Chapter 14

Managing roe deer and their impact on the environment: maximising the net benefits to society

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INTRODUCTION

In a world where many of the large mammal species are faced with extinction because of competition with people and livestock, the sharp increases of deer populations over the last century (in both north America and Europe, Gill 1990), provide a refreshing contrast. These increases are due to a combination of favourable land-use changes (increases in the area of forests and woodland and a reduction in extensive grazing) as well as to an improvement in game management. Measures implemented by hunters' organisations and wildlife professionals, including shorter hunting sea-sons, bag limits, reintroductions of deer, winter feeding and habitat management, have all helped bring about an increase in deer populations and re-present a success story for wildlife management. The resulting high deer populations are, however, now causing significant damage to other interests in the countryside (see for the case of the US McShea et al. 1997), and today the challenge is to include other stakeholders (e.g. foresters, hikers and nature conservationists) in the process of deer management.

This is made difficult by a number of factors, including the urbanisation of the majority of the people in these (democratic) countries, since urbanisation leads to life in surroundings of concrete and plastic, cut off from nature. This lifestyle has obvious advantages, in addition to convenience it encourages the emergence of civic virtues including more care for animals. The downside is that the vast majority of today's citizens in these countries have no personal experience of wildlife and wildernesses, and little under-standing of their ecological functioning. The idea of managing 'bambi' by shooting is unpopular especially among urban people, except among hunters themselves (at least in the United States (chapters in Warren 1997a)), so a wide range of alternatives is being explored, including trapping and re-location, fencing, birth control, reintroduction of natural predators and deer repellents.

The European Roe Deer: The Biology of Success
(Eds. R. Andersen. P. Duncan and J.D.C, Linnell).
Scandinavian University Press 1998.

In Europe, roe deer are a resource with great economic value for meat production and sport hunting. For example, in Sweden where the population has increased substantially over two decades, the annual harvest approached 400,000 deer in the early 1990s (Liberg et al. in press), and in Germany no less than 1 million (D.J.V. Handbuch 1996). In Sweden alone the venison from the annual harvest was estimated at 40-50 million $ US (Cederlund and Liberg 1995). Deer also have cultural value, for photography and other recreational activities, and ecological value as part of the bio-diversity of Europe including their role in the functioning of semi-natural ecosystems.

In parallel to the general increase in their range and numbers, however, deer are causing new problems, particularly damage to forestry and crops and collisions with vehicles. In Germany alone there are 50-100 000 reported accidents per year, costing perhaps 1 million $ US. In north America deer are also involved in the epidemiology of Lyme disease (13 000 cases reported in 1994, Conover 1997) and they may be in Europe too.

White-tailed deer *(Odocoileus virginianus)* have been termed a 'keystone' herbivore in the deciduous forests of the eastern United States since they alter substantially the structure and functioning of these ecosystems. Deleterious impacts on biotic communities have now been noted for more than half a century (Waller and Alverson 1997). The same may be true for roe. but data are woefully short: one of the great challenges facing European wildlife biologists is to document the impact of wild and domestic ungulates on our semi-natural ecosystems, to monitor trends over time, and to make the results known to the public so that early action can be taken to manage the populations. The experience from the US is that it takes a decade to alert biologists - and presumably as long again for the public!

In many areas of modern management of forestry and wildlife roe deer now are considered a source of unacceptable herbivory (Angelstam 1997). In most of Europe the natural balance between plants, roe, and predators no longer exists, so now that the roe are abundant, they generally require management. Objectives clearly vary between different management units, but tend to be to maximise the net benefits (Figure 14.1). Managers for

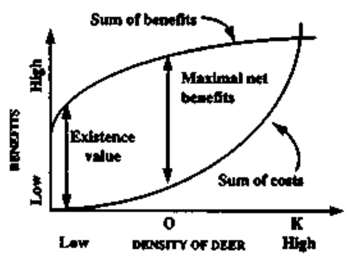

Figure 14.1. Schematic model of the costs and benefits of different densities of roe deer (after Conover 1997). **K** - the biological carrying capacity, **O** - the density at which the net benefits are maximised.

example, commonly try meet several (often contradicting) demands simultaneously, attempting to reduce damage, whilst maintaining high yields and hunting opportunities, so the process is not a simple one. Management in other areas of human activity commonly uses a modelling approach: management of roe deer (as for most European wildlife populations) has a good track record of successes, but is generally empirical. The tools needed as a basis for modelling, biological and mathematical (this volume), are be-coming available, so we can expect rapid steps forward.

This chapter reviews the issues and approaches to roe deer management, and addresses these questions:

- How do managers evaluate the state of the resource, roe deer populations?
- What damage do they cause?
- How are offtake rates determined?
- How can damage be reduced?

THE STATE OF THE GAME: NUMBERS AND TRENDS

Roe deer are known to be secretive and difficult to observe, particularly in forested habitats. In what now has become a classic, Andersen (1953) counted all the roe deer in a Danish wood by eliminating the whole population: prior estimates based on direct observations including drive counts had underestimated population density by a factor of three. Similar results have been reported elsewhere (Pielowski 1984; Ratcliffe 1987). In this section, we review methods which are widely used in roe deer management.

Capture-Mark-Recapture Methods (CMR)

The Petersen-Lincoln method, the simplest capture-mark-recapture (re-sighting) method (Petersen 1896; Lincoln 1930) has been used for many roe deer populations (Strandgaard 1967, 1972; Gaillard et al. 1986; Liberg et al. in press; Gill 1994; Andersen et al. 1995). This method can provide reliable estimates of population size as well as of confidence intervals if its assumptions are fulfilled, i.e. (1) a closed population, (2) an equal recapture or resighting probability among all individuals (especially for marked and unmarked animals), and (3) the number of marked animals in the population at any time is known (Caughley 1977; Seber 1982), and if a high proportion of animals are marked (around 60%, Strandgaard 1972; Gaillard et al. 1986). It is a method well suited for research projects because it allows estimation of survival rates as well as population size (Lebreton et al. 1992). However, its high costs make it prohibitively expensive for routine management.

More general CMR models than the Petersen-Lincoln method are now available, with user-friendly softwares like JOLLYAGE (Pollock et al. 1990), SURGE (available on the internet at http://www.biol.sfu.ca/wildberg/cmr/surge-guide.html) or Mark (available on internet at http://www.cnr.colostate.edu/~gwhite/software.html). These allow some of the assumptions of the Petersen-Lincoln method (closed populations. known numbers of marked animals) to be relaxed.

