

## ASSESSING THE RISK OF EXTINCTION FOR THE BROWN BEAR (*URSUS ARCTOS*) IN THE CORDILLERA CANTABRICA, SPAIN

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**Abstract.** The status of the brown bear (*Ursus arctos*) in Spain has suffered a dramatic decline during the last centuries, both in area and numbers. Current relict populations are suspected to be under immediate risk of extinction. The aim of our model is to attain an understanding of the main processes and mechanisms determining population dynamics in the Cordillera Cantabrica. We compile the knowledge available about brown bears in the Cordillera Cantabrica, northern Spain, and perform a population viability analysis (PVA) to diagnose the current state of the population and to support current management.

The specially constructed simulation model, based on long-term field investigations on the western brown bear population in the Cordillera Cantabrica, includes detailed life history data and information on environmental variations in food abundance. The method of individual-based modeling is employed to simulate the fate of individual bears. Reproduction, family breakup, and mortalities are modeled in annual time steps under the influence of environmental variations in food abundance, mortality rates, and reproductive parameters. In parallel, we develop an analytical model that describes the mean behavior of the population and that enables us to perform a detailed sensitivity analysis.

We determine current population parameters by iterating the model with plausible values and compare simulation results with the 1982–1995 time pattern of observed number of females with cubs of the year. Our results indicate that the population suffered a mean annual decrease of ~4–5% during the study period, 1982–1995. This decrease could be explained by a coincidence of high poaching pressure with a series of climatically unfavorable years during the period 1982–1988. Thereafter, population size probably stabilized. We estimate that the population currently consists of 25 or 26 independent females and a total of 50–60 individuals. However, our viability analysis shows that the population does not satisfy the criterion of a *minimum viable population* if mortalities remain at the level of the last few years of 1988–1995. The “salvation” of at least one independent female every three years is required.

The population retains relatively high reproductive parameters, indicating good nutritive conditions of the habitat, but mortality rates are higher than those known in other brown bear populations. The most sensitive parameters, adult and subadult mortality of females, form the principal management target. Our model shows that the series of females with cubs contains valuable information on the state of the population. We recommend monitoring of females with cubs as the most important management action, both for collecting data and for safeguarding the most sensitive part of the population.

**Key words:** brown bear; endangered species; extinction; individual-based stochastic simulation model; population dynamics; *Ursus arctos*; viability analysis.

### INTRODUCTION

The plight of the brown bear (*Ursus arctos*) in Spain has received much attention and generated much debate in recent years (Council of Europe 1989, Clevenger and Purroy 1991, Naves and Palomero 1993). The surviving brown bears in Spain are relics from a distribution that once covered the whole Iberian Peninsula (Nores 1988, Alonso and Toldrá 1993, Nores and Naves 1993). The remaining bears in the Cordillera Cantabrica are suspected to be at risk of extinction (Servheen

1990), and extinction appears imminent in the Pyreneas (Servheen 1990, Caussimont et al. 1993). In the Cordillera Cantabrica, the brown bear area has decreased considerably, from ~9000 km<sup>2</sup> at the turn of the century to 5000 km<sup>2</sup> at present (Naves and Nores 1997). In Asturias, bear numbers have declined from a possible (>)125 bears at the turn of the century (Nores 1993) to a total of 50–65 (Palomero et al. 1993). At present, these remaining brown bears are located in two small, apparently isolated populations, which makes them more susceptible to random demographic events and environmental variability.

The brown bear has been protected in Spain since 1973 and is listed in the National List of Threatened

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Species as being in serious danger of extinction. Despite the initiation of four Regional Recovery Plans (Naves and Palomero 1993) in the early 1990s, and considerable conservation efforts (establishing reserves, conducting long-term field research, mapping and monitoring bear distribution, habitat analysis, etc.), the situation of the brown bear is still critical in the Cordillera Cantabrica (Naves 1996).

Although there has been a considerable number of studies, both long-term field studies and theoretical models, including population viability analysis (e.g., Craighead et al. 1974, Shaffer 1983, Knight and Eberhardt 1985, Suchy et al. 1985, Eberhardt 1990, Dennis et al. 1991, Mattson and Reid 1991, U.S. Fish and Wildlife Service 1993, Eberhardt et al. 1994, Foley 1994, Boyce 1995, Doak 1995, Knight et al. 1995, Primm 1996), present knowledge on population dynamics and conservation of bears is still deficient (Harting et al. 1994, Boyce 1995) for several reasons. Firstly, life-spans of brown bears are long (up to two or three decades), whereas databases for assessing demographic data and population trends seldom exceed a decade. Secondly, low densities, secretive behavior, and high mobility make wild bears especially difficult to observe and to census. Thirdly, the high impact of environmental and demographic stochasticity and the susceptibility to random events become important if population numbers are low and make serious predictions extremely difficult.

However, the immediate threat to the Cantabrian bears requires courageous and active management that should be based on an understanding of the processes that determine the population dynamics. Decisions will be made, however, and it is better to found them on a prognosis based on limited current knowledge rather than to decide arbitrarily "out of the pocket" (C. Wisel, *personal communication*). In this paper, we compile the knowledge available about the brown bears in the Cordillera Cantabrica and perform a population viability analysis (PVA) by means of an individual-based stochastic population model to diagnosticate the current state of the population and to support current management.

#### *Population viability analysis (PVA)*

In recent years, PVAs have been attempted for a large number of species such as tigers (*Panthera tigris*; Kenney et al. 1995), African elephants (*Loxodonta africana*; Armbruster and Lande 1993), and gorilla (*Gorilla gorilla beringei*; Akçakaya and Ginzburg 1991, Harcourt 1995a). Perhaps the most famous are those for the grizzly bear (*Ursus arctos horribilis*; Shaffer 1983, Suchy et al. 1985, Boyce 1995) and the Northern Spotted Owl (*Strix occidentalis caurina*; Lande 1988, McKelvey et al. 1993, Boyce 1994). Nevertheless, current discussions have partly become polemic (e.g., Akçakaya and Burgman 1995, Harcourt 1995b, Walsh 1995) or imbued with some feeling of frustration. For

example, the new Grizzly Bear Recovery Plan (U.S. Fish and Wildlife Service 1993) was challenged as inadequate (Harting et al. 1994), partly because of the failure to perform a PVA. Boyce (1995) stated that none of the numerous studies he had reviewed constitutes a sufficient PVA for grizzly bears, yet Taylor (1995) stated, "We are not ready to use PVAs, as they are currently done, to classify species [based on their risk of extinction]." Both polemics and frustration may be attributed to unrealistically high expectations of the predictive power of PVA in face of the inherent complexity and unpredictability of ecosystems, the sensitivity of model results (e.g., extinction times or *minimum viable populations*) to model parameters and the scarcity of data, especially for bears, in combination with inherent environmental and demographic stochasticity. However, an insufficient concentration on an understanding of the processes that shape the species' dynamics, the lack of careful sensitivity analysis, unclear objectives (Boyce 1995), or insufficient knowledge and standardization of methods (Akçakaya 1993) may also account for the present situation.

Models related with PVA can be divided into three groups (Boyce 1995). Firstly, stochastic time series models (e.g., Dennis et al. 1991, Foley 1994) try to estimate growth and extinction parameters by taking information about the underlying stochastic process exclusively from the time series of population estimates. These models ignore most information on life history attributes, social behavior, and habitat. Secondly, structured population models often incorporate detailed information on life history traits and stochasticity of the basic processes that determine population dynamics. Models of this class include age-structured, nonstochastic iteration models that implicitly or explicitly use the Lotka equations (e.g., Sidorowicz and Gilbert 1981, Knight and Eberhardt 1985, Yodzis and Kolenosky 1986, Doak 1995), stochastic age-structured population models (e.g., Shaffer 1983, Suchy et al. 1985, Boyce 1995, Eberhardt 1995), and individual-based models (Knight and Eberhardt 1985, Kenney et al. 1995). Thirdly, spatially explicit population models (Akçakaya et al. 1995, Boyce 1995, Dunning et al. 1995) combine a population simulator with a landscape map that describes the spatial distribution of landscape features. The latter type of model considers both the species-habitat relationship and the arrangement of the habitat in space and time, and is especially promising because GIS data and advanced habitat analysis are becoming increasingly available.

However, with small populations in which chance events lead to a high degree of variability in possible outcomes, it is necessary to build stochastic models (Starfield and Bleloch 1991, Burgman et al. 1993, Kenney et al. 1995). Several general stochastic population models, like Vortex (Lacy 1993), RAMAS/stage (Ferson 1990), RAMAS/GIS (Akçakaya 1993), and ALEX (Possingham and Davies 1995), have been used in pop-

ulation viability analysis (e.g., Ginzburg et al. 1990, Boyce 1995, Maguire et al. 1995). These models are general and applicable for individual species. However, when detailed life history data are available and the social or territorial behavior of the species probably affects population dynamics, it may be more productive to create models especially for that particular species (Kenney et al. 1995), incorporating the available knowledge in an adequate way. Another problematic point, the question of how consistent predictions of population persistence are when using different demographically explicit PVA programs, was recently raised by Mills et al. (1996). They performed a PVA for grizzly bears with four frequently used population viability analysis programs based on a single data set. The results of the study were disillusioning. The parameterizing of the models from the given data set on its own lead to an enormous difference of 3% in the intrinsic growth rate. After adjusting these differences, density dependence caused substantial differences in predictions among programs.

In this paper, however, we advocate specially constructed, stochastic, individual-based models (DeAngelis and Gross 1992, Judson 1994, Uchmanski and Grimm 1996). First, they allow the efficient and lucid integration of most life history information into the model, and they consider important processes like demographic stochasticity in a natural way (because the unit of the model, the individual, is also the biological unit). Second, they can be easily extended toward a powerful, spatially explicit population model (T. Wiegang, *unpublished analysis*). For empiricists, individual-based models are intuitive in a way that matrices and differential equations are not (Judson 1994). However, perhaps the most serious problems of individual-based stochastic simulation models are (1) the lack of analytical lucidity in the face of almost infinite possibilities for modeling detailed behavioral aspects, and (2) problems in performing a complete and careful sensitivity analysis. To overcome these problems and to support the tractability of the simulation model, we have developed, in parallel, an analytical model that describes the mean behavior of the population and that enables us to perform a detailed sensitivity analysis.

#### *Site description and population*

The two brown bear populations studied are located in the Cordillera Cantabrica, northern Spain: a western population that occupies mostly the north-facing slopes of the Cordillera Cantabrica, and an eastern population occupying south-facing slopes (Fig. 1a). The shortest distance between the two areas is ~30 km, but the two populations are apparently isolated. Both populations occupy similar areas of ~2500 km<sup>2</sup> (Naves and Palomero 1993).

The mean altitude along the divide is 1200–1600 m. Average altitudes and gradients of north-facing and south-facing slopes are 700 m and 34% and 1300 m

and 21% slope, respectively. Proximity to the ocean results in high rainfall and humidity, especially on the north-facing slopes, where average annual rainfall ranges between 900 and 1900 mm, depending on the altitude, and temperatures are mild. The habitat occupied by the western population in the Cordillera Cantabrica is part of the Eurosiberian phytoclimatic region, but on its limits with the Mediterranean region. High elevations facilitate abundant snow during winter.

In general, cover is varied on the steep, north-facing slopes of the forest, with different oak (*Quercus robur*, *Q. petraea*, *Q. pyrenaica*, *Q. rotundifolia*), beech (*Fagus sylvatica*), and chestnut (*Castanea sativa*) species. Above 1700 m, climatic conditions prevent forest growth.

Human density in the range of the western bear populations is 12.1 inhabitants/km<sup>2</sup> (Reques 1993). The main economic activity is farming livestock, mostly cattle. Mining, tourism, and sports, including hunting, agriculture and timber harvesting, are more of local importance. Human activities have resulted in a conversion of former forest areas to grazing and brush (*Genista*, *Cytisus*, *Erica*, and *Calluna*). Total current forest covers 20–50% of the brown bear area.

In contrast to other brown bear populations, close interactions between bear and man have occurred over several thousand years in the Cordillera Cantabrica. As with brown bears in northern Sweden (Iregren 1988), the long-lasting persecution by man may have caused morphological, ethological, and ecological adaptations on an evolutionary scale (Naves 1996). Brown bears in northern Spain are smaller in size and less aggressive than their American co-species. The intense persecution by man may have forced relict populations to occupy habitats of inferior quality where only phenotypes of smaller size could survive. Alternatively, or in complement, this could be due to a selective process, because bigger and more aggressive individuals are more vulnerable to hunting (Mattson 1990, Naves 1996). The relations between humans and bears are intense and complex, and all mortalities are more or less influenced or caused by human activity (Elgmork 1987, Mattson et al. 1991, Naves 1996) because human presence accompanies the Cantabrian bears for their entire lives. For example, one adult male that was poached in 1981 had survived at least two former poaching attacks; a cartridge embedded in an upper facial bone and damage to the lower mandible were visible in his skull (Naves and Palomero 1993). Sightings of lame, wounded, and mutilated bears are not rare in the Cordillera Cantabrica, and a surprisingly high number of pathologies were found when living bears were compared with fossils (Ana Pinto, *personal communication*).

Brown bear habitat in the western Cantabrian population is limited (Fig. 1b). Similar to findings from studies with marked females (Pearson 1975, Mace and Waller 1997), analysis of the locations of females with cubs during the 1982–1995 period indicated that home

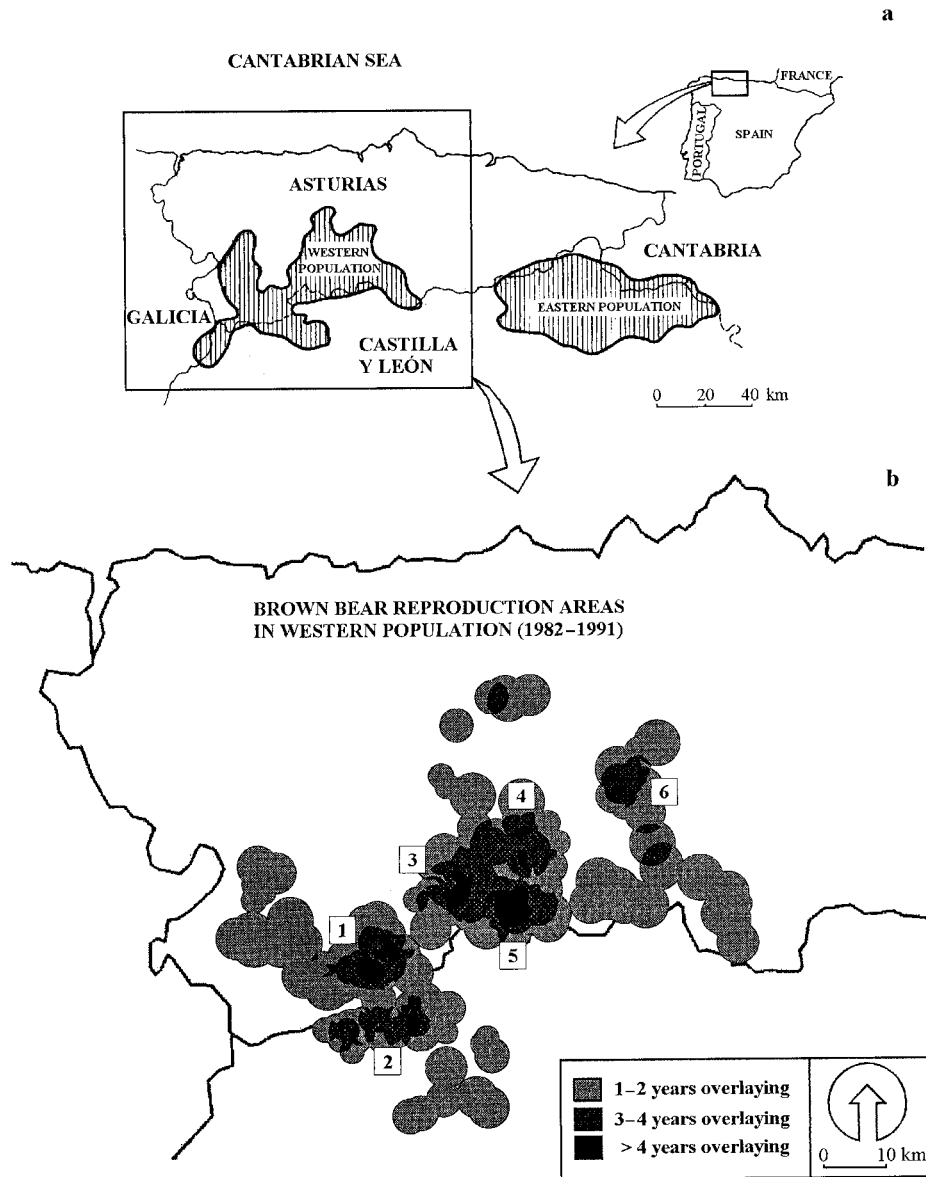


FIG. 1. (a) Area of distribution of the two brown bear populations (western and eastern) in the Cordillera Cantabrica, Spain. (b) Brown bear reproduction areas in the western population (1982-1991). By overlaying the reproduction areas from individual years, six principal reproduction nuclei (numbers 1-6) could be identified.

ranges of females with cubs rarely overlap. Analysis of the spatial distribution of females with cubs during the 1982-1995 period (J. Naves, *unpublished analysis*) suggested that space provided by the present habitat may support no more than 18 breeding females in the same year.

#### *Food availability*

Fecal analysis showed that plant foods dominate the diet of brown bears (Braña et al. 1993), providing >85% of the diet, by volume, in every season. Feeding of the Cantabrian brown bears falls into four seasonal periods, with sequential replacement of the major food

categories. In spring, the diet is mainly herbaceous; berries (*Vaccinium myrtillus*) and other pulpy fruits (*Rhamnus alpinus*) are added to the diet in summer; and in autumn and winter, the bears feed primarily on acorns (*Quercus* spp.), beechnut (*Fagus sylvatica*), and chestnut (*Castanea sativa*). The most frequently consumed animal prey are social hymenoptera and large herbivores, which were scavenged instead of preyed upon, in most cases. In the Cordillera Cantabrica, pregnant females hibernate during winter, living exclusively on body fat accumulated during the last year. Females with newborn cubs usually do not leave the den before April, as observed for other independent bears in the

Cordillera Cantabrica (Naves and Palomero 1993). Therefore, extensive consumption of dry fruits in autumn and winter is indispensable for the accumulation of reserves for the hibernation and posthibernation periods (Kistchinsky 1972, Elgmork et al. 1977). The abundance of selected parts of the diet, such as acorn, chestnut, and beechnut in the Cordillera Cantabrica, or fleshy fruits and pine seeds in the Yellowstone ecosystem, Wyoming, United States (Mattson and Reid 1991), is expected to be a key factor in determining reproductive success and cub survival (Rogers 1987, Servheen 1990). A correlation between food abundance and reproductive performance has been reported for grizzly bears (e.g., Bunnell and Tait 1981, Stringham 1986). Varying food abundance and long hibernation periods of pregnant females suggest similar correlations in the Cordillera Cantabrica.

