Habitat and population modelling of roe deer using an interactive geographic information system

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Abstract

Management of German roe deer (*Capreolus capreolus*) populations is a challenge for wildlife managers and foresters because population densities are difficult to estimate in forests and forest regeneration can be negatively affected when roe deer density is high. We describe a model to determine deer population densities compatible with forest management goals, and to assess harvest rates necessary to maintain desired deer densities. A geographic information system (GIS) was used to model wildlife habitat and population dynamics over time. Our model interactively incorporates knowledge of field biologists and foresters via a graphical user interface (GUI). Calibration of the model with deer damage maps allowed us to evaluate density dependence of a roe deer population. Incorporation of local knowledge into temporally dynamic and spatial models increases understanding of population dynamics and improves wildlife management. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The purpose of this study is to develop a tool for managing roe deer in Germany. Management of roe deer is controversial because foresters claim that high roe deer populations inhibit natural tree regeneration. In contrast, hunting organizations oppose reducing deer populations, and perceive environmental factors (e.g. acid rain) as the main constraint on forest regeneration. Sound management of roe deer populations is complicated by

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the difficulty of assessing the population density of roe deer in forested areas (Strandgaard, 1972; Vincent et al., 1991).

Roe deer are common throughout Europe and are the most important game species in Germany. The species is managed in administrative units usually not larger than 10 km². For each hunting unit, one hunter leases hunting privileges for 9–12 years. Under the current management system in Germany, the hunting administration prescribes the annual harvest for each hunting unit. The harvest plan specifies the number of roe deer to be harvested in three age classes for each sex. The hunting leaseholder must report every deer killed and is legally responsible for fulfilling the harvest plan (Ueckermann, 1988). The number of deer to be harvested is calculated from a spring population estimate by the hunting leaseholder under the assumption of a recruitment rate of 1.0 fawns per breeding female (fawn sex ratio 1:1). This procedure is not based on current scientific knowledge about roe deer population dynamics, such as density dependence. It does not capture the dynamics of roe deer populations, changes in habitat suitability, or previous hunting success. These shortcomings in the assessment of the harvest plans result in their low acceptance and poor fulfilment by many hunting leaseholders.

We present an improved approach to roe deer management, incorporating current knowledge of population dynamics and modelling techniques, to assess roe deer densities and harvest plans. Our goals are: (i) to develop a roe deer management model that links habitat suitability and population dynamics; (ii) to make the model adaptable to local conditions via a graphical user interface (GUI); and (iii) to assess whether harvest rates are adequate to prevent forest damage by roe deer browsing.

Roe deer prefer to forage near protective cover and are often found in early successional habitat and forest plantations. The presence of spatial structures (e.g. forest/field edges) determines habitat suitability of a management unit for roe deer. Thus a geographic information system (GIS) - based approach for assessing habitat for roe deer is appropriate.

GIS is often used to derive habitat suitability models from a set of GIS layers (Donovan et al., 1987; Pearce, 1987; Aspinall, 1991; Aspinall and Veith, 1993), that describe large areas on a relatively coarse scale (Heinen and Mead, 1984; Scott et al., 1993; Mladenoff et al., 1995). Most GIS models of wildlife habitat capture only one point in time rather than habitat dynamics over time (Ormsby and Lunetta, 1987; Aspinall, 1991). Dynamic models of wildlife habitat interactions often do not incorporate GIS functionality (Bhat et al., 1996; Bettinger et al., 1997; Stankovski et al., 1998). Dynamic GIS based models have only recently been developed (Ozesmi and Mitsch, 1997), and used to optimize wildlife habitat spatially (Nevo and Garcia, 1996; Garcia and Armbruster, 1997).

Roe deer of both sexes occupy small home ranges and adult males defend territories. In central Europe, yearling roe deer of both sexes disperse only short distances (Wahlström and Liberg, 1995). In several European studies, the majority of marked fawns were recaptured or harvested as adults within 1 km of the capture site. Dispersal distances of more than 10 km are rarely observed (Ellenberg, 1978, Danilkin and Hewison, 1996). The small hunting units and the small home ranges of roe deer require a management tool that operates at the local scale (1–10 km²). Previous GIS-based studies on deer species have operated on much broader scales, making their approach poorly suited for managing a species with small home ranges within small harvest units. (Tomlin et al., 1983; Leckenby et al., 1985; Milne et al., 1989; Huber and Casler, 1990; Wright and Boag, 1994). None of the existing roe deer habitat assessment tools for Central Europe are GIS based (Müller, 1964; Bobek, 1980; Ueckermann, 1988).

Early research on roe deer population dynamics by Strandgaard (1972) and Bobek (1977, 1980) neglected density dependence and assumed dispersal to be the primary regulator of population density. Recent evidence indicates that roe deer populations are not regulated by dispersal (Vincent et al., 1995; Wahlström and Kjellander, 1995; Wahlström and Liberg, 1995). The high emigration rates in Strandgaards' study appear to be due
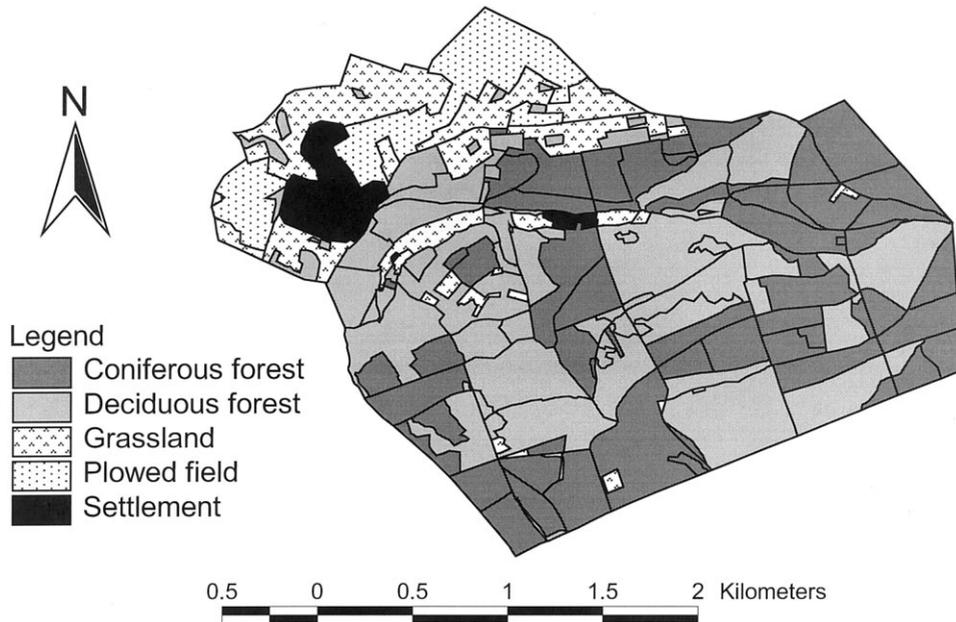
Fig. 1. Land cover of the Holzerath study site in 1993; derived from forest compartment maps and aerial photographs.

to the juxtaposition of the study area, where no harvest occurred, with the surrounding area, where harvest was high (Gaillard et al., 1993).

