping, stands unthinned for their entire rotation will remain susceptible for longer than thinned stands.

The causes of bark stripping

Deer population density

There are several reports of a positive relationship between bark stripping and deer population density (Ueckermann, 1960 and 1983; Szukiel, 1978; Kaji *et al.*, 1984; Kraus, 1985; Maizeret and Ballon, 1990). Unfortunately all of these studies suffer from the same problems reported for browsing damage, namely that the density estimation methods used are crude or unreliable and site or stand differences have been confounded with density

differences. The reported relationships only therefore give an approximate indication of influence of density on bark stripping.

Feeding and ranging behaviour

There are many studies which have investigated both the value of bark as food and the relationship between bark stripping and the availability of other food items.

Investigations into the nutritional value of bark have failed to provide a simple explanation for bark stripping. Bark has been reported to have comparable levels of starch, water, and digestibility to other food plants (Ueckermann, 1956; McIntyre, 1975), although some investigators have thought that either the water (Rijcken, 1965), sugar (König, 1967) or even phosphorus (Husak, 1985) content may be responsible for motivating stripping. However no relation between calcium, phosphorus, water content and bark stripping was found by Papageorgiou and Neophytou (1981). Furthermore, attempts to reduce bark stripping by improving the macromineral content of winter feed have not been successful (Missbach, 1977; Ueckermann, 1983). No relationship has yet been found between bark stripping and bark tannin content (Ueckermann, 1956; Szederjei, 1957). McIntyre (1975) however found that the *in vitro* digestibility of lodgepole pine decreased with increasing bark thickness, which offers an explanation for the age related changes in susceptibility reported for many tree species.

Bark of several species has been found to have high vitamin and micromineral contents but this too was not found to correlate with their vulnerability to bark stripping (Woodsak and Ueckermann 1955). Most vitamins (other than vitamin A) can in any case be synthesized by ruminants (Robbins, 1983). A serious case of bark stripping by cattle on rowan (Kinnaird *et al.*, 1979) may have been linked to a magnesium deficiency, since this element was often deficient in the area but appeared in high concentrations in the bark.

Bark stripping in spring sometimes coincides with a change to a more nutritious diet in deer and may therefore be taken to provide roughage to balance rumen pH (Van der Veen, 1973; Reijnders and Van der Veen, 1974). These authors found that summer bark stripping was higher both at times and in places where alternate roughage was not readily accessible. Keenan (1986) suggested a similar explanation for a sudden outbreak of bark stripping by horses when allowed to graze an irrigated pasture with a low fibre and high nitrogen content.

In general however, nutritional studies of bark fail to show any simple relation between bark nutrient content and damage. This is perhaps not surprising since many nutrients, particularly minor ones, are unlikely to determine diet selection unless they are seriously deficient, and bark normally forms only a tiny component of a deer's diet (Welch *et al.*, 1987). The evidence nevertheless suggests that the occasional outbreak of serious damage could be motivated by a nutritional deficiency. Furthermore, bark is

of sufficient quality to justify it as an acceptable winter food item (McIntyre, 1975), which is sufficient to explain the more chronically stable levels of damage.

Supporting the evidence of bark as food, a number of authors have reported more bark stripping in areas where shrubs or other browse are lacking, or *vice versa* (Van der Veen, 1973; Reijnders and Van der Veen, 1974; Jamrozy, 1980; Welch *et al.*, 1987; Miquelle and Van Ballenberghe, 1989). Tree stems may however develop more branches or thicker bark in areas where more light gets through the stand to provide more browse, particularly if the stand is unevenly spaced. Stem characteristics may sometimes therefore vary in association with browse supply.

Winter feeding is required by law in many central European countries (Gill, 1990), but its influence on bark stripping is contentious. Szederjei (1957) even asserted that hungry deer did not strip bark, but deer given a supplementary food source did. Several authors have however found that damage can be reduced, sometimes to very acceptable levels, by a comprehensive feeding programme (Strandgaard, 1967; Ueckermann, 1983). Red deer are being increasingly kept in enclosures during the winter in central Europe and this implies that feeding is often not effectively reducing damage.

There are several examples of the influence of ranging behaviour on the incidence of bark stripping. Deer are often reported to strip bark when seeking shelter from snow (Chard, 1966; Springthorpe and Myhill, 1985) or when seeking concealment from human disturbance (Van der Veen, 1973; Maizeret and Ballon, 1990). The failure of winter feeding to reduce damage has been attributed to the fact that it attracts and concentrates deer, resulting in damage to nearby trees (Bubenik, 1959). McIntyre (1975) found a positive association between faecal pellet density and bark stripping damage, with the most severely affected sites often having the best understorey vegetation. Deer can therefore be attracted by food sources which may not then be sufficient in quantity or sufficiently preferred to deter bark stripping. In this way ranging behaviour could balance out any effect of feeding preference (Holloway, 1967b; Maizeret and Ballon, 1990).

