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Modeling the brown bear population in Slovenia A tool in the conservation management of a threatened species

Klemen Jerina [a,*], Marko Debeljak [b], Sašo Džeroski [c], Andrej Kobler [d], Miha Adamič [a]

[a] *Department of Forestry, Biotehnical Faculty, University of Ljubljana, Večna pot 83, 1000 Ljubljana, Slovenia*
[b] *Nova Gorica Polytechnic, School of Environmental Sciences, Vipavska 13, 5000 Nova Gorica, Slovenia*
[c] *Jozef Stefan Institute, Jamova 39, 1000 Ljubljana, Slovenia*
[d] *Slovenian Forestry Institute, Večna pot 2, 1000 Ljubljana, Slovenia*

Abstract

In this paper, we address three aspects of the brown bear population in Slovenia: its size (and its evolution over time), its spatial expansion out of the core area, and its potential habitat based on natural habitat suitability. Data collected through measurement/observation of the bear population and from the literature are used. A model is developed for each aspect. The results are estimates of population size, a picture of the spatial expansion of the population and maps of its optimal and maximal potential habitat (based on natural suitability). Overall, the brown bear population has been increasing since the establishment of a core protective area and has been expanding outside this area. The habitat suitability maps show that there is room for further expansion. Based on habitat suitability and bear population density, as well as human activity and current damage reports, we recommend that the Alps should be temporarily kept free of the bears, until the necessary mitigation measures regarding human–bear conflicts are carried out. On the other hand it is of crucial importance to adapt human activities and improve bear management in the optimal habitat, with which the goals of successful conservation of the species might be achieved.

Keywords: Brown bear; Population size model; Spatial expansion; Habitat model; Management

1. Introduction

Due to direct persecution and economic exploitation, as well as habitat destruction and fragmentation, the brown bear (*Ursus arctos*) occurs today in only a small part of its historical range. Slovenia is among the few European countries with a preserved viable indigenous brown bear population, as well as populations of other large predator species, such as wolf (*Canis lupus*) and lynx (*Lynx lynx*). The Slovenian bear population is a part of the continuous Alps-Dinaric-Pindos population (Swenson et al., 2000). Vast forested areas of southern and southeastern Slovenia (Kočevska and Notranjski Snežnik), which represent the core habitat of the bear population in Slovenia, are connected with Gorski Kotar in Croatia in a unified block of bear habitat (Huber and Adamič, 1999). This bear population is important also because it represents the source for natural re-colonization or reintroduction of the bear into Slovenia's neighboring countries Austria and Italy.

Although severely endangered on several occasions, the bear never became extinct in Slovenia as in most other parts of Europe. At the end of the 19th and the beginning of the 20th century, the size of the bear population in Slovenia was estimated at about 30–40 animals (Simonič, 1992). Bears only survived in the

* Corresponding author. Tel.: +386-1-4250477.
E-mail address: klemen.jerina@uni-lj.si (K. Jerina).

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sparsely inhabited areas of south-central Slovenia. After its legal protection in 1931, the population started to grow gradually. At the end of the fifties, the population size was estimated at 160 animals (Švigelj, 1961). In 1966, the core bear management area of 3500 km^2 was established in south-central Slovenia. The yearlong protection of females accompanied by cubs, the supplemental feeding and the introduction of a yearly harvest quota were probably important triggers of the fast bear population growth and its expansion toward the north and west in the post-1966 period. In October 1993, "The act on the protection of threatened species in Slovenia", including strict regulations on the harvest of bears, was adopted.

The accelerated brown bear expansion was not without consequences. The increased extent of bear sighting, as well as the occurrence of other reliable signs of bear presence, caused fear and aversion among the people who live in the areas recently colonized by the bear (Adamič, 1999b; Korenjak and Adamič, 2000). Conflicts and uncomfortable feelings appeared also because of the increased number of bear attacks on livestock. Subjective and bear-hostile mass media reports introduced further strain into the already strained situation.

Although it is clear that the coexistence of people with brown bears, as well as with other large predators, bring problems to both sides, it should be emphasized that many of these problems can be solved or mitigated without a drastic reduction of the predator species. The state of Slovenia still supports the attempts to restore livestock pasturing on the western and northwestern edge of the bear range, although this is not compatible with the projects on the recovery of large carnivores. Despite being warned by the researchers, the range communities and the sheep-owners there still manage their flocks as if they were in predator-free areas (Adamič, 1996). The assumptions of a negligible extent of the damages that might be caused by the few bears living in the Slovenian Alps proved to be false. The greatest shares of compensation claims, which have to be reimbursed by State budget, take part in the areas with irregular occurrence of the bears, but with human activities exposed to an elevated predation risk.

Resolving the problems mentioned above is made more difficult by the lack of appropriate knowledge. Measures for improving the coexistence between man and brown bears should be based on objective information. The latter should include information about the size of the bear population and its spatial distribution, as well as the trends of these two parameters.

Population size is a very important attribute in the conservation management of brown bears and it should be thus estimated as objectively as possible. Previous estimations have been derived from visual estimates, which were influenced by the subjective impressions of the observers; some of them have been gained also by 'ad hoc' impression on the population size, without using or measuring any data about bear population.

Bears are difficult to census (Swenson et al., 2000); it is, therefore, hard to get realistic estimates of population size. Crude assumptions on the population size in Slovenia varied from 200 and up to 1000 individuals. Since 1994, one-night censuses of bears at registered feeding sites in the core area twice a year became a regular method of bear population estimation in Slovenia. We are aware that one-night censuses do not give precise figures on population size. But despite this, crucial population parameters (e.g. the share of females with cubs of the year, the share of yearling bears among the total of counted bears, the average litter size, etc.) have been collected in the course of the counts. The knowledge of these parameters has been used in a modeling approach to calculate the size of the bear population.

We were also interested in the process of spatial expansion of the brown bear out of the core protective area in the period after its establishment. Knowledge of this process might explain the potential of bears to reoccupy historical habitats, as well to settle in new habitats. At the same time, the sexual structure of the formed population nuclei was studied. The population sex structure helps to determine the population development stage in the process of colonization of new areas. So afterward the management-conservation status and importance of the newly formed sub-populations could be determined.

In our research, we also determined the range and distribution of habitat suitable for the bear. The carrying capacity has several aspects—among them the social tolerance, the political climate, the financial capacity and the natural habitat suitability. The aim of this part of the study was to address one of these aspects of Slovenia's carrying capacity for bears—the natural habitat suitability. This should be considered together with the model of the population size. We

attempted to map the potential habitat of the brown bear in Slovenia, regardless of whether it is currently inhabited by bears or not.

