



Expansion of brown bears (*Ursus arctos*) into the eastern Alps: a spatially explicit population model

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Abstract. We present a spatially explicit population model for analysing the expansion of brown bears (*Ursus arctos*) after the reintroduction program in central Austria. The model is based on field investigations into brown bears in Austria and Slovenia and on current knowledge of brown bears. The landscape of the eastern Alps is represented by a GIS-derived raster map defining local habitat suitability and five major spatial barriers to dispersal. The population model follows the fate of individual bears and simulates reproduction, dispersal, home range establishment, and mortality in annual time steps. We indirectly adjust unknown or uncertain model parameters with 10-year data on the number of females with cubs in central Austria and determine key variables of population dynamics, such as population sizes and growth rates within different population nuclei, dispersal distances, or mortality rates, for model parameterisations that reproduce the data on females with cubs. We estimated a current (1996–2000) growth rate of the population in Austria and adjacent parts of Italy of some 14%; a high proportion of this growth was due to immigration from Slovenia. Consequently, the growth rate of the subpopulation in central Austria, which probably is isolated functionally (i.e., no exchange of females) from the nuclei along the Austrian–Slovenian border, yielded some 7%. This subpopulation may comprise seven residents, and we estimated for females a 33% risk of extinction during the 1992–2000 period. Validation and confirmation of our model results with data on bear densities that were not used for model construction and parameterisation supported our findings. The high female mortality rates, together with the vulnerability of the small population to chance events (i.e., demographic stochasticity), are the most pressing threat for the population in the eastern Alps. Our approach could be widely applied for analysing dynamics of rare and endangered species in which the paucity of data precludes an appraisal of the state of the population using standard methods.

Key words: Extinction, Individual-based model, Landscape, Management, Population dynamics, Spatially explicit population model, *Ursus arctos*

Introduction

Brown bears (*Ursus arctos*) formerly occurred throughout continental Europe, but later disappeared from most areas as the human population grew (Breitenmoser 1998; Swenson et al. 2000). The remaining relict populations in southern, central, and western Europe (Figure 1) are small and highly fragmented (Servheen et al. 1998; Swenson et al. 2000). Today there is increasing public interest in their conservation, which even triggered three reintroduction projects: one in the central Pyrenees, where bears had been exterminated a decade ago (Camarra 1998), and two augmentations in central Austria (Rauer and Kraus 1993; Rauer and Gutleb 1997) and northern Italy (Mustoni and Genovesi 2001) to allow population recovery.

Bears were extirpated in Austria in the 19th century, but in almost every decade dispersing individuals from the bear population in Slovenia appeared (Rauer and Gutleb 1997; Gutleb 1998). Until 1971 those bears were shot. After that the bear became fully protected in Austria. The adjacent country of Slovenia changed its bear hunting policy in 1991 and banned the killing

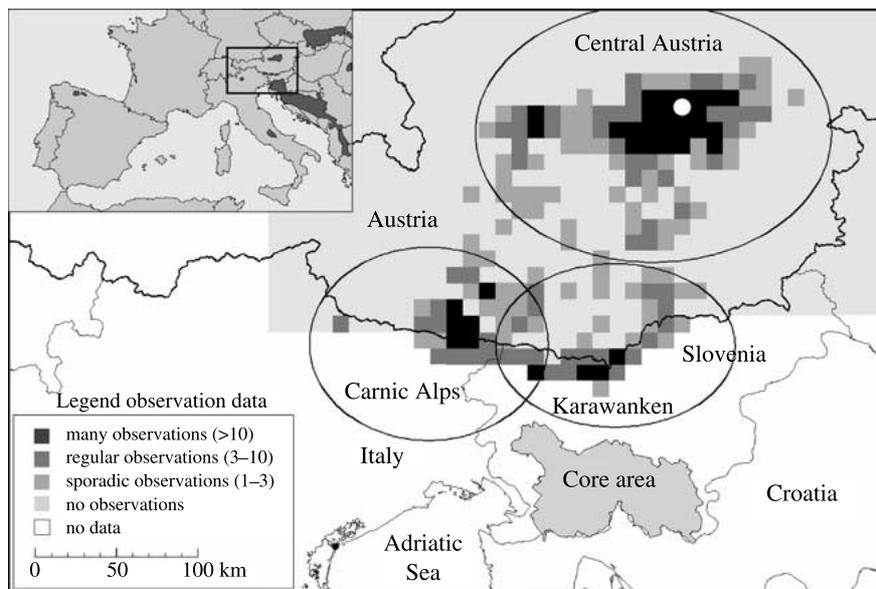


Figure 1. The study area. Small inlet figure: location of the study area in Europe with distribution of brown bears in Europe (dark grey, modified after Swenson et al. 2000). Main figure: details of the study area and the 1989–1999 bear observations data transformed to a 10 km × 10 km grid. The ellipses encircle detailed study areas of the simulation model in central Austria, the Carnic Alps, and the Karawanken Mountains. The bear management core area in Slovenia is shown in grey colour; the white dot in central Austria indicates the location of the bear releases.

of bears outside of a core management area. The latter event was of particular importance for bear recovery in Austria because without hunting along their immigration route, bears should be able to disperse unhindered from the large source population in southern Slovenia to the re-founded population in central Austria. In 2000 the population estimate was about 25–30 brown bears living in Austria. The long term goal for Austria is to establish a viable bear population, but the current Austrian population is far from viable (Arbeitsgemeinschaft Braunbär Life 1997), especially regarding the scarcity of female bears. Contrary to males, that may cover large distances during dispersal, females seem to settle largely in or adjacent to their natal range and therefore population expansion for females is much slower than for males (Taberlet et al. 1995; Knauer 2000).

The expansion of brown bears in Austria is a great challenge for wildlife managers and conservation biologists because they envisage a viable population, while reducing the conflicts that the species may generate to a minimum. Such complex, large-scale management problems require an understanding of the spatial and temporal dynamics of the population to efficiently co-ordinate management before conflicts arise (Tufto et al. 1999; Zedrosser et al. 1999). However, the population dynamics of brown bears in Austria are complex, because the key ecological processes operate on different spatial scales (involving the scales of an individual home range, a subpopulation, and the entire eastern Alps), and the habitat is fragmented and the population is unevenly distributed. Additionally, due to the secretive behaviour of brown bears and their low numbers, the information on the spatial and temporal dynamics of the Austrian population is scarce and uncertain.

One approach to analyse and understand such complex spatial and temporal population dynamics in fragmented landscapes is the use of spatially explicit population models (e.g., Pulliam et al. 1992; Dunning et al. 1995; Turner et al. 1995; Wiegand et al. 1999). This type of model provides a powerful tool for analysing the impact of spatial processes and landscape structure on population dynamics. Spatially explicit population models often use a geographical information system (GIS) database to compile maps on habitat quality, and apply a population model that relates demographics of the species explicitly to the landscape in which the organism lives.

In this article we present a spatially explicit population model with the aim to obtain an understanding of the dynamics of brown bears in the eastern Alps after the reintroduction program. More specifically we use a 10-year time series of females with cubs in central Austria to indirectly calibrate model parameters and to assess current key variables of population dynamics, such as population sizes and growth rates, dispersal distances, or mortality rates within different population nuclei. For model validation and confirmation we use data on bear densities that were not used for model construction and

parameterisation. Hence, we aim to study the past to be able to better manage the present and the future.

The study area

The study area includes the Austrian Alps, the eastern part of the Italian Alps, the German Alps, and the Alpine and Dinaric mountains in Slovenia and northern Croatia (Figure 1). This area is connected by suitable habitat in the South and the West. The Austrian Alps are separated into three landscape types. In the North and the Northeast there are large forested areas and most mountains do not reach the timberline. In the central part of the Alps the mountains are higher and reach heights over 3000 m. The forest there is limited to stripes along the valley bottoms. In the South the mountains are lower, but the forest is more fragmented by man than in the North. Sheep farming and bee keeping are practised in all parts, but the damage by bears in Austria is moderate (Zedrosser et al. 1999). In Italy the landscape resembles the respective parts in the Austrian Central and Southern Alps, and the Slovenian Alps are similar to the mountains in the South of Austria. Extensive sheep farming on open range is widespread in Slovenia, and livestock predation and property damage by bears outside the bear core area (Figure 1) have caused increasing conflicts and may result in changes of the bear management in Slovenia (Adamic 1996; Kaczensky 2000a).

The bear population in Slovenia is located at the link between the Dinaric Mountain Range and the Alps and is the only source for a natural recolonisation of the Alps. The population is estimated at approximately 300–500 individuals and is the northern tip of a contiguous bear population stretching down as far south as Greece and numbering about 2800 bears (Swenson et al. 2000). In Slovenia, a core management area with a range of $\approx 3500 \text{ km}^2$ was established in 1966, and expanded in 1992 to a total area of $\approx 5300 \text{ km}^2$ (Adamic 1996; Figure 1). Within the core area bears are fed and hunted under a quota system, whereas outside the core area they have been protected throughout the year since 1992.

Methods

Strategy of the model

We construct an individual-based spatially explicit population model that contains data on demographic processes, social structure, and dispersal behaviour of brown bears which were accumulated over many years of research on

brown bear populations (e.g., summarised in Swenson et al. 2000). Because the biology of brown bears is well known, the structural uncertainty (*sensu* Burgman and Possingham 2000) of our model is relatively low. However, because of scarce data on the expanding population in Austria the parameter uncertainty is high. To overcome this problem we use population-level data (the 10-year time series of females with cubs in central Austria) to indirectly adjust the unknown or uncertain parameters. To this end we follow the known history of the reintroduction as close as possible and include the spatial structure of the landscape in the eastern Alps, the specific management history (e.g., the release of three bears in central Austria), and other data (e.g., the known litters and mortality of females) into the model. For indirect parameter adjustment we apply the model with a large number of biologically plausible parameterisations, and the predicted time series of females with cubs are systematically compared with the observed time series. The population level data thus act as ‘filter’ that sorts out parameter combinations that are not able to reproduce the known dynamics (Wiegand et al. 1998, 2004 (this issue)).

