

Trends in number and distribution of brown bear females with cubs-of-the-year in the Cantabrian Mountains, Spain

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Abstract: Brown bears (*Ursus arctos*) in the Cantabrian Mountains of northwestern Spain occur in 2 small, isolated, and endangered populations: the western population (WP) and the smaller eastern population (EP) were studied from 1989 to 2004. We documented the number of unique females with cubs-of-the-year (F_{CUB}), the number of cubs per female, and the area occupied by F_{CUB} . The estimated number of F_{CUB} using the Chao mark–resight estimator was similar to a conservative number of F_{CUB} obtained using protocols to distinguish unique animals (\hat{N}_{Obs}). In the WP, \hat{N}_{Obs} increased during the period, whereas the trend suggested by the index in the EP did not differ from 1.0. The number of cubs per female was slightly higher in the WP (1.8) than in the EP (1.5). The area occupied by F_{CUB} initially decreased followed by a recovery in both populations. Nevertheless, the area occupied as of 1989–92 had not been completely re-colonized by 2001–04. The areas apparently abandoned by F_{CUB} were situated in the middle of the 2 populations, so the gap between them was wider in 2001–04 than in 1989–92. We conclude that brown bears in the Cantabrian Mountains are recovering, but the isolation of the 2 populations jeopardizes this recovery. Both populations are still endangered, especially the EP, for which we estimated only 0–3 breeding females/year. Conservation priorities include promoting recovery of range previously occupied by breeding females and increasing contact between the populations.

Key words: brown bear, Cantabrian Mountains, conservation, demography, distribution, females with cubs, trends, *Ursus arctos*

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Historically, in Europe the distribution of the brown bear (*Ursus arctos*) included roughly all of the broadleaved and coniferous forests (Curry-Lindhal 1972). Currently, several large populations persist in northern and eastern Europe, but in western Europe, the only 4 remnant populations are in the Apennines, the Alps, the Pyrenees, and the Cantabrian Mountains (Servheen et al. 1999).

In northern Spain, the brown bear populations in the Cantabrian Mountains and the Pyrenees became isolated between the 17th and the beginning of the 19th century (Nores and Naves 1993). From that point forward, the Cantabrian population suffered a steady, severe reduction in size and an increase in

fragmentation, which has led to the formation of 2 apparently isolated populations: the western population (WP) and eastern population (EP). Since the middle of the 20th century, the range of these populations has changed little. In 1993, the WP and the EP were separated by approximately 30 km of unoccupied habitat and occupied about 2,600 km² and 2,480 km², respectively (Palomero et al. 1993). Almost all of the area is within protected areas or in the Natura 2000 European Network. In the Cantabrian Mountains, brown bears occupy 4 administrative regions (Galicia, Asturias, Castile and Leon, and Cantabria), each of which has its own brown bear recovery plan. In addition, the 4 political entities share a general conservation strategy that is coordinated by the Spanish Ministry of the Environment. All the recovery plans advocate re-unifying

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the 2 populations by increasing their size and range through improvements in habitat conservation and the prevention of human-caused mortality.

Monitoring demographic and spatial trends of the populations, specifically counting annual number of females (F_{CUB}) with cubs-of-the-year (cubs) in the population, is central to evaluating the conservation measures implemented in recent decades. Currently the number of F_{CUB} present each year is estimated as the number of such animals actually observed (\hat{N}_{Obs}) using protocols to distinguish unique animals (Keating et al. 2002). Between 1986 and 1990, the average annual \hat{N}_{Obs} , using the protocol for discriminating among duplicate observations from 1989 onward, were 5.0 and 1.7 in the WP and the EP, respectively (Palomero et al. 1993). In the WP between 1982 and 1995, the estimated total population decreased an average of 4–5%/year (from ~95 to 56 individuals; Wiegand et al. 1998). The decline was most pronounced between 1982 and 1988, after which the population appeared to stabilize. Wiegand et al. (1998) found that the population was not viable if mortality rates remained at the level observed in their study.

The aim of our work was to identify the demographic and spatial changes of the 2 populations, 1989–2004, and to interpret the results in the context of the conservation measures applied to the brown bear populations in the Cantabrian Mountains. Specifically, we analyze data on \hat{N}_{Obs} and the number of cubs/year. In addition, we describe changes in the areas the 2 populations occupied and define the distance that separated them.