In this paper, we thus address three aspects of the brown bear population in Slovenia: its size (and its evolution over time), its spatial expansion out of the core area, and its potential habitat based on natural habitat suitability. The remainder of this paper is organized as follows. Section 2 describes the data available for our study, collected either through measurement/observation or from the literature. It also describes the methods used to model each of the three aspects mentioned. Section 3 presents the results of the three models: estimates of population size, a picture of the spatial expansion of the population and maps of its optimal and maximal potential habitat (based on natural suitability). Finally, Section 4 discusses the relevance of these results to the management of the Slovenian brown bear population.

2. Materials and methods

This section describes the data on the Slovenian brown bear population used in our study, collected either through measurement/observation or from the literature. It also describes the methods used to model each of the three studied aspects of the brown bear population in Slovenia: its size (and its evolution over time), its spatial expansion out of the core area, and its potential habitat based on natural habitat suitability.

2.1. Modeling the size of the brown bear population

To estimate the size of the brown bear population in Slovenia and its dynamics, i.e. changes over time, we have developed a difference equation model. This subsection describes data relevant to determining these parameters, collected either through measurement/observation (data on the number and age structure of shot bears) or from the literature (initial population size, sex structure, age structure, reproduction age, fertility and mortality of different age categories).

All extracted bears (shot by hunters or resulting from other causes of morality) are indicated in the Slovenian Central Register of Large Carnivores. This information is very reliable. Existing data on the population size are of lower quality, due to the subjective methods used for estimation. Data about the population parameters in the post-1950 period are mostly missing.

2.1.1. Population properties

The following population properties were selected as parameters of our model: the initial population size, the sex and age structure, the reproduction age, fertility and mortality (of several age groups). The available data relevant to determining these parameters are described below.

2.1.1.1. Initial population size. The size of the bear population in Slovenia was estimated to be 161 bears in the period between autumn 1957 and spring 1958 (Švigelj, 1961). This was chosen as the starting-point for our model and as initial population size. We believe that this first official estimate of the bear population size in Slovenia is credible enough to be used in our model since the professional district wildlife wardens systematically collected the data that were used in it. At that time the bear population was much smaller than nowadays and it was limited to the east-central Dinarics in southern Slovenia and thus easier to census. Therefore the results of the systematically performed spring and autumn counts of the bears represented good basis for an accurate estimate of the bear population size.

2.1.1.2. Sex structure. The birth sex ratio is approximately 1 to 1 in Eurasian and North American brown bears (Adamič, 1997). The sex ratio for shot bears is 66% males to 34% females. In the group of non-hunting mortality sources, the share of males is even higher (73% males, 27% females) (Adamič, 1997). Females are gradually becoming dominant in the sex structure because of the high male portion in the shot bears group.

2.1.1.3. Age structure. The expected life span for brown bears is 25 years (http://nature-net.com/bears/brown.html) and for black bears between 20 and 25 years. The expected life span for Slovenian bears is 16 years (Adamič, 1997).

Danilov et al. (1993) studied the age structure of the brown bear in the northeastern part of European Russia. He showed that the population contains 23.5%

newborns, 12.6% yearlings and 63.9% bears of 2 years and older. Unfortunately we do not have such information for Slovenia. Because of the differences in the living conditions between the Russian and Slovenian bear population, the use of the Russian bears' age structure for modeling the Slovenian bears' population would not be reliable.

From the bears harvested in Slovenia in the period 1994–2000, the first premolars (P1) have been extracted. The age of 336 bears has been established by cementum analysis, performed by MATSON's Laboratory, Milltown, MT, USA. We used the age structure of these harvested bears as a good approximation to the real situation. The relative frequencies, calculated from the raw data (fourth and fifth columns of Table 1) were used to perform nonlinear regression, yielding Eq. (1) for females and Eq. (2) for males. The relative frequencies for each age, as approximated by these equations, are given in columns six and seven of Table 1.

$$\mathrm{RF\,(age)} = 0.00112949 + \exp(0.8485986 - 0.6038906 \times \mathrm{age}) \quad [R = 0.9788] \qquad (1)$$

$$\mathrm{RF\,(age)} = 0.0007536337 + \exp(-0.001939656 - 0.379584 \times \mathrm{age}) \quad [R = 0.9906] \qquad (2)$$

2.1.1.4. Reproduction age. Bears are capable of reproduction at the age of 5 years (http://nature-net.com/bears/brown.html). The mean age of the first successful reproduction for females in Northern Sweden is 5.3 ± 0.5 years, and 78% of females give birth to their first litter at the age of 5 years (Swenson et al., 1998a). The results are consistent with Sæther et al. (1998), who found that the female reproduction age is 5 years in the north and 4 years in the south of Sweden. The reproduction age of the females in northwestern Russia is 3 years. Brown bear females in Slovenia give birth to their first litters at the age of 4–5 years (Švigelj, 1961).

2.1.1.5. Fertility. The brown bear litter size can be from one to four cubs, but the average is between two and three cubs and increases with the age of the mother (http://nature-net.com/bears/brown.html). Swenson et al. (1998a) report that the average litter size in northern Sweden is 2.4 ± 0.8, while the litter size is 1.65 on the Kola peninsula, 2.02 in the Karelia region and 1.97 in the Petersburg area (Danilov et al., 1993).

Švigelj (1961) studied the sizes of bear litters in the Wildlife Reserve Rog (600 km^2) and in the Wildlife Reserve Snežnik (270 km^2), both in south-central Slovenia for 1956, 1957, and 1958. He found that average yearly litter sizes were 1.82, 1.66 and 1.62, respectively. The estimation of the average litter size

Table 1
The relative age structure of shot bears in Slovenia between 1980 and 2000

Age (years)	Frequencies		Relative frequencies (raw)		Relative frequencies (from regression)	
	Males	Females	Males	Females	Males	Females
3	37	26	0.316	0.400	0.315	0.393
4	25	12	0.214	0.185	0.216	0.220
5	16	12	0.137	0.185	0.148	0.125
6	13	3	0.111	0.046	0.101	0.074
7	11	2	0.094	0.031	0.070	0.045
8	5	2	0.043	0.031	0.048	0.030
9	1	2	0.009	0.031	0.033	0.021
10	2	2	0.017	0.031	0.023	0.017
11	1	1	0.009	0.015	0.016	0.014
12	4	0	0.034	0.000	0.011	0.013
13	0	0	0.000	0.000	0.008	0.012
14	0	2	0.000	0.031	0.006	0.012
15	1	1	0.009	0.015	0.004	0.012
16	1	0	0.009	0.000	0.003	0.011

in both Wildlife Reserves was repeated in 1991: 21 females accompanied with 39 cubs were registered, which means 1.85 cub per female. Nineteen percent ($n = 4$) of observed female was accompanied with three cubs, 48% ($n = 10$) with 2 and 33% ($n = 7$) with one cub (Berce and Štrumbelj, 1994). Muhič (1999) estimated the average litter size for the Wildlife Reserve Medved Kočevje (ex-W.R. Rog) in the period between 1987 and 1998 and found 1.84 cubs per litter.