During the model simulations we scan the internal performance of the model and record, for example, the 1990–2000 population sizes in the sub-areas central Austria, Carnic Alps, and Karawanken (see Figure 1), mortality and reproduction events, mean and maximum dispersal distances, and bear densities. These internal relationships are secondary model predictions and we use them to investigate details of the spatial and temporal dynamics of the expansion. Our assumption is that the data on females with cubs do not only constrain model parameterisations, but also the internal model performance. With this indirect method we can therefore assess probable values for secondary model predictions which are otherwise not available. For model validation and confirmation we use the accumulated 1989–1999 data on bear observation (Figure 1) that were not used for model construction and parameterisation.

The spatially explicit population model

The model is hierarchical in design, being constructed at the population and landscape scales (Figure 2). The landscape of the eastern Alps is represented by a GIS-derived raster map of habitat quality and major large-scale dispersal barriers. Because population numbers are low in the eastern Alps, we select an individual-based model (Wiegand et al. 1998) to describe population dynamics. A demographic submodel determines the fate of individuals throughout life and simulates the life-history events of birth, death, independence and dispersal of young individuals, and reproduction and death for adults (Wiegand et al. 1998). Each of these demographic events is determined

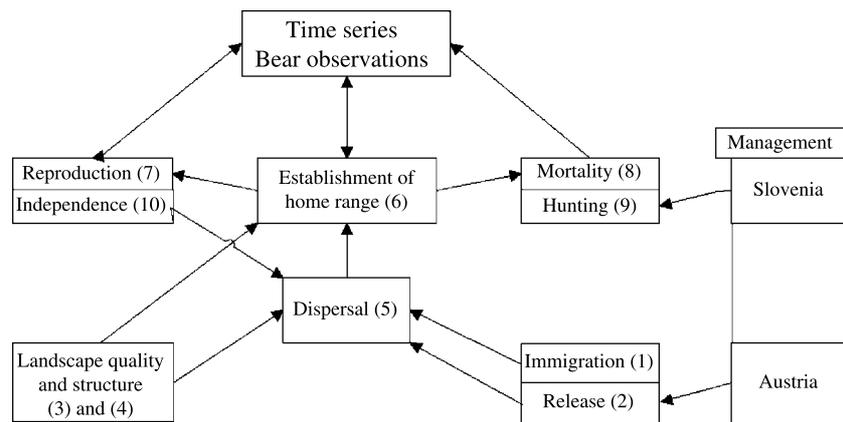


Figure 2. Flow-chart showing the different processes and management actions determining the number of females with cubs and bear observations. The numbers in parentheses refer to the number of the model rules.

stochastically. Mortality is modified as a function of home range size, and only females occupying a home range can reproduce. At the landscape scale, spatially explicit rules determine patterns of dispersal and establishment of home ranges (for a similar model, see Wiegand et al. 1999). These processes depend upon ‘habitat attractiveness’, as perceived by individuals while they move through the model landscape.

The spatial scale

To model variable home range sizes we select a resolution that is finer than the typical scale of a home range and choose an intermediate $10 \text{ km} \times 10 \text{ km}$ raster size as the spatial subunit for our model. With this scale we cover the eastern Alps ($\approx 120,000 \text{ km}^2$) with a grid comprising 36×54 cells. We define a square of nine cells ($\approx 900 \text{ km}^2$) as the maximum size of a female’s home range, and a square of 36 cells ($\approx 3600 \text{ km}^2$) as the maximum size of a male’s home range. These maximum sizes accord qualitatively with observations of telemetric studies in Austria (Rauer and Gutleb 1997) or Scandinavia (Wabakken et al. 1992), but are larger than bear home ranges in the core area in Slovenia (Kaczensky 2000a, b). The coarse 10 km scale enables us to concentrate on large-scale dispersal, and to neglect details of small-scale movements during dispersal or within home ranges.

Because males generally occupy home ranges several times larger than those of females and disperse considerably larger distances, we join a square of four cells to one ‘virtual’ cell and apply all the (following) rules for male dispersal and establishment of home ranges on this double scale.

The habitat model for the eastern Alps

Knauer (2000) and Kaczensky (2000b) developed the habitat model based on 1947 radiolocations of 23 bears that were trapped between 1993 and 1998 in Slovenia (Kaczensky 2000a, b). The habitat model is a descriptive model with a grid structure of 1 km² that followed the habitat evaluation procedure HEP (US Fish and Wildlife Service 1981). Knauer (2000) and Kaczensky (2000b) found that the only relevant habitat variables were percentage forest cover and forest fragmentation measured by the length of polygons inside a 1 km² cell. Variables related to human infrastructure like villages, single houses, and paved or forest roads had no additional influence. This does not mean, however, that human infrastructure variables have no influence on habitat suitability, but because they are highly correlated with forest cover and fragmentation (e.g., fragmented forests are ones crossed by more roads) they provided no additional information. We aggregated the original map with 1 km² resolution to the 10 km × 10 km resolution of the spatially explicit simulation (Figure 3) and scaled the index of habitat suitability in classes between 0 and 9 (Figure 3). We validated the model with an independent data set of five bears from central Austria (Rauer and Gutleb 1997) and found that 94% of all radiolocations from the five bears were in cells with habitat suitability values of 7–9.

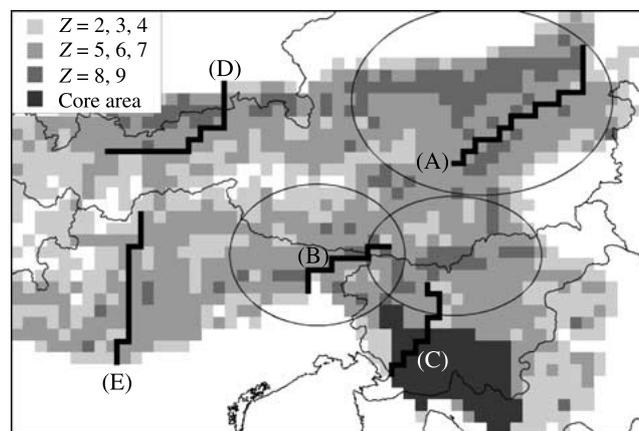


Figure 3. The habitat model for the eastern Alps on a raster basis of 10 km × 10 km. White: $Z = 0-1$, light grey: $Z = 2-4$, intermediate grey: $Z = 5-7$, dark grey: $Z = 8-9$, black: core area. The bold black lines show the barriers included into the model. The probability to cross a barrier during dispersal is reduced, and a home range cannot be crossed by a barrier (see rule (4)). The barriers: Mur-Mürz Valley (A), Villach-Udine (B), Ljubljana-Postojna highway (C), Inn Valley (D), and Etsch Valley (E).

Core area (1)

We do not attempt to model the dynamics within the core area in Slovenia in detail, but we include the source function of the core area, which is important for our aim. To do this, each year we place a number of s^F and s^M subadult females and males, respectively, at random locations at the northern border of the core area (Figure 1) and simulate their dispersal into northern Slovenia and Austria.

Bear management in Austria and fate of released bears (2)

During 1989–1993 WWF Austria released three bears in central Austria (Rauer and Gutleb 1997): in 1989 a 3-year-old female, in 1992 a 6-year old pregnant female, and in 1993 a 4-year old male. The release area was the Ötscher-region in the northern limestone Alps of central Austria (Figure 1). The first female had three cubs in 1991 and 1993; she died in 1993. The second female had two cubs in 1993, and she disappeared in 1994. To be able to more closely adjust the time series of females with cubs, we release bears of the same age and sex in the same area in the model, and we include the three litters and the subsequent death of the two released females deterministically.

Spatial social structure and home ranges (3)

To include a process that describes spacing of home ranges and attraction of males to females in a simple but reasonable way, we introduce the spatial variables attractiveness A^M and A^F that describe the attraction of a given $10 \text{ km} \times 10 \text{ km}$ area for dispersing males and females, respectively. For empty cells, the attractiveness is given through the index of habitat suitability Z (given by the map of habitat suitability), but for females it is reduced when already m males and f females share a cell:

$$A^F = Z e^{-ap} \quad \text{with } p = f + \frac{1}{4}m \quad (1)$$

and for males A^M is increased when more than one female (f) occupy the cell as home range:

$$A^M = (Z + f) e^{-am} \quad (2)$$

where a is a positive constant that determines the degree of possible overlap. Small values of a allow high overlap whereas larger values of a reduce the possible overlap.

Effects of spatial barriers on home ranges and dispersal (4)

Densely populated valleys and highways without many bridges or tunnels are spatial barriers that influence the spatial pattern of the expansion. Studies conducted in Slovenia showed that a highway poses a significant mortality risk

and is a barrier that is rarely crossed by resident bears, but may be crossed by dispersing subadult bears (Kaczensky et al. 1996; Kaczensky 2000a, b). None of the resident bears had a home range crossed by a highway (Kaczensky et al. 1996). In the eastern Alps, highways are expected to be a minor problem because there are more bridges and tunnels. We include five major spatial barriers into the model (see Figure 3) and consider two main effects on dispersal and home range establishment: (1) a home range cannot be bisected by a barrier, and (2) a barrier reduces the probability that a dispersing individual will cross. We assume different probabilities of crossing weak (b_w) and strong (b_s) barriers. We subjectively sorted barriers as weak or strong depending on highway characteristics (number of tunnels and bridges), density of human settlements, and availability of forest cover.

Dispersal (5)

After independence from the mother, subadults disperse and search for their own home range. During 1 year, they are allowed to perform up to S_{\max} site-sampling steps. They move one grid cell per step, selecting a neighbouring cell at random (Knauer 2000; Kaczensky 2000b) with a probability that is directly proportional to the attractiveness of the cell, relative to that of the other neighbouring cells. Dispersal of females continues until they encounter a home range, or until the maximum number of site-sampling steps per year (S_{\max}^F) is reached. By contrast, males accept a home range only with a probability

$$P_S = \begin{cases} \frac{s}{s_{100} S_{\max}^M} & \text{if } s \leq s_{100}, \\ 1 & \text{if } s > s_{100} \end{cases} \quad (3)$$

that increases linearly with the number s of site-selecting steps already performed. The parameter s_{100} gives the fraction of steps relative to the maximum annual steps S_{\max} at which the males take every acceptable home range. This rule describes the empirical observation that subadult males often disperse over long distances through suitable habitats before they eventually settle. Surviving individuals that do not find a home range continue dispersal in the next year.