Transect methods

Kilometric index

This method is based on the ratio of the number of observed animals to the distance travelled by the observer along a set of transects in the study area. Widely used in France (Groupe Chevreuil 1991). this method is commonly based on about one transect of c. 5km per 200ha; the circuits are covered al least three times for each sample period at times when roe are active (three hours after sunrise or before sunset). This intensity of coverage was used to test the method in areas of 1000-2 500ha: it may not necessary to maintain such an intensity in larger areas, provided that the transects are chosen to be representative of the whole area. For annual monitoring the end of winter is a good season.

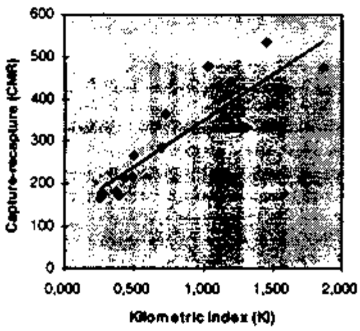

Figure 14.2. The relationship between an absolute estimate of population size (CMR. the Peterson-Lincoln index) and the kilometric index, KI (r = 0.88, van Laere et al. 1998) for the roe deer of Chizé forest, France.

In three areas in France (Chizé, Dourdan and Trois Fontaines) with different population trends, the correlation between the kilometric index and the known population sizes was about 0.85 (Groupe chevreuil 1991; Vincent et al. 1991. 1996: Gaillard 1988: van Laere et al. 1998: Figure 14.2). so about three-quarters of the real variations in population sizes over time were accounted for by yearly variations in this index. A change in shooting pressure (since it would make the deer more wary) or in the density of the vegetation during the period under study may result in bias error (Sage et al. 1983).

Spotlight road counts

Numbers counted at night using spotlights in vehicles have been used to estimate densities of roe deer (Cemagref 1984). However, while this method does allow a large number of roe deer to be counted, the reliability of these spotlight counts has been found to be very low. For example, after the removal of about 30% of the population in the forest of Chizé in France, densities measured by road counts showed no significant change (van Laere et al. 1998).

Line transects

The line transect method involves counting animals seen on both sides of a standardized transect of known length. For each object detected (individual or group), the distance between the object and the observer, the right-angle distance between the object and the transect, and the angle between the transect line and the direction of the object are measured. As long as the method's assumptions are fulfilled, in particular that (1) all objects on the transect are detected, in their (2) initial position, and (3) detections are independent events, then population density as well as its confidence interval can be estimated. These methods are statistically robust, and user-friendly softwares are available (e.g. DISTANCE, Buckland et al. 1993).

Line transect methodology is increasingly used for monitoring vertebrate populations (Seber 1992). however, it has not been used widely on roe deer (but see Zejda 1984, 1985 on field roe deer and Fandos et al. 1990 and Alvarez Jimenez 1988 on forest roe deer). A feasibility study on the Chizé population for which reliable CMR estimates of density were available led to encouraging results (Gaillard et al. 1993), however, wildlife professionals are often reluctant to use line transects. The small numbers of deer detected in most situations and the fact that the assumptions are difficult to meet (e.g. detecting roe deer in their initial position) are probably to blame.

Roe deer often respond to shooting pressure by becoming more secretive (Sage et al, 1983), which partly explains why they are so difficult to detect, and why they react quickly to observers. However, at night deer are often relatively tame, and may make more use of clearings than during daylight. This means that various forms of night vision equipment may be suitable for censusing roe deer. In a recent paper, Gill et al. (1997) combined the line transect methodology with thermal imaging equipment for censusing roe deer populations in Britain. The results they obtained suggest that the method allows accurate and precise assessment of roe deer population densities. It should now be tested against known density populations. However, the high costs of the thermal imaging equipment will limit the application of this method at the moment.

Pellet-group counts

These are used widely for estimating population sizes of large herbivores (Davis 1986). In theory this method has an advantage over many other indirect methods as it allows direct conversion from the number of pellet-groups (an index of abundance), to a number of animals per unit area (Mayle 1996).

In general pellet-groups are counted in winter, and different sampling techniques have been used (Aulak and Babinska-Werka 1990; Dzieciolowski 1976; Mitchell et al. 1985; Padaiga and Marma 1979; Wallin et al. unpublished data). It is important to estimate the rate at which pellets disappear (Plumtre and Harris 1995; Welch et al. 1990), or at least ensure that pellets do not decay between the time the plot is initially cleared and the date of counting. Defecation rate per roe deer-day is reported to vary between 10-23 in three different studies (17-23, Mitchell et al. 1985; 10-15. Padaiga 1979; 21.7 ± 1.36 S.E., Wallin et al. unpublished data).

An important assumption of the pellet-group method is that defecation rate is considered independent of factors like population density, age distribution, and type of forage consumed: recent studies on moose have shown that defecation rate varies, probably due to varying food quality (Jordan et al. 1993; Andersen et al. 1992). The method still needs to be carefully evaluated for roe deer: future studies should pay attention to these potentially confounding effects. At best it could be used for roe deer as a site-specific indicator of density changes between years.

Drive counts and other methods

The literature contains a large number of methods for censusing roe deer derived from hunting practices (e.g. drive counts, stalking, net-catches; De Crombrugge 1969; Boisaubert and Stoquert 1975; Boisaubert et al. 1979; Von Berg 1979; Cemagref 1984; Denis 1985; Blant 1987). In most cases, these have limited statistical bases, are likely to have low accuracy and precision: (1) they are ad-hoc methods without estimation procedures, so no confidence intervals are available, (2) sampling procedures are at best approximate, (3) they require a large number of people with inevitably different observational skills, and (4) double counting is difficult to avoid, especially at high population densities. When tested against populations of known size or populations for which reference methods are available, these methods have led to marked underestimates (Van Laere et al. 1998). Because of these problems, and despite the popularity of these methods among hunters, we do not consider them to be reliable for future research or management.

In conclusion, it is always costly to estimate absolute abundance accurately, since no single technique provides reliable estimates of roe deer densities in the range of conditions where they live, and the accuracy of all techniques is likely to vary from site to site. Since managers generally require re-liable population trends rather than inaccurate and imprecise density estimates, new approaches based on index methods merit attention.

Indicators of ecological changes

A set of indicators of ecological changes is being developed for roe deer populations and their habitats in France (Groupe chevreuil 199 6a). These parameters were selected as being easily measured and sensitive to changes in the balance between the population and its resources. By monitoring these over a number years, managers have a tool to assess trends and to select an appropriate harvest plan.

