Although the brown bear (Ursus arctos) is generally classified as an endangered species, the size and range of several bear populations are increasing in different parts of the world. Understanding how this occurs is essential for the species’ management. Using reliable signs of bear presence and models, we analyzed multiple aspects of the spatial expansion of the brown bear population in Slovenia from the Core Bear Protective Area (an area established in 1966 for the conservation of brown bears; hereafter, Core Area) toward the Alps and other parts of the country in 1945–1995. Bear population densities increased between 1945 and 1995, but densities decreased with distance from the Core Area. The observed proportion of females increased overall during the study period from 6% to 20%, but decreased with distance from the Core Area from 27% (0–10 km from the Core Area) to 5% (>70 km from the Core Area). This pattern likely is a consequence of male-biased dispersal, which can cause substantial changes in the sex structure of peripheral parts of populations in space and time. The population showed a net annual growth rate of 1.7%, and expanded spatially at an average rate of 1.6–1.9 km/year. Some females were recorded far from the Core Area (>80 km), suggesting that unlike in stable or declining populations, females in expanding populations can exhibit long-distance dispersal. However, the frequency of females that dispersed far was so small that it probably had little impact on the dynamics of the population expansion.

Key words: brown bear, dispersal, population density, population growth, sex-biased dispersal, Slovenia, spatial expansion, Ursus arctos

The brown bear (Ursus arctos) is generally classified as an endangered species, yet bear populations are increasing in several areas of the world (Servheen et al. 1999). In Europe, for example, all Nordic brown bear populations are increasing, whereas local expansions have been recorded in a part of the Carpathian population in Slovakia, a part of the northwestern population in European Russia, and parts of the Alps–Dinaric–Pindos population in Croatia, Italy, and Slovenia (Zedrosser et al. 2001). Moreover, numerous reintroduction projects aimed at increasing the sizes of bear populations are under way in different parts of the world (Clark et al. 2002; Pretoni et al. 2005). Several studies indicate that the demography, dispersal, and other ecological parameters of expanding populations of large predators can be different from those of stable or declining populations (Bales et al. 2005; Pletscher et al. 1997; Swenson et al. 1998). Recolonization of large predators into their historic ranges also can cause a disproportionate amount of economic damage and severe conflicts with local people (Kaczensky 1999; Kaczensky et al. 2004; Zimmermann et al. 2001). Studying the expansion of large predators is therefore essential for understanding their basic biology, and for their management.

The brown bear in Slovenia is a good example of a population of a large predator whose spatial expansion has caused management problems. The size and range of the population increased substantially after the Second World War. When the Core Bear Protective Area (hereafter, Core Area) was established in the south of the country in 1966 (Fig. 1), nearly the entire population, which had been estimated at 160 animals, lived within its boundaries (Švigelj 1961). Only about 5% of the animals lived outside the area. In the subsequent years, the population expanded from the Core Area to various directions toward the west, north, and northeast; individual animals were observed as far as in alpine regions in neighboring Austria and Italy (Adamčić 1992; Gutleb 1998; Perco 1992). The expansion sped up after 1992, when the brown bear was protected outside
The brown bear (Ursus arctos) population expanded after 1945 from the Core Protection Area (shaded part) to other parts of Slovenia and bordering parts of Austria and Italy. The analysis of spatial expansion is based on the shown locations (black dots), which are reliable signs of bear presence (harvested or recovered animals, sighted animals, or tracks) collected from 1945 to 1995. The figure also shows concentric belts around the Core Area in which local population density was estimated (see Fig. 4).

The Core Area as a result of international efforts to recolonize the species in the Alps (Simonič 1992). Consequently, the proportion of the population of brown bears outside the Core Area (hereafter: external population) has risen to 25% of the recently estimated population of 400–450 animals (Jerina et al. 2003). The state and dynamics of the external population is essential for Slovenia and other alpine countries because the external population links the great Dinaric bear population with small, isolated groups of animals in the Alps, and constitutes the single potential source of animals for the natural recolonization of the species in the entire Alps (Adamič 1992, 2003; Gutleb 1998; Percol 1992). However, it needs to be stressed that bear-caused damage in the newly populated areas outside of the Core Area has been so extensive it has had a negative impact on people’s general tolerance of bears, aggravating bear conservation efforts in the entire country (Adamič 2003; Krystufek and Griffiths 2003).