#### THE MODEL

##### *Aim of the model and model strategy*

We present a simulation model, based on long-term field investigations of the western brown bear population in the Cordillera Cantabrica, Spain. The aim of the model is to obtain an understanding of the main processes and mechanisms that determine population dynamics over long temporal scales, to assess the status of the population, and to support management decisions. Detailed information about life history attributes, family structure, interannual environmental variations in food abundance, mortality rates, and reproductive parameters are included in an individual-based, stochastic model that simulates the population dynamics in annual time steps.

The main problem that we face when assessing status of the population, determining values of the model parameters, requires special treatment. In a first step, we create a general framework, the set of rules, that determines the processes to be included in the model. However, the rule-set does not fix the values of the model parameters. In a second step, we determine the values of model parameters that are directly accessible from data from the Cordillera Cantabrica, and we estimate plausible values for all other model parameters through comparisons with data, mainly from Yellowstone bear studies. Based on these estimates, we determine the values of unknown parameters indirectly, in a third step, by matching up the number of females with cubs of the year (COY index) obtained from model simulations with the 14-yr time pattern of the observed number of females with cubs of the years from the Cordillera Cantabrica. The model simulations with the best adjustment of the COY index facilitate a detailed reconstruction and analysis of the population size development during the 1982–1995 period.

To assess the viability of the population and to define management goals, it is necessary to project model parameters from the current status quo into the future.

We do this by simulating population dynamics using the parameters determined in step three, but additionally we “rescue” certain numbers of independent females per year. The resulting overall mortality rates, together with the parameters determined in step three, deliver a series of reference parameter sets that give plausible scenarios for possible future developments in mortality rates. These scenarios are linked through the management-accessible variable, “number of females rescued per year.”

Based on these scenarios, we perform an extensive sensitivity analysis and estimate extinction times, minimum viable population sizes (MVP), and other management-relevant variables to define realistic management goals.

##### *Model structure*

In this section, we give a brief overview of the processes that are included in the model. In the next section, we define in detail how these processes are regulated.

The model follows the fate of individual bears throughout life and simulates the life history events of birth, weaning, litter production, and death, with stochastic determination of these processes. The age-specific probabilities for first reproduction and mortality and the probabilities for litter size are subject to interannual variation due to environmental fluctuations. Density-dependent regulation is considered by limiting the number of females that can breed simultaneously.

Fig. 2 shows the life history traits of female bears included in the model. 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. The probability for first reproduction of young females depends on food availability and the age of the female. Because brown bear habitat in the western Cantabrican population is restricted, only a limited number of females can breed simultaneously. After independence of their first litter, production of subsequent litters depends on the time since family breakup. Survival probability of orphaned cubs is lower than that of cubs within a family group.

We model independent bears as individuals and consider dependent cubs together with their mother. Thus, the model structure requires the characterization of independent females through the variables age, number of female cubs, number of male cubs, age of cubs, and time since last family breakup (Table 1).

The fate of a given individual is determined by (1) the variables that characterize the state of the individual (Table 1), and (2) the rule set, which determines how these variables change in the course of time, with dependence on the states of other individuals and on external factors such as food production, poaching, or management actions.

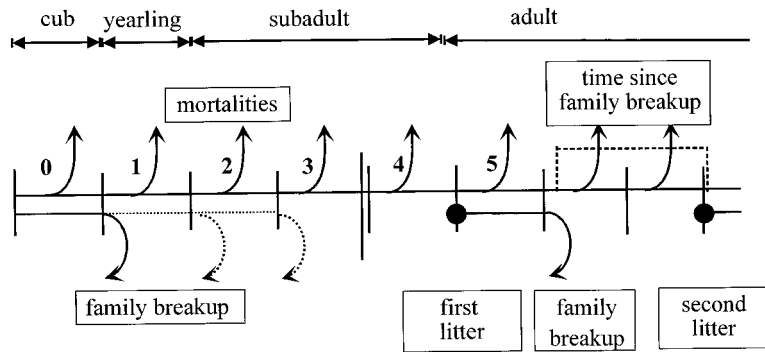


FIG. 2. Graph showing the life history traits of female bears considered in the model.

*The rule set*

The rules that follow determine, in detail, how certain variables change over the course of time. The rules provide a general framework for brown bear or grizzly bear population dynamics. Specific rules for a particular population can be made through a specification of the model parameters (Table 1). The rules are based on published and unpublished information on the population dynamics of the Cantabrian brown bears and on information about other brown bear and grizzly bear populations.

*Rule 1: Family structure.*—A family group stays together until the litter of age  $i$  becomes independent (probability  $i_i$ ), or until the entire litter dies.

*Rule 2: Reproduction.*—A female can only breed if not accompanied by a litter, if a “territory” is available (see rule 4), and if the population contains at least one adult male. 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 breakup. We assign the size  $j$  of a litter in accordance with probabilities ( $l_j$ ), and the sex of each cub

is determined randomly with an equal sex ratio. The probabilities  $f_i$  for first litter at age  $i$  and the probabilities  $l_j$  for a litter size  $j$  are modified by an environmental index IR, which describes food abundance (see rule 5).

*Rule 3: Survival.*—The annual survival of each individual is determined by choosing a random number from a uniform distribution [0, 1]. If the random number is below the probability of mortality at age  $i$  ( $m_i^f$  for females and  $m_i^m$  for males), then the individual dies. The mortality rates  $m_i^f$  and  $m_i^m$  at age  $i$  are modified by an environmental index IR (rule 5).

*Rule 4: Density-dependent regulation.*—Reproduction core areas are limited (Fig. 1b). Only a certain number of females ( $T_{max}$ ) can breed simultaneously. To determine which female can breed, we start with the oldest female and proceed with descending age until the maximal number of breeding females is reached. In this way, we consider that older females have an advantage over younger females.

*Rule 5: Environmental fluctuations.*—Food abundance from May (first appearance after hibernation) to

TABLE 1. Variables and parameters of the model for Cantabrian brown bears.

	Symbol	Range
A) Variables		
Age (yr)		0–26
Sex		male, female
Number of female cubs		0–4
Number of male cubs		0–4
Age of cubs (yr)		none, † 0, 1, 2, . . .
Time since last family breakup (yr)		none, † 0, 1, 2, . . .
B) Model parameters		
Probability of cubs becoming independent at age $i$	$i_i$	$i = 0, 1, 2, 3$
Probability of first litter at age $i$	$f_i$	$i = 4, 5, . . . , 9$
Probability of a litter $j$ years after family breakup	$h_j$	$j = 1, 2, . . . , 6$
Sex ratio, female : male	$s_f : s_m$	
Probability of a litter of $j$ cubs	$l_j$	$j = 1, 2, 3, 4$
Mortality rates at age $i$	$m_i^f, m_i^m$	$i = 0, . . . , 25$
Orphan’s mortality rate	$m_0^o$	
Maximal number of territories	$T_{max}$	
Environmental index	IR	–1 to 1
Environmental variation of mortality rates	$v_i$	$i = 0, . . . , 25$

† For males and young females that have not yet reproduced, “age of cubs” and “time since family breakup” are “none.”

December (beginning of hibernation) determines the nutritive state of the females and influences the probability of a first litter, litter size, and mortality. We employ an environmental index similar to an index used in Picton (1978) to correlate food abundance with precipitation. To keep our index simple and to avoid difficulties with adjustments for the different sources of food (e.g., beechnut, acorn, chestnut, or berries) without sufficient data available, we use only precipitation from May to December as a rough correlate that still keeps the essentials of the process. We use 1974–1995 rainfall data from the Cordillera Cantabrica to calculate the environmental index IR for a given year  $t$  as

$$\text{IR}(t) = c_t \left[ \bar{p} - \sum_{i=\text{May}}^{\text{Dec}} p(i, t) \right] \quad (1)$$

where  $\bar{p}$  is the 1974–1995 mean of the annual precipitation during the period of vegetation growth (May to December), the  $p(i, t)$  are the precipitation of month  $i$  and year  $t$ , and  $c_t$  is a constant that standardizes the mean variation for the period 1974–1995 as  $\text{SD}(\text{IR}) = 1$ .

We group years according to the index IR into good years ( $\text{IR} > 0$ ) and bad years ( $\text{IR} < 0$ ). Survival, the probability of first reproduction of young females in the next year, and the mean litter size in the next year, are below the mean rates in bad years when food is scarce, and above the mean rates in good years when food is abundant. We calculate the mortality rates in bad years ( $m_i^-$ ) as

$$m_i^- = m_i(1 + v_i) \quad (2)$$

and the mortality rates in good years ( $m_i^+$ ) as

$$m_i^+ = m_i(1 - v_i) \quad (3)$$

where  $v_i$  gives the environmental variation of the mortality rates at age  $i$ . We fix different sets of probabilities for a litter size of  $j$  cubs: (1) without environmental variation of litter size ( $l_j$ ), (2) for bad years ( $l_j^-$ ), and for good years ( $l_j^+$ ).

Calculation of the probabilities for the first litter are based on the following: (1) we assume for a “mean” female (disregarding individual differences) a minimal mass  $M_{\min}$  necessary for successful breeding and (2) we state that the mean mass  $M_m(i)$  of a female at age  $i$  may vary according to food conditions (index IR), with a factor  $v$ . The minimal mass at age  $i$  is  $(1 - v)M_m(i)$ ; the maximal mass is  $(1 + v)M_m(i)$ . Thus, the mass  $M(i, t)$  of females of age  $i$  at year  $t$  yields

$$M(i, t) = M_m(i)[1 + v\text{IR}(t)]. \quad (4)$$

Reproduction occurs only if the mass  $M(i, t)$  exceeds the minimal mass  $M_{\min}$ :

$$M(i, t) > M_{\min}. \quad (5)$$

Assuming that the index IR is equally distributed over

the interval  $(-1, 1)$ , the mean probability for first litter at age  $i$  yields

$$f_i = \frac{(1 + v)M_m(i) - M_{\min}}{2vM_m(i)}. \quad (6)$$

#### The simulation

In this section, we demonstrate how we transform the rule set into an individual-based simulation model. Before starting a simulation, we have to assign: (1) a parameter set; (2) an initial population with age, sex, number of male and female cubs, age of cubs, and time since last family breakup for each individual; and (3) a weather scenario that delivers the environmental index IR for each time step (year).

At the beginning of each time step (year)  $t$ , we initialize the parameters that depend on the environmental index IR. We choose, in accordance with last year's environmental index  $\text{IR}(t - 1)$ , the set of probabilities for litter size  $j$  (rule 5), we fix the mortality rates for year  $t$  (Eqs. 2 and 3; rule 5), and we determine the probabilities for first reproduction, dependent on the environmental index  $\text{IR}(t - 1)$  of the last year (Eqs. 4–6; rule 5).

Next we decide whether each female not accompanied by a litter reproduces or not (rules 2 and 4). We continue simulating the survivorship of each individual in accordance with rule 3. In the last step, we simulate the independence of cubs (rule 1) and update the variables age, age of cubs, number of female and male cubs, and time since family breakup for each surviving individual for the next year. The flow chart (Fig. 3) shows how and when a rule is applied.

As output variables, we record the number of independent females, the total population size, the simulated mortality rates per age class, and the number of females with cubs of the year (COY index). The cycle for one year is now complete, and we can proceed with simulating the cycle for the next year.

#### The analytical model

Central to an understanding of the dynamics of age-structured populations is the rate of increase  $\lambda$  that describes the “mean” behavior (growth rate) of the population. Even in cases in which environmental fluctuations and demographic stochasticity become important, the rate of increase remains a valuable tool, both for assessing functional relations between the parameters of the model and for performing a sensitivity analysis. We use an analytical method to calculate the rate of increase  $\lambda$  that considers all life history traits (Fig. 2) and parameters (Table 1) that are included in the individual-based simulation model, except for density-dependent regulation. The latter is unlikely to determine population dynamics in cases in which the population is decreasing ( $\lambda < 1$ ) or is only increasing slightly, or when population densities are far below the capacity of the habitat (Taylor 1994). The population

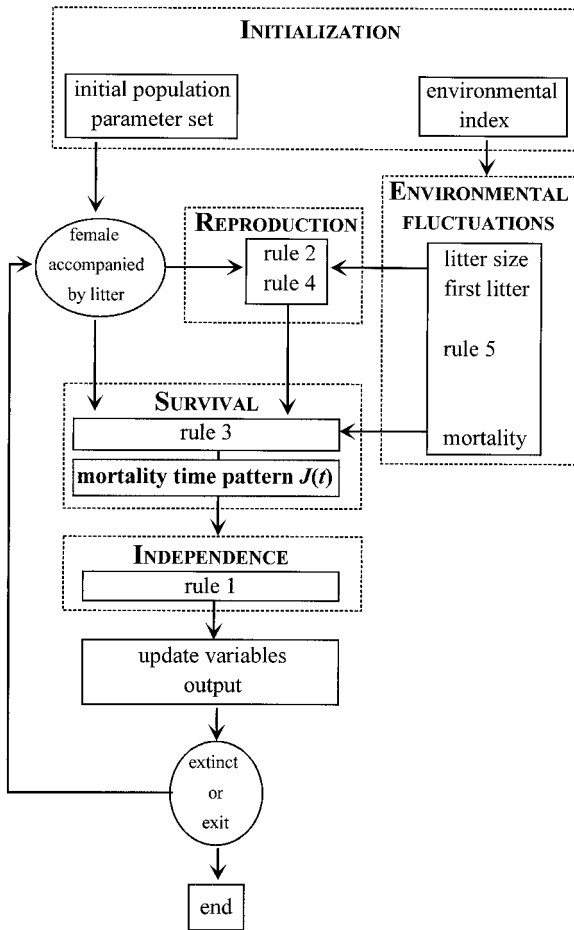


FIG. 3. Flow chart showing a time step iteration in the model.

in the Cordillera Cantabrica is probably decreasing, and the number of females with cubs has not exceeded 12 since 1982, whereas the capacity of the reproductive core areas is  $\sim 18$  (see rule 4).

We will fully exploit the analytical rate of increase  $\lambda_{th}$  that results from a given parameter set. We will use  $\lambda_{th}$  (1) to classify parameter sets during the adjustment of model parameters, (2) to perform an extensive sensitivity analysis with the analytical model, (3) to investigate minimum viable populations and the mean time to extinction, and (4) to classify plausible parameter scenarios. Additionally, we use the analytical model to calculate the initial state of the population.

We use the Lotka equation to calculate the rate of increase  $\lambda$ :

$$1 = \sum_{i=1}^{25} s_i y_i \frac{1}{\lambda^i} \quad (7)$$

where  $s_i$  is the survival rate of females up to age  $i$  and  $y_i$  is the fertility (number of female cubs) of a female at age  $i$ . The survival rates  $s_i$  are easily calculated from the mortality rates. The calculation of the fertility of a female at age  $i$  that considers reproduction in depen-

dence on the time since family breakup (either independence of litter, or mortality of the entire litter) requires a considerable analytical effort. In short, we sum up all possible combinations of litters that conform to our rule set. A detailed description of the analytical model is given in Appendix A.

The theoretical rate of increase  $\lambda_{th}$  calculated with Eq. 7 generally gave a good approximation of the rate of increase  $\lambda_{sim}$  that resulted from simulating population dynamics with the same parameter set, in the sense that it accords with the mean value of  $\lambda_{sim}$  of many simulations. However, due to environmental and demographic stochasticity, the dynamics of a single-model simulation may differ considerably from that predicted through the simple model of exponential growth with  $\lambda_{th}$ . In the section *Sensitivity analysis*, we compare simulated rates of increase with the corresponding rates of increase  $\lambda_{th}$  calculated with Eq. 7.

#### DETERMINATION OF MODEL PARAMETERS

The main problem when performing a population viability analysis of the brown bear population in the Cordillera Cantabrica (and for all endangered populations) is determining the model's parameters. The lack and inconsistency of data require specific, non-standard methods to exploit available knowledge in the most efficient and thorough way. In the next section, we tackle a first approximation of the model's parameters. We determine the values of model parameters that are directly accessible through data from the Cordillera Cantabrica, and we restrict the range of the probabilities of a first litter [ $f_i$ ] and the probabilities for litters  $j$  years after family breakup [ $h_j$ ] with empirical relations from the literature (Stringham 1990). Finally, we assess approximate values of the remaining model parameters through comparison with data from Yellowstone National Park, Wyoming, USA.

To determine the values of the uncertain parameters more precisely, we utilize additional information given through the observed 14-yr time series of females with cubs of the year (COY index). Basically, we perform a multiple-parameter fit by comparing the COY index obtained from model simulations with the 14-yr time pattern of real data from the Cordillera Cantabrica. We assign the parameter set that yields the smallest error as a reference parameter set.

#### First approximation of model parameters

*Family structure.*—Female brown bears in the western population normally wean their offspring as yearlings in May or early June (Palomero et al. 1993). Some family groups may stay together until the second year, but no reliable observations are known. Therefore, the probabilities for independence at the Cordillera Cantabrica are  $i_0 = 0$  and  $i_1 = 1$ .

*Reproduction.*—Mean litter size (in May) between 1982 and 1994 was 2.3 cubs, (two litters with one cub,

TABLE 2. Observed litter sizes in May and environmental index IR of the previous year between 1982 and 1994. The environmental index was constructed from rainfall data for 1975–1995.

A) Frequency distribution of litters					
Year of litter ( <i>t</i> )	Index IR of year ( <i>t</i> - 1)	Litter sizes (no. cubs)			
		1	2	3	4
1982	-0.44	0	1	0	0
1983	0.57	0	1	1	0
1984	-0.14	1	2	0	0
1985	0.61	0	1	0	0
1986	-0.73	0	2	0	0
1987	-0.31	0	3	0	0
1988	0.09	0	0	1	1
1989	-0.39	1	1	1	0
1990	-0.88	0	2	1	0
1991	0.17	0	0	1	0
1992†	0.08				
1993‡	1.00				
1994	0.53	0	1	1	0

B) Probability of different litter sizes					
Year quality	Mean litter size	Litter size probability, by no. cubs			
		1	2	3	4
Bad years	2.00	0.13	0.74	0.13	0.00
Good years	2.75	0.00	0.38	0.50	0.12
Mean	2.26	0.09	0.61	0.26	0.04
Mean‡	2.37	0.07	0.55	0.32	0.06

† Date of first observation of litter was later than May.