Body weight

Variation in body weight is crucial in explaining several life-history parameters, and hence population dynamics. Among roe deer fawn weights are known to be affected by summer temperature and density (Gaillard et al. 1996). The annual variation in fawn weights was negatively correlated with density ($r = -0.61$ for male fawns and $r = -0.58$ for female fawns). Vincent et al. (1995) report the same patterns where a decrease in average body weight of more than 20% was measured in fawns when the density increased from 5/km^2 to 25/km^2. The variation between sites is probably of such a magnitude that fawn body weight must be considered a site-specific index (see Andersen at al. this volume; Table 12.1). It is also important to correct for date, since fawns will continue to grow through the autumn and even the winter in some populations. The method has been used for several years in France as an index of roe deer/habitat relations (Maillard et al. 1989; Groupe chevreuil 1996b; van Laere et al. 1998).

Fecundity

Ovulation rate

Body weight clearly influences the fecundity of roe deer. Heavy does of all age classes are more likely to ovulate and/or implant larger litters than lighter does (Hewison 1996). Liberg et al. (in press) reported a significant response, with a decrease of 70% in ovulation rate among yearling does at high density (30 deer/km^2) compared to low density (12 deer/km^2). Similar results were obtained in the Chizé population (France, Gaillard et al. 1992a). Most studies report little variation in ovulation rates in adult females.

Fawn production

A substantial decrease in fawn production with increasing density has been observed in one study area in France (Vincent et al. 1995). The females > 2 yrs of age were counted each winter and the recorded fawn: female ratio decreased from 1.42 at low population density (5 deer/km^2) to 0.93 at high density (deer 25/km^2). A similar pattern has been reported in a non-hunted Swedish population at Ekenäs (Liberg et al. 1991). There was a good correlation between the number of fawns per mother and the population size (in March, CMR method) $r = -0.72$ in the Chizé forest (van Laere et al. 1998). The recruitment rate was calculated from observations of family groups, observed between the 1st of June to the end of November (see also Boutin et al. 1987).

Measures of skeletal size

There is a negative relationship between adult jaw length and the hindfoot length of fawns and density in the year of birth of a given cohort (Hewison et al. 1996; van Laere and Gaillard in press). The authors argue that this relationship reflects inadequate nutrition of juveniles at high population density. In conjunction with other methods these could possibly be used as in-dices of roe deer/habitat relations for large areas.

Browsing index

The browsing pressure of roe deer on the vegetation certainly increases with roe density. Monitoring the browsing impact on shrubs annually provides an index of the impact of roe deer on their habitat; it can also be used as a tool for quantifying the food availability (Mabille and Neet 1994; Ballon 1994; Groupe chevreuil 1996; Guibert 1997).

DAMAGE TO FORESTRY

Ungulates can have powerful effects on the species composition of deciduous and coniferous woodland and forests, natural and artificial, by brow-sing on shoots and foliage, fraying, debarking, trampling and scraping, and these ecological processes can cause financial losses to forestry (cf. Gill 1992a and b). It is important to distinguish between ecological interactions and damage, which has meaning only in relation to one or more economic or social objectives (see Reimoser and Gossow 1996 for a fuller discussion).

The impact of ungulates on plant communities is often reversible (e.g. by reducing ungulate densities), but there is increasing evidence that herbivory can cause some ecosystems to switch from one stable state to another. This is true in rangelands (Laycock 1991) and at least one forest ecosystem, the hardwoods of the Allegheny Plateau in the eastern United States, where heavy deer browsing since 1975 has been associated with a failure of tree regeneration in some areas, following invasion by herbaceous plants, ferns and grasses. Three processes have been identified as causes of this kind of switch: fire followed by heavy browsing, clear cutting followed by heavy browsing, and sustained, long-term suppression of regeneration by deer (Stromayer and Warren 1997).

In Europe, roe deer often coexist with other species, particularly red deer, which have similar browsing preferences, and which cause similar types of damage (Bobek et al.1979; Mitchell et al. 1982; Cederlund et al. 1980; Karpento 1980; Ammer 1996; Hernández and Silva-Pando 1996; Motta 1996). It is therefore often difficult to determine the effects due to roe. Their larger body size, and tolerance of lower quality forage, mean that red deer continue to damage the trees several years after the smaller roe deer have ceased to be a threat.

Though fraying is not negligible, damage to forestry by roe deer is caused mainly by browsing. Browsing of tree seedlings by roe has been reported across Europe and is often regarded as a severe problem in forest regeneration (Melzer 1974; Welch et al. 1988, 1991, 1992; Maizeret and Ballon 1990; Gill 1992a, b; Bergqvist and Örlander 1996). Here we focus on situations where roe deer are responsible for a large part of the observed damage.

Browsing by roe deer results in economic losses for forestry due to reduced timber quality, reduced growth, mortality, and changes in tree species composition. The leading shoot is often removed, resulting in a loss of apical dominance and ultimately timber defects, such as multiple trunks or stem sweeps, which seriously reduce the commercial value of the tree (Melzer 1974; Gill 1992b; Welch et al. 1992). However, technical defects on trees caused by roe deer browsing are probably less serious than those caused by larger cervids, because roe deer, unlike moose, seldom break trees (Heikkilä and Löytteniemi 1992). Due to their small size the defects caused by damage are located lower on the trees, so are less costly to prune.

Growth reduction varies considerably between tree species, but conifers seem to be somewhat more sensitive than deciduous trees (Mitscherlich and Weise 1982; Gill 1992b). Conifer species such as Sitka spruce *(Picea sitchensis)* which are relatively resistant may suffer from several years of browsing and only loose about a year of growth in height (Welch et al. 1992), while susceptible species such as silver fir (*Abies alba)* can be kept at a browsable height for several years or even decades (Roth 1996).

Changes in tree species composition due to browsing are caused by a combination of different feeding preferences between the browsers and of differences between tree species in response to, e.g. mortality and growth reduction (with a corresponding loss of competitive ability). For example, Scots pine *(Pinus sylvestris)* is more sensitive to browsing (Gill 1992b) and more often browsed than Norway spruce *(Picea abies)* in Sweden (Bergström and Bergqvist, in press) and thus heavy browsing pressure by roe deer in young mixed stands often results in a more or less pure spruce forest. Such effects have also been observed in other types of forests as in central Europe where young mixed silver fir and Norway spruce stands also ended up in a spruce-dominated forest due to browsing by roe deer and other ungulates (Ammer 1996).