Mimicry and learning behaviour may be important in some instances of bark stripping, because it may spread more rapidly if learnt from other individuals (Szederjei, 1957). Other authors have suggested that stress, caused by human disturbance or internal strife in the herd are involved (Bubenik, 1959; Van der Veen, 1973). So far, only anecdotal evidence supports these assertions.

Habitat and silviculture

Bark stripping by deer is unusual in North America. Although reports of deer bark stripping arise, particularly by wapiti on aspen (*Populus tremuloides*) (Lyon and Ward, 1982; Harestad *et al.*, 1986; Michael, 1987), surveys of forest wildlife damage make no mention of it (Crouch, 1969; Heidmann, 1972; Black *et al.*, 1979; Howard, 1982). Uniformly spaced monocultures are however also rare, particularly within the range of wapiti and the lower incidence of bark stripping has probably quite correctly been attributed to

differences in forest structure (Wolfe and Berg, 1988). Mixed age and species stands differ in a number of ways that may explain the lower incidence of damage. Vulnerable stems, for example, would be fewer and more randomly dispersed and an uneven canopy would allow better light penetration resulting in more branchy stems and a more effective browse distribution.

In Europe, damage has sometimes been reported to be worse in monocultures than in mixed crops (Van der Veen, 1973) and worse is planted than self-seeded stands (Szczerbinski, 1959). Lavsund (1974) however found that damage could occur in naturally regenerated Scots pine stands and in fact was greater where stocking density was high, probably because the bark remained thinner for longer. Bark stripping can also occur in national parks (e.g. Miquelle and Van Ballenberghe, 1989) so it is not solely a feature of man-made habitats.

FRAYING

The characteristics of fraying damage

Description

Fraying damage results from the removal of bark by the action of rubbing antlers or tusks up and down the stem. It is often associated with scent marking or velvet removal, and is sometimes referred to as rubbing or thrashing by other authors (Schloeth, 1968). The most common type of fraying in Britain is done by roe bucks to mark territories. Sika deer have the habit of scoring tree trunks with their antler points (Larner, 1977), which makes deeper, and more serious, wounds on the trunk.

Incidence and intensity

There are few published reports available to indicate how serious fraying can be in different tree crops, although it does appear to depend very much on the availability of suitable tree stems. In widely spaced broadleaved crops every unprotected tree can sometimes be damaged by roe deer (author's observation). Larner (1977) found that about 30 per cent of stems were damaged by sika deer in two woods in Ireland, but Schloeth (1968) reported only about 3 per cent damaged by red deer in Switzerland. Because such thin stems are used for fraying a large proportion may be completely girdled and subsequently killed (Turcek, 1962).

Species and sizes attacked

Red, sika and roe deer have all been reported to be selective among the trees they choose to attack (Thompson, 1969; Larner, 1977; Langvatn, 1982), and the same is probably also true of the other deer species. Physical characteristics appear to be more important than tree species.

Roe deer prefer springy, unbranched, sapling-sized stems for fraying (Thompson, 1969), and will attack almost any species (Turcek, 1962), although Thompson (1969) found western red cedar (*Thuja plicata*) and

rowan to be the most susceptible among 17 species available. Red deer select slightly larger trees than roe, mostly in the 50–250 cm height range, with some species (e.g. larch) susceptible at greater sizes than others (Schloeth, 1968; Langvatn, 1982). Sika deer appear to prefer smooth-barked stems greater than 30 cm d.b.h. (Larner, 1977); yew and rowan were found to be preferred to oak.

The size and species preferences can result in either dominant or suppressed trees being damaged more frequently than the stand average (Larner, 1977; Langvatn, 1982). Since sika select larger stems than the other two species dominants will be vulnerable for a much greater proportion of the rotation.

The causes of fraying by deer

Most fraying is done in relation to mating behaviour and is therefore intended either to display condition or status to a rival male, to mark a territory, or to leave scent (Schloeth, 1968; Cumming, 1974; Larner, 1977; Sempéré *et al.*, 1980; Langvatn, 1982). It is done much less frequently to remove velvet. The incidence of fraying by roe deer increases generally with population density, and occurs in two seasonal peaks, both at the onset of territory establishment in spring and during the rut in July or August (Sempéré *et al.*, 1980; Maizeret and Ballou, 1990). Fraying by red and sika deer occurs immediately before the rut in autumn, although another increase before antler drop has been reported in sika (Larner, 1977; Langvatn, 1982).

Since fraying is associated with rutting behaviour and consequently competition between males for access to females, it has been suggested that reducing aggression between males would alleviate fraying damage. This might be achieved by lowering the male:female sex ratio (Carter, 1981) or by shooting juvenile roe bucks in preference to established territory holding bucks (Prior, 1987). Clear evidence that either of these two measures reduces fraying damage is still however lacking. Unfortunately the function of scent marking by mammals is still not well understood, so the consequences of removing animals of a particular sex or status are not easy to predict.