Mortality during dispersal is considered in addition to age-dependent mortality and is modelled with a constant per-step probability of dying m_s .

Establishment of home ranges (6)

A potential home range is acceptable if the sum of the attractiveness of the block of nine cells, comprising the actual location of the individual and its eight neighbouring cells, exceeds a threshold A_{\min} . The home range is constructed from the collection of the cells with the highest attractiveness that,

as a whole, exceeds the threshold A_{\min} . Thus, establishment of home range size is primarily determined by habitat quality Z . By varying A_{\min} and the constant a in Equations 1 and 2 we can manipulate the number of potential home ranges within the landscape. Once a bear occupies a home range, it stays there until death.

Reproduction (7)

Only resident females that are not accompanied by a litter and with a home range near a male home range can reproduce. Proximity of males is defined as a distance of <7 cells between the centre of the female home range and one cell of the male home range. This allows males excursions up to 60 km, which is the maximal width of a male home range. The probability of a first litter (f_i) depends on the age i of the female, whereas the probabilities for subsequent litters (h_j) depend on the time j since family break-up. We assign the size k of a litter in accordance with probabilities (l_k), and the sex of each cub is determined randomly with an equal sex ratio.

Mortality (8)

The annual survival of each individual is determined stochastically according to age-dependent probabilities (m_i^f for females and m_i^m for males). Individuals with larger home ranges have to move more compared to individuals with smaller home ranges and may thus carry a higher risk of mortality. To consider these effects we multiply the age-dependent mortality rates given in Table 1 with a factor f that describes a reduction of the risk of mortality if home ranges are smaller than the maximum size:

$$f(size) = \frac{1 - c_m}{9} size + c_m \quad (4)$$

where $size$ is the size of the home range, and the parameter c_m defines the degree of reduction of mortality due to smaller home ranges. For $c_m = 1$ size does not influence mortality ($f = 1$), and for $c_m = 0$ mortality is directly proportional to size ($f = size/9$). For non-resident independent bears mortality is the same as for residents with maximal home range size (i.e., $size = 9$).

Bear management in Slovenia (9)

One management parameter that controls immigration into Austria and Italy is the annual probability J of bears being hunted outside the core area in Slovenia. To model the management practice before 1992 we assume hunting as an additional annual risk of mortality $J < 1$ independent of age or sex. In the case of protection outside the core area in Slovenia (the current management practice), we set $J = 0$.

Table 1. Variables and parameters of the model and their values considered for parameter adjustment.^a

	Symbol	Range or values
(A) Variables		
Index of habitat suitability for the landscape of the eastern Alps	Z	0–9
Attractiveness of a cell for dispersing bears	A^M, A^F	0–9 ^b
(B) Demographic model parameters		
Probability of cubs becoming independent at age i	i_i	$i_1 = 1$
Probability of first litter at age i	f_i	$f_3 = 0.9, f_4 = 0.9$
Probability of litter j years after family break-up	h_j	$h_1 = 1$
Probability of a litter of j cubs	l_j	$l_2 = 0.44, l_3 = 0.56^c$
Age-dependent mortality rates at age i^d	m_i	$m_0 = 0.20–0.50,$ $m_{1–4} = 0.08–0.28,$ $m_{5–16} = 0.08–0.18,$ $m_{17–25} = 0.26$
(C) Spatial model parameters		
Parameter describing degree of home range overlap	a	0.1–0.5
Attractiveness threshold for acceptable home ranges	A_{\min}^F, A_{\min}^M	$A_{\min}^F: 49–58,$ $A_{\min}^M: 50–65.$
Fraction of maximum steps at which males take every acceptable home range	s_{100}	0.5
Impact of home range size on mortality	c_m	0–1
Per-step mortality rate during dispersal	m_s	0.001–0.008
Maximum site-sampling steps during 1 year	S_{\max}^F, S_{\max}^M	$S_{\max}^F: 5–40$ $S_{\max}^M: 10–50$
(D) Parameter modelling core area and management		
Mean number of bears immigrating from the core area to northern Slovenia	s^F, s^M	$s^F: 0–0.75$ $s^M: 0–3.0$
Annual probability of being hunted outside the core area in Slovenia	J	0^f, 0.04–0.70

Table 1. (continued)

	Symbol	Range or values
(E) Dispersal barriers		
Probability of crossing a strong barrier (Etsch and Inn valley, Villach-Udine highway)	b_s	0.1
Probability of crossing a weak barrier (Mur-Mürz Valley, Ljubljana-Postojna highway)	b_w	0.8

^a Superscripts F and M indicate parameters for females and males, respectively. Bold-face indicates parameters, which are varied in the simulations.

^b Attractiveness depends on the index of habitat suitability Z and the number of females and males sharing the cell as home range (Equations 1 and 2).

^c Data from central Austria: four litters of two and five litters of three cubs.

^d Age-dependent mortality rates are modified by home range size (Equation 4).

^e One site-sampling step for males comprises two cells.

^f Protection of bears in Slovenia outside the core area 1992–2000.

Independence of cubs (10)

After birth, cubs stay together with their mother as a family group. Family breakup occurs if the entire litter dies or if the litter becomes independent (probability i_i).

One simulation run

At the beginning of each time-step (year), we determine the number of subadult females and males immigrating from the core area into northern Slovenia (1), we release bears in central Austria (2), and all non-residents older than 2 years disperse (3), (5) and search for home ranges (3), (4) and (6). If they survive dispersal (5), they settle or continue searching in the next year. Next, we decide for each resident female not accompanied by a litter whether these females reproduce or not (7). We continue by simulating the survivorship of each individual (8) and (9). In the final step we simulate the independence of cubs (10) and update the demographic variables for each surviving individual for the next year.

Plausible parameter ranges

Demographic parameters

In central Austria nine different family groups of females with cubs were observed. They consisted of five litters of three cubs, and four litters of two

cubs. In four verified (and one probable) cases the breeding interval was 2 years, and in one verified (and one probable) case females had their first litters at age 3 years. These data indicate high reproductive parameters. Similar observations were made in expanding populations in Scandinavia (e.g., Bjärvall et al. 1990; Sæther et al. 1998; Swenson et al. 2000). In Scandinavia, the majority of females come out with a litter the spring after family breakup (J. Swenson, personal communication). We therefore assume independence with 1.4 years ($i_1 = 1$), an interbirth interval of 2 years ($h_1 = 1$), and a high probability to have a litter at 3 years of age ($f_3 = 0.9$, $f_4 = 0.9$) (see Table 1).

In our model, mortality is influenced by dispersal and home range size. Therefore the age-dependent mortality parameters given in Table 1 are maximal mortality rates for resident and dependent bears (survivorship is higher in smaller home ranges), and minimal rates for dispersing bears (additional per-step mortality rate for each site-sampling step). There also seems to be a notable mortality in central Austria because many of the yearlings were not observed in later years. Because information on mortality rates is scarce (one bear probably was poached), we vary the mortality rates over wide ranges. For the cub mortality rate m_0 we assume a range of $m_0 = 0.2$ – 0.5 , for subadults a mortality rate m_{1-4} : 0.08 – 0.28 , and for adults $m_{5-16} = 0.08$ – 0.18 (Table 1). These values include the range of data reported from the managed grizzly bear population in the Yellowstone National Park ($m_0 = 0.11$ – 0.37 , $m_{1-4} = 0.14$ – 0.29 , $m_{5-16} = 0.087$ – 0.099 ; Craighead et al. 1974; Knight and Eberhardt 1985; US Fish and Wildlife Service 1993; Wiegand et al. 1998) and model results from northern Spain ($m_0 = 0.3$ – 0.5 , $m_{1-4} = 0.19$ – 0.22 , $m_{5-16} = 0.134$ – 0.171 ; Wiegand et al. 1998), but are higher than rates of Scandinavian bears ($m_0 = 0.04$ – 0.23 , $m_{1-3} = 0.05$ – 0.13 , $m_{4+} = 0.042$ – 0.08 ; Sæther et al. 1998).

Parameters describing dispersal

We vary the number of site-selecting steps for males between 10 and 50. For a random walk, this choice would yield mean dispersal distances between 65 and 145 km, and the latter includes the distance of some 300 km, which was covered in 1972 by the long-distant migrant ‘Ötscherbär’ from Slovenia to central Austria. For females, which usually settle in the neighbourhood of their mother’s home range (Swenson et al. 1994, 1998), we vary the number of site-selecting steps between 5 and 40. For a random walk, this choice would yield mean dispersal distances between 23 and 65 km. The parameter s_{100} , which describes the pattern observed that subadult males often disperse over long distances through suitable habitat before they eventually settle, only had a moderate impact on the spatial pattern of bear occurrence. We therefore designate an intermediate value ($s_{100} = 0.5$) of this parameter to describe the essence of the pattern observed.

Parameters describing establishment of home ranges

The adjustment of the attractiveness threshold of acceptable female home ranges (A_{\min}^F) (see rule (6)) has to be made relatively to the values of habitat suitability Z which define the landscape of the eastern Alps (=the habitat model). By changing the threshold A_{\min}^F we can manipulate in our model the area suitable for establishing home ranges. To obtain an estimate of how the potentially suitable areas change with the threshold A_{\min}^F we visit each cell of the area considered (Figure 1) and calculate an accumulated suitability index Z_9 , which is the sum of the habitat suitability indices Z of the cell and their eight next neighbours. Cells with $Z_9 \leq A_{\min}^F$ would not be suitable for a female home range. Next we investigate how the non-suitable area (=cells with $Z_9 \leq A_{\min}^F$) changes if A_{\min}^F changes (Figure 4A) and we compare the non-suitable areas with the non-observations of the bear observation data set. For attractiveness thresholds $A_{\min}^F < 49$ the suitable area would be too extended and comprise too much areas without females, especially along the Slovenia–Austrian border. In contrast, for $A_{\min}^F > 59$ the suitable areas would be too small, for example, they would allow no resident female in the area of the Carnic Alps (Figure 4B). For males we use a similar lower range ($A_{\min}^M = 50$), but because the attractiveness of a cell can be increased by the presence of females (see rule (3)), we allow a higher upper range ($A_{\min}^M = 65$). In the latter case males can settle only in areas with high suitability or in areas with many resident females.