The spatial expansion of animal populations depends on the current bear management policy and the spatial expansion of the bear population (Adamič 2003; Kaczensky 2000a, 2000b; Krystufek et al. 2003). Thus, the overall objective of this study was to examine the spatial and temporal patterns of the expansion of the brown bear population in Slovenia from the Core Area toward the Alps and other parts of the country after the Second World War. Specifically, we wanted to examine spatial (with distance from the Core Area) and temporal (in the 1945–1995 period) changes in the structure of the external population (population density and sex ratio); to establish the rate of the spatial expansion of the external population in the research period; and to determine the importance of newly formed bear population nuclei outside the Core Area for bear conservation in Slovenia and, more broadly, in Europe.

The spatial expansion of animal populations depends on factors that affect the growth of the population and the dispersal of individual animals (Lubina and Levin 1988; Swenson et al. 1998). In most (but not all) species of mammals, dispersal is male-biased (Brandt 1992; Pussey 1987; Wolff 1997), rarely female-biased (Clutton-Brock 1989), or equal (Dobson 1982; Greenwood 1980; Swilling and Wooten 2001). Studies examining dispersal of bears have yielded partially incompatible results. In stable and declining populations of brown bears or black bears (Ursus americanus) in North America, the dispersal characteristics of males and females are distinctly different (Lee and Vaughan 2003; Rogers 1987; reviewed in equal: Gardner and Gustafson 2004). Males frequently disperse far, whereas females tend to be philopatric and establish their home ranges in or close to the home range of their mothers. For example, Rogers (1987) reported that female black bears occupy the closest available area, if they disperse at all. In contrast, research on spatially expanding bear populations in Scandinavia and Finland shows that females can disperse far and their proportion among the emigrants is relatively large (Kojola et al. 2003; Kojola and Heikkinen 2006; Swenson et al. 1998). Based on the differences in dispersal by females between Scandinavian and other bear populations, Swenson et al. (1998) made the general prediction that long-distance dispersal of females occurs relatively frequently in spatially expanding populations, but is negligible in stable and declining populations. This prediction has so far been tested just for the bear population in Finland (Kojola et al. 2003; Kojola and Heikkinen 2006).

Spatially expanding populations, more individuals disperse from central parts into the outermost edges of the population than in an opposite direction, which also has been shown indirectly for large predators (Kojola et al. 2003; Pulliainen 1986). This pattern is also the premise of spatially explicit models of expanding populations of bears (Knauer et al. 2000; Wiegand et al. 2004). As a result, we can expect that the sex structure in expanding populations changes over space and time due to sex-biased dispersal. In our study, we predicted that the proportion of females in a population decreases with distance from the Core Area, because females disperse shorter and less frequently than males (hypothesis 1). During spatial expansion of the population to a previously uncolonized area, the proportion of females in this area should increase over time; thus, we predicted that the ratio of females in the external population should increase over the research period (hypothesis 2). As a result of the high harvest of bears in Slovenia, the external population was probably not saturated during the entire period covered by this research (Jerina et al. 2005). In line with the hypothesis of Swenson et al. (1998), which posit that the rate of philopatry of females increases as the population becomes saturated, we predicted that some females did disperse over large distances, meaning that at least a few will be recorded far from the Core Area (hypothesis 3).

This research also examined the rate of the spatial expansion of the central bear population. Several spatially explicit models of population expansion for various species of mammals have been published recently (e.g., Gardner and Gustafson 2004; Kramer-Schadt et al. 2004), including for the brown bear (Wiegand et al. 2004). However, the reliability of such models can be low due to their parameterization and structural
uncertainty (sensu Burgman and Possingham 2000) resulting from the complexity of factors that influence the speed of range expansion (Johnson and Gaines 1990; Lubina and Levin 1988; Wolff 1997) and because empirical evidence on the rate of expansion of bear populations or other species of large mammals is lacking. Furthermore, the effects of dispersal on the structure of populations are also quite poorly studied. Spatially explicit variation in the proportion of females has so far been described only for Nordic bear populations (Kojola and Heikkinen 2006; Swenson et al. 1998), whereas even less is known about changes in the sex structure of an expanding population in space and time for bears or any other species of mammals.