Factors affecting the extent of damage in plantations

The extent of damage varies enormously between plantations. In southern Sweden the frequency of damaged Norway spruce and Scots pine seedlings one year after planting varies from 0 to 100% (within and between studies, Karlsson 1991; Bergquist and Örlander 1996; see also Melzer 1974; Welch et al. 1991). A prime cause is often the density of the browsing ungulates: within habitats positive correlations are often found between browsing damage and roe deer density (Maizeret and Ballon 1990; Welch et al. 1991). When comparisons are made between plantations in different habitats similar results have been obtained (Motta 1996), though the relationship can be non-linear (for white-tailed deer, Tilghman 1989; sheep, Hester et al. 1996). However, in comparisons across habitat sites there is sometimes more damage when roe deer density is lower (cf. De Jong et al. 1995 and Bergquist and Örlander unpublished data), suggesting the causes are multiple (e.g. abundance of alternative food, nutritional value of the seedings).

The causes of these variations are not well understood, but stand characteristics appear not to be very important compared to seeding characteristics (Bergström and Bergquist in press). Browsing varies between *tree species:* among deciduous trees the genera *Quercus, Salix* and *Sorbus* are often reported to be more preferred than others, and among conifers *Abies* species are more preferred than *Picea* with *Pinus* and *Larix* usually intermediate (Bobek et al. 1979, Gill 1992a and b; Motta 1996; though *Pinus spp.* are sometimes relatively unpalatable, Motta 1996).

The *size of a seedling* is very important for the degree of damage to the leading shoot: damage increases with height of the seedling to a peak around 40 cm. Thereafter damage declines with almost none on the leaders of seedlings higher than 1.2 m (Welch et al. 1988, 1991). However, roe deer can feed on lateral shoots long after that. Little data is available about what shoot diameters roe deer prefer. Under Swedish conditions the average bite diameter for both conifers and deciduous trees seems to be in the 2-3 mm range. When snow is deep in Swedish winters, roe deer have been observed to feed on shoots up to 1 cm in diameter on both conifers and deciduous trees (J. Bergquist and R. Bergström, pers. obs.).

Roe deer often show preferences for seedlings grown in certain conditions. As a general rule, roe deer (Bergquist and Örlander, unpublished data), like other species (Danell et al. 1991; Roth and Newton 1996) show preferences for more *vigorous trees* and seedlings. Vigour is defined here as seed-lings with higher growth rate and/or healthier appearance (e.g. greener foliage, lower amount of visual signs of injuries or stress). Most silvicultural practices (e.g. scarification, weeding, genetic selection, fungicide and insecticide treatment) before or in connection with planting are done to facilitate growth and health of the seedling and enabling it to survive all other threats to its existence, thus probably increasing the browsing risk. Earlier browsed seedlings also seem to have an increased risk to suffer new damage compared to unbrowsed ones (Welch et al. 1991; Bergström and Bergqvist in press) which can (among other possible factors) be explained by a faster compensatory growth.

Perhaps as a consequence, naturally regenerated seedlings are usually browsed less than planted ones originating from nurseries (Gill 1992a; Reimoser and Gossow 1996; Bergström and Bergqvist, in press). Among planted seedlings bare-rooted seedlings seem to be less preferred than container-rooted ones. These differences in preference are most pronounced the first year after planting and also differ between tree species. In Sweden this pattern is much more pronounced for Norway spruce than for Scots pine (Bergström and Bergqvist, in press). However, the mechanisms under-lying this preference are unclear. Planted seedlings and naturally regenerated ones differ in morphology, chemical composition and spatial position. Naturally regenerated seedlings often grow with a clumped distribution, while planted seedlings are mostly regularly spaced and are often in scarified or weeded plots, which could explain part of these differences in preferences.

Seedlings growing in vegetation (even the field layer) tend to be less browsed than ones growing in the open (Huss and Olberg-Karlfass 1982; Welch et al. 1988; Reimoser and Gossow 1996; Bergquist and Örlander, unpublished data). This protective effect from *associated vegetation* is a consequence of the generalist nature of feeding by roe deer (Duncan et al. this volume), and is aided by factors such as physical protection, and the reduced nutritional value of the seedling due to competitive stress. Since these factors operate simultaneously, it is difficult to separate them. In at least one study (Bergquist and Örlander, unpublished data) competitive stress provided the best explanation for reduced browsing damage by roe deer on Norway spruce seedlings. However, this may vary considerably with tree species and vegetation type.

Large open areas tend to be avoided (Papageiorgiou 1978; Guillet et al. 1995), perhaps because this species requires *cover.* As a consequence, edge zones near older stands are often used very heavily (cf. Thirgood and Staines 1989; Reimoser and Gossow 1996) which results in more damage to seedlings growing there.

In conclusion, in spite of the considerable amount of information available, there is currently no quantitative model for the prediction of browsing damage, its severity and occurrence.

CHOOSING THE OBJECTIVES - MOVING FROM SPECIES TO ECOSYSTEM MANAGEMENT

The recent increases in roe deer populations in countries like France are an example of highly successful wildlife management at the species level. This involved fundamental changes (including legislative) in the way roe deer and other large herbivores are perceived: shooting seasons were reduced, bag limits imposed and extensive reintroductions carried out (the Chizé reserve alone exported three thousand live roe between 1978 and 1990). Today the damage caused by the resulting high densities is less and less acceptable to stakeholders other than hunters, especially foresters. This could be reduced by increasing offtake, but as found in the USA, the lag-time for human institutions to respond is long. More socio-economic research is required into the mechanisms of decision-making. Here we present the biological side of the picture.

Harvesting roe deer - how many to remove and which ones?

The literature contains many examples of harvest regimes focusing on single factors such as maximum hunting opportunities and trophy shooting. Qualitative shooting plans based on criteria like age, sex or antler size (e.g. von Raesfeldt 1985; Kurt 1991), as well as quantitative shooting plans based on fecundity data (e.g. Ellenberg 1974; Eiberle 1979; Blant 1991) have been proposed for managing roe deer hunting in specific areas.

The approach to be adopted when choosing appropriate harvesting rates depends on management objectives. It is important to distinguish between situations where *control* is required from those in which *exploitation* is needed, because different types of information about the population are required in each case. It is therefore important that these objectives are clear from the outset. The least demanding situations arise when only a modest level of exploitation and a minimal population reduction are required, for example to provide a limited harvest for trophy stalking. This may be achieved with only a knowledge of the minimum number of males known to be alive, a figure relatively easily obtained from counts. If, however, demand for hunting is substantial and the highest possible yield is required, then it is necessary to try to maintain the population in a state that yields the maximum yield. This demands information on recruitment rates and an understanding of the conditions that affect them. Lastly, if the management goal is to reduce damage to crops or forest vegetation then culling to control the population is needed. In this event, information on population size (particularly of females) is the most useful. Without this, reducing density to an acceptable level will be difficult (Ratcliffe 1987; Lubow et al. 1996).