2.1.1.6. Mortality and shooting mortality. Swenson et al. (1998a) report that the probability of surviving from spring as a yearling to autumn as a 5-year-old is 0.73. Population age-specific survival rates larger than 0.77 in all age classes, where more than 90% of the females of age 2 years and older survived, are reported by Sæther et al. (1998). Danilov et al. (1993) estimated that mortality of newborns is 19.2% and that of yearlings is 18.3%. It has been estimated that population density does not influence the survival rate, which depends mostly on the habitat quality (McLellan, 1994).

Švigelj (1961) estimated that 25% of newborn bears in Slovenia die in their first year. The structure of the shooting mortality over the time period between 1957 and 2000 is presented in Table 2. The sex of the shot bears has been recorded since 1979.

2.1.2. Model description

To estimate the size of the brown bear population in Slovenia and its dynamics, i.e. changes over time, we have developed a difference equation model. It uses the most probable values of the parameters described above. These are described below: the following selected attributes and their values were used to construct the model for population size prediction:

- The initial population size is 161 bears in 1957. The sex structure at this point is 1 to 1.
- The sex structure at birth is 1 to 1.
- The age structure for male and female bears is the same as age structure of shot bears, i.e. as in columns six and seven in Table 1.
- The expected life span of a bear is 16 years.
- The reproduction age is from 4 to 15 years; a female has her first litter when she is five and has a litter every second year afterwards.
- The shooting mortality for the period between 1957 and 2000 is as in Table 2.

Table 2
The number of shot bears in Slovenia between 1957 and 2000

Year	Total	Males	Females
1957	3		
1958	8		
1959	8		
1960	6		
1961	11		
1962	8		
1963	28		
1964	18		
1965	23		
1966	32		
1967	43		
1968	36		
1969	37		
1970	47		
1971	36		
1972	39		
1973	35		
1974	39		
1975	41		
1976	58		
1977	50		
1978	45		
1979/1980	47	35	12
1980/1981	47	36	11
1981/1982	46	34	12
1982/1983	33	29	4
1983/1984	50	34	16
1984/1985	30	18	12
1985/1986	55	39	16
1986/1987	37	26	11
1987/1988	49	34	15
1988/1989	39	30	9
1989/1990	35	26	9
1990/1991	41	28	13
1991/1992	29	23	6
1992/1993	35	33	2
1993/1994	42	30	12
1994/1995	37	24	13
1995/1996	28	21	7
1996/1997	37	24	13
1997/1998	40	26	14
1998/1999	58	38	20
1999/2000	56	36	20

For the following four parameters, different values were tried out, with each particular combination of values yielding one scenario of population development:

- For fertility, the values of 1.7, 1.8, 1.85, and 1.9 cub per litter per female in the reproduction period, were considered.

- For the mortality of cubs in their first year, the values of 15, 20, and 25% were considered.
- For the mortality of cubs in their second year, the values of 10, 15, and 20% were considered.
- For the natural mortality for bears older than 2 years (non shooting mortality reasons), the values of 5, 10, 15, and 20% of the shooting mortality were considered.

The parameters of the model have constant values over all the research period. Although the use of the constant (density invariable) population parameters (mortality and natality) does not take into account the compensatory mechanisms (intraspecific killing, mortality and natality rates, dispersion) that should temper the extremes of population growth and decline (see also Royana, 1992; Mitchell, 1994), we assume that in Slovene brown bear population the density-dependent intraspecific interactions that might influence the population's dynamics were not significantly changing within the analyzed period because:

- The bear population was intensively harvested through most of the research period. According to the statistical data published by the Hunters Association of Slovenia (*Statistical Yearbooks of the Hunters Association of Slovenia*, Ljubljana), more than 1500 bears, mostly sexually mature individuals, have been extracted within the research period. Population densities were thus regulated by the hunting, too.
- Slovene brown bear population was spatially expanding (this study; Jerina and Adamič, 2002) within all the research period analyzed in this paper, and the extreme population densities were most likely tempered also by the dispersion of the young bears that dispersed from the female-reproductive areas with bigger population densities into external areas with lower population densities.
- Due to natural afforestation of Slovenia, the area of the bear habitats was and is increasing rapidly. Since 1974 the percentage of the area covered by the forests has grown from 36% (Gašperšič, 1985) up to 64 % (Hočevar and Kobler, 2002).

Therefore we can assume that population densities were never high enough to reach the maximal habitat carrying capacity, so the compensatory mechanisms of the population size would come into force afterwards and would influence the population dynamics significantly (see also Jerina and Adamič, 2002).

The model for estimating the size of the brown bear population further respects the following constraints:

- The number of newborns is calculated for each year according to the number of fertile females in the population.
- The model respects different non-shooting mortality rates for different age groups, expressed as a percentage of the shooting mortality for the corresponding age group.
- The number and sex structure of shooting mortality is respected. The sex structure is not known for the period before 1979: for the period between 1985 and 1999 the sex structure of total shooting mortality rate is estimated at 624 males and 247 females.
- The age structure of male and female bears older than 2 years is conserved over time (from year to year) and is the same as predicted by the two regression models (cf. Table 1).
- Bears in a given age group are moved to the corresponding next age group in the following year. Half of the bears in the oldest age class (16 years) are excluded from the "next modeling year", while the remaining half is retained in the same age class.

2.2. The spatial expansion of brown bears

The spatial expansion of brown bears from the bear core protection area into the external regions was studied by analyzing data about sighted or extracted bears and data about registered bear attacks on domestic animals and other reported damage caused by the bears. The data were gathered from the archives of the Slovenian Hunters Association, the hunters' magazine 'Lovec' and our own databases. Although the data were not collected systematically in the past, we believe that the estimated population areas of activity and other findings fit well the actual spatial distribution and population dynamics characteristics of the brown bear within the observed period. Since the number of recorded locations was large enough ($n = 930$), we believe that the potential impact of the errors due to non-systematical gathering of earlier data is not strong.

This part of the study comprises the area of Slovenia out of the core bear's protection area and the border

regions in Austria within the period 1966–1995. The year 1966 was chosen as starting point of the study because the bear's core protection area was established at that time. In this area, law strictly protected the bear and hunting quotas were prescribed. But out of this area, the bear still remained without any protection until the beginning of the 1990s. Between 1963 and 1973, bear hunting out of the core protective area was intense and therefore the spatial expansion of the bear was inhibited: almost the entire Slovenian brown bear population was located in the core protective area.

When the bear population started to grow faster in the beginning of the 1970s, the bear started to expand faster also out of the core protective area. In order to study the qualitative and quantitative aspects of expansion, the following analyses were performed:

- spatial analysis of all recorded bears' locations,
- estimating the bear population size out of the core protective area,
- spatial analysis of recorded females' locations, and
- regression analysis of the share of females in relation to the time and the distance from the core protective area.