‡ Mean, assuming an equal distribution of good and bad years.

14 litters with two cubs, six litters with three cubs, and one litter with four cubs; Table 2A).

No data are available on the mean age of first litter in the Cordillera Cantabrica. However, data on 20 comparable brown bear populations given in Stringham (1990: Table 1) indicate significant linear correlations ( $y = 2.81 - 1.36x$ , and  $z = 1.82 - 0.77x$ ) between the logarithm of the mean litter size ( $x$ ) and the logarithm of the mean age at first litter ( $y$ ) and the logarithm of the litter interval ( $z$ ). A mean litter size of 2.3 yields a mean age of first litter of 5.3 yr and a litter interval of 3.3 yr. The earliest age of first litter is probably 4 yr for the Cantabrian brown bears.

In the Cordillera Cantabrica, reproductive cycles of 2 yr were observed (Palomero et al. 1993), but the majority are probably 3–5 yr. Reproductive cycles can be shorter in cases in which the entire litter dies. In the model, we do not use the litter interval as a parameter describing reproductive cycle, but rather we calculate the mean probability for reproduction  $h_j$ , depending on the time  $j$  since family breakup (rule 2).

*Survival.*—We only differentiate mortality rates for the following age classes: female and male cubs, females and males 1–4 yr old, adults 5–16 yr old, and old adults 17–24 yr old. The biological motivation for this classification is that: (1) mortality rates of cubs have been estimated for the Cordillera Cantabrica, and are important for the reproductive cycle because females that have suffered the death of the whole litter

TABLE 3. Survival to age 1 ( $S_1$ ), to age 5 ( $S_5$ ), to age 17 ( $S_{17}$ ), and to age 25 ( $S_{25}$ ) for female (f) and male (m) Yellowstone grizzly bears from different sources. Pooled mortality rates are given for three age classes:  $m_{1-4}$  for age class 1–4 yr;  $m_{5-16}$  for age class 5–16 yr; and  $m_{17-24}$  for age class 17–24 yr, calculated with  $S_i$ .

Variable	Craighead et al. (1974)		Knight and Eberhardt (1985)		U.S. Fish and Wildlife Service (1993)	
	f	m	f	m	f	m
A) Survival						
$S_1$	0.630	0.744	0.890	...	0.890	0.880
$S_5$	0.304	0.185	0.254	...	0.486	0.325
$S_{17}$	0.089	0.052	0.074	...	0.188	0.087
$S_{25}$	0.004	0.003	0.012	...	0.047†	0.049†
B) Mortality						
$m_{1-4}$	0.167	0.294	0.269	...	0.140	0.220
$m_{5-16}$		0.099		0.098		0.087
$m_{17-24}$		0.319		0.200		0.138†

Note: Original mortality data for males and females were pooled for  $m_{5-16}$  and  $m_{17-24}$  to facilitate a direct comparison with the mortality rates used in the model.

† The last age class in the U.S. Fish and Wildlife Service (1993) study was 18–23 yr instead of 18–25 yr.

in the first half of the year can breed 1 yr earlier than usual; (2) subadult females and males show different mortality patterns (see Table 3); and (3) mortality rates of young adults are lower than for non-adults and senescent adults (see Table 3). Any further differentiation would give the model a level of detail that cannot be supported by the data.

Mortality of cubs from 1982 to 1991 was analyzed for 150 cubs. To avoid problems with the first observation of family groups, the month of May (usually the first appearance of family groups with cubs) was chosen as a reference point. The staggered methodology of Pollock (Pollock et al. 1989) was used to include later appearances (J. Naves, *unpublished analysis*). The definition of the survival function required a clear definition of time and origin and a staggered entry of individuals into the calculation, depending on the time of initial location, together with consideration of previously applicable mortality rates (Pollock et al. 1989). The analysis yields a mean cub mortality rate of  $m_0 = 0.4$  from May of the first year to May of the next year. The observed mean cub mortality rate is high, but within the range observed for other brown bear populations. For example, Bunnell and Tait (1985) reported cub mortality rates between 0.3 and 0.4, and McLellan (1994: Table 4) listed observed cub mortality rates of 0.15 to 0.44 for 10 different grizzly bear populations in North America. Knowledge of the survival functions for other age classes is scarce. Table 3 summarizes mortality data for the Yellowstone grizzly bear population.

*Density-dependent regulation.*—Brown bear habitat in the western Cantabrian population is limited (Fig. 1b), and may support no more than 18 breeding females in the same year (J. Naves, *unpublished analysis*).

TABLE 4. Number of known and probable mortalities of independent individual bears due to poaching. The mortality numbers in parentheses give the number of dead females; cases of uncertain sex are considered as 0.5. Data are from our own mortality records; no official records were performed.

Year	Index IR of year $t$	Known mortal- ities	Probable mortal- ities	Total mortalities
1980†	-0.14	2 (1.5)	1 (1.0)	3 (2.5)
1981†	-0.44	2 (1.5)	2 (1.0)	4 (2.5)
1982	0.57	1 (0.0)	0 (0.0)	1 (0.0)
1983	-0.14	5 (3.0)	0 (0.0)	5 (3.0)
1984	0.61	0 (0.0)	0 (0.0)	0 (0.0)
1985	-0.73	1 (0.5)	0 (0.0)	1 (0.5)
1986	-0.31	6 (3.5)	4 (2.0)	10 (5.5)
1987	0.09	0 (0.0)	4 (2.0)	4 (2.0)
1988	-0.39	0 (0.0)	0 (0.0)	0 (0.0)
1989	-0.88	1 (1.0)	1 (0.5)	2 (1.5)
1990	0.17	2 (1.0)	1 (0.5)	3 (1.5)
1991	0.08	0 (0.0)	0 (0.0)	0 (0.0)
1992	1.00	0 (0.0)	0 (0.0)	0 (0.0)
1993	0.53	0 (0.0)	0 (0.0)	0 (0.0)
1994	-0.18	0 (0.0)	3 (1.5)	3 (1.5)
1995‡	0.72	0 (0.0)	0 (0.0)	0 (0.0)
Total, 1982–1995		16 (9)	13 (6.5)	29 (15.5)

† No data on females with cubs were available in 1980 and 1981, so the data in this table for these two years were not used in the analysis of the mortality time pattern (see The mortality time pattern  $J(t)$ ).

‡ No data.

Thus, we set  $T_{\max} = 18$ , which is the sum of the largest number of females with cubs observed in any year in each area (see Fig. 1b).

*Environmental fluctuations.*—A significant difference between cub mortality rates in bad years ( $IR < 1$ ) and cub mortality rates in good years ( $IR > 1$ ) was detected in the Cordillera Cantabrica (log rank test,  $P < 0.01$ ). The minimal cub mortality rate was 0.25 in the above-mean rainfall years, and 0.55 in years with below-mean rainfall. Thus, the environmental variation  $v_0$  of the cub mortality rate yields  $v_0 = 0.38$ .

Food shortage influences the survival of all age classes directly (through physical conditions) or indirectly (lack of food stimulates unusual movements, behavior, or diseases, etc.; Picton et al. 1986, Rogers 1993). Less experienced subadults that are in search of a home range move larger distances than do adults, and may be especially vulnerable to poaching during bad years. Records of mortalities in the Cordillera Cantabrica showed that 5 out of 6 subadult mortalities and 8 out of 12 adult mortalities occurred during bad years ( $IR < 0$ ). This situation yields environmental variations of the mortality rates of about  $v_{1-4} = 0.66$  for subadults and  $v_{5-25} = 0.33$  for adults. Selected data from the mortality records shown in Table 4 show 3.5 mortalities for females within the eight good years ( $IR > 0$ ) and 17 mortalities within the eight bad years ( $IR < 0$ ), indicating an overall environmental variation of the mortality rate for independent females of about  $v_{2-25} = 0.66$ . These differences in the recorded total mortalities

(Table 4) were significantly different between bad years ( $IR < 0$ ) and good years ( $IR > 0$ ) ( $U$  Mann-Whitney,  $0.05 < P < 0.1$ ). However, the basis for the estimates of  $v_i$  is weak; in the next section, therefore, we will test a variety of scenarios for the environmental variation  $v_i$  of the mortality rate.

Litter sizes observed in May of year  $t$  were significantly different between bad years ( $IR < 0$ ) and good years ( $IR > 0$ ) ( $U$  Mann-Whitney,  $P < 0.05$ ; Table 2A). In the model, we employ the probabilities of a litter of  $j$  cubs for below-mean rainfall years (Table 2B) if the environmental index IR of the last year was negative; otherwise, we use probabilities for above-mean rainfall years (Table 2B). If environmental variations are switched off, we use the resulting mean probabilities (Table 2B).

The mass of the bears varies seasonally, as losses in body mass during winter sleep and after emergence are rapidly replaced over the summer and fall months (McLellan 1994, Craighead et al. 1995). Most individuals attain their maximum annual mass shortly before denning (Kingsley et al. 1983, Blanchard 1987, Craighead et al. 1995). McLellan (1994), for example, reported that late fall mass of females was 1.28 times greater, on average, than early spring mass. Obviously, mass will be influenced by the quantity and quality of food resources available during summer and fall, and body mass predicts and strongly constrains reproductive performance and survivorship (Stringham 1990). In the model, we assume that food conditions influence the probability of a first litter, but not the probability of subsequent litters. Young females 4–7 yr old may not yet have reached their mature mass; thus, their reproductive success may depend critically on food abundance. Mature females, in contrast, have more experience and knowledge of alternative food sources, and thus may be able to smooth out the effect of food shortages.

To estimate the probabilities of a first litter at a certain age, we assume (1) that body mass varies with the environmental index IR (Eq. 4); and (2) that young females that have not yet reached their mature mass can only reproduce if their mass exceeds a certain threshold  $M_{\min}$  (Eq. 5). Using these assumptions, we can predict the mean probability  $f_i$  of the first litter at age  $i$  (Eq. 6), or, alternatively, we can use the probabilities  $f_i$  as a parameter to calculate the mean mass  $M_m(i)$  at age  $i$ . Because first reproduction is more intuitive and more widely used as a parameter, we use the probabilities for first litter as a parameter and calculate internally the mean mass  $M_m(i)$  and the threshold mass  $M_{\min}$ .

*The COY index.*—Because no telemetric studies were performed for the western population of the Cordillera Cantabrica, observations of family groups of females with cubs of the year (COY) were the principal source of demographic data. Annual litter sizes, cub mortalities, and COY indices were determined from these

TABLE 5. Number of females with cubs and number of observations.

Year	No. family groups	Total no. observations	No. valid observations per family group
1982	8–10	31	2–8
1983	8–11	34	2–7
1984	8–12	33	2–6
1985	no data	no data	no data
1986	6–7	55	4–18
1987	6–7	35	4–7
1988	3	26	3–14
1989†	4–6	24	2–13
1990	7	50	3–11
1991	6–7	30	2–6
1992	5–6	25	2–11
1993	4–5	19	2–9
1994‡	2	8	2–3
1995‡	6–8	31	3–6
Total	73–91	401	5.5–4.4

† One of the females with cubs was killed illegally, and the cubs were captured. In this year, the total observations were made with 3–5 family groups.

‡ No official census was performed. The given numbers of females with cubs are based on partial data (own observations and personal communications).

observations. Annual official censuses of females with cubs were performed between 1982 and 1993, with the exception of 1985, and were available from own data for 1994 and 1995. All official censuses were revised for this study. During this period, 401 valid observations of family groups were collected (Table 5). Since 1989, authors of observations were recorded: 24% of the observations between 1989 and 1995 were made by research teams, 30% by rangers, and 46% by local people. The distinction of family groups was based on characteristics of the family groups (number of cubs and morphologic characteristics), spatial distance between observations, the date of observations, and landscape features, such as large areas with human settlements or dams that have a barrier effect (Palomero et al. 1993). This method is similar to that used in Yellowstone National Park (Knight et al. 1995). Observations allowed the confident identification of 73 different females with cubs of the year and an identification of 18 probable females with cubs of the year. Family groups were considered as probable if (1) some valid observations in the same area could also have been other family groups; (2) in cases where only one single valid observation was made by a ranger or by local people; and (3) in cases of various nonvalid observations.

Because of the low numbers of family groups (2–12; Table 5) and a relatively high number of observations (with a mean of five observations per family group), the real number of females with cubs should be close to the observed number. For this reason, an adjustment of the number of females due to interannual changes in sightability or the use of Petersen estimates

was not necessary, as it was in Yellowstone (Boyce 1995, Eberhardt and Knight 1996). In comparison, 9–25 family groups were identified in Yellowstone during the 1976–1995 period (Boyce 1995: Fig. 1), with a mean of 1.8 observations per unmarked female (Craighead et al. 1995: Tables 19.3 and 19.4).

#### *Procedure for adjusting model parameters with the COY index*

In this section, we perform a multiple-parameter fit by comparing the COY index obtained from model simulations with the 14-yr time pattern of real data from the Cordillera Cantabrica. However, the procedure that allows for squeezing a maximum amount of information out of the COY index requires considerable methodological and computational effort.

*Justification of the approach.*—The number of females with cubs is related to the overall population size (Dennis et al. 1991, Foley 1994, Boyce 1995, Eberhardt and Knight 1996). Possible problems of “sightability” of family groups (Boyce 1995) are less serious in the Cordillera Cantabrica (see *First approximation of model parameter: the COY index*). Thus, we assume that the COY index closely approximates the “real” number of females with cubs of the year.

The idea behind the procedure of parameter adjustment is that a comparison of the simulated COY index with the data would eliminate all parameter sets that do not reflect the overall trend in the COY index. In this way, the COY index serves as a “filter” that distinguishes between probable parameter sets (“small” differences between the simulated COY index and data) and improbable parameter sets (“large” differences between the simulated COY index and data). We determine the best match by comparing the error

$$\Delta(\text{COY}) = \sqrt{\frac{1}{13} \sum_{\substack{t=1982 \\ t \neq 1985}}^{1995} (\text{COY}(t) - d(t))^2} \quad (8)$$

between the observed COY index,  $d(t)$  (Table 5), and the COY index obtained from simulations,  $\text{COY}(t)$ .

However, the COY index contains more usable information. To demonstrate this, we perform a small simulation experiment. Following the instructions for performing a simulation run (see section *The model: the simulation*), we run a series of 200 simulations. We use the same parameter set and the same initial number of individuals for each simulation run. We assign the initial reproductive state of independent females with the stochastic determination of Eqs. A.13 and A.14 (see Appendix A) and employ the same (randomly created) scenario for the environmental index  $\text{IR}(t)$  for each simulation run. We determine the mean and standard deviation of the COY index for the 200 simulation runs. Fig. 4 shows the results of the simulation experiment. The mean COY index shows a distinct time pattern with marked fluctuations. The pattern persists for long time spans, and the relatively low standard deviation

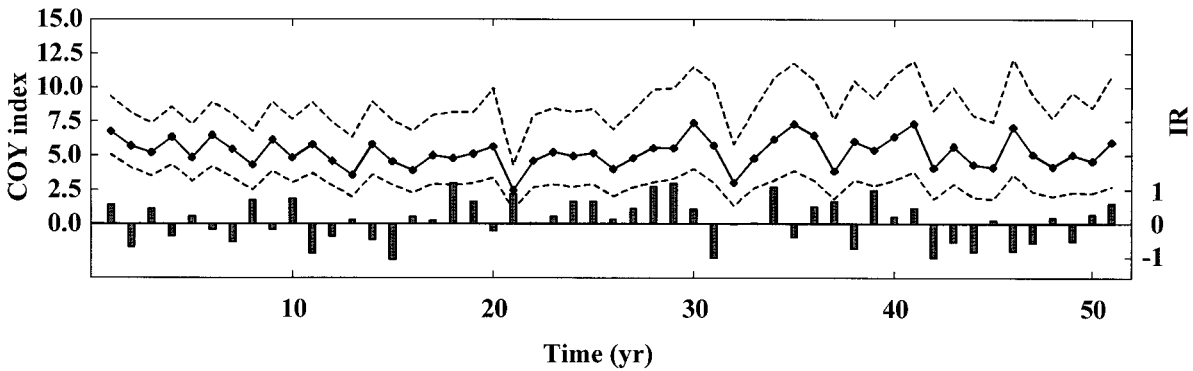


FIG. 4. An example of the mean COY index obtained from 200 simulation runs over 50 yr (solid line), the range given by the standard deviation (dashed line), and the environmental index (bars). The parameter set used had a rate of increase of  $\lambda = 0.993$ .

indicates that the COY indices of single simulations show basically the same pattern. Thus, the environmental fluctuations act as a “trigger” that shapes the COY index in a characteristic way.

Although a strong dependence of cub mortality, age of first litter, and litter size on the environmental index was built into the model, the correlation coefficient between the environmental index and the simulated COY index was generally not too high. In the example shown in Fig. 4, the Spearman correlation coefficient yields  $r_s = 0.45$  ( $P < 0.001$ ). This is because, in the model, the COY index is shaped in a complicated, non-linear way by the superposition of two time lags and the triggering force of the environmental fluctuations. The first time lag is caused by the litter interval, the second by the age of first litter. These cycles may be veiled by the influence of the climate on mortality and reproductive performance: bad years cause a repercussion of young females that cannot reproduce, and mortalities may differ considerably between bad and good years (see rule 5). Thus, the COY index contains “encoded” information about mortality rates, reproductive parameters, and climate. By building this code into the model and by using real climatic data and the observed number of females with cubs, we can hope to retrieve information about the model parameters.

*The mortality time pattern  $J(t)$ .*—To be able to consider additional information from the mortality records (Table 4), and to detect a possible mortality pattern that may differ from the mortality pattern caused by environmental variations, we proceed with a specific approach. We assign the environmental variation of subadult and adult mortality rates as zero ( $v_{1-4} = 0$ ,  $v_{5-25} = 0$ ) and introduce, instead, a mortality time pattern  $J(t)$  that gives the number of independent females that are killed additionally at simulation year  $t$ . More precisely, in the model we choose a fixed number of  $J(t)$  independent females at random from all ages at the end of the year  $t$  and kill them. With this procedure, we thus have two distinct sources of mortality: (1) mortalities given through the mortality rates  $m_i$ , and (2) the

additional mortalities from the mortality time pattern  $J(t)$  (see Fig. 3). To determine an optimal mortality pattern  $J_{op}(t)$  that minimizes the error between the observed COY index and the COY index obtained from simulations, we perform a multiple-parameter optimization (see Appendix B).