With all approaches, a knowledge of the variability in vital rates could be usefully applied to managing deer populations, particularly when attempting to achieve maximum sustainable yield. Unfortunately, key information on vital rates, particularly on survival and dispersal, has proved difficult to obtain and, so far, a general framework for long-term exploitation of roe deer populations that integrates the environmental stochasticity of recruitment, has not yet been proposed. However, the recent long-term studies of roe deer populations based on the monitoring of many marked animals performed in several European countries offer an opportunity to model roe deer harvests more realistically. With this aim in mind, we review here the general principles of hunting management and discuss them in the context of the current knowledge of roe deer population dynamics.

Managing for maximum sustainable yield (MSY)

Among the factors that affect variation in vital rates, density has received the greatest attention. Whatever the density-dependence function looks like, we can define (see Figure 14.3):

(1) a density at which the sustained yield of the population is maximised (Caughley 1977), and

(2) two densities at which no yield can be sustained over the long-term (a trivial one when there are no animals and a second one corresponding to the density at which recruitment rate is equal to death rate ($r = 0$), corresponding to the so-called carrying capacity (K) (e.g. McNab 1985).

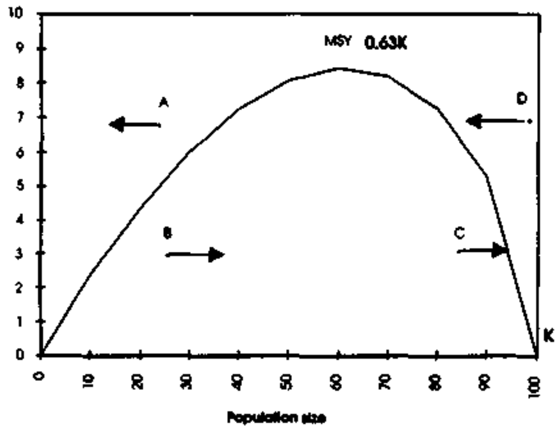

Figure 14.3. A density-dependent yield curve for roe deer (using empirical data, J.M. Gaillard unpublished). MSY is expected to occur at a density of 0.63K. Generation time is 4 years (Gaillard et al. 1992), average rate of increase per generation time is 0.25 (Fowler 1984). When sustained harvest is to the left of MSY, point A) exceeds rate of increase, the population is further reduced and goes towards extinction (as is the case if the harvest exceeds MSY); B) is lower than rate of increase and the population is increasing. When harvest is to the right of MSY the population tends to track back to equilibrium both for C) underharvesting and for D) overharvesting.

Knowledge of the relationship between yield and density is required when discussing sustained-yield harvesting (Caughley and Sinclair 1994). The shape of this relationship is a direct consequence of the density-dependence function. If roe deer populations behave like other large mammals, we can expect maximum growth rate to occur at high density (higher than K/2, Gilpin and Ayala 1973; Fowler 1981. 1987). This appears to fit the empirical data available for roe deer. From a very simplistic model of a French roe deer population with density-dependent responses, the population was expected to reach MSY at 63% of K (Gaillard, unpublished data; see Figure 14.3 for further explanations).

However, this figure includes total annual mortality, and hence the manager must compensate for non-hunting mortality when he decides the hunting quotas. It is evident that predators on roe deer can account for an appreciable component of total mortality (see Aanes et al., this volume).

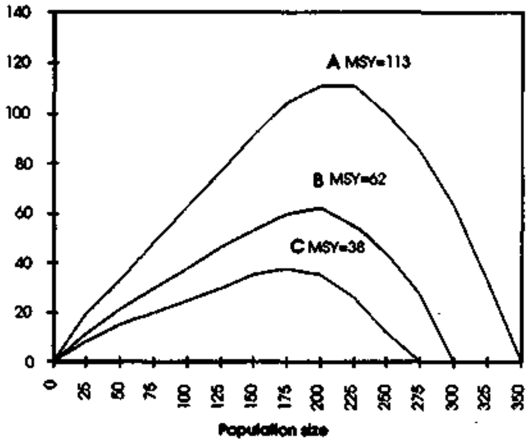

Figure 14.4. Theoretical density dependent yield curves for roe deer using data from central Sweden where the density is maximal (K in Figure 14.3). The three curves exemplify the effect on yield at different mortality rates:

A) maximum survival with mild winters (no or sporadic snow cover) and no fox predation;

B) mild winters with no mortality, but 50% fawn mortality in summer due to fox predation;

C) winters with permanent, moderate snow depth (<0,5 m snow cover over the entire winter); and winter mortality rates: 25% among male, 20% among female fawns, 10-20% for adults of both of sexes (depending on their age). Data collected in the study sites at Ekenäs and Bogesund, mid-Sweden (Cederlund and Liberg 1995; Liberg, unpublished data).

The examples given in Figures 14.4 and 14.5 clearly illustrate the dramatic reduction in the MSY if fox predation and/or winter mortality occurs.

However, environmental stochasticity has obvious effects on roe deer populations but it is not incorporated in these general principles. Harvesting at MSY will therefore lead to over-exploitation of the population, leading to accelerating decline and finally extinction. This illustrates one of the limits of such general models. In the case of roe deer, a more severe limitation is the difficulty of assessing MSY density in the field. If a re-liable assessment of density is not obtained (and roe deer are difficult to census - see the section entitled "The state of the game" above), it will be difficult to maintain the population at MSY. The set of indicators of ecological change described above can, however, be used to rank a given population on the sustained yield curve of Figure 14.4.

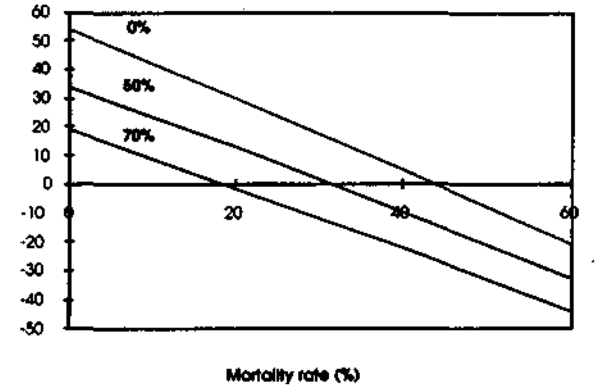

Figure 14.5, The theoretical effect of three different non-hunting mortality rates (i.e. 0, 50, 70% summer mortality of among female fawns due to fox predation) on the relation between mortality rate (due to hunting) and the annual rate of increase in the population of adult female roe deer. The horizontal line at zero indicates that the population is stable (annual rate of change = 0%). Above the line the population increases, below, it decreases.