2.2.1. Spatial analysis of all recorded bears' locations

All recorded locations were classified according to the year of bear's presence (from 1967 to 1976, from 1977 to 1986, from 1987 to 1995) and according to the sex of the animal (entire population, only females). For each period and group of animals, the population area of activity was determined by the use of Home Ranger (1999) software. This software employs the kernel method (Worton, 1989) and is used for fitting non-parametric distribution functions to two-dimensional spatial (X, Y) data. The software performs the calculation and graphic presentation of the area that corresponds to a chosen probability ($0 < P < 1$) of spatial use. Normally, it is used to determine the size and the shape of the home range of an individual or a population, or the core area for a fixed probability. Afterwards, the size, shape or structure of the determined areas of activity is compared between individuals or populations.

In this study, the population areas of activity were determined differently. We calculated a different probability of spatial use for each period, so that population densities were comparable among the calculated areas. If the population areas of activity were calculated as usual, the sizes of the determined areas within different periods would be almost equal (as shown by a pilot study), although the population size in the last period is almost three times larger than in the first one.

This is why the spatial expansion of the brown bear was studied as described below. For the last period (from 1986 to 1995), the population area of activity was calculated for the probability value of spatial use of 0.8. The calculation was first performed for all recorded locations, and then only for the recorded locations of females. For both estimated areas, the population densities were calculated by multiplying the estimated discrete (per pixel) two-dimensional probability function with the average external bear population size in this period. We recorded the lowest population density among the pixels still included in the estimated population area of activity for this period. We required the lowest population density in the population areas of activity for the other periods to be the same. Appropriate probability values of spatial use were calculated and used so that this criterion of population density was equal within all periods.

2.2.2. Estimating the bear population size out of the core protective area

The external population size needed for the calculation of the areas of activity was estimated as follows. For the year of 1957, the portion of the external population in the entire Slovenian bear population was determined on the basis of Švigelj's census (Švigelj, 1961) by counting the records of bears living inside and outside of the core protective area. For the year of 1995, the portion of external population in the entire Slovenian population was calculated from the data gathered by monitoring bears at feeding places. (This monitoring performed by the hunters comprised all bears habitats in Slovenia and lasted for 5 years: At least once per year the bears were counted at feeding places simultaneously.)

The portion of the external population was estimated by dividing the average number of recorded bears in the external area by the average number of recorded bears in the whole of Slovenia. Both calculated portions were linked with a linear function, assuming that the portion of the external population was growing linearly. The population size was calcu-

lated for each year afterwards by multiplying the corresponding portion of the external population with the size of entire Slovenian bear population (as predicted by the model described in the previous section). When determining the female population area of activity, we considered that not only the size of the entire population was increasing, but also that the portion of females was increasing with time.

2.2.3. Spatial analysis of recorded females' locations

The ratio of females was calculated on the basis of nonlinear regression analysis of the recorded locations. All recorded locations and the recorded locations of females were classified into two time frequency distributions. The ratios of females were calculated. A regression function was adjusted to the calculated ratios. The frequency of the class was used as a weight in the regression analysis. Several non-negative functions with a left and a right limit were tested. Among all of them, the Bertalanffy (1995) growth function fitted the empirical data best. This type of function was chosen also because we believe that its shape reflects what is actually happening in the nature.

Because of differential postnatal dispersion of the bear, most of the emigrants that colonize the new space are males (Swenson et al., 1998b). In the beginning of colonization, the ratio of females is very low or close to zero (left limit of function is equal to zero). After that, the ratio of females starts to grow until it stabilizes at its final value when the colonization is complete (the function converges and has a right limit).

2.2.4. Regression analysis of the share of females

The regression analysis of the ratio of females in relation to the distance from the core protective area was performed similarly. For all recorded locations the distance from the edge of the core protective area was determined. All locations were classified with respect to determined distance into two frequency distributions. The ratio of females was calculated within each distance class.

2.3. Potential brown bear habitat

A detailed description of the methodology has been given elsewhere (Kobler, 2000) and only an overview will be given here. In many points this method is related to the method presented in a previous pilot study (Kobler and Adamič, 2000). The differences between the two mostly stem from the fact that a much larger (i.e. countrywide instead of regional scale) and thus a more heterogeneous dataset was used for the study presented in this paper.

The habitat map was based on habitat suitability modeling, which took into account explanatory variables in the form of several GIS layers (i.e. land cover data, forest inventory data, settlements map, road map, digital elevation model). The target variable was binary (suitable/unsuitable). The modeling process took place in the context of a raster GIS with a 500 m × 500 m spatial resolution. Two GIS-based models were made—one to identify the optimal potential habitat (the "optimal" model) and the other to identify the maximal extent of the area that could potentially be inhabited by brown bears in Slovenia (the "maximal" model). Both models were induced automatically by top-down induction of decision trees (Quinlan, 1993), which can accommodate both continuous and discrete explanatory variables. This was an advantage given the available GIS data. An additional advantage of the method is its ability to present the learned information in an easily understandable form of sequential IF-THEN rules. The underlying assumption of the models is that the geo-located sightings of the animals inherently contain some information on bears' preferences regarding the location and quality of their habitat. This information can be extracted, given an adequate number of locations and a sufficient quality of data. A habitat model can then be induced by linking this information to other GIS layers containing factors relevant to habitat suitability.

The models were based on bear sightings data acquired in the last decade throughout Slovenia by the Hunters association for population monitoring (Adamič, 1999a). Some data also resulted from a previous radio-tracking project, which was done between 1993 and 1995 jointly by the Biotechnical Faculty of the University of Ljubljana, the Slovenian Forestry Service, the University of Vienna, and the Munich Wildlife Society (Kaczensky et al., 1995; Kobler et al., 1997).

Our attention was primarily focused on the cleansing of sighting locations data (7.326 points), because they were not all acquired in a similar fashion. There were differences in acquisition method, sampling in-

tensity, and location accuracy. These differences were manifested mostly between different geographic regions, while they were much less pronounced within regions. We were therefore subsequently able to stratify data only considering the geographic criterion. The data cleansing methods included the following:

- visualization of locations in GIS to eliminate obvious gross location errors and to shift out from the database the mistakenly repeated locations,
- overlaying each location over the scanned 1:50,000 topographical map and eliminating those locations, where geographic name attributed to the location differed from the name of the relevant geographic feature on the map,
- applying the same temporal sampling density (i.e. one location each 24 h) for all the radio-tracked bears,
- geographical stratification into four strata, defined by regions of homogenous data acquisition methods.

From the remaining locations we only picked locations of females (sightings with cubs), because we were interested in the "optimal" habitat, best presented by females with cubs. Males disperse over a larger area (Swenson et al., 1998b) and therefore tend to be less selective as to their habitat quality. The number of locations was thus reduced for 67%, from 7.326 to 2.396.