MATERIALS AND METHODS

Data.—We studied the expansion of the external bear population on the basis of locations of harvested and other dead bears (e.g., animals found dead and road- and railway-killed animals) and other reliable signs of bear presence (tracks and visual observations). We collected this data from official hunting registers of the Hunters Society of Slovenia, which professionals maintain, and from the Official Gazette of the past Socialist Republic of Slovenia, which published governmental decisions about bear harvest. We extracted data on signs of bear presence from the magazine Lovec (the only specialized hunting magazine in Slovenia issued monthly since 1910), which published numerous articles and comments on bear occurrences authored mostly by hunters, and from the database of national monitoring of brown bears (started in 1986), which was coordinated by the Forestry Institute of Slovenia and supported by the Hunters Society of Slovenia with local assistance from hunting clubs (described by Adamič [1992] and Adamič and Jerina [2006]). We also used published data on harvested bears or bear observations in the border regions of Austria and Italy (Adamič 1992; Anderluh 1990; Perco and Calo 1990; Švigelj 1961).

From these sources, we systematically extracted all spatially and temporally defined data on bear locations outside the Core Area in Slovenia and in the border regions of neighboring Austria and Italy in the period 1945–1995. For our analysis, we assumed that at the beginning of the research period, the Core Area coincided with the actual distribution of bears in Slovenia. This assumption is realistic, because the boundaries of the Core Area had been determined based on the actual range of the bear population (Švigelj 1961). The period covered by our study ends in 1995, because subsequent data are not directly comparable to older data because of changes in bear management and monitoring methods. Using a geographic information system, we calculated the distance of the locations from the nearest edge of the Core Area (Fig. 1).

We tried to determine the sex of the animals for each location. The category “females” includes locations that reliably belonged to females (females harvested by hunters or found dead, and visual observations or tracks of females with cubs), whereas the category “other” includes all other locations that could belong only to males (data on bears harvested by hunters or found dead) or where the sex could not be determined (other data). The actual proportion of females was probably underestimated by both sets of data. For the data on bears harvested by hunters, the proportion of females is probably underestimated because their hunting mortality is typically smaller than that of males (review in Adamič 1997). For example, the average proportion of females among harvested brown bears was 43% in the recent years, whereas their proportion in the population as determined by fecal sampling, the results of which, however, also may be biased (Bellemain et al. 2005), is 56% (Skrbišek et al. 2007). This underestimate does not reduce the usefulness of the data, because we studied the relative changes in the proportion of females, not absolute values.

Many people authored the primary sources of data for various purposes, which is why we meticulously filtered the data. We removed all duplicate data that denoted the same observation of a bear (same event) as well as incomplete data sets and data sets with logical errors. After filtering, we were left with 1,180 data points that included information on sex (196 females and 984 other signs), year of observation (1945–1995), and distance from the Core Area (0–98.9 km; Fig. 2). Of the 1,180 data points, 184 denote the locations of harvested bears or bears found dead, and the remaining 996 are from other signs of bear presence (tracks and visual observations). The proportion of females among the harvested or recovered animals (16.3%) was almost identical to the proportion (16.6%) recorded from other signs of bear presence.

To establish the rate of population expansion, we also used data from a spatially explicit model of brown bear habitat in Slovenia and a model of the external bear population size in the period after the Second World War, which Jerina (2002) and Jerina et al. (2003) described.