This approach allows for a more precise adjustment of the population trend, as would be possible with the variation of subadult and adult mortality rates with climate. Nevertheless, to compare both approaches, we also repeat the parameter adjustment for different scenarios of the environmental variations  $v_{1-4}$  and  $v_{5-25}$  of subadult and adult mortality rates with a zero mortality pattern [ $J(t) = 0$  for all years  $t$ ].

*The multiple parameter fit.*—In this procedure, we simulate the brown bear population dynamics for 22 yr using the environmental index IR from the Cordillera Cantabrica for the 1975–1995 period. Essentially, we compare the mean COY index obtained from a series of simulation runs,  $COY(t)$ , with the observed time series of the number of females with cubs,  $d(t)$  (Table 5), and determine the error  $\Delta$  (Eq. 8). The error  $\Delta$  serves as a criterion to distinguish between probable ( $\Delta$  small) and less probable ( $\Delta$  high) parameter combinations.

The multiple-parameter fit that aims to minimize the error  $\Delta$  requires the variation of (1) the initial population size  $P_0$ , (2) the model parameters, and (3) the mortality time pattern  $J(t)$ . A detailed description of this procedure is given in Appendix B.

*Parameter ranges.*—In the section *First approximation of model parameters*, we compiled information about the model parameters. We now use this information to determine plausible parameter ranges over which we vary during the parameter adjustment.

Data on cub survival are available, but the mortality rates of adults and subadults are unknown. To investigate the sensitivity of the fit with respect to cub mortality, we vary the range of the mean cub mortality rates ( $m_0^f$ ,  $m_0^g$ ) in the neighborhood of the observed data (0.40) between 0.36 and 0.44 (Table 6). We base the variation range of mortality rates of the other age class-

TABLE 6. (A) Grid in parameter space for parameter adjustment. (B) Scenarios for the environmental variation of cub ( $m_0$ ), subadult ( $m_{1-4}^f$ ), and adult ( $m_{5-16}^f$ ) mortality rates. Scenarios are presented for environmental variation of subadult mortality rate ( $v_{1-4}$ ), and environmental variation of adult mortality rate ( $v_{5-26}$ ).

A) Grid for parameter adjustment					
Variable	Parameter values varied				
	Value 1	Value 2	Value 3	Value 4	Value 5
Female mortality rates					
$m_0$	0.36	0.38	0.40	0.42	0.44
$m_{1-4}^f$	0.15	0.17	0.19	0.21	0.23
$m_{5-16}^f$	0.055	0.07	0.085	0.1	0.115
First litter at ages 4, 5					
$f_4$	0.00	0.06	0.12	0.18	0.24
$f_5$	0.80	0.90	1.00		
Litter 1, 2 yr after break up					
$h_1$	0.05	0.10	0.15		
$h_2$	0.40	0.50	0.60		
B) Scenarios for environmental variation					
Scenario	$v_0$	$v_{1-4}$	$v_{5-25}$		
S1	0.38	0.00	0.00		
S2	0.38	0.33	0.17		
S3	0.38	0.66	0.10		
S4	0.38	0.20	0.20		
S5	0.38	0.45	0.45		
S6	0.38	0.66	0.33		

es on data for the Yellowstone grizzly bear population (Table 3), and we vary the mortality rate of adult females ( $m_{5-16}^f$ ) between 0.055 and 0.115 and the mortality rate of subadult females ( $m_{1-4}^f$ ) between 0.15 and 0.23 (Table 6).

We estimated the mean age of first litter (5.3 yr) and the mean litter interval (3.3 yr) (see *First approximation of model parameters: reproduction*) using correlations between mean litter size, mean age at the first litter, and the litter interval. To test these estimates and to determine the probabilities of a first litter at ages 4 and 5 ( $f_4$  and  $f_5$ ) and the probability of a litter 1 and 2 years after family breakup ( $h_1$  and  $h_2$ ), we vary  $f_4$ ,  $f_5$ ,  $h_1$ , and  $h_2$  in a way that the resulting mean age of the first litter and the mean litter interval are close to our estimates.

#### RESULTS OF THE PARAMETER ADJUSTMENT

##### *Selecting the reference parameter set*

We perform the procedure described in Appendix B for each of the 16 875 possible combinations of the parameter values given in Table 6A. Since the mortality pattern  $J(t)$  already models a temporal variation of the overall mortality rates, we set environmental variations of subadult and adult mortality rates as zero ( $v_{1-4} = 0$ ,  $v_{5-25} = 0$ ). As an output of this procedure, we obtain a minimal error  $\Delta$  for each parameter set, together with an optimal initial population size  $P_0$  and an optimal mortality time pattern  $J_{\text{opt}}(t)$ .

We also repeat this procedure for the six scenarios of environmental variations of subadult and adult mor-

tality rates (Table 6B), but do not consider the mortality time pattern in this case (we set  $J(t) = 0$ ).

To present the results in a clear way, we classify the different parameter sets according to their (theoretical) rate of increase,  $\lambda_{\text{th}}$ , which we calculate with the analytical model (Eq. 7). The theoretical rate of increase  $\lambda_{\text{th}}$  is a property of the parameter set and does not consider the mortalities due to the mortality time pattern  $J(t)$ . Thus, the simulated rate of increase  $\lambda_{\text{sim}}$  is always smaller than the theoretical rate of increase  $\lambda_{\text{th}}$ , and both accord if  $J(t) = 0$ .

Fig. 5 shows the results of the parameter adjustment. We plotted a dot with the rate of increase  $\lambda_{\text{th}}$  for each parameter set on the  $x$ -axis, and the error  $\Delta$  that results from the multiple parameter fit (see Appendix B) on the  $y$ -axis. We found a marked boundary that limits the error  $\Delta$  for a given theoretical rate of increase  $\lambda_{\text{th}}$ . The points on the "borderline" represent the most probable parameter combinations for a given theoretical rate of increase. The corresponding  $(\lambda_{\text{th}}, \Delta)$  points of all other parameter combinations form a dense cloud above the boundary. Thus, for a given theoretical rate of increase, the transition from parameter combinations with a good agreement between the simulated COY series and the data to a poor agreement is continuous. This result assures us that we are not searching for a singular phenomenon, and that our "grid" in parameter space (Table 6) is dense enough to capture the essential behavior of the system.

The borderline declines almost linearly with increasing theoretical rate of increase  $\lambda_{\text{th}}$  before reaching a

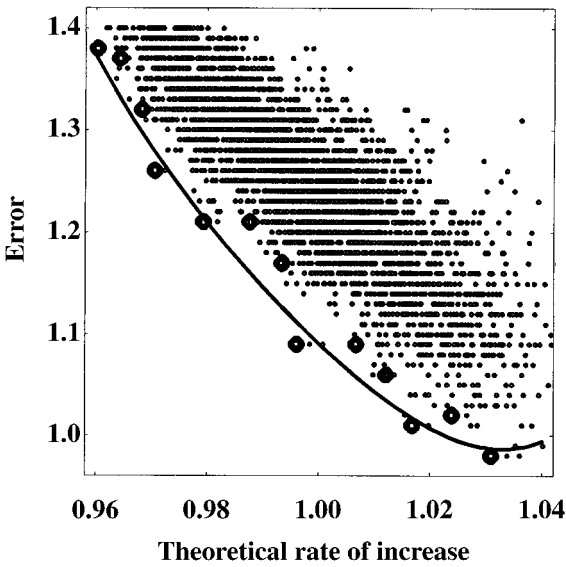


FIG. 5. Results of the parameter variation, showing the smallest error  $\Delta$  between the mean simulated COY index and the data, depending on the theoretical rate of increase  $\lambda_{th}$ . The solid line represents the fitted borderline; small points are the data points; large circles are the data points with  $m_0 = 0.4$ , which are close to the borderline.

minimum at  $\lambda_{th} \approx 1.03$  (Fig. 5). The minimum corresponds to the optimal parameter set and to an optimal mortality time pattern. All parameter sets on the borderline yield approximately the same number of total mortalities  $J_{tot}$  during the 1982–1995 period (Table 7). For parameter sets with a larger theoretical rate of increase  $\lambda_{th}$ , a higher fraction of mortalities ( $J_p$ ) were due

to the mortality time pattern  $J(t)$  (Table 7); thus, a higher fraction of mortalities could be “distributed” more specifically in time to acquire a better fit. Consequently, the error  $\Delta$  decreased with increasing  $\lambda_{th}$ .

To investigate the sensitivity of the borderline with respect to the mean cub mortality rate, we calculated the borderline based on all parameter sets given in Table 6 (solid line, Fig. 5) and plotted it, together with the data points with a mean cub mortality rate of  $m_0 = 0.4$  (large circles in Fig. 5). The best fits with  $m_0 = 0.4$  (large circles in Fig. 5) are in good accordance with the borderline. Thus, the observed data for cub mortality indeed deliver the best adjustments. This important result confirms the self-consistence of the observed data and of the adjustment procedure.

Tables 7 and 8 show details of the borderline parameter sets and summarize the simulation results for these parameter sets. As important results, we find that the simulated rates of increase  $\lambda_{sim}$  range between 0.946 and 0.960 (Table 8). This result indicates that the population suffered an annual decrease of  $\sim 5\%$  during the 1982–1995 period.

The parameter adjustment without the mortality time pattern ( $J(t) = 0$ ) delivered a minimal error  $\Delta$ , with  $\Delta > 1.4$  (Table 8) for all six scenarios (Table 6). The scenarios with low variations of adult mortality (scenarios S1, S2, and S3) have minimal errors  $\Delta$  of the same magnitude (cases R8–R11 in Table 8), but a high variation of the adult mortality rates (scenarios S4, S5, and S6) always results in worse fits, with errors  $\Delta > 1.5$ . A high variation of the subadult mortality rate (cases R10 and R11) yields the best fits, with the same errors  $\Delta$  as without variation of the subadult mortality

TABLE 7. Optimal mortality time pattern  $J_{op}(t)$  from 1982 to 1995 for “borderline” parameter sets R1–R7 (large circles) of Fig. 5, total probable and known mortalities (from Table 4), and total number of mortalities  $J_{tot}$  during the 14-yr simulation period. Variables are as follows:  $\lambda_{th}$ , theoretical rate of increase;  $J_{tot}$ , total number of mortalities, 1982–1995;  $J_p$ , total number of time-dependent mortalities, 1982–1995;  $v_0$ ,  $v_{1-4}$ , and  $v_{5-24}$ , coefficients of variation of cub, subadult, and adult mortality rates due to climate.

Set	$\lambda_{th}$	Simulated optimal mortality time pattern $J_{op}(t)$ , by year														$J_{tot}$	$J_p$
		1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995		
R1†	1.031	0	0	7	3	5	5	0	0	2	2	2	0	0	65.7	26	
R2	1.024	0	0	7	1	5	4	0	0	3	2	0	0	0	60.9	22	
R3	1.017	0	0	5	1	6	5	0	0	0	3	0	0	0	65.3	20	
R4	1.012	0	0	6	2	5	3	0	0	1	2	0	0	0	64.2	19	
R5	1.007	0	0	5	3	5	3	0	0	0	3	0	0	0	67.7	19	
R6	0.996	0	0	5	2	3	3	0	0	0	1	0	0	0	65.7	14	
R7	0.960	0	0	4	2	1	0	0	0	0	0	0	0	0	65.2	7	
Data‡		1	5	0	1	10	4	0	2	3	0	0	3	0	...	29	
Set	$\lambda_{th}$	Scenario	Simulations without mortality time pattern												$J_{tot}$	$J_p$	
R8	0.960	S1	$v_0 = 0.38, v_{1-4} = 0.00, v_{5-24} = 0.00$												64.6	0	
R9	0.952	S1	$v_0 = 0.38, v_{1-4} = 0.00, v_{5-24} = 0.00$												64.0	0	
R10	0.961	S2	$v_0 = 0.38, v_{1-4} = 0.33, v_{5-24} = 0.16$												66.2	0	
R11	0.967	S3	$v_0 = 0.38, v_{1-4} = 0.60, v_{5-24} = 0.10$												63.5	0	

Note: Parameter sets R1–R6 represent the borderline, with  $\lambda \geq 0.996$ , in contrast to the worst case of set R7, with  $\lambda = 0.96$ .

† R1 was selected as the reference parameter set.

‡ Observed data on the total number of mortalities (known and probable mortalities for independent males and females), in contrast to the simulated parameters (R1–R7). See Table 4.

TABLE 8. Parameters and simulation results for the “borderline” parameter sets (R1–R7) of Fig. 5, and for the four best cases (R8–R11) without time-dependent mortality. Variables are  $\lambda_{th}$ , theoretical rate of increase (not including the mortality time pattern  $J(t)$ ) calculated with Eq. 7;  $\lambda_{sim}$ , simulated rate of increase (including all mortalities);  $m_0$ , mean (male and female) cub mortality rates (at age 0);  $m_i^f$ , mortality rate of  $i$ -year-old females;  $f_i$ , probability of first litter at age  $i$ ;  $h_j$ , probability of a litter  $j$  years after family breakup;  $M$ , mean litter interval;  $R$ , mean age of first litter. The values in parentheses give the simulated overall mortality rates (including the mortality time pattern  $J(t)$ ) for the 1982–1995 period.

Set	$\lambda_{sim}$	$\lambda_{th}$	error $\Delta$	$m_0$	$m_{1-4}^f$	$m_{5-16}^f$	$m_{17-24}^f$	$h_1$	$h_2$	$f_4$	$f_5$	$R$	$M$
R1†	0.950	1.031	0.98	0.4 (0.42)	0.15 (0.21)	0.055 (0.144)	0.22 (0.31)	0.15	0.5	0.12	1	4.87	3.10
R2	0.954	1.024	1.02	0.4 (0.42)	0.17 (0.22)	0.055 (0.134)	0.22 (0.30)	0.15	0.6	0.12	1	4.87	3.01
R3	0.960	1.017	1.01	0.4 (0.41)	0.15 (0.19)	0.085 (0.153)	0.22 (0.30)	0.15	0.6	0.06	1	4.93	2.99
R4	0.956	1.012	1.06	0.4 (0.41)	0.17 (0.21)	0.070 (0.137)	0.22 (0.29)	0.10	0.5	0.18	1	4.81	3.17
R5	0.946	1.007	1.09	0.4 (0.41)	0.15 (0.20)	0.100 (0.171)	0.22 (0.29)	0.10	0.6	0.06	1	4.93	3.06
R6	0.952	0.996	1.09	0.4 (0.41)	0.19 (0.22)	0.085 (0.134)	0.22 (0.28)	0.15	0.5	0.12	1	4.87	3.08
R7	0.940	0.960	1.38	0.4 (0.41)	0.23 (0.25)	0.115 (0.142)	0.22 (0.25)	0.15	0.5	0.06	1	4.93	3.06
R8	0.951	0.960	1.42	0.42 (0.43)	0.20 (0.21)	0.150 (0.154)	0.30 (0.32)	0.15	0.6	0.18	1	4.79	2.94
R9	0.946	0.952	1.45	0.4 (0.40)	0.24 (0.25)	0.125 (0.126)	0.30 (0.31)	0.15	0.5	0.06	1	4.93	3.05
R10	0.965	0.967	1.46	0.4 (0.41)	0.20 (0.20)	0.125 (0.132)	0.30 (0.31)	0.10	0.4	0.06	1	4.93	3.25
R11	0.958	0.961	1.49	0.4 (0.41)	0.20 (0.20)	0.150 (0.152)	0.30 (0.31)	0.15	0.6	0.06	1	4.93	2.95

Note: Contrast the borderline sets (R1–R6) with the worst case set (R7) and the parameter sets without time-dependent mortality (R8–R11).

† Selected as reference parameter set.

rates (cases R8 and R9). Thus, we can reject the hypothesis of a high environmental variation of the adult mortality rates ( $v_{5-26} > 0.2$ ), but not the hypothesis of a high environmental variation of the subadult mortality rates (e.g.,  $v_{1-4} = 0.6$ , scenario S3).

A comparison of the parameter sets and the simulated overall mortality rates for the best fits (Table 8: R1–R6) shows a good accordance among the values of all parameters. The simulated overall mortalities range between 0.19 and 0.22 for subadults, between 0.134 and 0.171 for adults of the 5–16 yr-old age class, and between 0.28 and 0.31 for the 17–24 yr-old class (Table 8). The simulated overall mortalities for the best fits for the scenarios without mortality time pattern (R8–R11) are all within the same ranges. The mean age at first reproduction ranges from 4.79 to 4.93 yr, and the mean litter interval ranges between 2.94 and 3.25 yr.

The accordance of the results between different approaches increases our confidence in our adjustment of the model parameters. However, the “best parameter sets” should be similar, because they all optimally fit

the same time series of the COY index (Fig. 6). To capture the essence of the whole procedure of parameter adjustment, we designate the parameter set R1 with the smallest error  $\Delta$  (Table 8) as the reference parameter set.

Analyzing the mortality time pattern

In this section, we compare the simulated optimal mortality patterns  $J_{op}$  from the borderline sets (Table 7) and relate them to observed data from the mortality records (Table 4). The mortality pattern  $J(t)$  gives the number of females that we kill at simulation year  $t$  in addition to mortalities given through the mortality rates  $m_i^f$  (see Table 8 and Fig. 3). The introduction of the mortality pattern  $J(t)$  allows us to search for nonrandom temporal pattern in the mortality, as indicated by the mortality records (Table 4). The optimal mortality pattern  $J(t)$  (Table 7) and the mortality rates  $m_i^f$  (Table 8) together give the mortality regimes that deliver the best adjustments of the simulated COY index to the observed COY index.