Instead of using a cloud of sighting location points as the basis for the models, we decided to use the estimation of the inhabited area (IA), as represented by the area predominantly utilized by the bear population for feeding, mating, and rearing of cubs. Such an estimate gives a better representation of spatial preferences for a GIS-based model as compared to the simple point locations, because it minimizes the influence of random excursions. The IA was estimated separately for each stratum, using the kernel method (Seaman et al., 1998), which outputs the utilization distribution (UD), defined as a two-dimensional relative distribution of location frequencies (Van Vinkle, 1975). Incomparable sampling intensities were compensated by selecting appropriate UD percentage level for each geographical stratum, such that the estimated IA was proportional to the percentage of the bear population living within the geographical stratum.

The training datasets for automated induction of decision trees consisted of cases (i.e. pixels in the raster GIS), each case belonging to one class (suitable/unsuitable) and specified with the attribute values (i.e. linked to other GIS layers). The pixels belonging to the IA were the positive (suitable) cases, while a similar number of negative (unsuitable) cases were randomly sampled from the rest of the study area, which presumably is less (or not at all) suitable for bear habitat. To account for every possible land cover type, the negative cases were sampled in a stratified random manner with approximately similar number of cases per land cover type. Two training datasets were separately prepared—one for the "optimal" model and one for the "maximal" model. The difference between the two was in the percentages of the IA included. These percentages rested on expert opinion, which was based upon GIS visualizations of IAs at different percentage levels. The "optimum" dataset thus totaled 3.340 (positive and negative) cases, while the "maximum" training dataset consisted of 8.354 cases. Half of each dataset was (randomly) used for training while the other half was set aside for subsequent validation of the habitat maps.

Two decision trees were generated from the above training datasets, using the Rulequest's SEE5 software. None of the decision trees recognized the influence of forest fragmentation, which is generally considered to have an important influence on bear habitat suitability (Knauer and Kaczensky, 1999; Pazhetnov, 1993; Vaisfeld, 1993). This deficiency became obvious from the GIS-visualized decision tree models, which manifested many very small patches of "suitable" habitat. When we filtered these fragments out, the resulting maps not only looked more in accordance with existing knowledge of brown bear habitat in Slovenia, but also became more thematically accurate.

3. Results

This section presents the results of modeling the three aspects of the brown bear population in Slovenia: its size (and its evolution over time), its spatial expansion out of the core area, and its potential habitat based on natural habitat suitability. The results of the models are: an estimate of the bear population size, a picture of the spatial expansion of the population and maps of its optimal and maximal potential habitat (based on natural suitability).

3.1. Modeling the size of brown bear population

To estimate the size of the brown bear population and analyze its behavior over time, we simulated the developed difference equation model. The model has several parameters, as described in Section 2.1. The values for most of these were fixed, but 10 alternative combinations of four parameters were explored. These parameters were: fertility (number of cubs per litter), the mortality rate of cubs in their first year, the mortality rate of cubs in their second year, and the natural mortality for bears older than 2 years (non shooting mortality reasons), expressed as a percentage of the shooting mortality.

Ten combinations of parameter values are listed in Table 3, followed by the output of simulating the model for each of these combinations, listed in Table 4. Out of the 10 scenarios (simulation runs), six seem unlikely given the existing knowledge (and data) about the Slovenian brown bear population (see also the next two subsections). In scenarios 7, 8, and 10, the population dies out due to the high mortality rates. In scenarios 2 and 5, the population explodes. In scenario 3, the population size is stable and in the range between 150 and 190 bears.

The remaining four scenarios (1, 4, 6, and 9) seem likely to reflect the actual population development reasonably well. These are depicted in Fig. 1, together with the official estimates of the Slovenian brown bear population size. The latter are made by the Slovenian hunter association, which is responsible for the management of the brown bear. The model shows a continuous growth of population size since 1969, when stronger measures for bear protection came into force. The model also indicates a decreasing trend in the population size between 1963 and 1969, which is consistent with strong hunting pressure on bears outside the protected core area.

There is an obvious inconsistency between the official estimates and the model simulation results up to 1990, where—according to the official estimates—the population size oscillates between 275 and 325 bears. In that period official estimations of population size were determined 'ad hoc' (*Statistical Yearbooks of Hunters Association of Slovenia*, Ljubljana) without using or measuring any empirical data on bear population and were thus very coarse. Since 1991 the spring and autumn bear's population censuses have been introduced, and the estimates came closer to actual bear population size, what reflects also in better consistency with our model (scenario 1 and 4).

Of the four scenarios, scenario 1 is the most likely one: it has the most characteristic (likely) values of the parameters of the Slovenian brown bear population, selected according to existing knowledge about Slovenian bears. The next most likely scenario is scenario 4. Both are close to the official estimates in the period 1990–1997; based on these, we estimate the bear population size to be between 375 and 425 animals in the year 2000.

3.2. The spatial expansion of brown bears

As evident from Figs. 2 and 3, the brown bear has successfully colonized the area external to the core protective area within the research period. The external population has grown up from 10 to 60 bears, whereas the portion of females has increased from 5 to 19% (Fig. 2). The share of females declines with the distance from the core area. The population area of activity, calculated on the base of either all locations or the locations of females was increasing in time (Fig. 3). These results can be explained by the simultaneous

Table 3
The parameter values in the bear population dynamics model for 10 different development scenarios

Attributes	Scenarios									
	1	2	3	4	5	6	7	8	9	10
	Attribute values									
Fertility (cub per year)	1.7	1.7	1.7	1.75	1.85	1.85	1.85	1.85	1.9	1.9
Mortality of new-borns (%)	10	10	10	12.5	10	15	15	20	15	20
Mortality in second year (%)	5	5	5	7.5	5	10	10	15	10	15
Mortality of older bears (%)	5	10	20	10	10	10	15	10	15	10

Table 4
The 10 different scenarios (simulation runs), with parameter values as in Table 3