During the last decade, research groups in France (e.g. Gaillard et al., 1992, 1993; Vincent et al., 1995; Gaillard et al., 1996), Scandinavia (e.g. Wahlström and Liberg, 1995) and the UK (e.g. Hewison, 1996; Putman et al., 1996) have presented evidence for two density dependent factors influencing roe deer population dynamics. First, in regions of mild climate, there is an inverse correlation between body mass and population density (Blant, 1991; Gaillard et al., 1992, 1993; Vincent et al., 1995; Gaillard et al., 1996). Body mass is positively correlated with the probability of pregnancy in roe deer does younger than 20 months (Gaillard et al., 1992, Hewison 1996). Second, juvenile survivorship increases with decreasing population density (Fruzinski and Labudzki, 1982; Gaillard et al., 1992).

The main density independent factor in roe deer population dynamics is climate (Gaillard et al., 1993). Winter snow depth is negatively correlated with survival rates in all age classes (Fruzinski et al., 1983; Gaillard et al., 1993). In most German hunting grounds, winter mortality related to snow depth is reduced by supplemental feeding. Precipitation in April and May is negatively correlated with male fawn body weight (Gaillard et al., 1996) but precipitation in May and June is positively correlated with fawn survival rates for both sexes (Gaillard et al., 1997). These complex responses of roe deer populations to weather make their modelling difficult.

In summary, a management tool for roe deer useful at the local scale requires use of a dynamic habitat suitability model in a GIS that can incorporate habitat change. The model should provide a GUI to make it easily accessible and flexible for wildlife managers. Finally, the habitat model must be linked to a population model that incorporates density dependence. We describe such a model.

2. Study area

The study site, Holzerath, is located in western
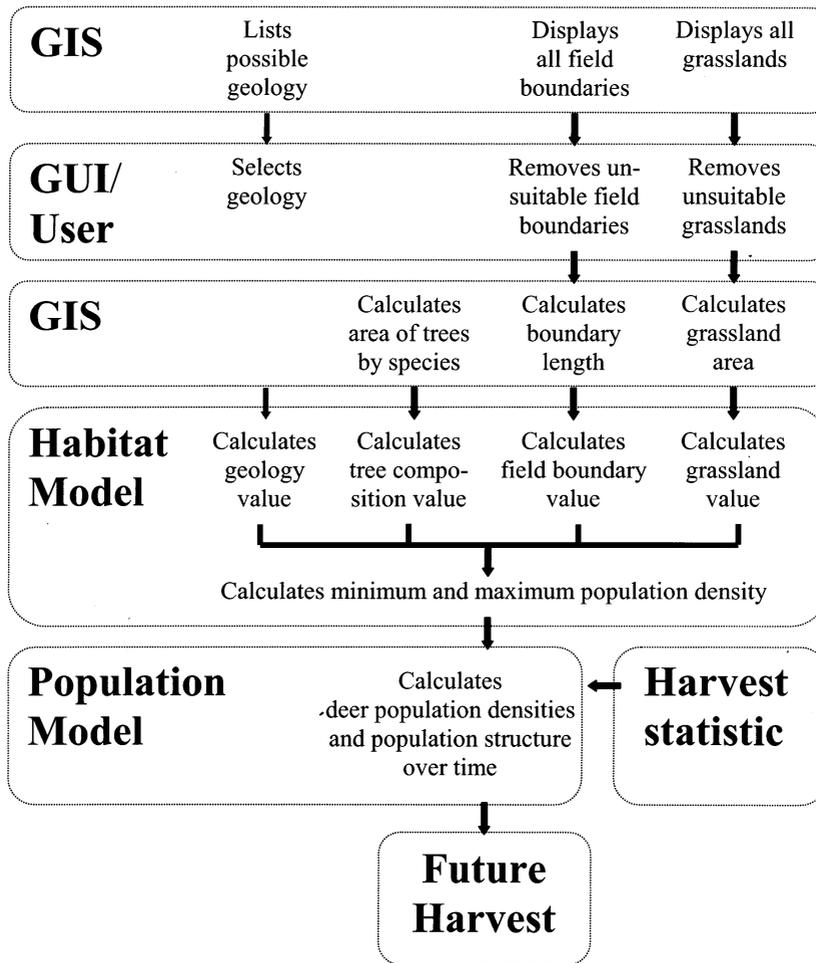
Fig. 2. Structure of the integrated habitat and population model based on a GUI in a GIS.

Germany, 50 km Southwest of Luxembourg city. It covers 673 ha, of which 513 ha are forested, 135 ha are agriculture, and 25 ha are covered by settlements (Fig. 1). The potential natural vegetation type is beech (*Fagus silvatica*) forest. Forests are managed in even-aged stands with rotation cycles ranging from 30 years for firewood up to 150 years for timber. Half of the forested area on the study site is dominated by conifers (primarily spruce (*Picea sitchensis*) and pine (*Pinus silvestris*)) and half by broadleaf species (primarily beech and oak (*Quercus robur*)). Roe deer and red deer (*Cervus elaphus*) are native to the area and

large predators are extinct. Wild boar (*Sus scrofa*) and red fox (*Vulpes vulpes*) may both predate roe deer fawns (Aanes and Andersen, 1996). Holzerath is in many respects a typical German hunting ground, which makes our study broadly applicable.

Detailed harvest statistics were available for our study site from 1978 to 1994. Throughout this period wildlife management was consistently the responsibility of one hunting leaseholder. Windthrow during two storms in winter 1989/90 affected 24 ha of the forest that improved roe deer habitat by increasing herbaceous cover.

3. Methods

Our roe deer model is structured in two major parts (Fig. 2). The first part is a spatially explicit habitat model, based on a GIS land cover data set. This part of the model includes an interactive GUI. The second part is an iterative population model that calculates population levels for single hunting units. The model output for our study area was validated by deer browse maps made by the Ministerium für Landwirtschaft, Weinbau, Umwelt und Forstwirtschaft Rheinland-Pfalz (i.e. the State Forest Service) in 1992 and 1995 (MLWF, 1995).