Spatial and temporal variation in the sex structure of the bear population.—We analyzed the variation in the sex structure of the external bear population with binary logistic regression in Statistica 6.0 (StatSoft, Inc., Tulsa, Oklahoma), which has the advantage of being robust and having relatively few assumptions regarding data distribution (Hosmer and Lemeshow 1989). The binary logistic regression model predicts the likelihood that for given values of independent variables (numeric or nominal) the dependent variable will take 1 of the 2 binary values. The method is thus suitable for our data, because the dependent variable sex is binary (female or other), whereas the independent variables time and distance from the Core Area are numerical. The model, which we adjusted to the data using binary logistic regression, predicts the likelihood that a randomly observed bear—at a certain distance from the Core Area and in a certain year—is female. The predicted value is functionally dependent on the linear combination of the variables time and distance from the Core Area. We analyzed the data separately including both time and distance, and for only time and only distance. The 1st analysis tested hypotheses 1 and 2, whereas the last 2 analyses were used to show variation in the sex structure of the external bear population in time and with regard to the distance from the Core Area. In addition to regression models, we examined the empirical proportion of females for time intervals and distance belts from...
Correction constants are quotients between the average size of multiply the location frequencies in all 32 time–distance belts. For the purpose of comparability, we relativized densities for both sex categories (all locations, females).

We calculated the rate of external population spatial expansion with data on bear density in time–distance belts that had been established for all locations notwithstanding the sex of the animals (Fig. 4, all locations). We did not know the shape of the function that relates bear density to distance from the Core Area, nor did we want to make any hard presumptions on it. Therefore, we built the regression models for several functions, including the linear, exponential, and Bertalanffy functions, that were all based on the general equation (Table 1, equation 1) described above. The linear model expresses local population density as a linear combination of the variables time and distance from the Core Area (Table 1, equation 3). The exponential model assumes that density depends on the exponent of the linear combination of independent variables.

### Table 1.

<table>
<thead>
<tr>
<th>Number</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>density = function((-A \times \text{distance}) + (B \times \text{time}))</td>
</tr>
<tr>
<td>2</td>
<td>$\Delta$ density = 0 $\Rightarrow$ ((-A \times \text{distance}) + (B \times \text{time}) = 0 \Rightarrow A \times \text{distance} = B \times \text{time} \Rightarrow \text{distance/time} = B/A = \text{rate of expansion}</td>
</tr>
<tr>
<td>3</td>
<td>density = ([(-A \times \text{distance}) + (B \times \text{time})]) + C</td>
</tr>
<tr>
<td>4</td>
<td>density = $\exp([-A \times \text{distance}) + (B \times \text{time})] + D) + C</td>
</tr>
<tr>
<td>5</td>
<td>$Y = A \times [1 - \exp(-B \times x)]$</td>
</tr>
<tr>
<td>6</td>
<td>density = $C \times (1 - (1 - \exp(-A \times \text{distance}) + (B \times \text{time}) + D)]^2$</td>
</tr>
</tbody>
</table>

the Core Area. We divided the locations into 7 equidistant categories, each 10 km wide (0–10, 10–20, . . . , 60–70 km) and an 8th, open-ended category (>70 km). Temporally, the locations were grouped into categories that included at least 30 locations and at least a 2-year interval each (Fig. 3).

**Spatial and temporal variation of bear population density and the rate of its spatial expansion.**—The analysis of the rate of spatial expansion of the external bear population is based on the following: as the population expanded, its density increased over time in concentric circles around the Core Area (if only 1 belt is observed) and decreased with the distance from the Core Area (if all belts are observed at once). Based on the population density in belts around the Core Area, the rate of expansion can be determined with a regression model in which density is expressed as a function of linear combinations of time and distance (Table 1, equation 1); the rate of expansion equals the quotient of regression coefficients of the variables time and distance (Table 1, equation 2) of this regression model. The rate of expansion of the external population is thus defined as the rate in which the 2-dimensional function that indicates population density with respect to distance is radially moving away from the Core Area in time.

We established the population density in individual time and distance (from the Core Area) belts (hereafter, time–distance belts) on the basis of the frequency distribution of bear locations, which we adjusted using data from the external bear population size model for the years included in the research and the spatially explicit model of bear habitat using the following procedures.