Density-dependent changes in attractiveness

Because we have little knowledge about the extent of home range overlap, we select a wide range of values ($a = 0.1, 0.2, 0.3, 0.4, 0.5$) for the parameter a that describes the degree of home range overlap. For $a = 0.1$ (0.5), the attractiveness of a cell drops by a factor 0.5 if eight (2.4) individuals of the same sex share a home range.

Dispersal mortality and home range size effects on mortality

We vary the per-step mortality during dispersal between $s_d = 0.001$, and $s_d = 0.008$. To describe the effect of home range size on mortality, we vary c_m over the entire range from $c_m = 1$ (mortality directly proportional to home range size) to $c_m = 0$ (no effect of home range size on mortality).

Barriers

Our preliminary simulation experiments showed that the effect of a barrier on the spatial pattern of bear occurrence was mainly characterised by the structural rule that a home range cannot be bisected by a barrier, and less by

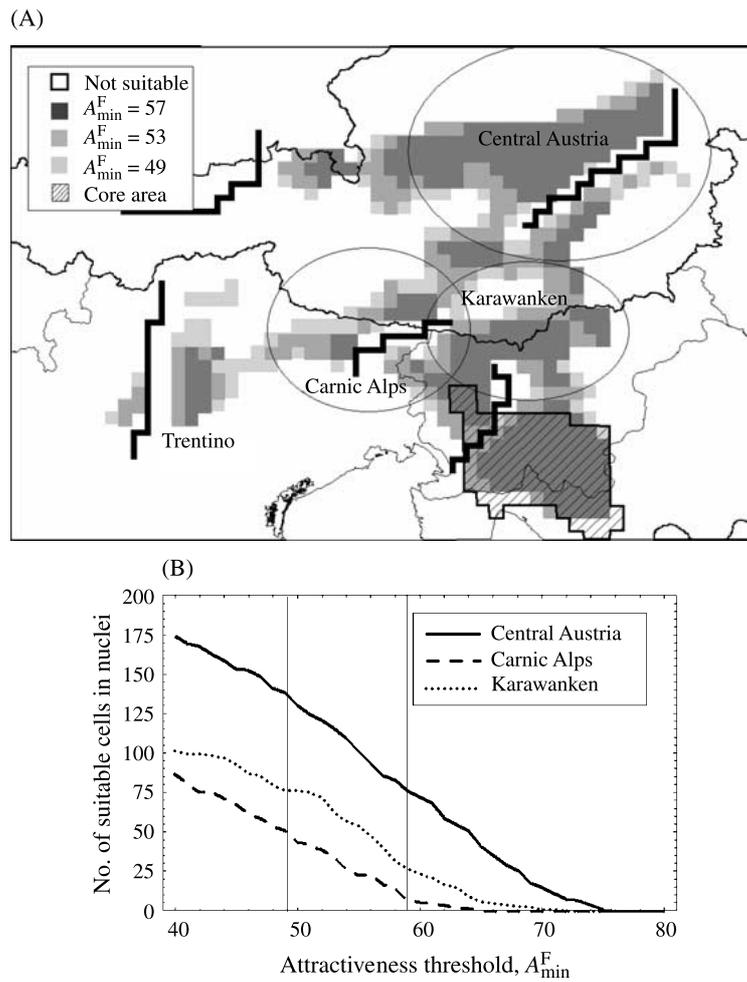


Figure 4. Adjustment of the attractiveness threshold A_{\min}^F for acceptable home ranges. (A) Cells suitable to be the centre of a female home range, in dependence on the attractiveness threshold A_{\min}^F . The barriers (see rule (4)) are shown as bold lines. The predictions are based on the habitat model and the rules for home range establishment (rules (4) and (6)). (B) Number of suitable cells ($Z_0 > A_{\min}^F$) for the three areas central Austria, Carnic Alps, and Karawanken, in dependence on the attractiveness thresholds (A_{\min}^F). The cell size is $10 \text{ km} \times 10 \text{ km}$.

reduced dispersal through the barrier. We therefore keep the probabilities of crossing a barrier unchanged and assume a low probability ($b_s = 0.1$) of crossing a strong barrier (Etsch Valley, Inn Valley, highway Villach-Udine) and a higher probability ($b_w = 0.8$) for weak barriers (Mur-Mürz Valley, Ljubljana-Postojna highway).

Hunting in Slovenia outside the core area

When bears are protected outside the core area in Slovenia, we set $J=0$, and when free bear-hunting is allowed, we assume an annual risk of mortality $J>0$ due to hunting. Because we have no detailed knowledge of hunting efficiency, we vary J over a wide range between 0.03 and 0.7.

Immigrants from the core area into northern Slovenia

Because we have scarce knowledge about the parameters s^F and s^M , we vary them over wide ranges and ‘release’ on average between $s^F=0$ to $s^F=0.75$ females and $s^M=0$ to $s^M=3$ males at the northern border of the core area each year (see rule (1)). Our preliminary simulation experiments showed that higher values of s^F and s^M yielded unrealistically high bear densities in northern Slovenia and southern Austria.

Procedure for model adjustment

We created a total of $n=28,172$ model parameterisations with random generation of the 13 uncertain parameter values, independently of each other, from uniform distributions within the ranges given in Table 1. The range of variation of each parameter reflects the scale of uncertainty in its estimate. For each model parameterisation we perform a number of replicate simulations and measure the errors between the simulated and observed time series of females with cubs. Because the population in central Austria started with only two females, it has a very high risk of extinction due to chance events, and the fact that the female population survived until 2000 is important. We record therefore only information from non-extinct replicate simulation runs (i.e., during 1991–2000 females did not disappear from central Austria) and we perform as many replicate simulations as necessary to obtain 35 non-extinct replicates. Thirty-five replicate simulations were sufficient, because the variance of the number of females with cubs in year t usually stabilised at about 20 (non-extinct) replicate simulations.

Time series of females with cubs

We use the time series $D(t)$ of females with cubs in central Austria from 1991 to 2000 (see Figure 2A in Wiegand et al. 2004 (this issue)) for parameter adjustment and compare it to the corresponding simulated time series $[S(t)]$ of non-extinct replicate simulations:

$$E^{\text{cub}} = \sqrt{\frac{1}{10} \sum_{t=1991}^{2000} \left[\frac{D(t-1) + D(t)}{2} - \frac{S(t-1) + S(t)}{2} \right]^2} \quad (5)$$

To define accordance between simulated and observed time series we compare the mean value of E^{cub} from the 35 replicates ($=E_{35}^{\text{cub}}$) with that of 35

time series obtained through randomisation of the observed data (for details, see Wiegand et al. 2004 (this issue)).

Data on bear observations

Bear observation data were collected during the bear monitoring program (Rauer and Gutleb 1997; Rauer et al. 2001) and include the telemetric data in central Austria. We use the 1989–1999 data on bear observations in Austria for model validation. Unfortunately, the number of observations does not reflect directly bear densities (e.g., Rauer and Gutleb 1997). This is because problem bears may cause more observations than secretive bears, more observations may be reported in areas where good contacts are maintained with forest managers and hunters, and more reports may come from areas that are just receiving their first immigrating bears because they are exciting and newsworthy. Therefore, we do not use this data set for model construction and calibration, but we use it to validate the habitat model and to confirm the simulated bear densities.

We use a coarse classification of bear observations within our $10\text{ km} \times 10\text{ km}$ grid and build four observation classes: (0) cells without bear observations ($n = 613$), (1) cells with sporadic observations of bears ($n = 84$, 1–3 observations), (2) cells with regular evidence of the presence of bears ($n = 62$, 4–10), and (3) cells with many observations ($n = 34$, > 10 observations). Figure 1 shows the resulting map with the bear observation data from 1989 to 1999 transformed to our grid.

To compare the data on bear observations with the simulated data we estimate the total time bears spent during 1989–1999 in every cell, and calculate the average over the 35 non-extinct replicate simulation runs. We assume that resident individuals divide their time equally among cells of their home ranges ($= 1\text{ year}/size$) with *size* being the size of the home range, and that time steps during dispersal have a constant length ($1\text{ year}/S_{\max}$). For dispersing individuals that settled during the current year t we add the contribution of the remaining time after settling to the measure for residents.

As a measure for the accordance between the data on bear observations and the simulated data we calculate the Spearman correlation coefficient for all cells i in the three areas central Austria, Carnic Alps, and Karawanken (Figure 1). Because the data on bear observations are only an index of relative densities, we use a correlation coefficient, which is also a relative measure. However, the information on absolute bear densities (e.g., there were no bears observed in a certain area) cannot be tested with this measure. Because the Spearman correlation coefficient does not resolve the problem of spatial autocorrelation, it may produce a Type I error, that is, we might find significant correlations, which is not real. We therefore define accordance between ob-

Table 2. Secondary predictions for variables of population dynamics, and R^2 -value and T statistics of the coefficients of the multivariate linear regression based on the $n = 88$ best model parameterisations with $E_{35}^{\text{cub}} < 0.5$.^a