For example, decreasing recruitment over 3 or 4 years will indicate that the MSY density will probably be overshot, while high body weights and high fecundity of individual females will indicate that population density is well below MSY density. As proposed by Clutton-Brock and Albon (1989) for red deer, a trial-error approach seems to be a practical option for most managers, who today operate without precise information on vital rates, habitat quality, and population history.

Managing to achieve population control

With recent increases in deer populations there is now growing concern for the impact deer have on forest vegetation, as well as an awareness that density-dependent regulation in the deer population may not on its own be sufficient to keep density below the level at which unacceptable damage occurs (Gill et al. 1995). Although it is sometimes advocated that culling effort may be simply raised until damage is reduced to an acceptable level, in practice this can be difficult to achieve. Damage levels are very dependent on the age, quality, and species of trees as well as being influenced by diet and habitat selection (see the section "Damage to forestry" above), so they cannot be expected always to reflect changes in deer numbers. A more satisfactory approach is to try to achieve and maintain control of the deer population whilst keeping unwanted impacts within broadly acceptable limits. Attempts at modelling the effects of culling on a deer population have demonstrated that effective control is easier to achieve if population size as well as other vital rates are known beforehand. This has been backed up by experience of control of deer in forests in Britain (Ratcliffe 1987). Since estimates based on counts are known to underestimate numbers, (and if relied on fail to achieve control), a method that yields unbiased estimates is required. Recently, efforts have been made to improve density estimation methods to ensure that this is possible (Vincent et al. 1996; Gill et al. 1997; Mayle pers. comm.). The cull required to maintain or reduce the population can be calculated using deterministic Leslie matrix models (Mayle 1996).

The harvest programme

Setting the harvest programme, usually on an annual basis for a species like roe deer with a life cycle scaled to one year, requires information on the two opposing flows of individuals, mortality and reproduction. In addition, the effects of emigration and immigration need to be assessed, since they, too, affect population growth. Almost all young animals disperse at the northern edge of roe deer distribution in Scandinavia (Wahlström 1995). Moreover, the number of individuals to be removed is not in itself sufficient to manage structured populations like those of roe deer. Demographic analyses have shown repeatedly that in iteroparous species with long generation times, changes in the numbers of adult females have much more impact on population growth rate than the same changes in the number of juveniles (Goodman 1981; Eberhardt 1985). For roe deer, the ratio is around 3 (Gaillard et al. 1992b).

When a high level of exploitation is desired a possible approach would be to skew the harvest in favour of males. This results in little or no reduction in females and therefore helps to ensure that a high yield or population growth rate can be sustained. This approach to management has been widely adopted in the USA, and to a lesser degree in parts of Europe, with the intention of providing the maximum possible number of hunting opportunities whilst protecting the deer population (Gill 1990). There does not appear to be any evidence that recruitment is affected by changes in the adult sex ratio in roe deer, although there is continued debate about the possibility of loss of genetic variation (see the subsection *The effects of harvesting* below).

Any useful model of roe deer population will recognise at least two age classes: fawns (0 to 1 year of age) and adults (older than 1 year). The manager should also pay attention to environmental stochasticity of vital rates for assessing his management rules. In particular, interactive effects of population density and harsh climatic conditions (like a severe winter) will decrease the population density much more than the decrease expected from the simple addition of the effects of population density and winter severity.

Up to now, numerous deterministic models have been used, either conceptually or using empirical data, to explore the effects of different harvest strategies on the dynamics of roe deer (e.g. Bobek 1980, 1984; Csanyi 1991; Georgii et al. 1992; Wotchikowsky and Schwab 1994; Cederlund and Liberg 1995). More recently, modelling has integrated CIS information to estimate densities and suggest future harvest plans for roe deer (Radeloff 1996). The next step is to develop a more predictive theory of harvesting roe deer, based on an approach conducted at a scale (regional or national investigations) larger than the population scale usually undertaken (Giles 1978).

The effects of harvesting

Human activities, especially shooting, can have negative effects on roe deer populations (Herbold 1990; Kurt 1991). Furthermore, although unverified for roe deer, there is a continued debate on the possibility that sex-biased harvest strategies in cervids could lead to a loss of genetic variation by reducing the effective population size (e.g. Ryman et al. 1981; Harmel 1983). Some indirect effects are described below.

Spatial use: In the light of the growing awareness that dispersal in roe deer could be inversely density-dependent over a range of high densities (Wahlström and Liberg 1994; Gill 1994), reducing population size is unlikely to limit dispersal, except at very low density (Wahlström and Liberg 1994). The highest rate of dispersal is observed at intermediate density, which could account for the observation that roe deer populations have ex-tended their distribution in Great Britain, Sweden, and Norway in spite of shooting pressure within their established range (Gill 1990).

The death of an adult roe deer is often followed by settlement of the same territory/home range by another deer of the same sex. This appears to occur in both sexes, but more quickly after the death of a male than after a female, especially during spring and early summer in view of the competition of territories (Bramley 1970; Strandgaard 1972). In contrast, an experimental removal of territorial bucks in August at Bogesund in Sweden gave little evidence for an immediate colonisation of new territory holders (Cederlund et al. 1993). Hunting in spring could therefore result in rapid recolonisation of favoured habitats in spite of local shooting pressure, ma-king a reduction in local density difficult (McIntosh et al. 1995; Fairweather 1997), while hunting in autumn might have stronger effects. To reduce populations, harvesting should be performed on areas of not less than 3-5 km² in high density areas (Cederlund et al. 1993).

Hunting selection: How will different harvest regimes affect population demography? A hunter may shoot a specific roe deer for several reasons, like antler size, body size, age, productivity, etc. If genetic attributes are assumed to be constant, genetic characteristics do not change in response to harvest programmes (but see Scribner et al. 1983). Therefore, the relative value of inheritance and the environment should be investigated. The selective shooting among bucks in central Europe to improve trophy quality is perhaps the best example of such an action. After more than 100 years of planned shooting in many areas there is not yet evidence that the desired effects have been obtained.