We separated all locations into 8 classes (0–10, 10–20, . . . , 60–70, >70 km) by distance from the Core Area and 4 intervals (1945–1966, 1967–1976, 1977–1986, 1987–1995) by time of occurrence. The frequency of locations was counted for each of the 32 classes thus created. The 1st time interval is longer, because the frequency of locations in it would otherwise have been so small that random events and potential errors in data could have had a significant impact on results. The number of recorded locations increased faster in the observed period than the size of the external population (data from Jerina [2002] and Jerina et al. [2003]). To correct for this bias in sampling effort, we calculated time-specific correction constants for all 4 time intervals and used them to multiply the location frequencies in all 32 time–distance belts. Correction constants are quotients between the average size of the external population and the frequency of all locations in an interval. With this procedure, we translated the frequencies into average sizes of the external population in all time–distance belts.

To calculate the rate of expansion, we needed data on population density. Size could have been translated to density in 2 ways: by dividing the number of animals by the surface of the given time–distance belt, and by dividing the number by the surface of land cover appropriate for bears within the given time–distance belt. Because the belts differ in terms of the proportion of bear habitat they contain, the 1st option would provide a poorer estimate of density, which would have been underestimated in belts with few appropriate habitats and vice versa. This is why we used the 2nd option. In transforming population size to density, we used data from the spatially explicit bear habitat model for Slovenia, taking into consideration the “maximum potential habitat.” Using binary values (habitat or nonhabitat), this model provides a maximum area that bears could potentially colonize in Slovenia. For belts that reach beyond Slovenia, we calculated density by assuming that the part of the belt that lies outside the country contains the same proportion of bear habitat as the part of the belt within the country. The area of research was determined from the 100% minimum convex polygon (White and Garrott 1990) adjusted to all bear locations by the use of Biotas 1.03 software (www.ecostats.com). Population densities in the time–distance belts are presented in Fig. 4 (all locations). We also used this procedure to calculate the density of females (Fig. 4, females).

For the probability of comparability, we relativized densities for both sex categories (all locations, females).
The generalized Bertalanffy function, also known as Chapman–Richards function (Richards 1959), describes sigmoid growth of the dependent variable (Table 1, equation 5). In theory, this function seems the most appropriate: on the one side it is limited by 0 (as the distance from the center increases, population density inevitably drops to 0 at a certain point), and on the other it is limited toward an arbitrary positive value (when colonization of a space ends, density stabilizes). We modified the Bertalanffy function to create a 2-parameter inverted sigmoid function (Table 1, equation 6), which we used in the analysis.

**RESULTS**

As predicted by hypotheses 1 and 2, the proportion of locations composed of females decreased with distance from the Core Area and increased with time. In the belt nearest to the Core Area (0–10 km), the proportion of locations comprised of females was 27% on average in the research period, but it was only 5% in the farthest belt (>70 km; Fig. 3). At the beginning of the research period (from 1945 through 1953), the proportion of locations composed of females was 8% on average, whereas it was 25% at the end of the research period (1994, 1995; Fig. 3). The 2 logistic models that include only 1 independent variable each (distance from the Core Area or time) predicted that the proportion of females decreased with distance from the Core Area from 30% (on the edge of the Core Area) to 1% (at a distance of 98.9 km) and in the research period it increased from 6% (in 1945) to 20% (in 1995; Fig. 3). The likelihood that a randomly observed bear is a female depends significantly on both independent variables regardless of whether they are included in the regression model individually or both at the same time (Table 2). When both variables are included in the model, the impact of each of them on the dependent variable is slightly lower than in the bivariate models, which is probably due to the correlation between independent variables. However, the impact of every independent variable is statistically significant in all models (maximum $P = 0.038$; Table 2).

Even though the proportion of females drops rapidly as the distance from the Core Area increases, some were occasionally observed far from the Core Area throughout the research period (Fig. 2). For example, a female was registered more than 65 km from the Core Area in 1953 and 1954. After 1960, 1 (or >1) female with cubs, which was shot 2 years later, was spotted in northwestern Slovenia 80 km from the Core Area, and other individual females were registered far from the Core Area in subsequent years.