3.1. Habitat model

We implement and augment the habitat suitability model by Ueckermann (1951, 1957, 1988) in a GIS because it incorporates spatial structures and is widely used by wildlife managers in Germany. Ueckermann's habitat model was derived from a correlation analysis of 171 German hunting grounds (Ueckermann, 1988). He assessed the habitat suitability index (HAB) by correlating the weight of roe bucks older than 3 years with environmental parameters. The underlying assumption is that these bucks have held a territory for at least 2 years and thus are indicators of local habitat suitability. Ueckermann explained 82% of the variation of male body weights using a multiple regression of four parameters (Table 1).

$$HAB = GEO + TRE + FPB + GRA \qquad (1)$$

The four parameters are dimension-less; Ueckermann (1988) weighted them so that perfectly suitable habitat has a HAB value of 100. In practice values between 40 and 85 occur in Germany. Geology (GEO) represents a qualitative measure of soil fertility and is an indicator of browse quality of the herbaceous layer. Relative tree species composition (TRE) indicates browse quality in winter and also herbaceous browse quality in summer due to different shade regimes. The frequency of boundaries between forest and plowed fields (FPB) is also an indicator of forage quality. Parcels of plowed fields in the vicinity of forests improve habitat. Grassland enclosed by forest (GRA) is important for forage and for the first two weeks of life during which fawns need tall grass as cover. The values for the four parameters under different conditions are presented in Table 1; for further details about the model and the underlying analyses refer to Ueckermann (1951, 1957, 1988).

Ueckermann related his habitat suitability index to roe deer population densities by assessing two density values for each habitat suitability class (Ueckermann, 1957, 1988). His economically acceptable density is a subjective value at which

Table 1
Values for the four parameters of the habitat suitability index (after Ueckermann 1988)

Parameter	Value
Geology (GEO)	
Sandy outwash plains	14
Other glacial deposits	18
Sandstone, granite, chalk	20
Basalt, gneiss, slate, loess	23
Jurassic deposits	30
Limestone	35
Tree composition (TRE) (*the average is taken if two cases are true*) (%)	
Spruce >50	10
Pine >50	13
Beech >50	15
Oak 0–30	15
Oak 31–40	18
Oak 41–50	21
Oak 51–60	24
Oak 61–100	25
Oak <30 and no other tree species >50	15
Forest/plowed field boundaries as a percentage of all forest edges (FPB)	
0	7
1–20	8
21–40	11
41–60	13
61–80	16
81–100	18
Grasslands enclosed by forest as a percentage of total forest area (GRA)	
0–1	9
1–4	10
5–10	13
11–20	17
21–100	22

Table 2
Estimated roe deer population densities (no./100 ha) for various habitat values (after Ueckermann 1988)

Habitat value	Habitat quality	Economically acceptable density	Maximum density
41–45	Poor	3	7
46–50	Poor	4	8
51–55	Poor	5	9
56–60	Medium	6	10
61–65	Medium	7	11
66–70	Medium	8	12
71–75	Prime	9	13
76–80	Prime	10	14
81–85	Prime	11	15

deer browse damage is limited. The maximum density is the density at ecological carrying capacity (Table 2).

Implementing Ueckermann's model in a GIS allows annual calculations of HAB so that habitat change can be monitored. This led us to modify the estimation of the GRA parameter of Ueckermann's model by including the area of young forest plantations in the class of enclosed grasslands. In the first five years after forest harvesting, the tree crowns are not closed and the herbaceous vegetation of plantations fulfills an ecological function similar to grasslands (Gill et al., 1996). Our modification allows more accurate modelling of forest changes (e.g. storm damage and clear cuts).

All parameters necessary for determining habitat quality are contained in forest compartment maps that are geometrically rectified aerial photographs (1:10 000) with superimposed stand boundaries. Polygons for forest stands, grasslands, and plowed fields are digitized in a GIS (ARC/INFO). The attributes for each polygon are stored in a relational database (INFO). The need to incorporate habitat changes requires the ability to relate land cover types and tree species with their occurrence dates. The table structure applied is tuple level versioning (Langran, 1992); one table stores geometric information for each polygon and a second table contains starting and ending dates of land cover types for each polygon.

The parameter TRE is calculated annually from the GIS land cover data set, as forest management changes tree species composition. Furthermore, some grasslands were re-forested during our study period so that the total area of forest changed.

3.2. Graphical user interface

The GUI is programmed as a macro in ARC/INFO using ARC macro language (AML). It utilizes two windows, a command window, where instructions to the user are also presented, and a display window, where habitat maps are presented, and where the user can interactively select spatial objects, such as grassland polygons.

Our model assesses the GEO by prompting the user for major rock types (e.g. slate, limestone) and their relative abundance. This procedure is done only once per model run.

GRA and FPB may change from year to year and both are calculated annually. To determine these parameters accurately, knowledge about local habitat selection by roe deer needs to be incorporated in the model.

Forest/plowed field boundaries (FPB) can easily be selected in a GIS. However, forest/plowed field boundaries that are disturbed by humans must be excluded from the calculations. The reaction of roe deer to disturbance is highly variable (Herbold, 1990). Furthermore, disturbance patterns are determined strongly by leisure activities (mountain biking, jogging etc.). This variable response is difficult to simulate in a computer model. Using a GUI, the local wildlife manager

eliminates unsuitable boundaries by selecting them with the cursor while all possible boundaries are highlighted on screen. Finally, automatic distance calculation and partial habitat value estimation is done.

The same concept of combining field knowledge, computer pre-selection, and automated calculation is applied for assessing grassland enclosed by forest or within a 200 m buffer from forest edge (GRA). The GUI is used to identify unsuitable enclosed grassland polygons.

3.3. Population Models

The design of our roe deer population model is a compromise between ecological realism, i.e. the incorporation of as much detail as possible, and practical applicability, i.e. limiting the input data demands to a level which can be provided by wildlife managers. Our model does not require collection of data beyond that normally recorded by the German hunting administration (annual harvest separated into both sexes and three age classes).

We assume that the percentage of young breeding females and fawn survival are the main density dependent factors in roe deer population dynamics (Gaillard et al., 1992; Vincent et al., 1995; Gaillard et al., 1996; Putman et al., 1996). Dispersal is not included because it is not a density regulating factor and because dispersal rates are generally low (Wahlström and Liberg, 1995). Reproductive rates for does and survival rates for adults (> 2 years.) are assumed to be constant (Gaillard et al., 1993).

We developed two models. The first, a more theoretical model, investigates fawn survival rates and age class distributions in an un-harvested population. The second, a practical model, is used to estimate population densities of roe deer populations that are harvested.

Both models divide the population by sex and age class and operate on an annual basis. Population values are estimated for April 1st of a given year. This date is routinely used by the German hunting administration for population estimates.