The optimal mortality time patterns  $J(t)$  are similar

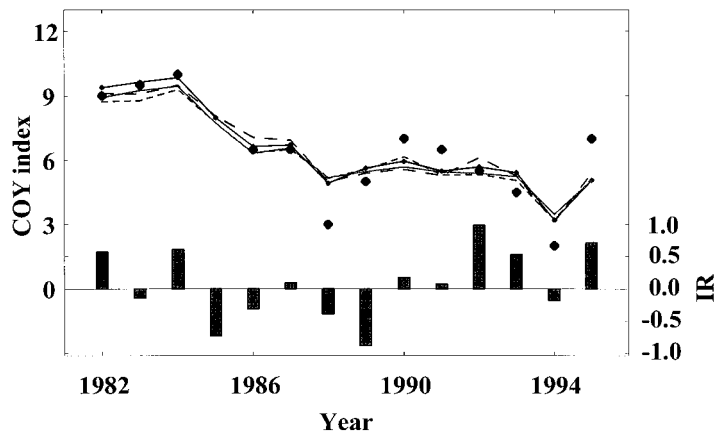


FIG. 6. Observed number of females with cubs of the year (large data points, COY index), the environmental index IR (bars), and the simulated COY index for four borderline parameter sets: R1 (solid line), R2 (small dashes), R3 (long dashes), and R4 (gray solid line).

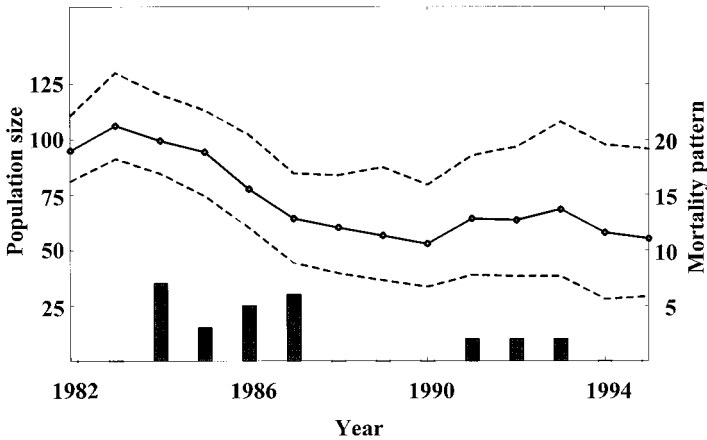


FIG. 7. Simulated total population sizes (solid line), standard deviation (dashed lines), and mortality pattern (bars) for the reference parameter set R1. For male subadults, the mortality rate was  $m_{1-4}^m = 0.22$ .

in all cases (Table 7). Qualitatively, the patterns consist of five blocks: the periods 1982–1983, 1988–1990, and 1993–1995, with low mortality pressure; and the periods 1984–1987 and 1991–1992, with high or intermediate mortality pressure. The 1984–1988 period coincides with the period of the dramatic decline of the COY index from 10 (1984) to 3 (1988) (see Table 5).

A comparison of the simulated optimal mortality time pattern with observed data from the mortality records (Table 7) shows a good qualitative agreement. Only for three years (1983, 1989, and 1994) does the model predict a considerably lower number of mortalities than the observed data. In these cases, the observed data indicate at least one or two mortalities, whereas the model predicts none. For nine years, data and prediction are in quantitative agreement; only for two years (1984, 1985) are the observed data considerably lower than the prediction of the model. However, the detected mortalities (Table 4) give only minimal numbers, and real mortalities may be higher.

Nevertheless, the qualitative agreement between known mortalities due to poaching and the mortality pattern predicted from the model simulations supports an identification of the mortality time pattern with an index of poaching.

#### Total population size

The simulations performed in the last section provide means for determining probable overall population

sizes for the 1992–1995 period and, thus, for reconstructing population dynamics during this period. From our simulation results, we calculated the mean overall population size, the standard deviation of the overall population size, and the mean number of dependent cubs, independent females, and independent males for the four borderline cases with  $\lambda_{th} > 1$  and  $m_0 = 0.4$  (R1–R4; Table 8). For these simulations, we assumed the same mortality time pattern for males as for females. Because we were not able to fit the mortality rate for subadult males, we assume an optimistic case with  $m_{1-4}^m = 0.22$  (from the U.S. Fish and Wildlife Service 1993) and a pessimistic case with  $m_{1-4}^m = 0.29$  (from Craighead et al. 1974; Table 3). Fig. 7 shows the reconstructed total population sizes for the reference parameter set R1. Simulation results for all four cases were in good agreement (Table 9).

Our simulation results indicate that the overall population size declined during the 1982–1988 period from ~95 individuals in 1982 to a minimum of 52 individuals in 1990, and recuperated slightly to ~60 individuals in 1995. We found that this rapid decline could be explained by a coincidence of the high poaching pressure during the 1984–1987 period (Fig. 7) and a series of bad years, 1985–1989 (Fig. 6), with high cub mortality and low reproductive output. However, simulation results shown in Fig. 7 indicate that the population stabilized in the early 1990s after the decline during the late 1980s. Our results suggest that this sta-

TABLE 9. Reconstruction of the mean population sizes for 1982 and 1995. The estimates are based on model simulations for the four borderline parameter sets R1–R4 from Table 8. Values for total population sizes and numbers of independent males are based on an optimistic value for the mortality rate of male subadults ( $m_{1-4}^m = 0.22$ ). Values given in parentheses are based on a pessimistic value ( $m_{1-4}^m = 0.29$ ).

Set	Total population		Dependent cubs		Independent females		Independent males	
	1982	1995	1982	1995	1982	1995	1982	1995
R4	95 (83)	58 (51)	25	13	40	26	30 (18)	19 (12)
R3	89 (82)	56 (51)	25	14	38	25	26 (18)	17 (12)
R2	94 (82)	60 (56)	25	15	40	26	29 (17)	19 (12)
R1	95 (86)	56 (49)	27	14	40	26	28 (21)	16 (10)

bilization may be partly due to a period of more favorable climatic conditions (Fig. 6) and to the considerable management efforts (Naves and Palomero 1993) that resulted in reduced rates of poaching. Later, we will tackle the essential question of whether or not the actual population size is sufficient for a minimum viable population.

The trends in overall population size predicted from our model simulations (Fig. 7) coincide largely with trends in the observed data of the number of females with cubs (Fig. 6, Table 5). The observed number of females with cubs declined during the 1984–1988 period from ~10 (1984) to 3 (1988); thereafter, the observed COY index stabilized.

Our estimates for the total population size depend on the unknown male subadult mortality rate (Table 9). Therefore, it appears more precise to characterize the population size only by the number of independent females instead of by the total population size.

Similar estimates for population size can be obtained by using a simple method based on the observed COY index, the breeding interval, and the percentage of adult females within the population (Dennis et al. 1991, Foley 1994, Boyce 1995). Based on the reference parameter set R1 (Table 8), the analytical model yields a fraction of ~28% adult females ( $\geq 4$  yr old) within the population. In Yellowstone, the fraction was ~27% adult females (Boyce 1995). With these estimates, an observed 3-yr mean of 4.5 females with cubs in 1995 (Table 5), and a breeding interval of 3.1 yr, we obtain a total of 50 individuals. For 1984, the observed 3-yr mean of 9.5 females with cubs yields a total of 105 individuals. However, this method only allows a crude estimate of the total population size and is very sensitive to the assumed age structure of the population.

#### *Creating a series of mortality scenarios*

In the last sections, we adjusted the unknown model parameters and reconstructed the population dynamics during the 1982–1995 period. To assess the viability of the population (calculating minimum viable populations and mean extinction times) and to define management goals, however, we need to project from the status quo into the future. To do this, we presume that most population parameters will remain unchanged, but we assume different scenarios for mortalities of independent females, because mortality rates are the parameters that are most likely to change in response to management. To link the different scenarios for the mortality rates with a variable that is directly management accessible (the mortality records), we perform a series of simulation experiments in which we basically repeat the simulations for the reference parameter set R1 (Table 8). Instead of employing the optimal mortality pattern (Table 7), however, we use a random environmental index IR for every simulation run, and a random mortality pattern  $J(t)$  with a fixed number  $J_p$  of time-dependent mortalities. In this step, we cannot

TABLE 10. Mortality rates and simulated rate of increase for the different mortality scenarios P0–P5 and for reference parameter set R1 from Table 8.

Scenario	$J_m$	$\lambda_{\text{sim}}$	$m_{1-4}^f$	$m_{5-16}^f$	$m_{17-24}^f$
P0	0.00	1.036	0.15	0.055	0.22
P1	0.31	1.022	0.16	0.070	0.24
P15	0.46	1.014	0.165	0.080	0.25
P2†	0.69	1.006	0.17	0.090	0.26
P25	0.85	0.999	0.175	0.098	0.27
P3	0.92	0.993	0.18	0.105	0.28
P35	1.15	0.977	0.19	0.125	0.29
P4	1.38	0.962	0.20	0.145	0.30
P5	1.77	0.938	0.22	0.170	0.33
R1	2.00‡	0.950	0.21	0.144	0.31

*Notes:* The mortality rates resulted from simulating population dynamics with random mortality time patterns  $J(t)$  with a mean annual number of time-dependent mortalities  $J_m$ , random environmental indices IR, and an initial number of 25 independent females. Variables are:  $\lambda_{\text{sim}}$ , simulated rate of increase (including mortality time pattern);  $m_i^f$ , and mortality rate of  $i$  year-old females.

† Approximation of the present situation of the western population at Cordillera Cantabrica.

‡ A direct comparison of values of  $J_m$  is not possible because simulations for R1 started with 40 independent females (Table 9).

use specific scenarios for the environmental index and the mortality pattern because we do not know how climate, mortality, and poaching will develop in the future in the Cordillera Cantabrica. We adjust the initial population size to 25 independent females, our model estimate for the approximated number in 1995.

The resulting scenarios for the overall mortality rates (Table 10) predict future mortality rates that are projected from the present state of the population (current population size, current reproductive parameter, etc.) for different possible (hypothetical) developments of poaching. From this exercise, we gain the ability to link these mortality scenarios via the management-accessible variable “numbers of females killed or saved.” Dynamics of both models differ only in that simulations in the section *Selecting the reference parameter set* were based on one specific realization of the mortality pattern  $J(t)$  and the observed data for the environmental index IR, whereas simulations with random mortality pattern and random environmental index cover all plausible realizations of  $J(t)$  and IR.

Our simulations indicate that population size has stabilized since 1988 (Fig. 7) to a level of ~25 independent females, and the optimal mortality pattern  $J_{\text{opt}}(t)$  between 1988 and 1995 yields a mean of  $J_m = 0.75$  mortalities per year (Table 7). Scenario P2 with  $J_m = 0.69$  is a good approximation of the present state of the population, with  $J_m = 0.69$  (Table 10). The corresponding rate of increase of  $\lambda_{\text{sim}} = 1.006$  also reflects the stabilization of the population trend. Comparison of the overall mortality rates from scenarios P0 to P5 with the overall mortality rates from reference parameter set R1 (Tables 8 and 10) shows that the entire 1984–1995 period can be approximated with a mortality scenario between P4 and P5. The resulting overall

TABLE 11. The full reference parameter sets:  $i_i$ , probability of litter becoming independent at age  $i$ ;  $f_i$ , probability of a first litter at age  $i$ ;  $h_j$ , probability of litter  $j$  years after family breakup;  $s_f$  and  $s_m$ , fractions of female and male cubs;  $l_j$ , probability of a litter size  $j$  without environmental variations;  $m_i^m$  and  $m_i^f$ , male (m) and female (f) mortality rates at age  $i$ ,  $m_0^m$ , mean orphan's mortality rate. S1, S2, and S3: scenarios for environmental variation of subadult ( $v_{1-4}$ ) and adult ( $v_{5-26}$ ) mortality rates (see Table 6). The mortality rates in parentheses are for the mortality scenarios (P0, P1, . . . , P5).

Symbol	Reference parameter sets			Associated means
$i_i$	$i_0 = 0; i_1 = 1$			Mean independence age = 1.86 yr†
$f_i$	$f_4 = 0.12; f_5 = 1.00; f_6 = 1.00$			Mean age at first litter = 4.87 yr†
$h_j$	$h_1 = 0.15; h_2 = 0.5; h_3 = 0.9; h_4 = 1.0$			Mean litter interval‡
$s_f, s_m$	$s_f = 0.5; s_m = 0.5$			
$l_j$	$l_1 = 0.07; l_2 = 0.55; l_3 = 0.32; l_4 = 0.06$			Mean litter size = 2.37§
$l_j^+$ (good years)	$l_1^+ = 0.00; l_2^+ = 0.38; l_3^+ = 0.50; l_4^+ = 0.12$			Mean litter size = 2.75†
$l_j^-$ (bad years)	$l_1^- = 0.13; l_2^- = 0.74; l_3^- = 0.13; l_4^- = 0.00$			Mean litter size = 2.00†
$m_0$	(0.4, 0.4, 0.4, 0.4, 0.4, 0.4)			
	(0.22, 0.23, 0.24, 0.25, 0.27, 0.29)			
$m_{1-4}^m$	(0.15, 0.16, 0.17, 0.18, 0.20, 0.22)			
$m_{1-4}^f, m_{5-16}$	(0.055, 0.070, 0.090, 0.105, 0.145, 0.170)			
$m_{17-25}$	(0.22, 0.24, 0.26, 0.28, 0.30, 0.33)			
$m_0^m$	0.5			
Scenario	$v_0$	$v_{1-4}$	$v_{5-26}$	
S1	0.38	0.00	0.00	
S2	0.38	0.33	0.16	
S3	0.38	0.66	0.10	

Notes: Maximal number of territories = 18; initial population size = 25 independent females.  
 † Values calculated with the analytical model.  
 ‡ Mean litter interval = 3.11, 3.10, 3.08, 3.07, 3.04, and 3.02 yr for scenarios P0–P5 (calculated with the analytical model).  
 § Bad and good years are assumed to be equally distributed.

mortality rates for all scenarios (Table 10) are within the ranges given through data from Yellowstone (Table 3).

The adjustment of model parameters is now complete. Table 11 summarizes the reference parameter sets that include the mortality scenarios P0–P5. In the next section, we can proceed with a detailed sensitivity analysis of the model parameters given in Table 11, and calculate minimum viable populations and extinction times for the different mortality scenarios to investigate the viability of the population.

RESULTS OF PVA

Sensitivity analysis

One of the fundamental elements of every population viability analysis is a sensitivity analysis (Grand 1986, Boyce 1992). Knowing how sensitive the model's results are to its key parameters is essential to obtaining a sufficient understanding of the processes that determine population dynamics. If simulation models alone are used for the viability analysis, the execution of a careful sensitivity analysis may involve an exhaustive simulation effort and, thus, is often neglected.

Our analytical model (Eqs. A.1–A.12) calculates the deterministic rate of increase and describes the mean behavior of the population for a given parameter set without considering demographic and environmental stochasticity. The analytical model allows the variation of a high number of parameters with little computational effort, and is therefore a suitable tool for performing a sensitivity analysis. To test the analytical model, however, we also perform a series of simula-

tions and compare the simulation results with results from the analytical model. For this purpose, we start our simulations with a high number of independent females (500) and switch off the density-dependent regulation. For each parameter set, we perform 50 replications of the simulation and we calculate the simulated rate of increase  $\lambda_{sim}$  with the Lotka equation (Eq. 7), using the simulated fertility and mortality rates.

We analyze the sensitivity of the rate of increase with respect to mortality rates, reproductive parameter, and independence of cubs. Although we vary the probabilities of litter size ( $l_j$ ), independence ( $i_i$ ), first reproduction ( $f_i$ ), and reproduction after family breakup ( $h_j$ ), we use the more intuitive parameters, mean litter size ( $L$ ), mean litter interval ( $M$ ), mean age at first reproduction ( $R$ ), and mean age of independence ( $I$ ), as the basis for sensitivity. As a first step, we determine the slope of the rate of increase with respect to a parameter  $p$  at point  $p_0$  with

$$s(p, p_0) = \left. \frac{d\lambda}{dp} \right|_{p=p_0} \quad (9)$$

Fig. 8 shows the slope of the key parameters based on the reference parameter set P4 given in Table 11. The agreement between rates of increase predicted by the analytical model and simulated rates of increase is high; thus, the analytical model is an extremely powerful tool for predicting the mean behavior of the population. However, because of demographic and environmental variability, variations between single simulation runs may be considerable.

A sensitivity index needs to consider both the pure

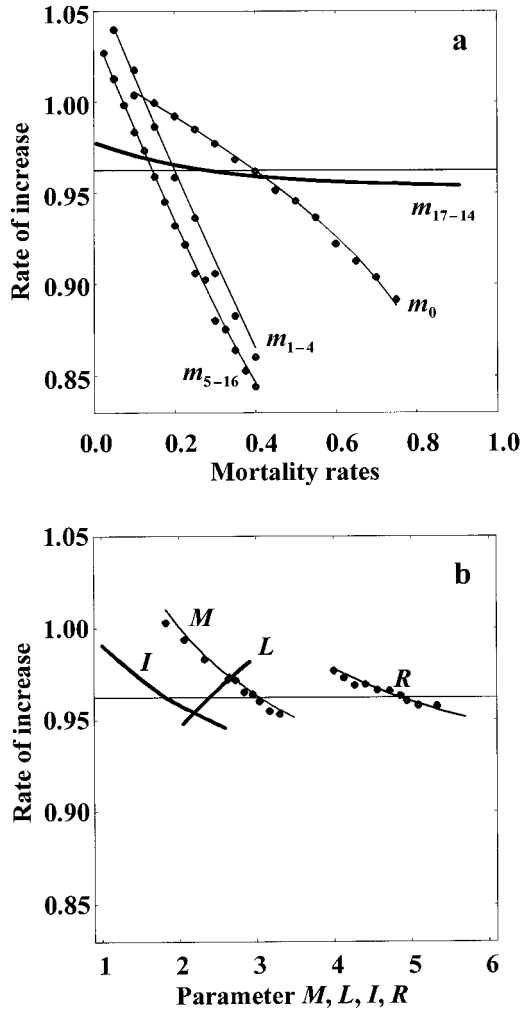


FIG. 8. Sensitivity analysis of the rate of increase, depending on various parameters, performed with the analytical model (lines) and with the simulation model (●). (a) Mortality rates are shown as solid lines from left to right: adult mortality rate ( $m_{5-16}$ ); female subadult mortality rate ( $m_{1-4}$ ); cub mortality rate ( $m_0$ ); and adult mortality rate ( $m_{17-24}$ ). (b) Reproductive parameters, shown as solid lines from left to right: mean age of independence ( $I$ ); mean litter size ( $L$ ); mean litter interval ( $M$ ); and mean age at first reproduction ( $R$ ).

sensitivity of the parameter (the slope) as well as the level of uncertainty of the parameter. We define the sensitivity index of a parameter  $p$ , within point  $p_0$  as  $\rho(p, p_0) = s(p, p_0)\Delta(p)$ , where  $s(p, p_0)$  is the slope and  $\Delta(p)$  is the approximate uncertainty of the parameter  $p$ . The parameters from the best fits of the parameter variation (Table 8) give the uncertainty of the parameters varied. We obtain  $\Delta(m_{1-4}) = 0.03$ ,  $\Delta(m_{5-16}) = 0.037$ ,  $\Delta(m_{17-24}) = 0.03$ ,  $\Delta(R) = 0.14$ , and  $\Delta(M) = 0.31$ . For the cub mortality rate, we assume that  $\Delta(m_0) = 0.04$ , and we assume approximate parameter ranges of the litter size and the mean age of independence of  $\sim 0.2$ .