The relative density of the external bear population increased steeply in the observed period and decreased with distance from the Core Area (Fig. 4). In the nearest belt around the Core Area, it was on average 6.4 times higher than in the outermost belt; in the final period analyzed (1986–1995) it was 5.1 times greater on average than in the 1st period (1945–1966). In the 1st period, the bear population density outside the Core Area was relatively low in all belts and individual animals were widely dispersed in a large part of the study area (Figs. 2 and 4). The density of the external population initially started increasing more rapidly close to the boundary of the Core Area, whereupon it started rising in progressively distant belts. The spatial expansion of males and females did not proceed equally. Females started to expand later and their density dropped sharply as the distance from the Core Area increased; males spread sooner, further, and were present in small numbers in...
TABLE 2.—Logistic regression models of the proportion of females relative to time and distance from the Core Area for the external brown bear (Ursus arctos) population in Slovenia in 1945–1995. In all 3 models the dependent variable is binary (females or other) and the independent variables are numeric (time or distance from the Core Area). The predicted values of the 1st and 2nd models are shown in Fig. 3.

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimate</th>
<th>SE</th>
<th>Odds ratio (unit change)</th>
<th>Odds ratio (range)</th>
<th>P</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>$-3.85 \times 10^{-2}$</td>
<td>$5.53 \times 10^{-3}$</td>
<td>0.962</td>
<td>0.021</td>
<td>&lt; 0.001</td>
<td>48.6</td>
</tr>
<tr>
<td>Constant</td>
<td>$-8.36 \times 10^{-1}$</td>
<td>$1.21 \times 10^{-1}$</td>
<td>0.433</td>
<td></td>
<td>&lt; 0.001</td>
<td>48.0</td>
</tr>
<tr>
<td>Year</td>
<td>$2.92 \times 10^{-2}$</td>
<td>$8.55 \times 10^{-3}$</td>
<td>1.030</td>
<td>4.179</td>
<td>&lt; 0.001</td>
<td>11.7</td>
</tr>
<tr>
<td>Constant</td>
<td>$-4.14$</td>
<td>$7.53 \times 10^{-1}$</td>
<td>0.016</td>
<td></td>
<td>&lt; 0.001</td>
<td>30.2</td>
</tr>
<tr>
<td>Distance</td>
<td>$-3.01 \times 10^{-2}$</td>
<td>$5.72 \times 10^{-3}$</td>
<td>0.970</td>
<td>0.049</td>
<td>&lt; 0.001</td>
<td>27.7</td>
</tr>
<tr>
<td>Year</td>
<td>$1.80 \times 10^{-2}$</td>
<td>$8.66 \times 10^{-3}$</td>
<td>1.018</td>
<td>2.410</td>
<td>0.038</td>
<td>4.3</td>
</tr>
<tr>
<td>Constant</td>
<td>$-2.52$</td>
<td>$7.41 \times 10^{-1}$</td>
<td>0.080</td>
<td></td>
<td>&lt; 0.001</td>
<td>11.6</td>
</tr>
</tbody>
</table>

The rate of the spatial expansion of the external population was assessed with 3 regression models in which population densities were expressed as a function of linear combinations of time and distance from the Core Area (Table 1). The linear model explained 72% of the total variation of bear population densities, the modified Bertalanffy function explained 92%, and the exponential model, which fits the data best of all 3, explained 95% (Table 3). All 3 estimates of the rate are similar and equal 1.6 km/year for the linear model, 1.9 km/year for the Bertalanffy model, and 1.7 km/year for the exponential model.

**DISCUSSION**

Our study is based on data on bear harvest or recovery and other reliable signs of presence of bears. In Slovenia, it is mandatory to report every harvested or found-dead animal of large game species. Data on bear presence were not systematically collected in the field, but this charismatic species has always triggered interest from various groups of people (Korenjak and Adamič 2000), especially hunters, who consider the bear as the most prestigious game. In addition, the hunters’ association was tasked with the preparation of management proposals, which included analysis of the status of the bear population. Sightings have therefore been regularly reported, especially in the study area, where bears were rare. The area also is divided into many (176) hunting clubs and is densely populated (64 inhabitants/km²), making the likelihood rather small that the presence of bears would go unreported.