Year/scenario	Official estimate	1	2	3	4	5	6	7	8	9	10
1957	161	161	161	161	161	161	161	161	161	161	161
1958	–	169	169	169	168	171	168	168	165	168	166
1959	–	173	174	173	172	177	171	171	166	172	167
1960	–	184	185	183	183	190	182	181	174	182	176
1961	–	198	200	197	197	207	196	194	185	196	187
1962	–	208	210	206	206	219	205	203	191	205	194
1963	–	222	225	220	220	237	218	216	201	219	204
1964	–	216	220	212	214	236	212	208	191	213	195
1965	–	221	227	216	219	246	217	211	191	217	196
1966	–	222	229	215	220	253	218	211	186	217	192
1967	–	214	223	205	212	251	210	200	172	209	179
1968	–	194	206	182	193	240	190	178	146	187	154
1969	300	181	196	178	181	236	177	174	148	181	154
1970	288	186	186	180	183	232	181	174	145	183	152
1971	284	188	196	180	185	231	183	175	142	184	150
1972	281	189	199	179	185	239	183	173	136	184	145
1973	266	192	204	181	188	249	185	173	132	186	142
1974	283	196	209	182	192	255	188	174	128	188	139
1975	298	200	216	185	196	275	191	176	124	191	136
1976	302	204	222	186	199	289	194	176	118	194	132
1977	285	205	226	184	200	302	194	173	110	193	124
1978	314	202	226	178	197	313	190	166	96	188	112
1979	321	202	229	174	196	318	188	160	83	185	101
1980	286	204	235	173	199	346	189	158	73	186	92
1981	297	208	244	173	202	368	192	157	62	187	83
1982	327	211	251	172	204	383	192	153	49	187	72
1983	288	222	267	178	215	417	201	157	43	196	68
1984	328	226	276	176	218	453	203	153	27	196	55
1985	280	227	288	167	219	501	200	141	16	191	37
1986	327	232	295	169	223	528	204	142	18	194	23
1987	300	234	302	164	224	581	203	133	13	191	14
1988	299	239	317	160	228	629	204	126	16	191	15
1989	292	247	327	159	235	695	208	122	13	193	13
1990	277	256	354	159	243	777	213	118	12	197	12
1991	272	266	369	157	251	863	218	112	13	199	13
1992	255	276	401	160	259	973	227	109	10	207	10
1993	324	307	431	173	288	1092	247	117	11	225	11
1994	311	323	471	175	302	1221	257	113	12	232	12
1995	314	334	511	172	310	1372	257	104	11	235	12
1996	363	358	566	175	330	1550	276	99	10	240	10
1997	–	377	619	175	345	1741	287	91	12	253	12
1998	–	395	675	172	358	1952	298	81	13	259	13
1999	–	413	718	164	379	2167	304	63	18	260	18
2000	–	417	770	149	388	2411	305	38	18	256	18

processes of population growth, spatial expansion and postnatal differential dispersion.

For the brown bear and many other mammalian species, it is characteristic that young, mostly yearling males, represent the majority of emigrating individuals (Swenson et al., 1998b). Emigrant bears seek for new living space. Habitats in the surroundings of reproductive females are often occupied by dominant males, which behave intolerantly towards young males inside their home ranges. Because of this, adolescent males often have to travel long distances after being chased away. Due to postnatal differential dispersion,

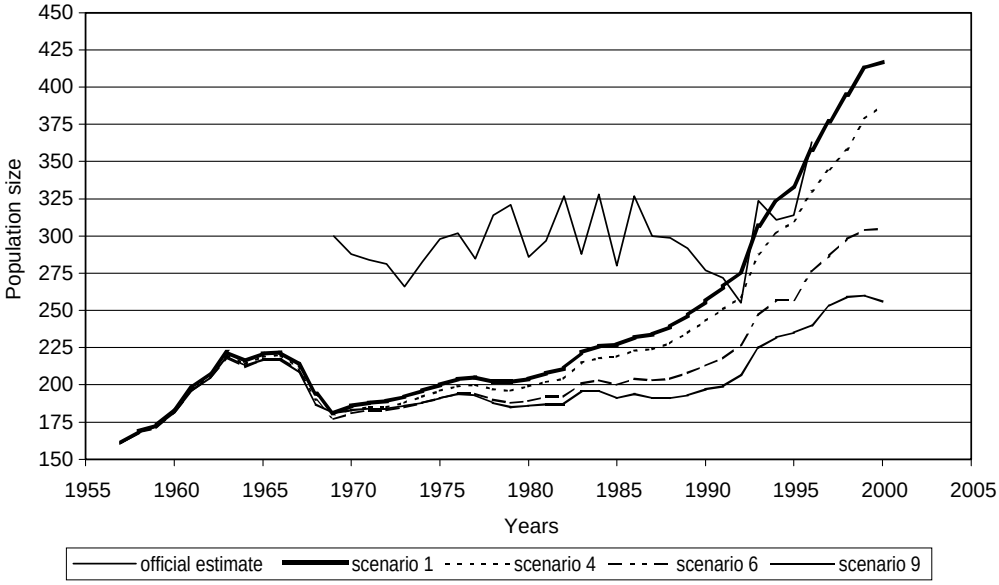

Fig. 1. Four different development scenarios and the official estimates of the brown bear population size in Slovenia.

the population's sex and age structure vary with the distance from the population's core area, which is determined with the presence of the adult fertile females. The share of young males increases with distance from the core area (Swenson et al., 1998b).

At the beginning of the research period (year 1967) almost the entire (92%) Slovenian brown bear population lived in the core protective area. Because of the low portion of females (10% of observations, Fig. 2) and the fact that only the regions near the core protective area were colonized with higher densities (Fig. 3), we believe that emigrants from the core area represented the majority of the external population at that time. The female density was so low, that it did not

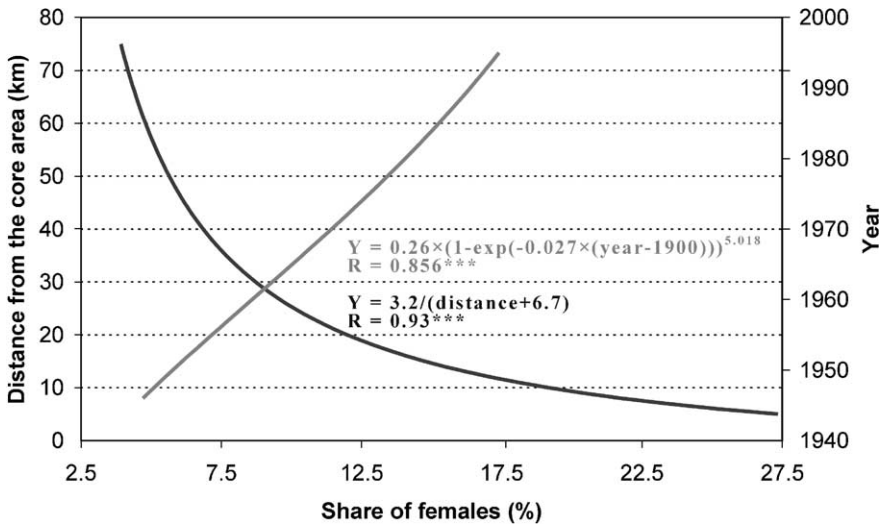

Fig. 2. The share of observed females out of the core area in relation to time (raising curve) and to distance (descending curve) from the core protective area.