Prediction Unit	Mean \pm SD	Min	Max	R^2	J	s^{F}	s^{M}	a	$A_{\text{min}}^{\text{F}}$	$A_{\text{min}}^{\text{M}}$	$S_{\text{max}}^{\text{F}}$	$S_{\text{max}}^{\text{M}}$	c_{m}	m_0	m_{1-4}	m_{5-17}	$1/m_s$	
N_{total}	Bears	32.3 ± 11.3	13.7	65.5	0.73	-6.0	9.5	3.6	0.1	-3.3	-1.4	-0.8	-1.5	-2.7	-1.4	-6.3	-2.9	3.7
R_{Kalk}	Bears	6.7 ± 1.3	4.5	10.9	0.81	-4.3	3.0	3.8	-13.6	-5.1	-7.3	1.3	2.6	-2.1	-1.9	-8.8	-4.1	3.9
R_{Carn}	Bears	3.3 ± 1.4	0.6	7.8	0.78	-4.9	9.2	3.2	-4.5	-8.1	-3.0	3.0	0.4	-3.2	0.2	-5.3	-3.5	-0.3
R_{Kara}	Bears	5.8 ± 2.5	2.1	14.9	0.80	-4.2	5.9	1.1	-11.1	-8.8	-0.6	1.1	1.4	-0.8	0.3	-3.7	-2.7	-1.2
Flux ^M	Bears/year	1.4 ± 0.6	0.0	2.9	0.83	-5.1	7.0	12.4	-1.5	-4.9	0.9	-2.4	-1.5	-0.7	-0.3	-2.1	-1.0	6.7
Flux ^F	Bears/year	0.4 ± 0.2	0.0	1.0	0.79	-6.5	12.3	1.4	1.2	-1.2	2.1	2.6	0.5	-2.8	-2.0	-4.3	-2.5	-0.1
r_{Lotka}		0.080 ± 0.038	0.9964	1.1755	0.76	-2.1	3.0	1.5	-3.1	-4.0	-3.6	-3.4	-1.0	-2.4	1.0	-11.7	-2.3	4.9
r_{total}		0.137 ± 0.035	0.0671	0.2355	0.75	1.9	5.7	-4.7	-4.9	-2.3	0.5	-1.8	-0.2	-0.8	-2.7	-7.4	-3.4	0.6
r_{Kalk}		0.065 ± 0.021	0.0162	0.1307	0.55	-0.3	1.9	-3.8	-5.8	-1.0	-1.5	2.3	-1.1	0.8	-0.8	-3.4	-2.5	-0.9
ext	%	16.7 ± 6.9	3.0	35.0	0.63	-0.6	-2.0	1.5	-1.2	2.5	-0.6	-0.8	0.3	3.1	0.9	7.3	-0.8	0.5
c_0	Cubs	1.48 ± 0.28	0.98	2.35	0.73	-3.2	3.4	1.7	-2.0	-4.0	-2.7	-2.8	-0.9	-2.7	1.0	-10.3	-3.4	4.0
c_3	Cubs	2.68 ± 0.33	2.01	3.44	0.60	-4.8	6.0	2.3	-0.2	-2.9	-2.7	-0.6	-1.2	-3.4	0.7	-5.4	-2.7	1.4
$d_{\text{mean}}^{\text{M}}$	km	118 ± 17	7.2	14.6	0.81	-0.8	1.4	8.0	3.7	-1.0	5.1	-3.7	6.4	-0.3	0.5	-0.6	-0.1	5.3
$d_{\text{mean}}^{\text{F}}$	km	46 ± 11	1.3	6.7	0.76	-3.0	7.9	2.5	8.5	6.5	0.7	8.4	0.0	-3.5	-0.8	-3.0	-1.1	0.1
d_{95}^{M}	km	236 ± 23	16.0	28.0	0.70	-0.2	-2.0	6.3	2.4	0.2	3.9	-3.5	3.8	-0.2	1.0	0.7	-0.2	4.4
d_{95}^{F}	km	110 ± 26	4.0	16.0	0.71	-2.4	6.4	2.6	6.7	6.4	0.1	8.2	0.1	-3.5	0.2	-2.0	-1.0	-0.4

Table 2. (continued)

Prediction	Unit	Mean \pm SD	Min	Max	R^2	J	s^F	s^M	a	A_{\min}^F	A_{\min}^M	S_{\max}^F	S_{\max}^M	c_m	m_0	m_{1-4}	m_{5-17}	$1/m_s$
floater ^M	%	56.0 \pm 19.5	1.0	92.0	0.89	-4.7	9.6	2.2	11.7	9.7	-1.4	-8.1	0.4	-4.1	-2.1	-4.5	-1.5	0.6
floater ^F	%	65.7 \pm 20.6	5.0	97.0	0.82	-2.2	3.0	4.8	5.2	-1.4	9.0	-2.0	-8.6	-1.4	-0.9	-2.4	-0.3	6.5
Q_{HR}		6.8 \pm 0.3	6.2	7.3	0.73	2.7	-2.6	-0.2	-0.4	11.5	-0.1	-1.4	0.4	0.4	0.7	1.4	1.3	-1.5
s_{HR}^F	km ²	840 \pm 20	7.4	8.7	0.81	-3.3	4.2	3.0	2.7	15.6	-1.0	2.1	-0.6	-1.7	-1.7	-4.5	-1.6	2.8
s_{HR}^M	km ²	3390 \pm 700	7.9	9.0	0.86	-3.1	2.8	6.8	0.5	-1.0	14.3	-1.1	1.5	-0.4	0.0	-1.5	-0.1	2.4
O_1^F	%	78.9 \pm 10.3	47	92	0.82	-1.2	6.1	0.5	15.2	5.9	-0.6	2.4	-0.7	-1.9	-1.3	-1.2	-0.3	0.7
O_2^F	%	19.3 \pm 7.2	8	34	0.84	2.3	-8.2	0.1	-16.0	-5.1	0.4	-3.2	0.1	2.0	2.1	0.8	-0.3	0.0

^a For symbols of the model parameters, see Table 1. N_{total} : total number of individuals in Austria and Italy; R_{Kalk} , R_{Carn} , R_{Kara} : number of residents in central Austria, Carnic Alps, and Karawanken, respectively; Flux^M , Flux^F : mean flux of males and females from Slovenia to Austria given in individuals per year; r_{Lotka} : growth rate in Austria and Italy based on all mortality and reproduction events between 1992 and 2000; r_{total} , r_{Kalk} : growth rate of the population in Austria and Italy and central Austria, respectively, based on the simulated 1995–2000 total bear numbers in the respective area; ext : number of replicate simulations where females went extinct in central Austria; c_i : mean expected number of cubs of an i -year-old female; d_{mean}^M , d_{mean}^F : mean dispersal distances and 95%-percentile for males and females; floater^M, floater^F: % disperser that do not find a home range in the current year; Q_{HR} : mean attractiveness of female home ranges; s_{HR}^F , s_{HR}^M : mean size of a female and male home; O_i^F : % of cells with i overlapping female home ranges.

served and simulated data if the correlation coefficient has a conservative P -value of <0.001 .

Sensitivity of model predictions to model parameters

To analyse the dynamics of the expansion in detail we record different variables of population dynamics (Table 2). We calculate the mean value and the standard deviation of these variables based on the 35 non-extinct replicate simulations of the model parameterisations that satisfied the observed time series of females with cubs. To investigate how the uncertainty in the model parameters impacts the secondary predictions we performed linear regressions with secondary predictions (k) as dependent variables and the 13 parameters (i) as independent variables. Because of compensatory effects between model parameters, we may expect multicollinearity among the independent variables p_i of the linear regression (the parameters) which can cause instability in the estimates of the regression coefficients $\beta_{k,i}$. To test for multicollinearity we perform a principal components analysis of our independent variables. It is important to note that the resulting relations between a model prediction and model parameters do not tell us how the prediction will change, if the parameter changes (i.e., a sensitivity analysis), because we base the regression only on the limited set of cases that satisfy the observed data. For a global sensitivity analysis of the model, see Wiegand et al. (2004, this issue). A model parameter p_i with a high regression coefficient $\beta_{k,i}$ has a strong impact, but if the standard deviation SD_i of the coefficient is high the strong effect can be diffused. A good measure that can be used to rank the parameters according to their relative impact on a given model prediction is the T -statistic $T_{k,i} = \beta_{k,i}/SD_i$ that balances both effects. To investigate whether two parameters p_i and p_j impact secondary predictions in a similar way, we construct for each model parameter i a vector $v_i = (T_{1,i}, \dots, T_{23,i})$, where $T_{k,i}$ is the T -statistic for parameter i and secondary prediction k , and calculate the correlation coefficients between all vectors v_i and v_j .

Results and discussion

Model adjustment

Confidence thresholds for the time series of females with cubs

We found that 35 replicate simulations that produced an error $E_{35}^{\text{cub}} < 0.50$ can be considered to be in good accordance with the observed data (for details, see Wiegand et al. 2004 (this issue)).

Secondary model predictions of non-spatial variables

Only 88 (0.3%) model parameterisations satisfied the condition $E_{35}^{\text{cub}} < 0.50$, indicating that the time series data of females with cubs contained a high degree of quantitative information that allowed sorting out a high number of biological plausible model parameterisations. The 88 remaining model parameterisations and their secondary predictions of internal model relations represent the state and the uncertainty of our current knowledge, given our habitat model, our model structure, our parameter ranges, and the data of females with cubs.

The mean values and the standard deviation of the secondary predictions were in general not sensitive to the selection of the threshold of E_{35}^{cub} that defined whether or not the time series data were matched. Using, for example, the less restrictive criterion $E_{35}^{\text{cub}} < 0.54$, we obtained 505 model parameterisations that satisfied the criterion, but the secondary predictions did not change more than 5%. The number of residents \pm SD in central Austria was $R_{\text{Kalk}} = 6.702 \pm 1.264$ for $E_{35}^{\text{cub}} < 0.50$ and $R_{\text{Kalk}} = 6.617 \pm 1.286$ for $E_{35}^{\text{cub}} < 0.54$ (Figure 5A), and the growth rate for this population was $r_{\text{Kalk}} = 0.0652 \pm 0.0218$ for $E_{35}^{\text{cub}} < 0.50$ and $r_{\text{Kalk}} = 0.0663 \pm 0.0236$ for $E_{35}^{\text{cub}} < 0.54$ (Figure 5B). Figure 5 shows two typical examples of how the variables depend on the error E_{35}^{cub} between observed and simulated data. The range of variation of the variables declined with decreasing error and stabilised inside the envelopes of standard deviation. If there were too many or too few residents in central Austria, differences between observed and simulated time series of females with cubs would be marked, and even if the overall

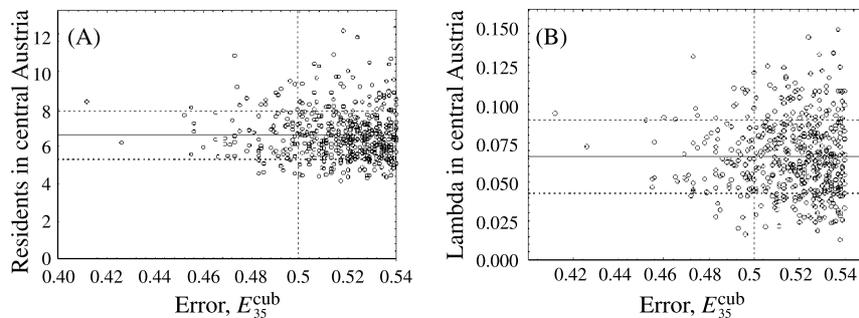


Figure 5. Secondary prediction of the number of residents in central Austria for the year 2000 (A) and the growth rate in central Austria (B), both in dependence on the error E_{35}^{cub} between observed and simulated patterns. Each circle represents the result from 35 replicate simulations. The solid horizontal gives the mean value calculated from the $n=88$ model parameterisations that satisfied $E_{35}^{\text{cub}} < 0.5$, the dashed lines give the range of the standard deviation. Shown are the results for all $n=505$ model parameterisations that satisfied $E_{35}^{\text{cub}} < 0.54$; the $n=88$ best parameter sets are left from the vertical line.

population trend was matched, ‘wrong’ model parameterisations could cause clear differences between the shape of the observed and the simulated time series (e.g., produce wrong minima and maxima in the time series).