The first, more theoretical, model contains eight age classes; fawns (< 1 year), yearlings (1–2 years), prime adults (2–3 years), prime adults (3–4 years),..., prime adults (6–7 years), and senescent adults (> 7 years) for each sex, and does not incorporate harvest.

Survival rates from the roe deer population in Chizé (Gaillard et al., 1993) are used (Table 3). They are separated by sex and age class into Sv_{Yf} and Sv_{Ym}, the survival rate for female and male yearlings, Sv_{Af} and Sv_{Am}, the survival rate for prime adult females and males, and Sv_{Sf} and Sv_{Sm}, the survival rate for senescent females and males (Begon et al., 1996). The number of individuals in each category is calculated using standard equations (Gotelli, 1995:66).

We assume a 1:1 sex ratio at birth, which is an average value (Danilkin and Hewison, 1996). We also assume E, the number of embryos per breeding female, to be constant at a value of 1.8, an average reported in several studies (Kurt, 1968; Stubbe and Passarge, 1979; Danilkin and Hewison, 1996; Hewison, 1996).

YP_y, the percentage of young females breeding in year y, is density dependent (Gaillard et al., 1992). We assumed a linear function between an upper and a lower boundary for young breeding female percentage; YP_{max} and YP_{min}. We use $D_{min} = 10$ (no./100 ha) and $D_{max} = 20$ for the following calculations. These are density values for which Gaillard et al. (1992) reported the percentage of young breeding females. We assumed YP_y to be YP_{max} for a population density $D_y < D_{min}$, and YP_{min} for a $D_y > D_{max}$ (Fig. 3). Between D_{min} and D_{max}, YP_y is determined by:

$$YP_y = YP_{max} - \left(\frac{D_y - D_{min}}{D_{max} - D_{min}} (YP_{max} - YP_{min}) \right)$$

(2)

Table 3
Annual survival probabilities of juveniles (8–20 months old), prime age adults (20 months–7 years old) and senescent adults for roe deer in the Chizé population (from Gaillard et al. 1993)

	Juvenile stage	Prime adult stage	Senescent stage
Males	0.739	0.864	0.833
Females	0.770	0.967	0.726
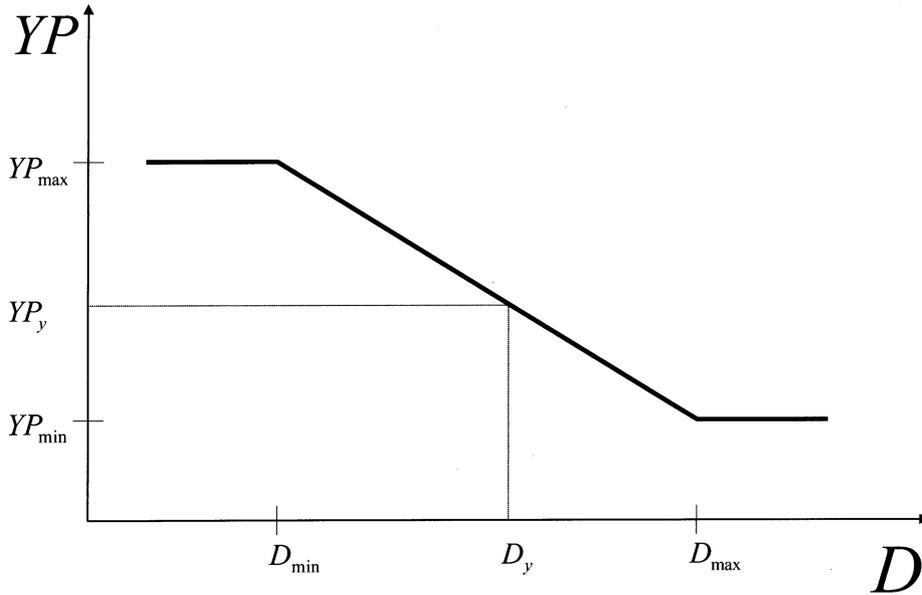
Fig. 3. General relationship between the percentage of pregnant yearlings (YP_y) to population density (D_y). Habitat suitability determines maximum and minimum densities (D_{min} and D_{max}).

Calculation of the fawn survival rate $SvFa_y$ is done similarly:

$$SvFa_y = SvFa_{max} - \left(\frac{D_y - D_{min}}{D_{max} - D_{min}}(SvFa_{max} - SvFa_{min}) \right) \tag{3}$$

The calculation for the male population numbers follows this same structure. The number of male and female fawns is equal due to the 1:1 birth ratio. We do not distinguish between male and female fawn survival rate. Male survival rates are lower than female survival rates during the prime adult stage and higher during the senescent stage (Gaillard et al., 1993; Table 3).

The available hunting data does not distinguish prime adult and senescent age classes, so it is necessary to derive a weighted average adult survival rate (Sv_{Wf} and Sv_{Wm}) We used the theoretical model to analyze population dynamics in an un-harvested roe deer population and estimated average age class distributions. A sensitivity analysis was performed to evaluate upper and lower boundaries for YP_y and $SvFa_a$

The results of the theoretical model runs are used to parameterize our practical model. This second model is designed to be used in wildlife management practice and incorporates roe deer harvest. Harvest data is available only for three age classes, fawns, yearlings, and adults, and our model was adjusted accordingly.

The survival rate of females older than 2 years is calculated using the age class distribution that results from running the first model for 50 years. The percentage of young breeding females YP_y and the fawn survival rate $SvFa_y$ are calculated using Eq. (2) and Eq. (3).

Incorporating HFf_y, the harvest of female fawns, Yf_y, the number of female yearlings, is calculated by:

$$Yf_y = (Ff_{y-1} - HFf_y)SvFa_{y-1} \tag{4}$$

where Ff_{y-1} is the number of female fawns in the previous year. The numbers for the male population are derived similarly, again assuming a 1:1 birth ratio and an identical fawn survival rate for both sexes. The population density D_y is thus:

$$D_y = \frac{Yf_y + Ym_y + Af_y^{>2} + Am_y^{>2}}{AR} \tag{5}$$
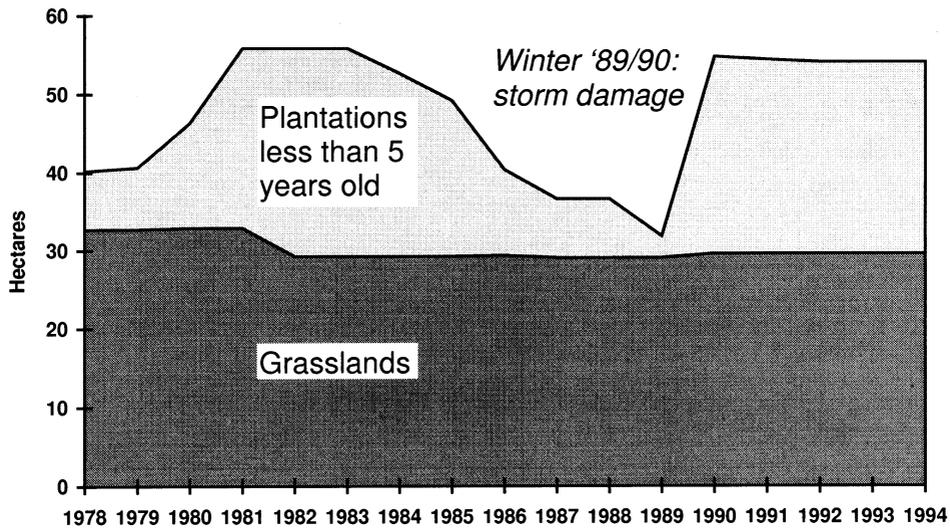
Fig. 4. Changes of functional grasslands (grasslands plus regenerating forest stands < 5 years old) over time.

where Y_{my} is numbers of male yearlings, $Af_y^{>2}$ is adult females, $Am_y^{>2}$ is adult males and AR is area.

A sensitivity analysis for the practical model was performed on the following variables: D_{min} and D_{max}, initial population level, survival rates of adults, and harvest.

4. Results

4.1. Habitat suitability

The habitat suitability index is comprised of four components: geology, tree composition, grassland, and forest/plowed field boundary (Ueckermann, 1988). The geology value of the study site Holzerath is 20 (sandstone). The tree species composition was relatively stable during the study period; the calculated value was 15 (oak < 30% and no other species > 50%). The total length of the forest boundary was 6.72 km, with 0.17 km of forest/plowed field boundary. These values also remained stable; the forest/plowed field boundary of 2.6% yielded a value of 8 (Table 1). The grassland category, which includes young plantations (Fig. 4), experienced the most change, due to both timber harvest from 1980–83 and

severe storm damage in winter 1989/90. Despite these changes, the value of grassland varied only slightly from 17 for 1981–83 to 13 throughout the rest of the study period.

The combined habitat value was 56 (1978–80, 1984–94) or 60 (1981–83), which indicates habitat of medium quality. According to Ueckermann (1988) (Table 2), this corresponds to a maximum density of 10 (no./100 ha) and an economically acceptable density of 6.

4.2. Population model sensitivity analysis

We explored the sensitivity of the theoretical model to minimum and maximum values for density, percentage of young females breeding and fawn survival rates (Fig. 5a, b, c). The maximum density boundary D_{max} is the density at carrying capacity. D_y, the estimated population density of a non harvested roe deer population, will level off at this threshold (Fig. 5a). If D_{min} is close to D_{max}, D_y reaches D_{max} slightly later.

The model is robust to changes in the minimum percentage of young breeding females YP_{min} (Fig. 5b). When using $YP_{min} = 0.67$, the smallest value reported by Gaillard et al. (1992), D_y peaks after 6 years at 20.72 (no./100 ha) and levels off after 14 years at 19.88. A larger YP_{min} results in a
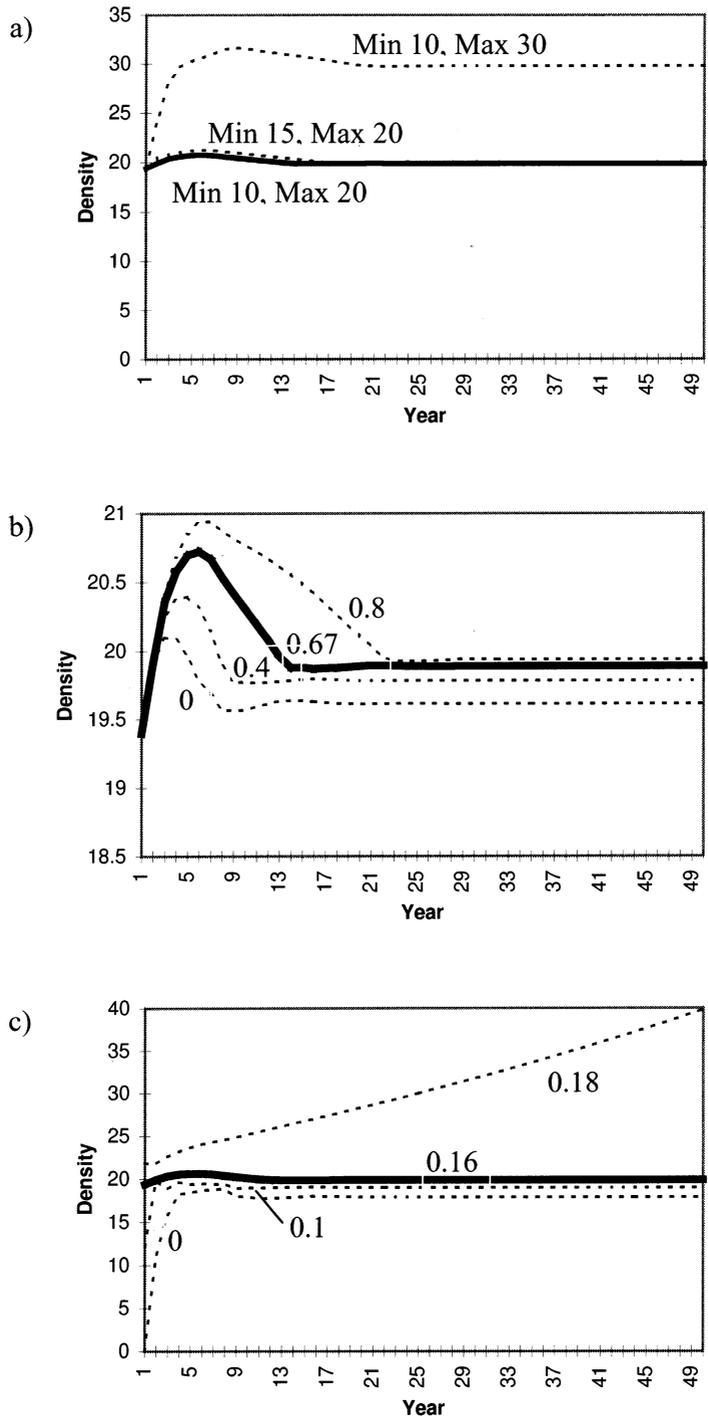
Fig. 5. Sensitivity of the theoretical model to: (a) different levels of minimum and maximum density (D_{min} and D_{max}); (b) different minimum percentages of pregnant yearlings (YP_{min}); and (c) different minimum fawn survival rates ($SvFa_{min}$); (densities in no./100 ha).