Study area

The study area is located in the Cantabrian Mountains, northwestern Spain, where brown bears appear to prefer habitat that is a complex of deciduous forests, shrubs, and grasslands at 1,100–1,400 m, which is above areas of intense agricultural activity but below the subalpine zone (Clevenger et al. 1992; see also Naves and Palomero 1993, Wiegand et al. 1998, Naves et al. 2003). In the area, forests are mainly composed of oaks (*Quercus petraea* and *Q. pyrenaica*; in the WP, also *Q. robur* and *Q. ilex*) and beech (*Fagus sylvatica*). Above the treeline, *Vaccinium myrtillus*, *V. uliginosum*, *Arctostaphylos uva-ursi*, heather *Erica* sp., *Cytisus* sp., *Genista* sp., and *Juniperus communis* shrubs cover

vast areas. In the WP and the EP, average human population densities are 12.1 and 6.2 inhabitants/km², respectively (Reques 1993). The main economic activities in the region are tourism and livestock (mainly cattle) farming. Mining is of some importance locally, and hunting is a popular activity for residents of the region. Almost all of the area used by the brown bears falls within protected areas, mainly natural parks.

The area occupied by the WP has more diverse forests, some at lower altitudes than those of the EP. Thus, food availability is higher and habitat quality in general is better for brown bears in the WP than in the EP (Naves et al. 2003). In addition, forests are more patchily distributed in the WP than in the EP.

Methods

Detecting and discriminating females with cubs

We attempted to detect and characterize all groups of F_{CUB} throughout the area covered by the populations every year. A monitoring team that consisted mainly of rangers and technicians from wildlife agencies of the regional governments, the Fundación Oso Pardo (FOP, Brown Bear Foundation), and other NGOs (non-governmental organizations) collected field data throughout the Cantabrian Mountains where brown bears could potentially reproduce. The 16-year study was divided in four 4-year periods to have enough samples to analyze distribution patterns. Assuming that the effort applied by occasional qualified observers (mainly other rangers in their vigilance work) remained more or less constant in the study, we used the number of totally dedicated qualified observers per year as an index of effort: 1989–92, 2–6 observers/year (1 in the WP and 1–5 in EP); 1993–96, 2–11 observers per year (1–8 in the WP and 1–4 in the EP); 1997–2000, 11–19 observers per year (9–13 in the WP and 2–6 in the EP) and 2001–04, 18–25 observers per year (10–16 in the WP and 8–9 in the EP).

To locate F_{CUB} , we used a 2-step procedure. First, the team obtained information from hunters and others within the areas occupied by the bear populations. Second, the most skilled members of the team carefully prospected areas where females with cubs or their sign had been observed and where females reproduced in previous years. In the WP, the main method for detecting F_{CUB} was to look for family groups by scanning from elevated vantage

points using telescopes. In the EP, detecting bears through direct sighting was more difficult because of the greater forest and shrub cover; therefore, the main method for detecting F_{CUB} was to search for footprints.

We differentiated the groups of F_{CUB} by 4 criteria (Knight et al. 1995). When the differentiation was uncertain, we applied the most conservative criterion.

Number of cubs. Most groups were observed for several days, for prolonged periods, which provided high probability of accurately determining the number of cubs. For example, in 2004 groups were observed an average of 11.1 days (range = 1–22). Mortality of cubs during the year may mislead investigators; to avoid duplications, when a female with cubs was observed in the same area that a female with more cubs had been previously observed, we assume that both sightings were of the same female (which may have lost some cubs), unless there was evidence to indicate otherwise.

Six of the 128 bear families were first detected when the cubs were yearlings. In all 6 cases, the yearlings were deemed unique because all F_{CUB} detections the previous year within a 14.5-km radius (see below) were simultaneously observed accompanied by yearlings.

Distance between sightings. Just 1 native F_{CUB} was radiomonitored, during November 1997–April 1998 (the bears did not den); the mean straight-line distance between 144 daily consecutive locations was 0.55 km (Naves et al. 2001). In addition, 90% of straight-line movements during 7 days of 2 radio-monitored F_{CUB} in southcentral Europe were <3 km in spring and 7.25 km after spring (A. Ordiz, Norwegian University of Life Sciences, Ås, Norway, personal communication, 2006). To be conservative, we estimated the average maximum travel distance as twice this figure (14.5 km) and used this distance to judge whether 2 females with the same number of cubs were distinct. In addition to straight-line distance, we considered the sighting history of every female during the season and the orography. Nevertheless, in the Cantabrian Mountains F_{CUB} are frequently clumped, so other criteria are needed to distinguish F_{CUB} .