For an analysis of population expansion, the sampling effort (the density of sampled locations/bear population density) should be constant in space and time. Because this condition was not fulfilled we converted the location frequencies into average population sizes in time–distance belts. Sampling effort also may vary due to differences in bear population densities, people’s attitude toward bears, and motivation in the reporting of observations (e.g., Mattson 1997; Solberg et al. 2006). For example, a study in Sweden showed that the public was more likely to report bears where there were more people and where bears were less common (Solberg et al. 2006). This potential source of error was probably insignificant in our study, because the densities of hunters and inhabitants are high. Furthermore, because time–distance intervals cover large, internally heterogeneous areas and long periods, nonsystematic differences in sampling error are balanced in averages. The results also could be affected by systematic spatial differences in sampling error. If they exist, one would expect that they would be dependent on the density of bears. However, this would primarily affect the shape of the regression function that describes the relative density of bears in relation to distance from the Core Area, not the estimated rate of expansion. Nevertheless, this potential source of error cannot be entirely ignored. The estimated relative population densities should thus be viewed as indices rather than actual values.

Although the proportion of females in our data is probably underestimated, this does not reduce the usefulness of the data because the study examines relative values. The underestimation also should be constant in space and time. Because there are no data on the actual proportions of females, this premise could not be verified directly, but several indices suggest that it is correct. The slopes of linear functions depicting the proportion of females were not different between data on bear harvest and recovery and other data, either in time ($P = 0.23$) or in space ($P = 0.35$). Thus, data from 2 sampling methods yield the same patterns. Furthermore, the proportions of females among harvested or recovered bears (16.3%) and among other data (16.7%) were not different ($P = 0.98$). Thus, possible temporal–spatial variation of the relative frequency of both data types could not have had a significant impact on the results. Furthermore, the proportion of females among harvested or recovered bears in the Core Area was substantially (on average 73%) larger ($P < 0.001$) than in the external population, yet the difference between the proportions of females in these 2 areas decreased over time (Jerina 2002). Finally, the proportion of females increased more than 3-fold during the study period and was 4 times greater near the Core Area than in the parts of the study area farthest from the Core Area. We believe the probability that these results are an
artifact of sampling error is negligible, and therefore consider our data appropriate for examination of the research objectives.

Our results strongly support our hypotheses, which predict that sex-biased dispersal causes temporal and spatial variations in the sex structure of peripheral parts of the population. Studies of ungulates and primates (but not bears) have reported other factors that can affect the sex structure of populations, such as sex-specific habitat selection (review in Ruckstuhl and Neuhaus 2002), or variation in maternal condition that causes differences in the sex ratio of their offspring (Clutton-Brock 1985; Kohlmann 1999; Mysterud et al. 2000; Wauters et al. 1995). The changes in the proportions of females observed in our study are too large to be explained by any of the alternative hypotheses. Moreover, they occurred across great distances simultaneously in time and space. The increase in proportion of males (especially of subadults, which are the most active dispersers) from the central parts of the populations toward the edges also has been found in Nordic bear populations (Kojola et al. 2003; Swenson et al. 1998). In addition, our study has shown that the sex structure in the spatially expanding population also changes over time due to sex-biased dispersal.

Even though the proportion of females decreased quickly with distance from the Core Area, some females were recorded far from the Core Area throughout the study period. This supports the hypothesis of Swenson et al. (1998), which states that in populations with presaturation densities females do exhibit long-distance dispersal. It should also be stressed that bears were close to extinction in Slovenia at the beginning of the 20th century, when only around 30–40 animals survived in the south of the country (Simonič 1992). Females far from the Core Area therefore cannot be a remnant of a past population. Rather, these individuals dispersed from or from near the Core Area. Considering our results and past descriptions of the bear population (Simonič 1992; Švigelj 1961), we estimate that some dispersed as far as 60 km. Similar maximum dispersal distances were estimated in telemetry studies in Scandinavia (Støen et al. 2006). Examination of our data indicates that dispersal patterns of females seem to occur at the same spatial scale in Slovenia as in Nordic countries (see Kojola et al. 2003; Swenson et al. 1998). This is noteworthy, because Nordic bears use home ranges several times larger than those of Slovenian bears (Dahle and Swenson 2003; Kaczensky 2000b).