Table 4
Age classes specific densities for a non-harvested population after running the theoretical model for 50 years

	Fawns	Yearlings	Prime age adults						Senescents
Age	0–1	1–2	2–3	3–4	4–5	5–6	6–7	>7	
Female	12.95	2.16	1.67	1.61	1.56	1.51	1.46	5.14	
Male	12.95	2.16	1.87	1.61	1.40	1.21	1.04	5.39	

higher peak (20.94 in year 7), and a slightly higher final level ($D_y = 19.94$) at later date (year 22). When YP_{min} is reduced, D_y varies less, and the final level is lower and is reached earlier. YP_{max}, the maximum percentage of young breeding females, had no notable effect on the population in the theoretical model because D_y is always high, and YP_y always close to YP_{min}. We chose $YP_{min} = 0.67$ and $YP_{max} = 0.93$ (Gaillard et al., 1992) for the practical model.

The minimum fawn survival rate $SvFa_{min}$ is the variable to which our model is most sensitive (Fig. 5c). D_y grows infinite for $SvFa_{min} > 0.17$. For $SvFa_{min} = 0.16$, D_y levelled off at 19.86, for $SvFa_{min} = 0.1$ at 19.03, and for $SvFa_{min} = 0$ at 17.91. The maximum survival rate $SvFa_{max}$ has no notable influence on D_y. We chose $SvFa_{min} = 0.16$ and $SvFa_{max} = 0.8$ for further analysis, the highest value found by Fruzinski and Labudzki (1982).

Using these values, the theoretical model was run for 50 years to investigate the age class distribution of an un-harvested population (Table 4) and to calculate a weighted average adult survival rate. The survival rate for all adult females older than two years was 0.87 and all adult males was 0.85.

The values derived with the theoretical model are incorporated in the second practical model which also incorporates roe deer harvest (Fig. 6a). The low harvest in 1989–92 was due to an increasing wild boar population that resulted in a shift of hunting activities. Harvest rate targets were set high in 1993 and 1994 due to concerns that browsing would prevent tree regeneration on the wind damaged areas. The consistently low harvest of male fawns is due to the interest in trophy males. The same motivation results in generally higher male than female adult harvest.

When incorporating harvest, the fawn survival rate $SvFa_y$ was never as low as $SvFa_{min}$ but stayed between 0.26 and 0.54, values which have been previously observed (Ellenberg, 1978; Fruzinski and Labudzki, 1982).

The maximum density D_{max} has a strong influence on the estimated population density D_y (Fig. 6b). D_{min} has less influence and is assumed to be $\approx 50\%$ of D_{max}. We compared the calculated habitat suitability for our study site ($D_{min} = 6$ and $D_{max} = 10$) with values from Ueckermann (1988) for poor and prime habitat (Table 2) and with the substantially larger values reported by Gaillard et al. (1992), $D_{min} = 10$ and $D_{max} = 20$). In all cases, D_y levels off at a value below D_{max}. The impact of harvest is strongest for the lowest values of D_{max}. All further calculations assumed $D_{max} = 10$; this sensitive point is discussed further below.

As is apparent in Fig. 7a, the population in the starting year may influence the results for a number of years. No information about the roe deer population in our study site before 1978 is available. We assumed equal total numbers for both sexes and a roe deer population with 45% fawns, 23% yearlings, and 32% adults, an average composition of hunted roe deer populations. The comparison of a high (132 individuals), a medium (100 individuals), and a low density population (62 individuals) in the study area reveals that the effect of the starting population lasts for a maximum of 10 years. We chose the medium level starting population for further analysis because its population density is comparable to subsequent years and we had no evidence for different harvest regimes or habitat quality before 1978.

The age class distribution of a roe deer population is difficult to estimate. Our approach to derive a weighted average for the adult survival rates assumes that a harvested population has the
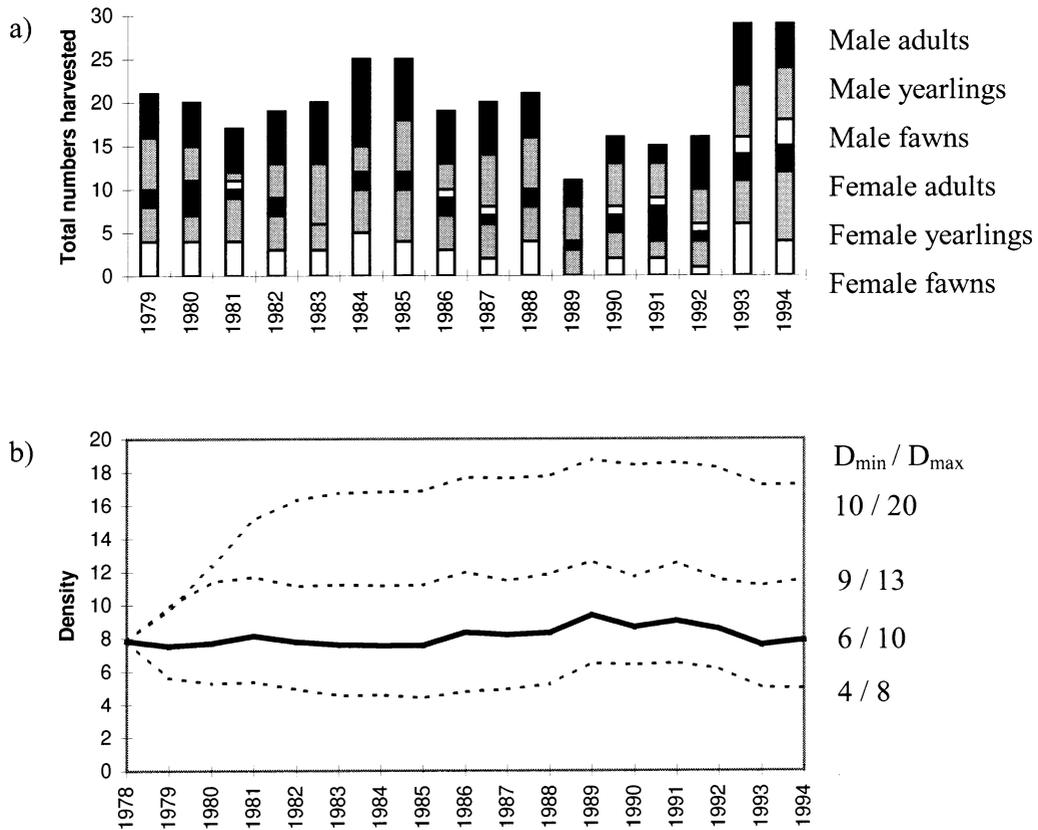
Fig. 6. (a) Roe deer harvest in the study area Holzerath; and (b) sensitivity of the practical model to different levels of minimum and maximum density (D_{min} and D_{max}). Four density ranges are explored; the habitat suitability model resulted in:$D_{min} = 6$ and $D_{max} = 10$ (densities in no./100 ha).

same age class distribution as an unharvested one. We explored the effect of highly skewed populations where either all adults are in the senescent stage or all adults are in the prime adult stage and used the survival rates reported by Gaillard et al. (1993) (Table 3) for these age classes (Fig. 7b). Maximum differences in D_y are about $\pm 14\%$, average differences are $\pm 10\%$.