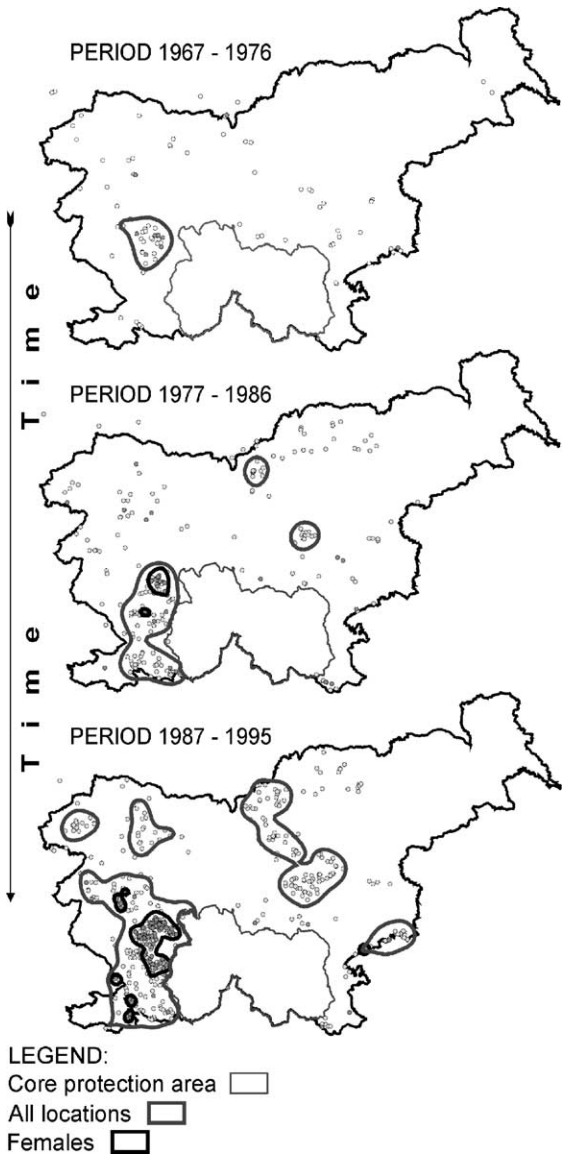

Fig. 3. The spatial expansion of the brown bear in Slovenia in the period 1967–1995.

reach the critical value anywhere (Fig. 3). The stability of population units in the external area probably mostly depended upon a flux of dispersals from the core protective area.

The external area started to lose the status of a typical sink habitat in the second period (1977–1986), when the first reproductive nuclei with higher female densities appeared also outside the core protective area (Fig. 3). The ratio of observed females increased to 15%, while the whole population grew up to 35 animals (Fig. 2). Males started to colonize with higher densities also the regions further away from the core protective area. The population areas of activity, calculated either on the bases of female or on all recorded locations, increased.

The areas, which were colonized mostly by the males in the first period changed into the reproductive—female areas within the last (1987–1995) period. The portion of observed females increased to 17%, which represents already 86% of the value of the stable population (data calculated on the bases of records of the entire Slovenian bear population). The new female and ‘all location’ areas of activity were formed also far away from the core area. The external population increased and contained over 70 bears at the end of the last period.

3.3. Potential brown bear habitat

This subsection presents the results of modeling natural habitat suitability for the brown bear. Decision trees were induced from data on bear presence (as described in Section 2.3), predicting optimal and maximal habitat. These trees were then applied to data from the appropriate GIS layers to obtain habitat suitability maps.

The “optimal” decision tree (Fig. 4a) accounted for differences in surrounding forest matrix size, forest abundance in each pixel, predominant land cover type, sub-regional density of human population, and predominant forest association within each forest pixel. The “maximal” decision tree (Fig. 4b) was much simpler, accounting only for predominant land cover type, forest abundance, and proximity to settlement. The thematic accuracy for the former decision tree was 89, and 84% for the latter. After filtering out the very small patches from the corresponding habitat maps, the accuracies slightly increased to 89 and 85% (Fig. 5). The optimal habitat covers 12.3% of Slovenia’s territory, mostly in the southern part, bordering to Croatia. The possible maximal habitat extent includes additional 26.4% of the territory, mostly in the alpine region in the northern and western part of Slovenia, thus totaling 38.7% of the country. The only region completely unsuitable to bears seems to

```
FOREST_MATRIX_AREA > 175 km2:
:...REGION = "Alpine"
:   :...HUMAN_POP_DENSITY_1991 > 39 inhabitants/km2: Unsuitable
:   :   HUMAN_POP_DENSITY_1991 <= 39 inhabitants/km2:
:   :   :...FOREST_ABUNDANCE <= 80 %: Unsuitable
:   :       FOREST_ABUNDANCE > 80 %: Suitable
:   REGION = "Other": Suitable
FOREST_MATRIX_AREA <= 175 km2:
:...FOREST_ABUNDANCE <= 60 %:
    :...FOREST_ASSOCIATION = {QUERCO ROBORI - CARPINETUM, CARICI ELATAE - ALNETUM GLUTINOSAE,
            CARICI BRIZOIDI -ALNETUM GLUTINOSAE, ALNETUM GLUTINOSO-INCANAE, ALNETUM INCANAE,
            SALICI - POPULETUM, SALICETUM GR., QUERCO - CARPINETUM VAR. HACQUETIA, QUERCO -
            CARPINETUM VAR. LUZULA, etc..... : Unsuitable *
        FOREST_ASSOCIATION = {ADENOSTYLO - FAGETUM, FAGETUM SUBALPINUM}: Suitable
    FOREST_ABUNDANCE > 60 %:
        FOREST_ASSOCIATION = {QUERCO ROBORI - CARPINETUM, CARICI ELATAE - ALNETUM GLUTINOSAE,
            CARICI BRIZOIDI -ALNETUM GLUTINOSAE, ALNETUM GLUTINOSO-INCANAE, ALNETUM INCANAE,
            SALICI - POPULETUM, SALICETUM GR., QUERCO - CARPINETUM VAR. HACQUETIA, QUERCO -
            CARPINETUM VAR. LUZULA, etc.....: Unsuitable *
        FOREST_ASSOCIATION = {MELAMPYRO VULGATI - QUERCETUM, ADENOSTYLO - FAGETUM, FAGETUM
            SUBALPINUM, QUERCO - FAGETUM, ABIETI - FAGETUM DINARICUM}: Suitable
```

(a)

* these branches are truncated

```
PREDOMINANT_LAND_COVER = "Other": Unsuitable
PREDOMINANT_LAND_COVER = "Forest":
:...FOREST_ABUNDANCE <= 60 %: Unsuitable
    FOREST_ABUNDANCE > 60 %:
    :...PROXIMITY_TO_SETTLEMENTS <= 1,5 km: Unsuitable
        PROXIMITY_TO_SETTLEMENTS > 1,5 km: Suitable
```

(b)

Fig. 4. (a) The “optimal” decision tree, (b) the “maximal” decision tree.