Model predictions of non-spatial variables and their sensitivity

Principal components analysis of our independent variables showed that collinearity did not occur; the lowest eigenvalue had a value of 0.26, and accounted for 2% of the variation. The uncertainty in the estimates of the secondary predictions depended to a different extent on the model parameters (Table 2). The parameters m_0 , m_{5-17} , c_m , S_{\max}^F , and S_{\max}^M contributed little to the remaining uncertainty, the parameters m_s , J , s^M , and A_{\min}^M were of intermediate impact, and the parameters a , s^F , A_{\min}^F , and m_{1-4} had the strongest impact. This result points to the information which is most urgently lacking for further reducing the uncertainty in the secondary predictions; an estimate of the carrying capacity (a , A_{\min}^F), female immigration (s^F), and mortality of subadults and young adults (m_{1-4}).

The parameter a controlling overlap of home ranges and the threshold A_{\min}^F for acceptable female home ranges impacted the secondary model predictions in a similar way; we found a positive relation (correlation coefficient = 0.64) between their vectors v_i and v_j . This result is reasonable because the consequences of decreasing a and A_{\min}^F are the same for population dynamics; the carrying capacity increases. We also found strong relations (correlation coefficient > 0.7) between the vector of the parameter J that describes hunting outside the core area in Slovenia before 1992 and the vector of the number s^F of females immigrating from the core area into northern Slovenia (negative sign), and between the vector of the number s^M of males immigrating from the core area into northern Slovenia and the vector of the per-step mortality rate m_s (positive sign). In all other cases we found correlation coefficients smaller than 0.7.

Population sizes

Our model prediction is that the total year 2000 population size in Austria and eastern Italy might be some 32 bears with 11.4 ± 4.7 independent females, 13.2 ± 4.2 independent males, and 7.3 ± 2.3 cubs (mean \pm SD). This prediction corresponds well with current population estimates for this area (Zedrosser et al. 1999; Swenson et al. 2000). In central Austria we estimate some seven resident bears, in the Carnic Alps some three residents, and in

the Karawanken area some six residents (Table 2). Our estimate for central Austria depended mainly on the parameter a determining the overlap of home ranges, the mortality rate m_{1-4} , and the threshold for acceptable male home ranges A_{\min}^M (Table 2). The parameters a and A_{\min}^M are related to the carrying capacity of this nucleus, a variable we cannot further assess with our data. The population estimates for the other areas depended additionally on the mean number of females s^F that immigrated from the core area into northern Slovenia (see rule (1)). This is a reasonable result because the suitable areas along the Slovenia–Austrian border could be reached by females dispersing from the core area (Table 2 and Figure 4A) and are directly impacted by influx from the core area, and because the data used to filter model parameterisations contained no information on population sizes in this area. Consequently, the uncertainties in the population estimates (Table 2), given through the relation between standard deviation and mean value, were much larger for the Carnic Alps (0.42), the Karawanken (0.43), Austria, and eastern Italy (0.35) than for central Austria (0.19).

Growth rates

The growth rate of the subpopulation in central Austria (r_{Kalk}) may have been some $6.5 \pm 2\%$ (mean \pm SD). The uncertainty in this growth rate was mainly due to the parameter a that controls the overlap of home ranges. The simulated growth rate r_{total} of the entire population in Austria and eastern Italy yielded some 14%, and was larger than r_{Kalk} . This might be mainly due to immigration of males and females from Slovenia. The uncertainty in this growth rate was mainly due to mortality of young bears (m_{1-4}), and to a lower extent to the parameter a that controls the overlap of home ranges and immigration of males (with negative sign) and females (with positive sign) from the core area in Slovenia (Table 2). Alternatively, we calculated the growth rate r_{Lotka} for the area of Austria and Italy with the Lotka equation:

$$1 = \sum_i s_i y_i \frac{1}{r_{\text{Lotka}}^i} \quad (6)$$

where s_i was the simulated survival rate of females up to age i and y_i was the simulated fertility (number of female cubs) of a female at age i , determined from all mortality and reproduction events in Austria and Slovenia between 1992 and 2000. This growth rate did not consider immigration and yielded only some 8% growth. The estimate of r_{Lotka} depended mainly on the subadult mortality rate m_{1-4} , but also to a lesser extent on the threshold for acceptable home ranges A_{\min}^F and the per-step mortality during dispersal (Table 2). As expected, the impact of immigrants from the core area in Slovenia disappeared.

Dispersal

The average distance between the mother home range and the own home range for males averages in our model was 120 km, with 5% of them dispersing more than 240 km (Table 2). This distance is about the distance between the core area and the area where bears were released in central Austria (Figure 1). In contrast to males, females dispersed less (Table 2). The mean female dispersal distance in our model was some 46 km, and 5% of all females moved more than 110 km. In comparison with data from Scandinavia, this estimate seems to be too high. In Scandinavia, where the home range sizes are similar to those in the Alps, the mean maximum dispersal distance was 29 km ($n = 11$) and the 95%-percentile 34 km (Taberlet et al. 1995). As expected, the female dispersal distances depended on parameters determining the carrying capacity of the landscape (a , A_{\min}^F), and on the number of site-sampling steps S_{\max}^F . The positive dependence of the dispersal distances on the number of individuals immigrating from the core area into northern Slovenia (s^F , s^M) may be caused by the fact that these individuals have to move farther to find unoccupied home ranges because previous immigrants already settled close by. The impact of the per-step mortality rate during dispersal (m_s) on dispersal distances remained weak and influenced only the mean dispersal distance of males. On average, 56% of all dispersing females and 66% of all dispersing males did not settle within the current year (Table 2). Consequently, the parameters giving the number of site sampling steps (S_{\max}^F , S_{\max}^M) have only a minor influence on the remaining uncertainty of our secondary model predictions (Table 2). However, the high number of dispersing individuals that did not find a home range during the current year led in our model to ‘old’ dispersers of more than 5 years (Figure 6), which is unrealistic for females. The possibility for females to disperse over many years caused the relatively high dispersal distances in our model. Consequently we have to correct the rule on dispersal in forthcoming model analyses.

A large proportion of the population seems to be immigrants from Slovenia (Figure 6A). Some of these immigrants are ‘second generation’ immigrants that moved in our model from their mothers’ home range in northern Slovenia (outside the core area) to Austria and Italy, because we released only 2–3-year-old females and 2–4-year-old males at the northern border of the core area to disperse into northern Slovenia (see rule (1)).

Extinction and mortality rates

We also recorded the number of extinct replicate simulations and find that there was a notable risk of extinction of the female population in central Austria. On average, 17 replicate simulations went extinct, which yields a 33% risk of extinction. Remember that we performed as many replicate

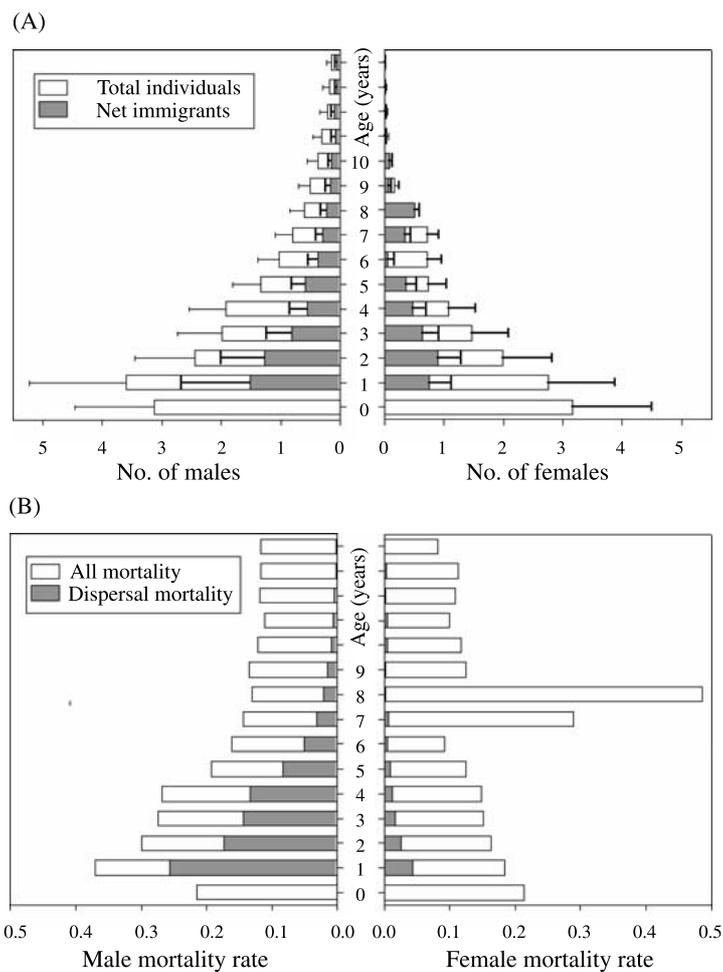


Figure 6. Simulated age structure and simulated mortality rates taken between 1992 and 2000 in Austria and Italy. (A) Mean age structure with envelopes of standard deviation and number of net immigrants from Slovenia (=immigrants – emigrants) based on the variation from simulations of the $n = 88$ best model parameterisations. Values are scaled to the expected population size in 2000 (=32.2 individuals). (B) Simulated mortality rates and fraction dispersal mortality calculated with the pooled data from the $n = 88$ best parameter sets. The high simulated mortality rates of 7- and 8-year-old females are caused by the deterministic death of the released 7-year-old female in 1993 and the 8-year-old female in 1994.

simulation runs as necessary to obtain 35 non-extinct replicates. The uncertainty in the risk of extinction was strongly determined by the subadult mortality rate m_{1-4} (Table 2).