Estimating the effect of different harvest schemes is presumably the most important aspect of a population model for a wildlife manager. We compared five harvest schemes: the actual harvest (Fig. 6a), an increase and decrease by 20%, no harvest and the official culling plan of the hunting administration for our study area (Fig. 8a). D_y, the total density for the no harvest case levels off

at $D_{max} = 10$. The culling plan of the hunting administration, if not adjusted, leads to extinction after 10 years. The actual harvest results in a D_y between 7.6 and 9.4. Varying the harvest by $\pm 20\%$ changed D_y by a maximum of 11.7%; increasing the harvest has stronger impact than decreasing it.

When using the chosen values for all variables and the actual harvest scheme as input, the changes of the roe deer population in our study site can be explored in detail (Fig. 8b).

The validity of our model, using actual harvest rates from 1978–92 with a resulting D_y of 7.6–9.4 (no./100 ha), was estimated using detailed roe deer browse maps. The German forest service (MLWF) made these available for 1992 and 1995.
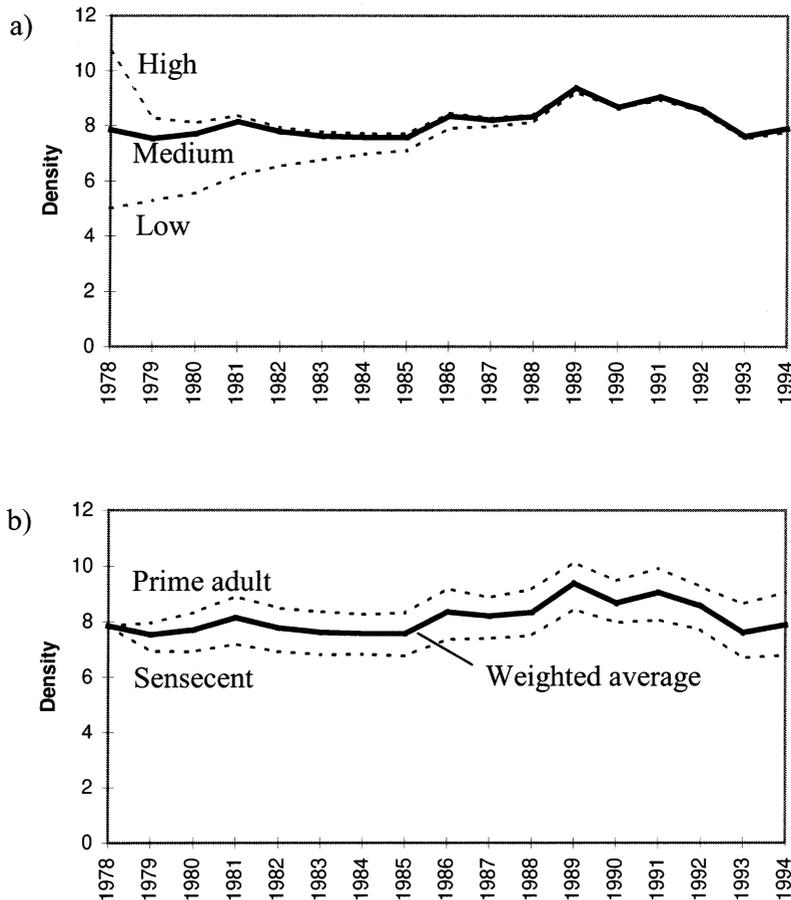
Fig. 7. Sensitivity of population densities calculated by the practical model to (a) population density (D_y) in the initial year; and (b) adult survival rates (Sv_{Wf} and Sv_{Wm}); (densities in no./100 ha).

At predicted carrying capacity, saplings would sustain heavy deer damage. In 1992, 300 saplings on six transects were sampled; of these 32 (10.7%) were browsed; in 1995 deer damage was lower (Buss, 1994, and personal communication) as was deer density. A value of 10% browsed trees results in 50% damaged trees before saplings grow out of reach, at about 5 years (trees previously browsed are not counted again). When interpreting deer damage maps, the MLWF makes a recommendation from four standardized management options; strongly increase, increase, maintain, or reduce harvest rates. For our study site, the recommendation in 1992 was to increase roe deer harvest rates due to sapling damage (Buss, 1994).

5. Discussion

We chose the study site Holzerath partly because of the habitat changes due to windthrow which resulted in an increase of the culling plan by 30% in anticipation of a major increase in the roe deer population. We assumed the habitat value would change substantially. Contrary to this assumption, changes in the habitat value, as assessed from the Ueckermann (1951, 1957, 1988) habitat model, were small. Whether Ueckermann's model is not sensitive enough or vegetation changes were not as extreme as anticipated is unclear. It is noteworthy that the dramatic event of storm damage led to a change in harvest management, however planned clear cutting,
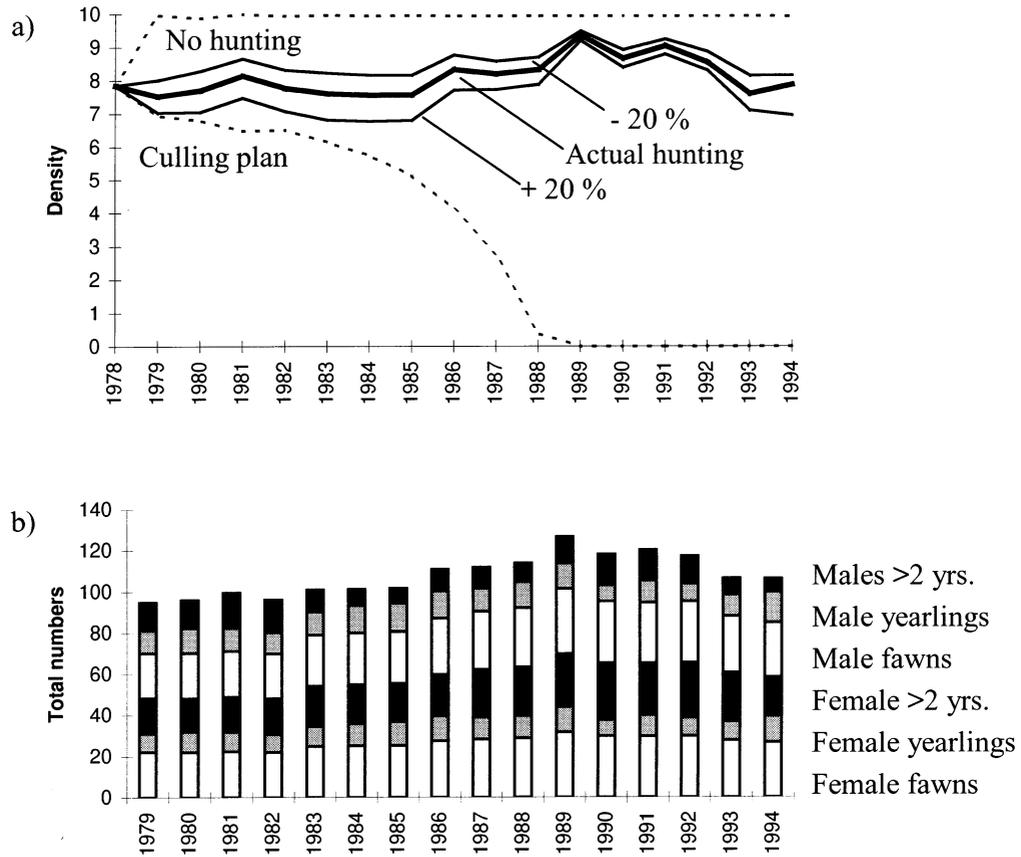
Fig. 8. (a) Effects of different harvesting schemes on population density D_y (in no./100 ha); and (b) population structure (classified into: $Am_y^{>2}$, Y_{my}, $Af_y^{>2}$, Y_{fy}, and Ef_y) resulting from the actual harvest.