Hunting may affect the population dynamics if directed towards specific sex or age classes, thereby potentially leading to changes in life-history traits such as onset of fecundity and body growth (e.g. Gadgil and Bossert 1970; Bell and Coufopanou 1986), and maybe also in adult sex ratio and mating systems. Large selection processes might act on the composition of the population even in a relatively short ecological time scale (e.g. Endler 1986). In one of the few studies addressing hunting versus evolutionary response, Skogland (1989) suggested that directional selection among wild reindeer lowered mean body weight by removing large phenotypes from the population.

Managing roe deer - are we doing the right thing?

As humans place increasing demands on wildlife populations for food and recreation, managers need much more precise information about population dynamics and ecology on the species they manage (e.g. Caughley 1982; Dodds 1990; Klein 1989). Moreover, in a decision-making process it is also important to understand how people value wildlife, if nothing else, to be better equipped to defend and justify the importance of management actions taken (Heberlein 1992; Filion 1992). This includes the integration of wildlife management to landscape management (Rodiek 1992).

What level of ambition should future roe deer management aim at? Should we consider roe deer as a medium-sized game species with high stochasticity in population performance and treat it as such (with low ambition for specific harvest quotas) or should we try to control populations with the ambition to stabilise a desired level and with a specific composition? No matter what, the scientist's role should be to inform the manager of possible options and then leave him to decide his own priorities (c.f. Clutton-Brock and Albon 1989). It may seem disappointing that Clutton-Brock and Albon (1989) and McCullough et al. (1990) after several years of research on deer concluded that the best advice given to a deer manager might be to operate by trial and error, i.e. the rate of sustained yield was best achieved after manipulation of annual harvest and monitoring the effects of this population size.

Why is population dynamics theory, for example the well-known matrix models (Caswell 1989), not successfully used for roe deer? The most probable answer, common for most ungulates was given by Eberhardt (1991): lack of data. The strength then of demographic analyses is a matter of the quality of the information available for a given population.

One problem is that the manager can not easily assess (1) if the mortality, fecundity, and survival rates are density-dependent, (2) the effects of harvesting on mortality and survival; (3) changing habitat quality (Gill 1994). If there are also cohort effects or other stochastic sources affecting the dynamics (Gaillard et al. this volume) as well as there might be effects of selective harvesting on the vital life-history variables, these must be known and if possible quantified in order to further assess the population dynamics and increase the accuracy of the management plans. As pointed out in Gaillard et al. (this volume), deterministic management models should be used cautiously, or replaced with stochastic models.

It is evident that populations dynamics of roe deer include high spatial and temporal variation that must be taken into account when managing on a local scale. In view of the impact on landscape structure and biodiversity, and the animal's potential to rapidly reach high densities, we can expect roe deer, like other ungulates, to strongly affect composition and standing crop of the vegetation in an interactive way (see Caughley 1979). Therefore, in times when we alter forestry practices and composition of the crops the vital rates of roe deer populations are expected to change. This is important for the manager to know, especially if variation in growth and fecundity might be accounted for more by habitat changes than by population density (Gill 1994).

Finally, to improve roe deer management from a theoretical standpoint, there are at least two fields of future research. First, we must learn more about the long-term effects of roe deer-plant interactions where we account for both variation in demographic variables and changes in the plant composition and standing crop, preferably including a spectrum of roe deer habitats (Duncan et al. this volume). Second, to measure the effect of an increasing hunting pressure on roe deer populations. In this context it is of less importance to estimate the immediate variations in age and sex composition or total density, but rather the effects on general life-history patterns due to persistent selective harvesting of certain categories of roe deer (e.g. sustained harvesting of adult bucks for trophies). In addition, it is important to improve existing methods for estimating the vital rates in roe deer demography and, if necessary, find new ones which have been tested rigorously.

REDUCING DAMAGE

The obvious means is to reduce the number of roe deer: this is often difficult since hunters might not be co-operative since they often want to maintain high populations (see the section "Choosing the objectives" above). A further complicating factor is the variable (and sometimes high) dispersal rate among roe deer that may increase immigration to areas of locally low abundance (McIntosh et al. 1995), however this is not a problem in all species of deer (McNulty et al. 1997).

The principles underlying management for the reduction of damage by roe deer (and indeed other ungulates) are:

(1) exclusion of the browsers;

(2) attracting them to other areas;

(3) choice of less sensitive seedlings; and

(4) reduction of the apparency of the seedlings.

Exclusion and protection

Fencing is commonly used to protect vulnerable tree species. Net fences are efficient if they are well designed. To exclude roe deer they should be 1.5 m high with a spring-steel line wire and a mesh of less than 20 cm (Anon. 1981; Pepper 1992 and pers. comm.). The high costs of setting up, maintaining, and taking down a net fence can seriously reduce the profitability of forestry. Electric fences are normally cheaper to construct than conventional deer fencing but experiments with a suitable design for roe deer has not yet yielded a satisfactory specification. Roe deer coats are more resistant to electrical current than red deer (Butt et al. 1998) and a fence with a low enough current to be safe for human contact will not deter roe deer (H.W. Pepper pers comm.). However, cheaper fencing, for example without spring-steel line wires, or of a lower height (1.2m) will be effective at eliminating or at least reducing damage if the fenced enclosure is small (<5 ha), and thus may keep browsing pressure to an acceptable level.

Protecting individual seedlings

Perhaps the commonest way of protecting seedlings from deer damage is to place something on or around then that repels the animals or physically hinders them from feeding on the seedlings. Such methods vary considerably from country to country and the scientific basis for them is often weak. Protecting individual seedlings makes it easy to design reasonably reliable and cheap tests in order to determine which repellents have the best effect. Repellents are generally designed to deter all types of deer species but at present little is known of the responses of roe deer to any of them.

Physical protection on or around the seedling can be used to protect both conifers and deciduous trees (Cemagref 1981; Putman 1994). Branches and stones available nearby can be placed close to the seedlings, or seedlings can be planted in naturally inaccessible spots. Artificial obstacles (such as stakes or plastic tubes) have also been designed for the same purpose: these usually provide better protection than natural materials (Pepper et al. 1985).

Attracting the deer to alternative areas - a sometimes dangerous tactic

Different types of alternative feeding are sometimes proposed, either artificial feeding or by facilitating attractive vegetation. Even if winter feeding is sometimes practised, the main intention is often to maintain high deer densities with protection only as a secondary priority (if this is considered at all), thus making it hard to estimate possible protective effects. Research in this field is, however, lacking: one can only guess through knowledge from other cervid species (Gill 1992a) that it's better to place the food source away from the area one wants to protect. Concentrating the animals by artificial feeding can cause increases in damage.