The simulated cub mortality rates, $m_0 = 0.22$ (Figure 6B), are within the range observed from Scandinavian bears and grizzly bears in Yellowstone

National Park, the simulated female subadult mortality rates ($m_{1-4} = 0.167 \pm 0.05$) are slightly higher than in Scandinavia. Our results suggest a high mortality of dispersing males, averaging $m_{1-4}^{\text{dM}} = 0.186 \pm 0.09$ for subadult males. Our estimates of overall female mortality rates ($m_{1-4}^{\text{F}} \approx 0.17$, $m_{5-16}^{\text{F}} \approx 0.15$, Figure 6) are considerably higher than female mortality rates reported from the expanding population in Sweden ($m_{1-3} = 0.05\text{--}0.13$, $m_{4+} = 0.042\text{--}0.08$; Sæther et al. 1998), but are similar to those modelled in the decreasing western population in the Cantabrian Mountains, northern Spain ($m_{1-4}^{\text{F}} = 0.19\text{--}0.22$, $m_{5-16}^{\text{F}} = 0.134\text{--}0.171$; Wiegand et al. 1998).

Female and male home range sizes were mostly of maximum size ($s^{\text{F}} = 8.4 \pm 0.2$, $s^{\text{M}} = 33.9 \pm 0.7$) and showed little variation (Table 2). This result indicates that the rules connected with differences in home range size played a minor role in determining population dynamics and could be simplified. Consequently, the parameter c_{m} that related mortality of residents to home range size had no influence on the secondary model predictions (Table 2).

Secondary model predictions of bear densities

We used the data collected by the virtual observer to calculate the expected mean densities of resident and dispersing female and male bears during the 1992–2000 period (Figure 7). The mean density of dispersing and resident females was relatively low and exceeded values of 0.07 individuals per 100 km² and year only in the core area of central Austria (Figures 7A and C). In Scandinavia, for example, there are about 1.0–1.2 females per 100 km² on an area of 4100 km² (J. Swenson, unpublished data). As expected, the spatial pattern of resident females and males was strongly confined by the pattern of suitable habitat (cf. Figures 4A and 7A and B). Whereas males may have dispersed over wide areas (Figure 7D) and may settle in most of the suitable areas (Figure 7B), the predicted distribution of females was more restricted to the existing nuclei in central Austria, the Karawanken and the Carnic Alps (Figures 7A and C). However, there seems to be a connection between the female population along the Slovenian–Austrian border and the population in central Austria, which is not in accordance with our current knowledge of distribution of female bears. In the field, no females were observed in the area indicated by the dashed box in Figure 7A and C. We use this knowledge for additional model evaluation (see section ‘*Model validation, bear densities between southern and central Austria*’).

We can use the data presented in Figure 7 to further assess the plausibility of internal model relations. Swenson et al. (1998) developed a method to identify core and peripheral areas for brown bears, based on the sex and age structure of hunted bears. Inside of core areas, based on 90% harmonic mean

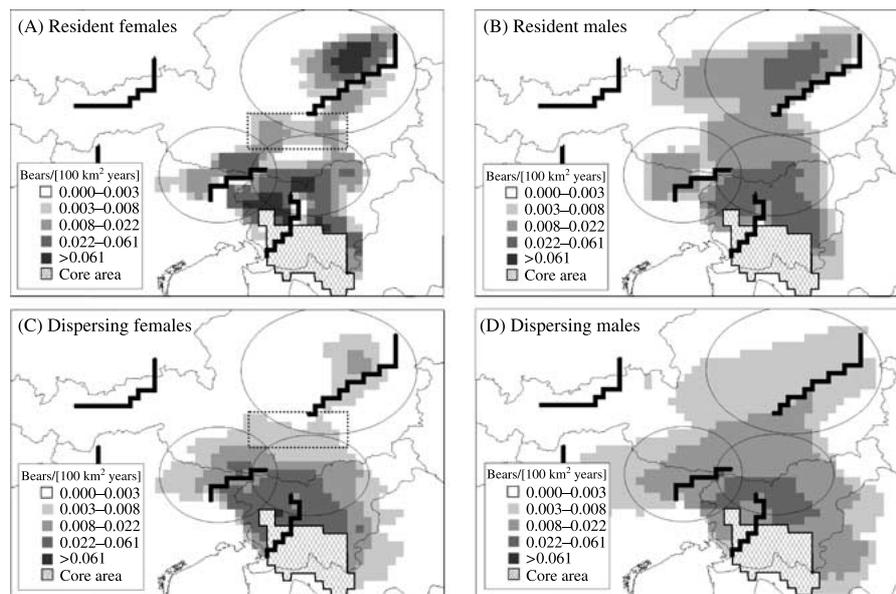


Figure 7. Secondary predictions of bear densities. Mean simulated bear densities within $10 \text{ km} \times 10 \text{ km}$ cells during the 1992–2000 period, based on the 88 model parameterisations that satisfied the observed pattern of females with cubs: (A) mean density of resident females, (B) mean density of resident males, (C) mean number of visits of dispersing females and (D) mean number of visits of dispersing males. The density classes are on a logarithmic scale. The dashed boxes in (A) and (C) indicate an area where no females were observed. We used the mean female densities inside these boxes for model validation.

areas of hunted females, one expects a 50:50 sex ratio, whereas males should dominate peripheral areas. In Sweden, there were 48% hunted females inside the core area, and 23% outside the core areas (Swenson et al. 1998). We tested our model output for this pattern separately for the entire area of Austria and Italy, the area of central Austria (Figure 1), and for the transition area between southern and central Austria (dashed boxes in Figure 7). We defined core areas as areas that contain 90% of the simulated resident females shown in Figure 7A and calculated the sex ratio of dispersing females shown in Figure 7C and dispersing males shown in Figure 7D inside and outside of the core areas. For the entire area of Austria and adjacent parts of Italy we found 45% females inside the core areas and 26% females outside the core areas. This result is in good accordance with the findings of Swenson et al. (1998). For the subpopulation in central Austria we obtained 38% females inside the core area, and 20% outside. The higher proportion of males in the core area in central Austria was expected because of immigration of males from Slovenia. For the transition area we found 26% dispersing females inside the core area and 26% outside, indicating that this area was peripheral.

These results met the expectations for the different population nuclei derived from the framework presented in Swenson et al. (1998) and showed that the internal relations regarding bear densities produced by our model are consistent.

Model validation and confirmation

Habitat model

To validate the habitat model that was constructed with data from Slovenia we used the part of the Austrian data on bear observation classes that was not used for calibrating the thresholds A_{\min}^F and A_{\min}^M for acceptable home ranges (i.e., classes 1–3 in Figure 1). We investigated whether or not cells with higher predicted habitat suitability were indeed cells with more observations. To do this, we determined the percentage of cells with observations that had an accumulated suitability index $Z_9 < A_{\min}^F$ (Figure 8; see also section ‘*Plausible parameter ranges, parameters describing establishment of home ranges*’). We observed that the majority (i.e., 90%) of all observations made in class 3 (many observations) satisfied the condition $Z_9 > 48$, indicating that the best areas in our habitat model (i.e., areas with $Z_9 > 48$) were indeed areas where virtual bears were observed. Thirty percent of all cells with sporadic and regular observations were cells with low predicted habitat quality (i.e., areas with $Z_9 < 49$). The relation of bear observation classes with habitat suitability classes (Figure 8) accorded well with the relation one may expect theoretically; observation class 3 occurred more frequently in good areas, followed by class 2, and class 1. This result increased our confidence in the habitat model and in the data set on bear observations.

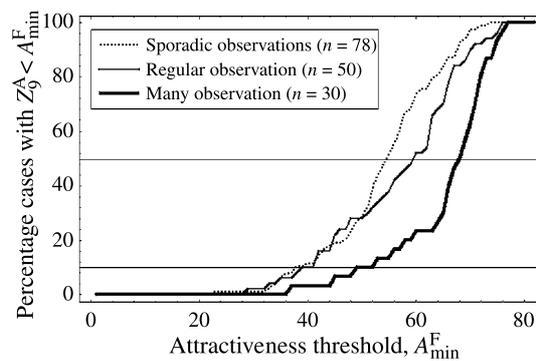


Figure 8. Percentage of cells within observations of classes 1 (sporadic observations), 2 (regular observations), and 3 (many observations) (see Figure 1) that yielded $Z_9 < A_{\min}^F$.

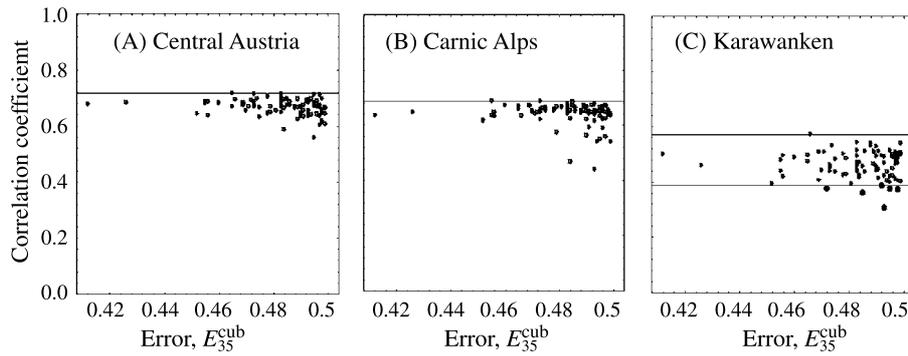


Figure 9. Model validation for the $n = 88$ best model parameterisations. Shown are the Spearman rank correlation coefficient between observation classes (0: no observations, 1: sporadic observations, 2: regular observations, 3: many observations) and the simulated bear densities in central Austria (A), the Carnic Alps (B), and the Karawanken (C), plotted over the error E_{35}^{cub} (Equation 5). The horizontal lines give the maximum value of the correlation coefficients. All correlation coefficients in (A) and (B) were significantly different from 0 with $p < 0.001$. The lower horizontal line in (C) shows the $p = 0.001$ significance threshold.