Unlike most other studies on bear dispersal (e.g., McLellan and Hovey 2001; Proctor et al. 2004; Støen et al. 2006), our study shows how far females can disperse into an unpopulated area or areas with low population densities. This information is important because it enables predictions of the species’ capability to survive in a fragmented environment and its ability to form metapopulations (Lidicker and Koenig 1996). Moreover, long-distance dispersal of females into unpopulated areas can markedly increase the rate of population expansion (Goldwasser et al. 1994). The latter gives rise to the question of how far from the original source population emigrants can form new breeding subpopulations. The expansion of the external bear population was rather slow and gradual. All newly established subpopulations far from the Core Area eventually failed during our study, even though some included females with offspring. Only subpopulations close to the Core Area (<10 km) expanded and turned into stable population units (Fig. 4; see also Jerina et al. 2003). To answer the previously posed question, examination of our data suggests that long-distance dispersal by females does not significantly accelerate the spatial expansion of the population. However, it needs to be stressed that the external population was not protected by law for almost the entire study period, until 1992. The harvest rate was very high, which probably had a profound impact on the population’s expansion.
Generalized pictures of population expansion fronts, similar to the one we have shown for brown bears in Slovenia (Fig. 4), have been described for several other species. In American mink (Neovison vison—Usher 1986), Eurasian beavers (Castor fiber—Hartman 1995), and raccoon dogs (Nyctereutes procyonoides—Helle and Kauhala 1991), for example, the expansion front is flat due to long-distance dispersal. In contrast, the population density decreases over short distances for sea otters (Enhydra lutris—Lubina and Levin 1988) and nutria (Myocastor coypus—Usher 1986) due to their shorter dispersal distances. Effects of dispersal on the spatial structure of populations are probably quite common. Dispersal characteristics can differ within and among species due to factors such as population density, body mass, feeding strategy, taxonomic group, social organization (Sinclair 1992; Støen at al. 2006; Sutherland et al. 2000; Travis et al. 1999; Trewella et al. 1988), and even kin-related social structure (Støen at al. 2005). Differences in the structure of peripheral parts of populations could partially be a consequence of inter- and intraspecific variation in dispersal.

The approach we used to calculate the rate of spatial expansion of the population is analytically more demanding than the traditional one in which the presence/absence of a species or another threshold value of population density is measured in space and time (e.g., Eraud et al. 2007; Hill et al. 2001). Yet it has an important advantage because it does not require an arbitrary determination of threshold density values, and it responds to the variation in all values of density, not just threshold values. Therefore, the results are probably more robust.

In establishing the rate of expansion, we assumed that it occurred in an even, radial fashion from the border of the Core Area, and that the rate was constant through time. However, a visual comparison of the border of the Core Area, the current range of the population, and the population’s spatially explicit habitat model (Jerina et al. 2003; Kobler and Adamicˇ 2000) indicates that expansion in proceeded faster in better habitats. A similar conclusion derives from a model of gray squirrel habitat model (Jerina et al. 2003; Kobler and Adamicˇ 2000) and even kin-related social structure (Støen at al. 2005). The rate of spatial expansion of the population probably also depends on the population growth rate. All demographically increasing bear populations in the Nordic countries, the Carpathian Mountains, and Ukraine are spatially expanding (Pulliainen 1983; Swenson et al. 1998). In contrast, no similar spatial expansion was reported for 3 stable or declining populations in central Italy and Spain (reviewed in Swenson et al. 1998). The net average (geometric mean) annual growth rate of the bear population in Slovenia was 1.7% in the study period. Given a higher growth rate, the population would probably provide an additional boost to political decisions to significantly increase hunting in the past years. The increased harvest has brought the expansion of the external bear population to a complete stop (Filacorda et al. 2004; Marenˇce et al. 2007).

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