Another way to dissuade roe deer from using an area is to introduce devices that produce sounds or visual signals that frighten the animals away. This type of protection has the advantage of being cheap, but there is little evidence, if any, of long-term efficacy.

Choosing less palatable seedings

A very common method to reduce browsing damage is to use seedling types that are little used by the deer. However, forest managers must consider more than browsing damage when regenerating an area and thus the freedom to select different types of seedlings is often restricted. For instance, large seedlings are less vulnerable to browsing damage but are generally more costly to produce, transport, and plant.

Vulnerable tree species are often avoided in regeneration projects. As an example forest managers in southern Sweden avoid planting Scots pine even on sites where pine would normally be more economically beneficial than the main alternative species, Norway spruce. This reinforces the change in tree species composition initiated by higher browsing damage on Scots pine.

The production of seedlings of low feeding value is often suggested. One way could be to grow a less nutritious seedling through lower doses of fertilisers in the nursery. Practical experiments have been done in southern Sweden with such 'starved' seedlings and roe deer seem to avoid them, but the seedlings grow very slowly and they suffer from other types of damage (Staffan Nilsson, pers. comm.). Another way to produce unpalatable seed-lings, with high concentrations of natural feeding deterrent compounds, is through breeding, cloning or genetic engineering. This approach is controversial (and subject to criticism from the public); it can also be costly as the-re is a negative correlation between growth rate and concentrations of deterrent compounds (Danell et al. 1991).

Repellents

Chemical repellents are used mainly to protect conifers (Pepper 1978, 1981; Andelt et al. 1991, 1992; Bergquist and Örlander 1996). They are usually applied by spraying or smearing on the shoots of the seedling and deter animals through taste or smell. There are also examples of systemic repellents, which means that the agent is taken up through the roots and gives a deterrent taste or smell to the foliage. Even if many tests have demonstrated significant deterrent effects for several products, there are also factors reducing their practicality. Phytotoxic effects by chemical repellents have been described (Karpento 1980; Bergquist and Örlander 1996), and studies on other deer species have shown that chemical repellents may function poorly: their efficacy seems to be reduced when a large proportion of the seedlings in an area are treated (Conover 1984; Gillingham et al. 1986); repellents lose efficacy with time because deer get used to them (Melchiors and Leslie 1985; Andelt et al. 1992) and/or by dilution through precipitation (Sullivan et al. 1985; Andelt et al. 1991); a lack of alternative food can force deer to feed on treated seedlings (Andelt et al. 1991, 1992); and the response may also vary between individuals (Harris et al. 1983) or groups of animals, and such effects have been indicated for roe deer (Bergquist and Örlander 1996). Chemical repellents are probably more suitable in protecting conifers, since conifers are dormant during the period of highest browsing pressure and thus probably less sensitive to phytotoxic effects, and no fresh unprotected foliage is produced. Most conifers retain their needles during winter thereby offering a larger attachment surface for the repellent.

Some repellents are also coloured (Pepper 1978; Bergquist and Örlander 1996) to give a visual signal to the animals. White or fair colours are mostly used for this purpose then in combination with chemical or physical repellents.

In a study by Swihart and Conover (1990), it was found that white-tailed deer soon lost their respect for different smelling soaps, and there is no reason to believe that roe deer should react differently (see Duncan et al. this volume). Such methods might be useful when used during short, distinct damage periods such as browsing in early summer on fresh conifer shoots; otherwise these methods are generally of little practical value.

Fraying damage

Roe deer males rub their antlers on young trees and the bark is often severely damaged. This type of damage occurs during summer (Cemagref 1981; Maizeret and Ballon 1990; Johansson et al. 1995) and is mainly connected with mating behaviour (i.e. territorial defence). Bucks prefer seedlings of about 2-3 cm in diameter (Cemagref 1981; Johansson et al. 1995; Motta and Nola 1996) and damage typically occurs at 10-80 cm in height (Anon. 1981; Motta and Nola 1996). *Pinus* spp. are often preferred (Mitchell et al. 1982; Nilsson and Gemmel 1989, Johansson et al. 1995, Motta 1996), but preference varies between studies. Rare species (Nilsson and Gemmel 1989, Johansson et al. 1995) and exotics (Nilsson and Gemmel 1989) tend to be frayed more often than dominant and/or native species. This damage is often more severe (and is often lethal for the tree), but in most cases it is less frequent than browsing damage.

The most obvious measure to prevent fraying damage is to reduce the number of males. There is a lack of knowledge about how large a proportion of the males that must be removed to reduce damages since only a portion of them defend territories and a shot territorial buck will soon be replaced by a former non-territorial one. If two or more weaker males replace a territorial male that has been shot and divide its territory, fraying damage may even increase.

CONCLUSIONS

Deer densities in the USA have been high for some time, and though the animals are perceived to be causing serious damage, there is not yet a consensus on the aims and tools to use to manage the deer herds. In much of Europe, north and south, deer densities have risen only recently which suggests that our problems are just starting. It is essential that rigorous monitoring of the populations and habitats is carried out to provide managers and the public with solid information on which to base decisions.

Estimates of absolute densities (which are useful for management) are currently either inaccurate or expensive, but new developments (e.g. transect counts combined with a thermal imager) hold promise, as do recent developments of indicators of ecological change. Further work is needed ur-gently to test these developments.

There are few European ecosystems where it is known whether roe deer (or indeed the other ungulates) are 'keystone species' (i.e. have a strong impact on the structure and functioning of the ecological systems). More in-formation on this issue is needed urgently to evaluate the effects of these ungulates on biodiversity conservation. Damage to forestry varies greatly in time and space, yet there is no quantitative model currently available for the prediction of browsing damage, its severity and occurrence.

As humans place increasing demands on wildlife populations for food and recreation, managers need better information about the population dynamics and ecology of the species they manage, so that they can use quantitative methods for determining offtake. Currently, damage prevention is achieved mostly by fencing, which is costly. Recent research on the ontogeny of food selection suggests new approaches to the search for repellents.

In spite of the gaps in our knowledge outlined above, there is today a reasonable biological basis for the management of roe deer populations. Management of roe (and wildlife in general) needs to become part of landscape (or system) management. More attention needs to be paid to understanding how people (especially the urban majority) value wildlife and their attitudes to the different methods of management, and to informing the public about the issues and the options available.

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