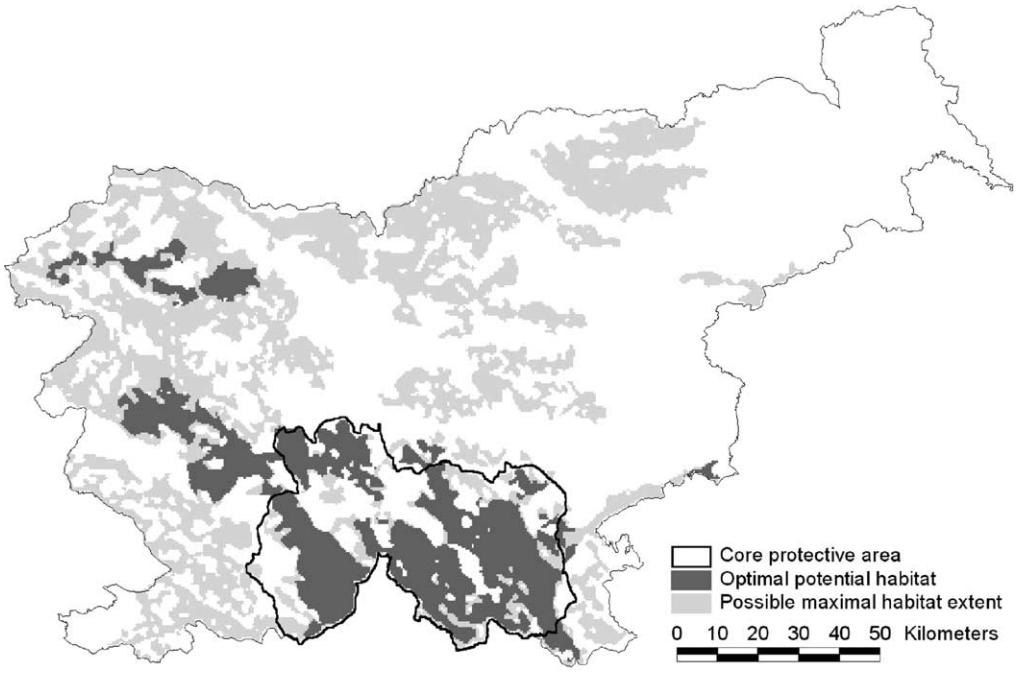

Fig. 5. Potential naturally suitable habitat for the brown bear in Slovenia.

be the Pannonian region in the eastern part of the country.

It can be gleaned both from the decision trees as well as from the final habitat maps, that the bear habitat suitability in Slovenia largely depends on the presence of dense forest cover, while it depends less upon food availability. This agrees with Swenson et al. (1998a), who maintain that the brown bears are found in forested areas with low human density, but the population survival is determined more by the presence of a protective forest cover than by the availability of food. Considering the increasing trend of forest cover in Slovenia, and assuming a continuation of high reproduction rates, we could even expect a further expansion of bear-inhabited areas in the future. We additionally conclude that a significant area of the optimal habitat in the west and northwest lies outside of the official brown bear protection area; therefore an expansion of protection area may be advisable. It is furthermore obvious that the 6-lane Ljubljana–Trieste highway cuts through the optimal habitat at two vulnerable bottlenecks, disrupting the dispersion corridors towards the Alps. This can be seen from a large number of bear related traffic accidents on the highway.

4. Conclusions

The results of our study, although coarse in several respects, can be used as support for future conservation management of the brown bear in Slovenia. In the post-1993 period, questions concerning:

- the habitat suitability of different areas and their importance for the conservation of bears,
- the expected spatial expansion of bears and the necessary extent of its control,
- the past, present, and future population dynamics and its triggers (e.g. the impact of supplemental feeding, surplus harvesting of male bears, etc.),
- optimal population size, etc.,

have been raised and discussed by state agencies, politicians and local communities in Slovenia. Some of these questions have been answered in our paper, and we have made progress towards answering those questions that were not answered completely. But it depends on the State Agencies whether or not these results will actually be taken into account in future bear management.

According to the outcomes of our study it is likely that the bear has already colonized or will colonize in the near future the Eastern Alps (northwestern part of the Slovenia) and other regions far away from the core protective area. So one of the crucial decisions in the future would be whether to allow the bear to re-occupy the Eastern Alps or not. Previous studies of the bear habitat suitability in the western half of Slovenia (Kobler and Adamič, 2000) has shown that the Slovenian Alps (northwestern part of the country) contain a very small portion of total optimal bear habitat. So this area will probably always represent sink habitat for the bears, since its characteristics are not suitable for the establishment of the reproductive part of the bear population. Although our habitat model is, as all the other habitat models of this kind, potentially biased toward the characteristics of currently bear-inhabited areas, (and is therefore valid only for the nowadays situation that might, either due to habituation of the bears or to changes of environment, become different in time), it still indicates that these areas are not crucial for the current conservation of a viable brown bear population in Slovenia. The latter might partly change in time if the bear is still allowed to expand, and if the reproductive females settle in those areas.

Bears' population densities and the share of females in the areas far away from the core protective area (like Slovenian Alps) are low (Jerina and Adamič, 2002; this study). Currently Slovenian Alps contain only 5–6% of estimated bear population, but account for about 67% of reported bear damages in the period 1994–2000 (Jonozovič and Adamič, 2002). It thus represents an important obstacle for the implementation of the species conservation strategy at the State level. Mass media produced daily reports on sheep depredation of the bears and on other kinds of 'bear threatening of human welfare' that triggers negative attitude toward bears and an un-proportionally high amount of compensation claims are, at our opinion, currently a too high 'price' for the conservation of sparse bear population in Alpine region. Therefore our suggestion to the relevant state agencies, arising also from this paper, is to extract any problem bear, repeatedly preying sheep in the Alps. At the same time mitigation measures that could prevent frequent bear-caused damages

must be evaluated and put into force, so that in time some parts of recent bear expansion areas might become a part of the area under protection.

On the other hand it is of crucial importance to adapt human activities and improve bear management in the optimal habitat, with which the goals of successful conservation of the species might be achieved. In future research on the brown bear in Slovenia, we will have to take into account the impacts of supplemental feeding of bears on the population dynamics and on the bear's human-related behavior. Also stockbreeding should be more strictly regulated (fencing of the flock and other mitigation measures) in the bear's core protective area in order to reduce the damage caused by the bear.

From our study, it is also evident that the spatial frames of the bear core protective area, established in 1966, are not suitable any more (Fig. 4). Habitat characteristics inside and outside the core protective area have changed—improved due to a natural afforestation—in time. The bear core protective area should be enlarged to comprise also parts of the estimated optimal habitat in the external area. Although it was proposed already in 1998 to the Ministry of Slovenia for the Agriculture and Forestry to adjust the spatial frames of the bear conservation management area (core protective area) in Slovenia nothing has changed so far. Our study proves again that an adjustment of the bear conservation system in Slovenia should be considered.

The results of our study presented in this paper are among the first steps towards long-term conservation of the brown bear in Slovenia.

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