which caused stronger habitat alteration, did not result in a change of the management plan.

Assuming that a population density below 6 adult roe deer per km^2 is the economically acceptable density, the harvest was not sufficient (Fig. 8a). Especially from 1989 to 1992, harvest was less than half that necessary to prevent browse damage in our study area. The increased harvest in subsequent years did not reduce the population density adequately. However, harvest was sufficient to keep the population density 6.3–23.9% below carrying capacity. This is consistent with the browse damage mapping. Damage is present but not overwhelming. The estimated decrease in population density between 1992 and 1994 coincides with the reduced browse damage in 1995. However, the browse damage mapping data

should not be over-interpreted. A higher sampling density, and more time steps, would be needed to fully validate our model.

A wildlife manager can use the results to plan future culling and can explore various harvest schemes in the modelling framework. Our approach assesses roe deer population densities more realistically than the current management practice, which is based on subjective estimates by the hunting leaseholder. The prescribed culling plan would have extirpated roe deer if actually implemented. Our model can calculate future roe deer population densities under different harvesting levels by adding years to the hunting data table. The effect of habitat changes on roe deer populations can be explored by changing the land-use table in the GIS. However, our model is

not specifically designed to optimize spatial habitat allocation (Nevo and Garcia, 1996; Bettinger et al., 1997; Garcia and Armbruster, 1997).

The population model is a compromise between ecological realism and limited available input data. Not included is the probable negative correlation between litter size of young females in relation to both their body weight and probably population density (Hewison, 1996). Density-independent factors such as weather cause fawn survival rates to vary widely (Gaillard et al., 1997). We decided against including these two processes into our model, partly because of the limitation on input data driven by our goal to derive a model suitable for management, and partly because of the lack of repeated studies on these processes.

Little has been published on the percentage of yearling pregnancies relative to population density. Our model incorporates the minimum rate of yearling pregnancies from Gaillard et al. (1992). However, it is unclear if this value is indeed the lowest possible case and if it is constant among populations. The same applies to the survival rates that were taken from Gaillard et al. (1993).

We employ the density values provided by Ueckermann (1988) (Table 2). In the context of recent research, these values are too low (Vincent et al., 1995; Danilkin and Hewison, 1996; Gaillard et al., 1996; Gill et al., 1996). We did not change these values, lacking data on population densities in a variety of habitats, but we tested the effect of higher maximum densities on our result (Fig. 6b). The general population trends hold for larger maximum densities but future research on better estimation of the carrying capacity in different habitats is clearly needed.

It was beyond the purview of our study to estimate population densities directly and compare those with our model predictions (Latham et al. 1996). Nor did we attempt to derive a more precise habitat model. Both steps are valuable areas of further research and probably necessary steps before our model can be implemented widely.

The strength of our model is that all input required can be derived from forest maps, which are available throughout Germany, and harvest statistics, which exist for every hunting unit. Furthermore, our model operates at the scale used for wildlife management in Germany, which makes it widely applicable. The nation-wide digital forest coverage of Germany, currently under development, will simplify future studies.

Our habitat suitability model is spatially explicit and one of the first designed for ungulate management (Turner et al., 1995). A better understanding of dispersal and habitat selection by roe deer would make the population model spatially explicit as well (Byron, 1981; Thor, 1990; Bideau et al., 1993; Holt et al., 1995). Individual-based habitat selection models could improve knowledge about the social structure of roe deer populations (Sandell and Liberg, 1992; Turner et al., 1993). Cohort effects observed in red deer (Albon et al., 1992) are also found in roe deer populations, which exhibit a strong relationship between adult jaw length to population density at the time of birth (Hewison et al., 1996). Our model encompasses the major aspects of our current scientific understanding of roe deer population dynamics, but future research will certainly lead to improvements of our approach.

6. Conclusion

We developed a GIS model at the local scale for managing roe deer populations in Germany. The model offers a tool for resolving conflicts about roe deer densities, harvesting levels, and browse damage, between forest managers, wildlife managers, and hunters. It translates current scientific understanding into a management tool suitable for every-day use by wildlife managers. Compared to the current management practice, our model improves the assessment of roe deer population densities by calculating annual habitat changes and by incorporating previous harvest. This allows estimation of more realistic harvest plans than under the current management practice.

Whether a harvest plan is actually implemented by hunters will depend on their acceptance of it. An important and novel component of our model is its use of a GUI that allows use of GIS on the

local scale and by local resource managers. "Perhaps the greatest need in species modelling is to incorporate the collective knowledge of field biologists" (Stoms et al. 1996:447). Current GIS systems are too complicated to be used routinely by the majority of field biologists. Our model provides a framework to incorporate their knowledge into GIS technology and wildlife management models. Interactive models increase user acceptance of GIS modelling over purely automatic approaches, an important consideration in attaining compromise between conflicting resource management plans. We strongly feel that the incorporation of the location-specific knowledge of field biologists is a key step in improving GIS wildlife models, and thus improving wildlife management.

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