We obtain a clear hierarchy of sensitivity (slopes on

TABLE 12. Sensitivity analysis of key parameters from Table 11 for the reference parameter set P4. Variables are  $m_0$ , mean (male and female) cub mortality rates (age 0);  $m_i^f$ , mortality rate of  $i$ -yr-old females;  $R$ , mean age of first litter;  $L$ , mean litter size;  $M$ , mean litter interval;  $I$ , mean age of independence.

Parameter $p$	$p_0$	Slope $s(p, p_0)$	Uncertainty $\Delta(p)$	Index $\rho(p, p_0)$
High sensitivity				
$m_{5-16}$	0.144	0.512	0.037	0.0189
$m_{1-4}$	0.21	0.506	0.03	0.0152
Intermediate sensitivity				
$M$	3.10	0.027	0.31	0.0084
$L$	2.26	0.041	0.2	0.0082
$m_0$	0.40	0.161	0.04	0.0064
$I$	1.86	0.029	0.2	0.0058
$R$	4.87	0.029	0.14	0.0041
Low sensitivity				
$m_{17-24}$	0.30	0.031	0.03	0.0009

Table 12). The female adult and subadult mortality rates are the most sensitive parameters, whereas cub mortality is of intermediate sensitivity and mortality of old females is of low sensitivity. The reproductive parameters range over intermediate levels.

*Minimum viable population sizes*

In the last sections, we focused on the (deterministic) rate of increase  $\lambda$  that determines the mean behavior of the population. However, demographic and environmental stochasticity have a strong impact on the outcome of individual simulation runs. Although a population might have a rate of increase greater than 1.0 and would increase deterministically, there still remains a certain probability of extinction. This is because of unfavorable chance events, especially at low population sizes. The minimum viable population (MVP) size is a concept that especially emphasizes this property. It is intended to be an estimate of the minimum number of individuals needed for a population to have a good chance of surviving for a relatively long period of time.

In this section, we investigate the classical question of MVP. For the purposes of illustration, we define a minimum viable population as “the smallest isolated population having at least a 95% probability of surviving at least 100 years” (Shaffer 1983). For this reason, we perform a series of simulation experiments in which we vary the initial population size and determine the probability of extinction after 100 yr. We repeat this simulation exercise for the reference parameter sets P0, P1, P15, and P2 that have a deterministic rate of increase  $\lambda > 1$  (Tables 10 and 11). For parameter sets with  $\lambda < 1$ , no MVP exists, since the population is already doomed to extinction deterministically. The approximate capacity of the habitat may be  $18 \times 3 \times (1 + 1/1.8) \approx 84$  independent females, if we assume that 18 females can breed simultaneously (see rule 4), that

TABLE 13. Minimum viable population sizes for the reference parameter sets P0, P1, P15, and P2 and scenarios S0, S1, S2, and S3 of environmental variation. Results are arranged in matrix form and show, for a given scenario of environmental variations (columns), and for a given parameter set (rows), the population sizes (number of independent females) that have a risk of extinction of 5% within 100 years.

Set	$\lambda_{det}^\dagger$	$J_m^\ddagger$	$f^\S$	MVP (no. independent females), by scenario			
				S0	S1	S2	S3
P0	1.036	0.00	0.413	10	10	10	11
P1	1.022	0.31	0.399	13	13	17	20
P15	1.014	0.46	0.391	21	21	28	32
P2	1.006	0.69	0.383	32	34	41	52

Note: Numbers of independent females can be scaled to total population sizes by dividing by the fraction  $f$  of independent females.

$^\dagger$  Deterministic rate of increase.

$^\ddagger$  Mean number of time-dependent mortalities.

$^\S$  Fraction of independent females.

|| Scenario S0 has no environmental fluctuations; scenarios S1–S3 have environmental fluctuation (see Table 6).

the litter interval is 3 yr, and that the population contains a ratio of  $\sim 1.8:1$  adult to subadult females.

To investigate the influence of environmental variation of subadult ( $v_{1-4}$ ) and adult ( $v_{5-24}$ ) mortality rates on MVP, we repeat the simulation experiment for the case without any environmental variations (scenario S0) and for the three possible scenarios S1 ( $v_{1-4} = 0$ ,  $v_{5-24} = 0$ ), S2 ( $v_{1-4} = 0.33$ ,  $v_{5-24} = 0.16$ ), and S3 ( $v_{1-4} = 0.6$ ,  $v_{5-24} = 0.1$ ) shown in Table 11. With environmental variation, the mortality rates are  $m_i(1 + v_i)$  in bad years and  $m_i(1 - v_i)$  in good years. Because of the uncertainty of the male subadult mortality rate, we base our analysis on the number of independent females and not on the total population size. With the aid of the analytical model, however, we can calculate the mean fraction  $f$  of independent females within the population (Table 13) and can thus scale up to total population size.

Fig. 9a shows the probability of extinction, depending on the initial number of independent females for parameter sets P0, P1, P15, and P2 and scenario S3. In all cases, the risk of extinction decreases exponentially with increasing population size. Fig. 9b shows the correlation between the minimum viable population and the deterministic rate of increase. For all scenarios of environmental variation (S0, S1, S2, S3), the population size with a 5% risk of extinction after 100 yr decreases with an exponential law in dependence on the deterministic rate of increase (Fig. 9b). We can use the results from this simulation experiment to assess the viability of the population in the Cordillera Cantabrica and to investigate the sensitivity of the key parameters with respect to the MVP.

We estimated a current population size of 25 independent females and diagnosed that current population parameters are approximated through parameter set P2.

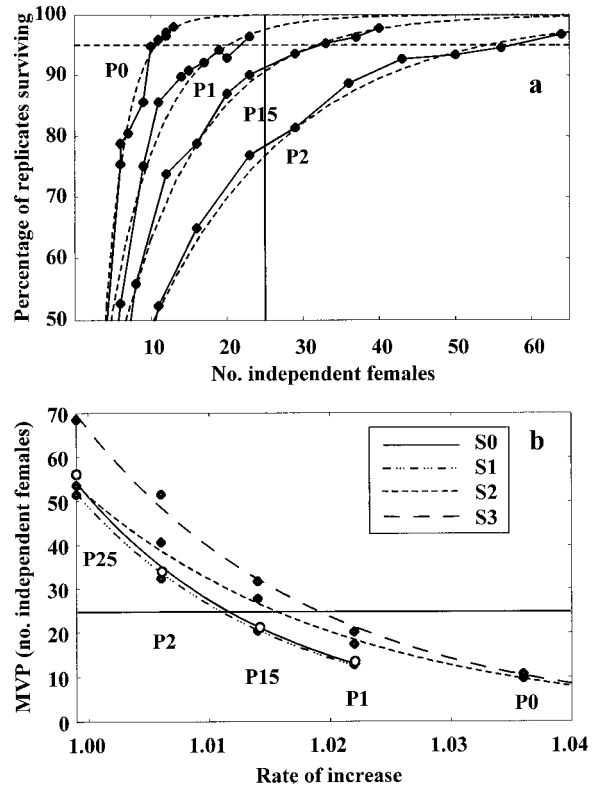


FIG. 9. Minimum viable population. (a) Percentage of 1600 replicates surviving the 100-yr test period vs. population size (number of independent females) for reference parameter sets P0, P1, P15, and P2, and scenario S3 of environmental variations. The dashed horizontal line gives the limit for 5% risk of extinction; the vertical line shows the estimated population size in 1995. All simulations with  $>95\%$  survival (data points above the 5% limit) satisfy the criterion for a viable population. Dashed lines indicate the fit of the simulated data points with exponential functions. (b) Correlation between minimum viable population (number of independent females) and deterministic rate of increase. Solid circles represent data from the simulation experiments for the reference parameter sets P25, P2, P15, P1, and P0. Open circles are data from scenario S0; the lines are interpolations of data points for scenarios S0–S3. The solid horizontal line represents the reconstructed population size in 1995. A population with a certain number of independent females and a certain parameter set satisfies the criterion of a viable population for a certain scenario (S0–S3) of environmental variations if the simulated data point is above the line that corresponds to the selected scenario of environmental variations.

Fig. 9b and Table 13 show that a population described through parameter set P2 satisfies the criterion of a minimum viable population if the population comprises  $\geq 32$  independent females (for scenario S0) or  $>52$  independent females if scenario S3 is assumed. Thus, our analysis shows that the western population of the Cordillera Cantabrica does not satisfy the criterion of a MVP. The risk of extinction exceeds the 5% limit within 100 yr.

The relationship shown in Fig. 9b can be used to define management goals. Minimal population sizes for

parameter set P1 are <25 independent females for all scenarios of environmental variations. The different reference parameter sets were linked through numbers of females “rescued” (Table 10); the difference between parameter set P2 and P1 yields  $(0.69 - 0.31) = 0.38$  independent females per year. This is equivalent to the salvation of one independent female every three years. Thus, the salvation of one independent female every three years (relative to the present mortality regime) would be the management goal that is required to lower the risk of extinction below the 5% limit within 100 yr for the western population of the Cordillera Cantabrica. To put these figures in the right context, the simulation of parameter set P2 yields a mean mortality of 3.5 independent females per year. These numbers also highlight the dramatic loss that every female found dead means for the survival of the population.

The influences of environmental variation on litter size, cub mortality, and age at first reproduction on MVP are weak (Fig. 9b; scenarios S0 vs. S1), but variations of adult and subadult mortality due to bad and good years (Fig. 9b; scenarios S1 vs. S2, S3) increase the MVP considerably (see also Table 13). Mortality records and the results of parameter adjustment (see *Results of the parameter adjustment: selecting the reference parameter set*) indicated substantial variation of mortalities between bad and good years, and favored scenarios S2 or S3, with high variation of subadult mortality.

Our simulation results show that a viable population size in the western population of the Cordillera Cantabrica, under the current mortality regime, must consist of >41 or 52 independent females (Table 13, Fig. 9) for the probable scenarios of environmental variation S2 or S3, respectively. Total population sizes for these estimates are 107 (for S2) and 136 (for S3), with an approximate fraction ( $f = 0.383$ ) of independent females within the population (Table 13). The salvation of one female every three (parameter set P1), or every four years (parameter set P15) would reduce the minimum viable population size to 32 independent females (for parameter set P15 with S3), or to 20 independent females (for P1 with S3). The corresponding total population sizes are ~82 and 50 individuals, respectively.

Boyce (1995) provided a review on population viability and MVP for grizzly bears. The first PVA for any species, conducted by Shaffer (1983), estimated a population size of 35 grizzly bears at Yellowstone as minimum viable population size, but because of uncertainty associated with the estimation of mortality rates, Shaffer (1983) suggested that the estimate should be increased to 50. Shaffer and Samson (1985) later re-estimated the MVP to 50–90, and Suchy et al. (1985) used 1975–1982 radiotelemetry data to update Shafer’s (1983) PVA. MVP from Suchy et al. (1985) varied between 40 and 225 individuals, depending on the mortality scenarios assumed. Suchy et al. (1985) recommended that a population size of 125 be maintained to

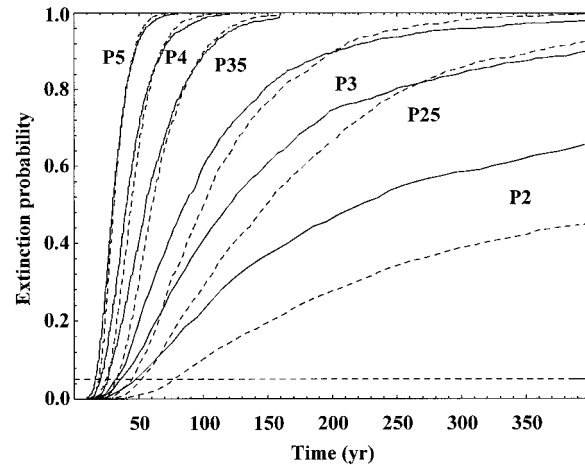


FIG. 10. The probability of extinction of a population with 25 independent females, depending on the number of years of simulation, for the different parameter sets P2–P5 under scenario S0 (dashed line, no environmental variation) and scenario S3 (solid line, maximal environmental variation). The horizontal dashed line shows the 5% limit.

ensure a high probability of a viable population for at least 100 years. Our estimates for MVP are within the range for MVPs estimated for grizzly bears. However, probably because of the high uncertainty associated with the estimations of total population sizes and model parameters, especially for mortality rates, and the resulting variation in the MVP estimates (35–225 individuals), the concept of MVP was largely neglected in later studies.

#### Time to extinction

A second concept that highlights the influence of stochasticity on the risk of extinction is the time to extinction. Starting with the estimated actual population size of 25 independent females, we performed a series of 1600 simulations for the parameter sets P15 to P5 and determined the probability of extinction for a given time step. As for MVP, we repeated the simulation experiment for different scenarios (S0, S1, S2, S3) of environmental variation. The initial population was calculated with the analytical model (see Appendix A.) and consisted of 9 subadult females, 7 subadult males (2–4 yr old), 16 adult females, and 11 adult males (5–15 yr old).

Fig. 10 shows the probability with which a population containing 25 independent females (a total population size of ~60 individuals) will suffer extinction after  $t$  years. The results of these simulation experiments again show that the western population in the Cordillera Cantabrica, with an estimated present population size of 25 independent females, is not “viable.” For the present mortality scenario (parameter set P2), the risk of extinction reaches the 5% limit after ~50 yr with (or 70 yr without) environmental variation of adult and subadult mortality; the risk of extinction after

TABLE 14. Mean extinction times for a population with an initial number of 25 independent females for different reference parameter sets and different simulation scenarios. The deterministic rate of increase is indicated by  $\lambda_{\text{det}}$ , and  $T_0$  is the deterministic extinction time calculated with Eq. 10.

Set	$\lambda_{\text{det}}$	$T_0$	Mean extinction time (yr), by scenario				
			M	S0	S1	S2	S3
P15	1.014	$\infty$					
P2	1.006	$\infty$					
P25	0.999	3005	275	185	230	231	202
P3	0.993	428	164	116	122	115	111
P35	0.977	129	87	66	67	64	62
P4	0.962	78	62	46	47	46	44
P5	0.938	47	44	32	33	32	32

Notes: Scenario M is the same as scenario S1, but reproduction does not depend on presence of adult males; scenario S0 has no environmental stochasticity; and S1–S3 are scenarios with environmental fluctuation (see Table 6).

100 yr is  $\sim 23\%$  (11% without environmental variation).

The probability of extinction increases rapidly for parameter sets P5, P4, P35, and P3, which have a rate of increase of  $\lambda < 1$  (Fig. 10). Environmental variation of female adult and subadult mortality has a considerable impact on the risk of extinction (Table 14).

Curiously, mean extinction times are longer in scenarios with environmental stochasticity than in the scenario without environmental stochasticity (c.f. scenarios S0 and S1 in Table 14). This is because variation of cub mortality with the climatic index (Eqs. 2 and 3) has a nonsymmetric effect on demography. In bad years, more females lose their entire litter and can breed earlier (see rules 1 and 2). This effect lowers the mean litter interval and has a positive impact on population growth and, consequently, increases mean extinction times. Interestingly, the analysis of extinction times for the different scenarios (S2 and S3) with considerable variation of subadult and adult mortalities shows a weak impact of environmental stochasticity (Table 14). In contrast, environmental variation of subadult and adult mortalities had a considerable impact on the risk of extinction (Fig. 10) and on MVP (Fig. 9b, Table 13). This is because the mean extinction time equilibrates earlier extinction (due to series of bad years) with prolonged survival (due to series of good years), whereas the 100-yr limit of MVP only captures earlier extinctions.

To further investigate the influence of stochasticity on the mean extinction time, we calculate the deterministic extinction time  $T_0$  of a decreasing population with initial population size  $N_0 = 60$  and a rate of increase  $\lambda$  as

$$T_0(\lambda) = \frac{\log[N_{\text{ext}}/N_0]}{\log[\lambda]} \quad (10)$$

where  $N_{\text{ext}}$  gives the assumed extinction threshold. We choose  $N_{\text{ext}} = 3$  because an ideally distributed popu-

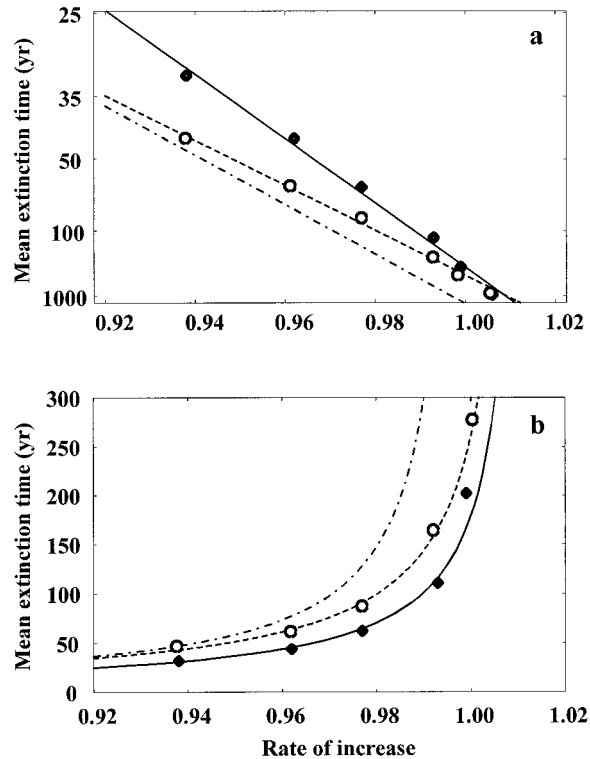


FIG. 11. Mean extinction times for a population with 25 independent females, depending on the rate of increase: (a) transformed to a linear relation with Eq. 11; and (b) indicating the original nonlinear relation. Solid circles are the simulation results, with the solid line fit for scenario S3; open circles represent scenario S1, but with reproduction not dependent on the presence of adult males (dashed line). The dot-and-dash line shows the deterministic case without any stochasticity, and the dashed line presents scenario S1, but with reproduction not dependent on the presence of adult males.

lation with three individuals contains one independent female. We plot our data with the following transformation:

$$T_0 \rightarrow \exp[1/T_0] \quad (11)$$

which makes Eq. 10 linear for  $\lambda$  (Fig. 11a). The linear relation also holds for the results of the stochastic simulations. Stochasticity shifts the deterministic threshold of  $\lambda = 1$  (here, the extinction time becomes infinity) to a value of about  $\lambda = 1.013$  (Fig. 11a). The threshold  $\lambda = 1.013$ , where mean extinction times become infinite for stochastic simulations, coincides with the rate of increase of parameter set P15 (Table 10) that yields a minimum viable population for the S1 scenario of environmental stochasticity.