DISCUSSION

Although this review has revealed many known causes of damage, it nevertheless remains difficult for forest managers to predict both the severity of damage as well as the reduction in damage that might be achieved by culling. There are two main reasons for this, each of which is discussed in turn. Firstly, methodological problems have sometimes led to a poor appreciation of the relative importance of each factor, and secondly, for a

forester, there are often simply too many interrelated factors to consider, making it difficult to predict damage effectively.

Limitations to identifying the causes of damage

Many studies of damage have used several sites for comparison or replication and therefore may have failed to detect the significance of a factor because adequate control proved impossible. Variables such as deer density, tree girths or heights, vegetation, hiding cover and soil fertility are often confounded and it is therefore not easy to assess the influence of each factor independently.

Two areas where further research would improve our understanding of the causes of damage are better deer density estimation methods and the influence of vegetation.

Culling is a widely adopted method of damage prevention and yet the information relating all three forms of damage to deer density is weak. The available evidence nevertheless suggests that there may often be a threshold density below which virtually no damage occurs and that the slope of the damage–density relationship may differ between habitats or stand types. This implies that the benefit of culling to a particular density may be variable. A weak slope, for example, would indicate that culling would reduce damage very little and therefore fencing, would be a more effective option, whereas a steeper slope would suggest that culling would be better.

It will not however be possible to provide this information to forest managers without a sound method of estimating deer density. Furthermore, better density estimation methods would bring the influence of other factors into sharper focus.

In some conditions, relating culling effort to damage is possible without estimating density at all. König and Baumann (1990), for example reported a good negative correlation between browsing damage on silver fir seedlings and the roe deer cull on a range of regeneration sites in southern Germany over a 13-year period. Unfortunately this approach is not suitable in plantation forests, because the loss of each plant is costly and therefore culling is best carried out in anticipation of damage, rather than in response to it. Furthermore, the effect of a cull would be difficult to detect where site differences would be confounded with year to year changes in density.

The influence of vegetation has a complicated influence on both browsing and bark stripping damage. The main habitat features clearly affect habitat selection and areas providing good food and cover often suffer the most damage, but other plants can reduce damage by providing an alternative food source. In general, it appears that damage is influenced more by habitat selection in red deer, which are more mobile, and more by diet in roe, which are more sedentary and selective. The influence of vegetation is also complicated by its composition, and therefore each community could have a different effect on browsing. It would be difficult to unravel all the

preferences deer show for native food plants, and making use of these would be further complicated by the imponderable aspects of foraging, such as how the dispersion of food plants provokes diet switching. However, the abundance of the most preferred food plants could be an important determinant of where and when damage becomes serious, especially for the most selective deer species, and a simple method devised to assess the abundance of these plants may prove to be essential if the risk of damage is to be assessed accurately enough.

Effective prediction of damage

Most reports and investigations of damage (and indeed most of this paper) have focused on particular aspects of the problem; identification of tree vulnerability, surveys of damage, investigations of some of the causes, and so on. It remains for a manager to assemble all the factors that contribute to damage and assess its likely severity. There have been remarkably few studies which have addressed this problem and attempted to demonstrate its feasibility.

Most of those available consist of statistical analyses of the variability in damage and the proportion explained by various factors, and were not strictly intended to serve a management function. They nevertheless provide an useful assessment of the feasibility of predicting the amount of damage.

In his study of bark stripping by red deer, McIntyre (1975) was able to explain between 51 and 87 per cent of the variation in percentage of damaged trees with 17 site variables, the most important being the proportion of larch. For leader browsing, Welch *et al.* (1991) found up to 51.2 per cent could be explained by just three variables; deer density, ericoid shrubs and the number of trees, although the precision was worse if plots, rather than sites were selected for analysis. Maizeret and Ballon (1990) chose a simple response variable (high or low damage) and found that a multivariate model could correctly predict the level of damage in 69–76 per cent of cases.

Although each of these models could be of value to management within the forest type from which they were derived, the examples given are not generally applicable and are either sensitive to spatial scale or have relatively weak predictive power. Furthermore, they demonstrate that different factors are important in different situations.

Since damage is influenced by factors that are both temporal (tree age, ground vegetation biomass) and spatial (stand types, site fertility, snow depth, roads) it could be more effectively predicted with a process model interfaced with a geographic information system. Although expert systems linked to geographic and forest databases are being increasingly used for forest management (Kourtz, 1990), so far there appears to be only one example of their application to mammal damage (Saarenmaa *et al.*, 1988). In this case, artificial intelligence methods were used to simulate moose behaviour; the

animals themselves chose where to forage in response to their needs and to what was available in the forest around them.

Such models have the flexibility to demonstrate how damage is related to direct management action such as culling, as well as indirect action, such as fertilizer application, road building or fencing nearby land. Unfortunately there are none yet available with proven accuracy. The most serious obstacle to developing models for damage prediction is likely to be obtaining data that faithfully enough relates damage in different crop types to deer density, ranging and foraging behaviour. This would probably be best achieved by linking model development to field research on the causes of damage.

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