Data on bear observations in three subareas

We used the data on bear observations (Figure 1) that were not used for model construction and parameterisation for model validation and tested the relation between bear observation classes and the simulated bear density with the Spearman rank correlation. We found that all of the $n = 88$ model parameterisations that reproduced the observed time series data of females with cubs also satisfied the pattern of bear observations in central Austria and the Carnic Alps, and all except six model parameterisations satisfied the pattern of bear observations in the Karawanken Mountains (Figure 9). The correlation coefficients in the Karawanken were generally lower than in the other two areas. By regressing the correlation coefficients over the values of the model parameters (see Table 2), we obtained a negative relation with the threshold for acceptable home ranges A_{min}^F ($R^2 = 0.15$), and a positive relation with the number s^M of males immigrating from the core area into northern Slovenia ($R^2 = 0.14$). In both cases the population size in the Karawanken would increase.

Bear densities between southern and central Austria

We used the mean simulated densities F_R of resident females and the mean simulated densities F_D of dispersing females in the transition area between southern and central Austria for additional model validation. We obtained $F_R = 0.0074 \pm 0.0054$ females per 100 km^2 and year, and $F_D = 0.0038 \pm 0.0032$ females per 100 km^2 and year. The high ratio between mean value and standard deviation indicates a high uncertainty in F_R and F_D . Some 14% of

the uncertainty in the density of resident females F_R in this area was explained by the threshold for acceptable home ranges A_{\min}^F , and 21% by the number s^F of females immigrating from the core area into northern Slovenia. For the density of dispersing females F_D , 15% of the uncertainty was explained by the annual probability J to be hunted in northern Slovenia before 1992, 12% by the parameter a describing degree of home range overlap, and 22% by the number of females s^F immigrating from the core area into northern Slovenia. Thus, a large proportion of the remaining uncertainty in F_R and F_D is due to parameters (J, s^F) which we cannot calibrate with the number of females with

Table 3. Validation of secondary predictions given in Table 2 with the additional patterns of the density of resident females (F_R) and dispersing females (F_D) in the transition area between southern and central Austria (see box in Figures 7A and C).

Variable	Mean \pm SD ^a	Mean \pm SD ^b	Relative change
R_{Kalk}	6.7 ± 1.3	6.8 ± 1.4	1.01
R_{Carn}	3.3 ± 1.4	2.7 ± 1.2	0.82
R_{Kara}	5.8 ± 2.5	5.5 ± 2.9	0.95
N_{total}	32.3 ± 11.3	24.6 ± 6.6	0.76
r_{Lotka}	0.080 ± 0.038	0.070 ± 0.032	0.88
r_{total}	0.137 ± 0.035	0.126 ± 0.038	0.92
r_{Kalk}	0.065 ± 0.021	0.064 ± 0.024	0.98
ext	16.7 ± 6.9	19.0 ± 6.9	1.14
M	1.4 ± 0.6	1.2 ± 0.6	0.86
F	0.4 ± 0.2	0.25 ± 0.2	0.6
c_0	1.5 ± 0.3	1.4 ± 0.2	0.93
c_3	2.7 ± 0.3	2.5 ± 0.2	0.93
d_{mean}^F	46 ± 11	39 ± 12	0.85
d_{95}^F	110 ± 26	99 ± 29	0.9
m_0	0.22 ± 0.05	0.23 ± 0.05	1.03
m_{1-4}^F	0.14 ± 0.04	0.14 ± 0.04	1.01
d_{1-4}^F	0.03 ± 0.02	0.02 ± 0.02	0.82

For symbols of the secondary predictions, see Table 2. m_0 : cub mortality rate, m_{1-4}^F : female subadult mortality (without dispersal mortality), d_{1-4}^F : female subadult dispersal mortality.

^a Mean value and standard deviation based on the $n = 88$ best model parameterisations that satisfied the time series of females with cubs in central Austria.

^b Mean value and standard deviation based on the $n = 42$ model parameterisations that reproduced the time series of females with cubs in central Austria and had low residents and dispersing female densities in the transition area.

cubs in central Austria. Therefore we use the bear densities in the transition area between southern and central Austria to correct and/or validate the values of the secondary model predictions given in Table 2.

To validate the secondary model predictions given in Table 2 we selected 42 model parameterisations with a low density of resident ($F_R < 0.0082$) and dispersing ($F_D = 0.0041$) females in the transition area between southern and central Austria and repeated the calculation of the variables of population dynamics only based on the data from this subset of model parameterisations (Table 3).

We found that using the additional pattern of female densities in the transition area only altered two estimates of variables of population dynamics (Table 3) by more than 20% (Table 3): the flux of females from Slovenia to Austria and the total population size in Austria and Italy. Both are directly linked to the number of females in the transition area between southern and central Austria. However, we used only local information on females with cubs in central Austria for model adjustment (females in central Austria are not directly linked to the dynamics in Slovenia and southern Austria), and therefore we cannot expect to accurately adjust the flux of females from Slovenia to Austria.

General discussion

The state of the population

Our analysis provided a clear picture of the dynamics of the brown bear population in the eastern Alps after the reintroduction program. The current population in Austria and adjacent parts of Italy may comprise 11.4 ± 4.7 independent females, 13.2 ± 4.2 independent males, 7.9 ± 3.5 resident females, 6.8 ± 2.5 resident males, and 7.3 ± 2.3 cubs (mean \pm SD, Table 2). We estimated a demographic growth rate of the population of some 8% per year, although the effective growth rate, including immigrants from Slovenia, may be some 14%. The subpopulation in central Austria may currently comprise 6.7 ± 1.3 resident individuals, 3.4 ± 0.6 of them are resident females. This subpopulation may grow at 6.5% annually. Because of demographic stochasticity due to the low population size, the female population in central Austria faces a high risk of extinction; in 33% of all replicate simulation runs females were extinct in 2000. A simple extrapolation of the 6.5% growth rate would yield, for example, an expected number of 6.4 resident females in 10 years time (in 2010), which is still quite low. Because of its low numbers and apparently high female mortality rates, the small bear population of Austria is currently far from being viable.

The available data on age of first reproduction and the interbirth interval from the subpopulation in central Austria indicate a high reproductive potential similar to the populations in northern Spain (Wiegand et al. 1998) and Scandinavia (Sæther et al. 1998). However, the good conditions for reproduction are contrasted with apparently high mortality rates, which indicate a high human impact on the population. This situation is typical for large carnivores where deaths are mainly caused by humans (e.g., Woodroffe and Ginsberg 1998), whereas nutritional condition determines the reproductive rate. As a consequence, a poorly perceived high risk of human-caused mortality in otherwise good habitats (where resources are abundant and reproductive potential could be high) may create attractive sinks (Delibes et al. 2001). Therefore an analysis of factors influencing reproduction and (human-caused) mortality would be important to identify and manage possible attractive sinks and to reduce the high mortality.

Since further reintroduction has been strongly opposed, the future of the Austrian bear population depends on immigrants from Slovenia. However, the net influx of females from Slovenia into Austria is small. We estimated that one female may immigrate to Austria roughly every 4 years (Table 3). Our estimate of a mean distance between the mother home range and the immigrant's own home range is some 40 km, with only 5% of all females dispersing more than 100 km (Table 3). Therefore it might take a long time before the female bears from Slovenia immigrate to central Austria. The female population in central Austria is functionally isolated from females in southern Austria and northern Slovenia. This isolation makes the subpopulation in central Austria even more vulnerable to chance events due to demographic stochasticity. Since an increase of landscape connectivity is not possible on such large scales and because the possibility of further reintroduction has been strongly opposed, a reduction of the high mortality rates forms the principal management target.

Application of our approach

Our approach can be widely applied for investigating population dynamics in fragmented landscapes, and is especially powerful in situations where paucity of data precludes an appraisal of the state of the population using standard methods (Wiegand et al. 1998). For a more detailed discussion on problems with uncertainty in spatially explicit population models, see Wiegand et al. (2004, this issue). For model construction and analysis we followed the pattern-oriented modelling strategy (Grimm 1994; Grimm et al. 1996; Wiegand et al. 2003). In the context of population dynamics in fragmented landscapes this approach involves (1) the construction of a realistic

(individual-based) population model that includes the key processes of population dynamics and describes the response of individuals to landscape structure, (2) a habitat map that represents the spatial structure of the landscape, and (3) independent population level data (=observed patterns) that capture key features of population dynamics for adjusting the unknown parameters. Our approach is most effective in situations where the model has a high parameter uncertainty, but a low structural uncertainty. This is because our approach can access a broader range of data for model parameterisation as conventional approaches which rely on point-estimates of parameter values (Wiegand et al. 2004, this issue). Clearly, the degree to which the initial parameter uncertainty is reduced depends on the amount of information that is carried by the independent population level data (the observed patterns), and on how well the model describes the most important processes and the major constraints that generate the observed patterns. Our approach is especially powerful when data on multiple features of population dynamics are used (e.g., Kendall et al. 1999; Railsback and Harvey 2002; Wiegand et al. 2004 (this issue)). Whereas it might be relatively simple to reproduce one feature of a system, the simultaneous fulfilment of several characteristic features of the system is by far non-trivial.

Because our approach requires the construction of a model that produces an output that is directly comparable with field data (i.e., the patterns), model results can be analysed in the same way as field data. This feature provides the possibility to perform an extensive analysis of internal model relations (secondary predictions) and the impact of model parameters on them, thereby facilitating a deep understanding of population dynamics (Wiegand et al. 2003). An important gain of this is that the researcher can identify data which are most urgently lacking for prognosticating the state of the population; for brown bears in Austria we identified estimates of the carrying capacity (a , A_{\min}^F), female immigration (s^F), and mortality of subadults and young adults (m_{1-4}) as such research priorities. Such interplay between modelling and field work is an essential part of adaptive management (Walters 1986, 1997).

The availability of population level data (the patterns) will be different for each population. Therefore, our approach requires specially constructed models, and a proper analysis of the detailed secondary model predictions, which is necessary for obtaining an understanding of population dynamics, may be time consuming. However, applied questions on complex systems, such as population dynamics of species in fragmented landscapes, can only be properly analysed if the model reflects the essence of the complexity. Therefore we have to accept the additional effort in model construction and analysis for obtaining deeper insights.

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