Fig. 11a demonstrates that behavioral rules, such as the presence of adult males for reproduction, can have some impact on calculated extinction times. Interestingly, extinction times without this rule shift between deterministic extinction times, if rates of increase are low, and the stochastic case, if rates of increase are

high (Fig. 11a), because this rule only becomes important if population sizes are very small.

#### DISCUSSION

##### *Benefits and shortcomings of the model*

*Benefits of the model structure.*—We created a “minimalistic” model balanced between the two antipodes of too many and too few parameters (Boyce 1991): enough parameters to capture the processes that are essential for the aim of the model on the level of description chosen, but not too many parameters to minimize the degree of freedom for parameter estimation and to keep the model manageable. The choice of a specially constructed, individual-based model (DeAngelis and Gross 1992, Judson 1994) facilitated incorporation of the knowledge available in a natural and direct way. We were not faced with the problem of parameterizing available PVA computer programs (Boyce 1995, Mills et al. 1996) and could incorporate a great deal of structural knowledge. For example, the way in which we modeled the independence of cubs and next reproduction of females is much closer to the biological process and draws on more biological knowledge than does assuming certain probabilities for certain litter intervals. Including these simple behavioral rules automatically delivered us the complicated stochastic structure of female fertility at different ages and probabilities of different litter intervals. Otherwise, one has to assume, “off the cuff,” some possibly erroneous stochastic distributions.

Mills et al. (1996) stated that

*a biologist fortunate enough to have data to parameterize a simulation model that is qualitative and demographically explicit has the potential advantage of being able to capture the interacting factors that influence population persistence. In most cases, however, there is neither the time nor expertise to develop a complex, species-specific PVA computer program; the reality is that biologists must choose from more generalized and readily available programs.*

This statement illuminates strikingly one of the current dilemmas of PVA. We have shown that squeezing as much information as possible out of the available data and knowledge requires specific methods and specially constructed species-specific models. This is still true if we consider the imminent and intrinsic lack of data in conservation biology. Without such a case-specific approach, PVA may lose its predictive power. In such cases, PVA can, however, greatly contribute to better understanding of population dynamics by the ability to make intuition explicit, that is, to incorporate a number of factors that influence population growth, thereby suggesting potential consequences of a range of management options (Mills et al. 1996). However, avoiding confusion, polemics, or even frustration about the value of PVA requires a clear statement of objectives (e.g.,

quantitative predictions, yes or no, etc.), clarity about the capacity of the model or program used, and realism about the data that form the basis of the PVA. As one wears out guesswork or adds complicated factors that cannot be parameterized properly, the analysis of results becomes incomprehensible. This is also the weak point of generalized and readily available MVP programs. The user can select from a variety of readily available mechanisms and processes (e.g., multiple populations, genetics, inbreeding depression, Allee effect, different forms of environmental and demographic stochasticity, shape and slope of density-dependent regulation, sex-specific and age-specific vital rates, etc.) and may get lost.

However, the main problem that we faced, when performing a population viability analysis of the brown bear in the Cordillera Cantabrica, was the determination of the model parameters. The lack and uncertainty of data required specific, nonstandard methods to exploit available knowledge in the most efficient and exhaustive way. We first determined the model parameters that are directly accessible through data from the Cordillera Cantabrica, and approximated the remaining model parameters through comparison with data from the literature. To determine the values of the unknown parameters more precisely, we utilized additional information given through the observed 14-yr time series of numbers of females with cubs of the year (COY index). To do this, we incorporated environmental variations in our model that were correlated across litter size, age at first reproduction, and mortality. The nonlinear interaction of environmental variations among these three processes resulted in a complicated pattern of the numbers of females with cubs (COY index). We found that the COY index contains information about reproductive parameters and mortality in an encoded way that one cannot usually decipher and that is thus lost. Building the code into the model and comparing the simulated COY index with the 14-yr time pattern of observed data enabled us to extract additional information that was consistent with other data and quantitative observations. However, such a specific exploitation of available knowledge would be impossible with general PVA computer programs. The gains from this immense exercise were a credible reference parameter set, a series of probable mortality scenarios that are linked to management relevant variables, and an estimate of the actual population size; both were the basis for our viability analysis. Our approach of simultaneous parameter adjustment allows for a more precise determination of population parameters than would be possible with other methods that estimate population parameters independently. This is because the “filter” of the COY index considers relationships between parameters and excludes much of the confidence ranges for each of the single-parameter estimates.

The somewhat artificial distinction between mortal-

ities (mortalities via the mortality rates  $m_i$  and mortalities via the mortality time pattern  $J(t)$ ) during the process of parameter adjustment allowed for a precise adjustment of an annual mortality pattern that we could relate to existing mortality records. Furthermore, this approach enabled us to study the evolution of the population size in more detail. We found that the population trend was more of a nonlinear process, with a dramatic decline during the mid-1980s and a subsequent period of relative stabilization, rather than a continuous process of decline. Although the COY index shows the same trend, the evolution of the total population size does not necessarily follow the COY index (Eberhardt and Knight 1996). Finding a probable population trend had important implications for an assessment of the actual state of the population and, thus, for management.

*Deterministic model.*—The deterministic model that describes the mean behavior of the population turned out to be a valuable tool for analyzing the simulation output, and it enabled us to perform an extensive sensitivity analysis. Our results demonstrate that the underlying structure is always revealed by the deterministic model, but clearly is modified by stochastic and annual mortality patterns. The considerable effort required to include behavioral rules in the deterministic model was fruitful, as proven by the good accordance between predictions from the deterministic model and mean simulation outcomes. Having the deterministic model in the background enabled us to perform an “intelligent analysis” of our simulation model, and knowing the relationships behind the parameters saved a lot of simulation time. Furthermore, the deterministic model provided means for assessing the influence of stochasticity, specially on extinction times, and was a vitally important tool for detecting programming and logical errors in the simulation model.

*Environmental variation.*—We use one simple climatic index (Eq. 1) to correlate food abundance via climate with the probability of first litter, litter size, and mortality. On the first glance, however, it might be more favorable to construct several indices that relate probability of first litter, litter size, and mortality more specifically to the different sources of food. However, this would give our model an inadequate level of detail, and there are not enough data available to calibrate the different indices. Therefore, we decided to use only one simple index that roughly summarizes the relationships between climate, mortality, and reproduction, but that still keeps the essentials of the processes. However, our data show reasonable differences between observed cub mortality and mean litter sizes (Table 2A) in bad and good years, as defined by our simple climatic index. A similar climatic index (Picton 1978) has been used by Picton and Knight (1986) to predict grizzly bear litter size in Yellowstone. Picton et al. (1986) considered that variations in climatic data, especially precipitation, could be used as an index for the variation

of food availability. They argued that lack of food may stimulate unusual movements of bears into areas with higher human densities, which are normally avoided, and thus may increase considerably the probability of human-caused mortalities (see also Mattson and Reid 1991, Rogers 1993, Primm 1996). This type of index has also been used for various species of large ungulates to connect survival of neonate cubs with food abundance (Picton 1984, Douglas and Leslie 1986).

We found a considerable impact of environmental variation in adult and especially subadult mortality on MVP and the risk of extinction. However, the influence of environmental variation of cub mortality, litter size, and first reproduction on MVP remained weak (Fig. 9b, Table 13). Our sensitivity analysis can explain the high impact of variations in subadult mortality. For scenario P2, which describes the current situation in the Cordillera Cantabrica, and coefficients of variation from scenario S3 ( $v_{1-4} = 0.66$ ,  $v_{5-24} = 0.33$ ), we obtain total variations of cub mortality ( $\Delta(m_0) = 0.3$ ), subadult mortality ( $\Delta(m_{1-4}) = 0.22$ ), adult mortality ( $\Delta(m_{5-16}) = 0.02$ ), litter size ( $\Delta(L) = 0.75$ ) and first reproduction ( $\Delta(R) = 1$ ). The resulting sensitivity index  $\rho$  yields maximal variations of the rate of increase of about  $\rho(m_0) \approx 0.05$ ,  $\rho(m_{1-4}) \approx 0.11$ ,  $\rho(m_{5-16}) \approx 0.03$ ,  $\rho(R) \approx 0.03$ , and  $\rho(L) \approx 0.03$ . Thus, the potential impact of subadult mortality on the rate of increase is twofold or threefold that of the other varied parameters.

Several clues, from model results, data, and literature, indicate that subadult mortality may indeed vary strongly between bad and good years. Firstly, parameter variations with coefficients ( $v_{1-4} = 0.66$ ,  $v_{5-24} = 0.10$ ; Table 8, R11) did not result in significantly worse fits than did scenarios without environmental variation of adult and subadult mortality (Table 8, R8 and R9). Secondly, the mortality records indicate high coefficients of variation between bad and good years (5 out of 6 subadult and 8 out of 12 adult mortalities were during bad years). Thirdly, there is evidence that food shortages may indirectly influence adult, and especially subadult, survival. Lack of food may stimulate unusual movements of inexperienced subadults into areas with higher human densities that are normally avoided. Such movements increase the risk of human–bear encounters and thus the probability of human-caused mortalities (Mattson and Reid 1991, Rogers 1993, Primm 1996). In Yellowstone, the number of adult female deaths escalates substantially during poor food years (Knight et al. 1988, Blanchard 1990, Mattson and Reid 1991), when there are fewer rich feeding opportunities and subordinate or security-conscious bears are displaced by adult males to less secure, lower elevation areas near human facilities.

We suspect two reasons for the weak impact of environmental variation of cub mortality, litter size, and first reproduction on MVP. Firstly, bad and good years are not the same for mortality and reproduction. A good year for reproduction (high litter size and earlier first

reproduction) was defined through food abundance of the previous year, whereas a year with high food abundance was a year with low cub mortality. This 1-yr delay for reproduction in relation to mortality causes a desynchronization of environmental variations and may soften its effect. Secondly, the life history strategy of bears emphasizes long life, reducing the impact of variability in recruitment rates and cub survival on population growth rate (Taylor et al. 1987). The long time delay of 4–5 yr to maturity and the long reproductive stage of ~10 yr buffer some of the environmental variations that operate on an annual basis.

The impact of environmental variations on mean extinction times was weak (Table 14), although environmental variations increased the risk of extinction considerably on scales of up to 200 yr (Fig. 10). Earlier extinction due to a series of bad years can be balanced out by prolonged survival due to a series of good years.

*Density-dependent regulation.*—Although evidence for density dependence among black, brown, and polar bear populations on present population sizes is scarce (Derocher and Taylor 1994, Garshelis 1994, McLellan 1994), density-dependent regulation will ultimately affect every population at the limits of its carrying capacity. For bears, an array of life history parameters may be affected by density, including age at first reproduction, litter size, fraction of available females that mate and produce cubs, and survival (Taylor 1994). Cub production and cub survival are the parameters most likely to be reduced by density effects, and the parameters most likely to be affected by density are those most likely to be affected by environmental variation (Taylor 1994). However, if major effects of density on life history parameters and population growth rate occur near carrying capacity (Fowler 1981, 1987), then population densities of human-impacted populations may be sufficiently low that changes in vital rates and population growth rate may stem from stochastic factors rather than density effects (Taylor 1994).

We did not include density dependence in the (sometimes controversially discussed) way that most PVA and grizzly bear models did (Shaffer 1983, Harris et al. 1986, Akçakaya 1992, Downer 1993, Lacy 1993), but we considered the essentials of density dependence that were obvious for the Cantabrian population. The spatial pattern of females with cubs during the last 14 yr indicates that a maximum of ~18 females could breed simultaneously. By designating this limit for the number of successful breeding females, we affect the age at first reproduction, because older females breed first (see rule 4). However, a maximum of 11 females with cubs was observed in 1984, and current numbers of females with cubs did not exceed 7. Although present bear densities are far below the carrying capacity, our rule prevents unrealistic model outcomes for MVP and extinction times, without being the object of such irritation, as recently reported by Mills et al. (1996), that was caused by “projecting

ignorance about specific functions of density dependence and carrying capacity.”

*Genetics and inbreeding.*—We agree with Boyce (1992), Shaffer (1983), and Lande (1988) that modeling genetics is not likely to be as important as modeling demographic and ecological processes. This does not imply that genetic considerations are not important (Frankham 1995); rather, because of the missing link between genetics and demography (Boyce 1992), we do not yet have the data and the understanding to include genetics quantitatively in brown bear or grizzly bear models (Boyce 1995).

#### *The state of the population*

Our analysis provides a clear picture of the state of the Cantabrian brown bears. Our reconstruction of the population dynamics during the 1982–1995 period indicates that the population suffered a decrease of ~41% (Fig. 7) during the 1982–1995 period, from ~95 individuals down to a total of ~56 individuals. This is equal to an annual decline of ~4 or 5%. A comparison of the initial and final 3-yr means of the observed COY index indicates the same trend. Nevertheless, the evolution of the total population size does not necessarily follow the trend of the COY index (Eberhardt and Knight 1996).

However, our simulation results show that the situation during the first years of the study (until 1989) was especially serious. A high poaching pressure coincided with a series of climatically unfavorable years. Simulation results indicate that poaching, high cub mortality, later first reproduction, and small litter sizes caused an annual decrease of ~7% between 1982 and 1990. Thereafter, population size seems to have stabilized, but our MVP analysis shows that the population, which may, following our reconstruction, currently consist of 25 independent females, is not “viable” if mortalities remain at the level of recent years (1988–1995). The salvation of one independent female every 3 yr would keep the risk of extinction within 100 yr below the 5% limit of the MVP concept.

With the help of the simulation model, we uncovered the patterns and processes that led to the nonlinear regression of population size, and we were able to reproduce the essential aspects of the decline.

Our model estimates that the mean age at first reproduction in the Cordillera Cantabrica is lower than data from the bear literature (Le Franc et al. 1987; but see Bjärvall et al. [1990] for early sexual maturity of Scandinavian bears). This may indicate a relatively good nutritive state of the habitat, but it could also result from the demographic regression of the population (lack of females and unoccupied breeding habitat) or from population-specific life history traits that give rise to earlier breeding. In other species with deferred sexual maturity (e.g., large raptors, strongly *K*-selected species), high percentages of subadult or young adults within the breeding portion of the pop-

ulation have been observed when adult females have been removed from territories by human action, or when feeding conditions were especially good (Newton 1979). On the other hand, latitude may contribute to early maturity in the Cordillera Cantabrica. Stringham (in Bjärvall et al. 1990) found a negative correlation between age of sexual maturity and latitude.

Observed cub survival in the Cordillera Cantabrica is lower than that reported from other populations (see Table 3). This may be due to earlier breeding of inexperienced, young females. Also, females with cubs of the year may use poor-quality habitats. Wielgus and Bunnell (1994) found that adult females, especially females with offspring, avoid immigrant males, and this may lead females to use food-poor habitats. Also, if only a few adult males are present, subadult males may immigrate and kill cubs (Wielgus and Bunnell 1994).

However, mortality, especially that of adult females and, to a lesser degree, that of subadult females, turned out to be the most important factor in determining population dynamics. A similar result was found by Eberhardt et al. (1994) and Eberhardt (1995) for grizzly bears in Yellowstone. Generally, adult mortality is the most sensitive demographic trait of long-lived species with respect to the growth rate (e.g., Emlen and Pikitch 1989, Lande 1991, Lebreton and Clobert 1991). Both estimated subadult and adult mortality rates at the Cordillera Cantabrica are clearly higher than those of other endangered brown bear populations (Craighead et al. 1974, U.S. Fish and Wildlife Service 1993).

#### *Implications for management*

The critical condition of the population requires urgent and courageous management. Similar to Knight and Eberhardt (1985) and Eberhardt (1995), we found that adult female survival is the key to the recovery of the population, and thus forms the principal management objective. Consequently, a continuous monitoring of females with cubs appears to be the management action of highest priority, not only from the viewpoint of monitoring population size, but also as guardianship and guarantee of the survival of family groups.

Our analysis of MVP showed that the population is not viable if the mortality rates remain at the level of the last few years. As a rule of thumb, it appears necessary to save one independent female every three years to obtain a MVP. Simulations of population dynamics for the 1982–1995 period yielded a mean of ~4.7 mortalities of independent females per year (Table 7), and the mean number of registered mortalities for the 1982–1994 period was 1.2 deaths/yr (Table 4). Thus, approximately one in four mortalities was detected. The mortality records of the last few years (1988–1994) detected a total of 4.5 independent females (Table 4), with a mean mortality of 0.64 female/yr. The mean number of detected mortalities of independent females can be used as an index to control management success. Assuming equal detectability of

mortalities over the years, the management goal of “save one female every three years” would reduce this index from the present 0.64 females/yr to 0.56 females/yr.

Censuses of females with cubs and mortality records (sure and probable) are important sources of data about the state of the population and contain information about demographic parameters and their variation with climate in an encoded form. Thus, performance and the methodological perfection of the census appear to be indispensable for assessing demographic parameters and monitoring the evolution of the population. Concerning the census of females with cubs, the situation has been aggravated since 1994, when the official census was stopped, and the current management plans do not consider the compilation of mortality records. Although the mortality records contain qualitative information (e.g., differences between bad and good years, and differences between age classes), their utility for determining demographic parameters remains limited. Nevertheless, mortality is a key factor for population dynamics, and major efforts are necessary to improve mortality data collection, e.g., by means of long-term telemetric marking and tracking of individuals.

The census of females with cubs, as well as data on mortality, should be the subject of permanent revision and actualization. The analysis performed in this paper points to differences between the observed values of females with cubs and the estimates of the model (Fig. 6). The differences may also hint at deficits in the census, far beyond the limitations of the model, and recommend a revision, e.g., the case of 1988 (Fig. 6), which seems to be an outlier.

In our model, we used a simple rainfall index as an indicator for interannual environmental fluctuations, and with respect to mortality and litter size, we differentiated only between bad and good years (Eqs. 2 and 3, Table 2A). This assumption is a rough approximation that considers the impact of environmental variations on mortality and litter size in the simplest way. However, although this index contains reliable correlations with aspects of the demography and the biology of the Cantabrian bears (e.g., cub mortality, litter size, and mortality records), it is apparently necessary to use more direct relations between demographic parameters and the availability of trophic resources and their variation in space and time. This would, however, require temporal and spatial monitoring of the habitat.

The recovery plans for the Cordillera Cantabrica contain the option of providing additional food during years with food shortages. Yet, the reproductive parameters determined in this paper point to relatively good nutritive conditions in the habitat and do not support this management option. Furthermore, providing additional food brings additional risks, and our sensitivity analysis showed that a variation of fecundity does not contribute significantly to variations in the population's rate of increase.

Boyce (1993) offers PVA for grizzly bears as an example of adaptive resource management. Boyce (1995) argues that adaptive resource management is a never-ending process of iterating models with management and monitoring, and that it is clearly time for a new iteration of modeling. For grizzly bears, previous modeling efforts postulated that management targeting mortality reduction would allow the bear population to increase (Knight et al. 1988). This appears to have worked, and chance events may not be as serious a concern for the future of grizzly bears in the Rocky Mountains as the deterministic erosion of habitats for the species associated with human development and resource extraction (Boyce 1995). As a new iteration of modeling, Boyce (1995) recommended habitat-based PVA that will allow management to follow up on land use changes and to document the consequences for grizzly bear populations. We found that mortality is still the most pressing threat for the Cantabrian bears, but degradation of bear habitat can also be assessed and understood in terms of human access to bears and resultant bear mortality (Primm 1996). However, we do not know if and how mortalities, especially poaching, are connected with habitat quality or the degree of human presence. An identification of areas that carry a high risk of human–bear contacts and an evaluation of the influence of such sinks (Pulliam and Danielson 1991, Doak 1995) on population dynamics are needed to eradicate the most immediate threat to the Cantabrian bears: human-caused mortalities. Thus, bear management in the Cordillera Cantabrica should include the analysis and monitoring of the habitat, including the spatiotemporal availability of trophic resources and human activity. For evaluating long-term population viability, a subtly differentiated view of habitat quality (Mladenoff et al. 1995) and risk areas, habitat cutting, or source–sink features (Doak 1995), as well as long-term habitat changes (Mattson and Craighead 1994, Boyce 1995) appears to be indispensable. We will extend the present nonspatial model toward a spatially explicit population model (Dunning et al. 1995) that allows us to perform a habitat-based PVA and to fulfill the new iteration of modeling demanded.

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## APPENDIX A

To calculate the fertility  $y_i$  of females at age  $i$ , we proceed with the following hierarchical scheme. We start with the highest level (fertility  $y_i$ ) and determine the immediate variables (situated “one level lower”) that are necessary to calculate the variable one level higher. For example, to calculate the fertility  $y_i$ , we need to know the fraction of females accompanied by a first litter at age  $i$  and the probability that two litters are  $k$  years apart. To calculate the probability that two litters are  $k$  years apart, we need to know the fraction of females with a litter interval of  $j$  years. To calculate the fraction of females with a litter interval of  $j$  years, we need to know the fraction of family breakups with cubs of age  $k$  and the fraction of females that reproduce  $j$  years after the last family breakup. In this way, we proceed until we can calculate all the variables of the analytical model with the model parameters given in Table 1.

*Fertility.*—For the calculation of the fertility  $y_i$  of females at age  $i$ , we consider the life history traits of females shown in Fig. 2. To calculate fertility for a given age  $i$ , we sum all possible combinations of litters up to age  $i$  that include a litter at age  $i$ :

$$y_i = \begin{cases} \left( F_i + \sum_{k=4}^{i-1} F_k B_{i-k} \right) s_f Z & i = 4, \dots, 15 \\ \frac{s_f Z}{M} & i = 16, \dots, 25. \end{cases} \quad (\text{A.1})$$

$F_i$  is the fraction of females accompanied by a first litter at age  $i$ ,  $B_k$  is the probability that two litters are  $k$  years apart (no matter how many litters there were in between),  $Z$  is the mean litter size,  $s_f$  is the probability that a cub is female, and  $M$  is the mean litter interval. We approximate fertility of females >15 yr old with a simpler method using mean litter interval.

*Probability for two litters  $i$  years apart.*—We calculate the probabilities  $B_i$  by summing all possible combinations of one, two, three, four, or five litters. As a first step, we define the sum  $BB_{p,i}$  that gives the probability that two litters are  $i$  years apart, but with a total of  $p + 1$  litters:

$$\begin{aligned} BB_{1,i} &= b_i & i=1, \dots, 7 \\ BB_{2,i} &= \sum_{k=2}^{i-2} b_k b_{i-k} \\ BB_{3,i} &= \sum_{\substack{k+l+m=i \\ k \geq l \geq m}} b_{klm} b_k b_l b_m \\ BB_{4,i} &= \sum_{\substack{k+l+m+n=i \\ k \geq l \geq m \geq n}} c_{klmn} b_k b_l b_m b_n \\ BB_{5,i} &= \sum_{\substack{k+l+m+n+o=i \\ k \geq l \geq m \geq n \geq o}} d_{klmno} b_k b_l b_m b_n b_o \end{aligned} \quad (\text{A.2})$$

with

$$b_i = 0 \quad i \geq 8.$$

The  $b_i$  are the fraction of females with a litter interval of  $i$  years, and  $b_{klm}$ ,  $c_{klmn}$ , and  $d_{klmno}$  are coefficients (Table A.1). To obtain the final formula for the probabilities  $B_i$ , we consider cases with 0, 1, or 2 occurrences of a litter interval of 1 yr. We neglect cases with more than two litters that have a litter interval of 1 yr, because the probability  $b_i$  for a litter interval of 1 yr is always small. There are  $p + 1$  possibilities of placing one litter within a sequence of  $p + 1$  litters, and  $(p + 1)(p + 2)$  possibilities of placing two litters within a sequence of  $p + 1$  litters. Thus, the total probability  $B_i$  that two litters are  $i$  years apart, no matter how many litters are in between, yields

$$\begin{aligned} B_i &= \sum_{p=1}^5 BB_{p,i} + b_1 \sum_{p=1}^5 (p + 1) BB_{p,i-1} \\ &+ b_1 b_1 \sum_{p=1}^5 (p + 1)(p + 2) BB_{p,i-2}. \end{aligned} \quad (\text{A.3})$$

*Litter interval.*—The fraction of females with litter interval  $i$  is

TABLE A1. The non-zero coefficients  $b_{klm}$ ,  $c_{klmn}$  and  $d_{klmno}$ .

$i$	$(k, l, m)$	$b_{klm}$	$(k, l, m, n)$	$c_{klmn}$	$(k, l, m, n, o)$	$d_{klmno}$
6	222	1				
7	322	3				
8	332	3				
8	422	3	2222	1		
9	333	1	3222	4		
9	432	6				
9	522	3				
10	433	3	3322	6	22222	1
10	442	3	4222	4		
10	532	6				
10	622	3				

$$b_i = \begin{cases} \sum_{k=0}^{i-1} U_k H_{i-k} & i < 8 \\ 0 & i \geq 8 \end{cases} \quad (\text{A.4})$$

where  $U_k$  is the fraction of family breakups with cubs of age  $k$ , and  $H_j$  is the fraction of females that reproduce  $j$  years after the last family breakup. To calculate the mean litter interval  $M$ , we have to consider the mortality of females that cannot complete a full cycle; thus,

$$b_i^* = \sum_{k=0}^{i-1} m^i U_k H_{i-k} \quad (\text{A.5})$$

and

$$M = \frac{\sum_{i=1}^7 i b_i^*}{\sum_{i=1}^7 b_i^*} \quad (\text{A.6})$$

where  $m$  is the mean mortality rate of adult females. We calculate  $m$  as

$$m = \frac{\sum_{i=5}^{26} m_i^f s_i}{\sum_{i=5}^{26} s_i} \quad (\text{A.7})$$

where  $m_i^f$  is the female mortality rate at age  $i$  and  $s_i$  is the fraction of females surviving to age  $i$ .

*Fraction of family breakups.*—Family breakup occurs if the entire litter dies or if the litter becomes independent; thus, the fraction  $U_i$  of females that reproduce  $i$  years after the last family breakup is

$$U_i = \left[ 1 - \sum_{k=0}^{i-1} U_k (E_i + (1 - E_i) I_i) \right]_{i=1,2,3} \quad (\text{A.8})$$

where the  $I_i$  is the fraction of litters that become independent at age  $i$ , and  $E_i$  is the fraction of entire ( $i$ -yr-old) litters lost.

*Fraction of litters lost.*—The entire litter has died with age  $i$  if at least one cub has died at age  $i$  and no cub reaches age  $i + 1$ ; thus,

$$E_1 = \sum_{i=1}^4 w_i D_0^i \quad (\text{A.9})$$

$$E_2 = \sum_{i=1}^4 w_i [(D_0 + D_1)^i - D_0^i] \quad (\text{A.10})$$

$$E_3 = \sum_{i=1}^4 w_i [(D_0 + D_1 + D_2)^i - (D_0 + D_1)^i] \quad (\text{A.11})$$

TABLE A2. The variables and parameters of the analytical model.

Variable	
$s_i^f, s_i^m$	fraction (females, males) surviving to age $i$
$y_i$	fertility at age $i$
$\lambda$	rate of increase
$F_i$	fraction of females accompanied with first litter at age $i$
$B_k$	Probability of two litters being $k$ years apart
$Z$	mean litter size
$s_f$	probability of cub being female
$M$	mean litter interval
$b_k$	fraction of females with litter interval $k$
$U_k$	fraction of family break-ups with litter $k$ years old
$H_k$	fraction of females reproducing $k$ years after family break-up
$E_i$	fraction of entire ( $i$ year old) litters lost
$I_i$	fraction of litters becoming independent at age $i$
$D_i$	fraction of cubs dying to age $i$
$w_k$	probability of litter size $k$
$m$	mean mortality rate of adult females
$o$	fraction of orphans
$S_i^{\text{none}}$	probability that a female of age $i$ has no litter
$S_i^k$	probability that a female of age $i$ had the last litter $k$ years ago

where the  $w_i$  is the probability for a litter size  $i$  and the  $D_i$  is the probability that a cub has survived to age  $i - 1$  but dies at age  $i$ ; and

$$\begin{aligned} D_0 &= (1 - o) \frac{(m_0^f + m_0^m)}{2} + om_0^o \\ D_1 &= \frac{(s_1^f + s_1^m) (m_1^f + m_1^m)}{2} \\ D_2 &= \frac{(s_2^f + s_2^m) (m_2^f + m_2^m)}{2} \end{aligned} \quad (\text{A.12})$$

where  $o$  is the fraction of orphan cubs;  $m_0^o$  is the mortality rate of orphans;  $s_i^f$  and  $s_i^m$  are the survival rates up to age  $i$  for females and males, respectively; and  $m_i^f$  and  $m_i^m$  are the corresponding mortality rates at age  $i$ . The fraction of orphans is approximately the mean mortality rate of adult females (Eq. A.9).

*Initial state of the population.*—Before running a simulation, we have to specify the initial reproductive state of the females. We can do this by using results from the analytical model. First, we calculate the probability  $S_i^{\text{none}}$  that a female of age  $i$  has no litter (“age of last cubs” = “none” and “time since family breakup” = “none”; see Tables 1 and A.2) as

$$S_i^{\text{none}} = 1 - \sum_{j=4}^i F_j \quad (\text{A.13})$$

where  $F_j$  is the fraction of females with first litter at age  $j$ . The probability  $S_i^k$  that a females of age  $i$  had the last litter  $k$  years ago (“age of last cubs” =  $k$  and “time since family breakup” =  $k - 1$  for  $k > 1$  and “none” for  $k = 0$ ) yields

$$S_i^k = \frac{1}{s_f Z} y_{i-k} \left( 1 - \sum_{j=1}^k B_j \right) \quad (\text{A.14})$$

where  $Z$  is the mean litter size,  $s_f$  the probability that a cub is female,  $y_{i-k}$  the fertility of a female at age  $i - k$  (see Eq. A.1) and  $B_j$  the probability that two litters are  $j$  years apart (see Eq. A.3).

APPENDIX B

To find the parameter set that minimizes the error between the simulated COY index and the data (Eq. 8), we combine simulations with a theoretical optimization. We search each parameter set for an optimal initial population size  $P_0$  and an optimal mortality time pattern  $J_{op}(t)$  that minimize the error  $\Delta$  between the simulated COY index and the data. Fig. B1 shows the flow chart of this procedure.

In a first slope (internal box), we iterate the optimal initial population size  $P_0$  for a given parameter set and for a given mortality time pattern  $J(t)$ . In each iteration step, we perform 200 simulation runs and calculate the resulting error  $\Delta$  between the mean COY index,  $COY(t)$ , of the 200 simulations and the data. To minimize possible effects of the initial population, we start all simulations in 1975. The seven additional simulation years, 1975–1981 (data for the COY index are

only available since 1982) add a sufficient degree of environmental “history” and ensure that the simulated COY index of the subsequent period (1982–1995) does not depend on the particular initial population we have chosen.

In the second slope (outer box), we optimize the mortality time pattern  $J(t)$  and perform a theoretical optimization of  $J(t)$  (box “optimization mortality pattern” in Fig. B1). The basic idea of this step is that a slightly different mortality pattern  $J^*(t)$  (e.g., one additional mortality in the year  $t^*$ ) may result in a slightly different COY index,  $COY^*(t)$ . If we could predict the approximate relation between one additional mortality in the year  $t^*$  and the resulting changes of the COY index [ $k(t, t^*)$ ],

$$COY^*(t) = \sum_{t=t^*}^{1995} [COY(t) + k(t, t^*)] \quad (B.1)$$

with

$$J^*(t) = \begin{cases} J(t) & t \neq t^* \\ J(t) + 1 & t = t^* \end{cases} \quad (B.2)$$

then we could search for alterations  $\delta(t)$  of the initial mortality time pattern that shapes the COY index in such a way that the error  $\Delta$  of Eq. 8 becomes minimal. We found

$$k(t, t^*) = \begin{cases} -0.267 + 0.0082(t - t^* - 1) & t > t^* \\ 0 & t \leq t^* \end{cases} \quad (B.3)$$

Eq. B.3 was obtained by running several series of simulations with optimal initial population sizes  $P_0$  and with different parameter sets. The coefficients were basically independent of the parameter set used.

Thus, a mortality time pattern  $J^*(t)$  that differs from the initial mortality pattern  $J(t)$  in  $J^*(t) = J(t) + \delta(t)$  changes the initial COY index  $COY(t)$  to approximately  $COY^*(t)$ :

$$COY^*(t) = \sum_{t=1982}^{1995} \sum_{t=t^*}^{1995} (COY(t) + \delta(t^*)k(t, t^*)). \quad (B.4)$$

The search for alterations  $\delta(t)$  that minimize Eq. 8 is a classical problem of finding a minimum in a multidimensional space. We employ the Powell algorithm (Press et al. 1993), with the additional constrain  $\delta(t) < J(t)$  (no release or immigration of females), to find the optimal alteration  $\delta_{opt}(t)$  so that the resulting COY index ( $COY^*(t)$ ) minimizes Eq. 8.

After finding a better mortality time pattern  $J^*(t)$ , we return to the starting point and reenter the internal box, but we now simulate with the mortality time pattern  $J^*(t)$  instead of  $J(t)$ . We continue iterating until the resulting error  $\Delta$ , at iteration steps  $i$  differs only slightly from the error in the next step ( $\Delta - \Delta_{i+1} < 0.025$ ).

Usually, we needed four or five iteration steps of the internal box to find an optimal initial population size  $P_0$ , and two or three iterations of the outer box to find the optimal mortality time pattern  $J_{opt}(t)$ . Thus, the optimization procedure for a single parameter set required the performance of ~3000 simulation runs. Because the values of the mortality time pattern are restricted to positive numbers (no immigration), each parameter set had a typical error  $\Delta$  that could not be further diminished.

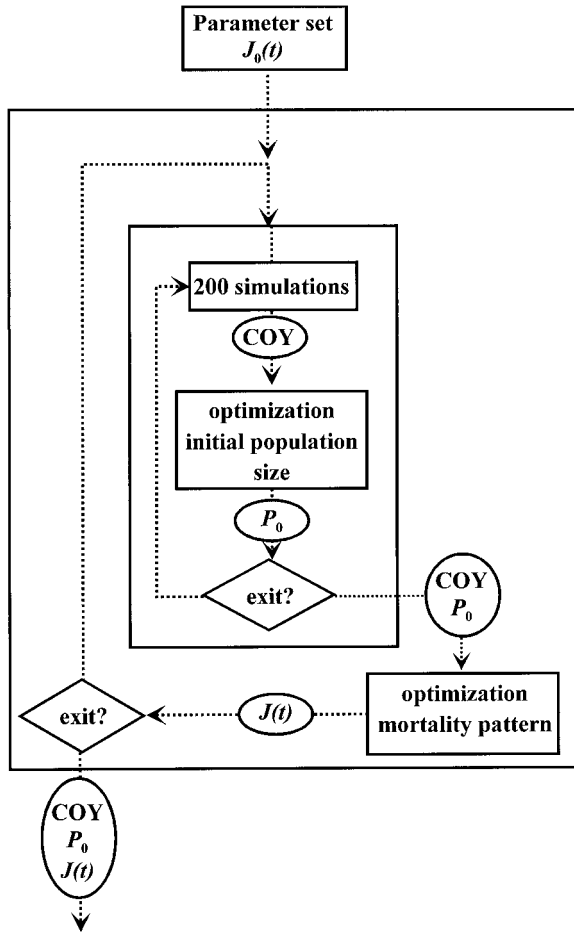


FIG. B1. Flow chart for the parameter variation.  $J_0(t)$  is the arbitrary initial mortality time pattern; COY is the mean simulated COY index;  $P_0$  is the initial population size; and  $J(t)$  is the mortality time pattern obtained from the Powell algorithm.