Concurrent sightings. When we doubted differentiation of F_{CUB} , we tried to perform concurrent sightings by different groups of observers who communicated by radio.

Physical features. To discriminate family groups, we searched for distinctive, clear, and

durable physical features on the female and cubs, such as size, color patterns, spots, or marks, which can be problematic because bears gain and lose weight quickly and color perception depends on light conditions. When possible, family groups were videotaped or photographed by digiscoping.

For example, in 2004, 11 females with cubs were located in the WP and 2 in the EP. The nearest family groups in the WP and the EP were 119.5 km apart. The females in the EP were differentiated by the number of cubs (1 and 2). In the WP, there were 2 females with 3 cubs, 8 with 2 cubs, and 1 with 1 cub. The nearest observations of females with 3 cubs were 16.1 km apart, in different slopes of the Cantabrian Mountains. The females with 2 cubs were >14.5 km apart, except in 6 cases (Table 1). Female 6 (F6) was just 4 km from F7 and 8.8 km from F2. Eventually, they were discriminated when F6 lost a cub. Since 20 August 2004, F6 was seen 8 times with just 1 cub, but F7 and F2 were seen 3 and 14 times with 2 cubs. F1, F2, F4, and F7 were videotaped and photographed and had distinctive features; in addition, F4 was in the southern slope of the Cantabrian Mountains (all the rest, in the northern one). F2 was light-colored with a distinctive dark strip along the back and the hump; F1 was uniform dark brown, and her cubs lacked distinctive features; F4 had 1 cub with a distinctive white collar and the other with a white spot on the neck. F7 was dark brown with light spots on the neck; 1 cub was light- and the other dark-colored.

The estimated number of family groups was conservative. F_{CUB} for which there was too much uncertainty to confidently classify as unique or a duplicate observation were excluded from the analyses. Using field observations, we estimated the annual number of F_{CUB} using Chao's non-parametric procedure described by Keating et al. (2002), which estimates F_{CUB} never detected (f_0). This procedure has the advantage of providing an estimate that is largely independent of sampling effort.

$$\hat{N}_{Chao1} = \hat{N}_{Obs} + \frac{f_1^2}{2f_2} \quad (1)$$

Where \hat{N}_{Obs} is the number of F_{CUB} observed in a given year; f_1 is the number of F_{CUB} seen only once, and f_2 is the number of F_{CUB} seen twice. When $f_2 = 0$, the equation gives $f_0 = \infty$. In this case we used the corrected formula

Table 1. Matrix of distances (km) between females with 2 cubs located in 2004. Entries in the matrix are distances between pairs of females with distances <14.5 km in bold (see text). Days separating the closest observations of the pair of females are in parentheses.

| Females (days observed) | Distances between females, km (days separating closest observations) | | | | | | |
|----------------------------|--|------------------|------------------|-----------------|------------|-----------|----------|
| | F1 | F2 | F4 | F6 | F7 | F9 | F10 |
| F1 (1) | | | | | | | |
| F2 (22) | 9.7 (55) | | | | | | |
| F4 (16) | 16.6 (37) | 14.3 (2) | | | | | |
| F6 (15) | 17.5 (50) | 8.8 (1) | 15.6 (0) | | | | |
| F7 (3) | 20.3 (8) | 10.8 (43) | 13.8 (25) | 4.0 (38) | | | |
| F9 (12) | 37.9 (130) | 28.7 (0) | 30.1 (17) | 19.8 (0) | 17.6 (118) | | |
| F10 (9) | 43.2 (27) | 35.4 (0) | 41.2 (0) | 28.3 (0) | 25.7 (35) | 15.4 (1) | |
| F11 (14) | 58.6 (81) | 50.1 (0) | 51.6 (3) | 41.9 (0) | 38.7 (89) | 22.0 (20) | 18.7 (5) |

$$\hat{N}_{Chao2} = \hat{N}_{Obs} + \frac{f_1^2 - f_1}{2(f_2 + 1)} \quad (2)$$

The original Chao estimator is high compared with the bias-corrected estimator, especially with small sampling efforts, although both results tend to converge with increasing observation intensity (Keating et al. 2002), as happened in our case. Although the Chao estimator is more robust than other parametric estimators and requires fewer assumptions (Keating et al. 2002), our data did not strictly fit the requirements of its application because some were not obtained randomly. (Some of our field work, linked to conservation efforts, was influenced by specific efforts to differentiate F_{CUB}). For this reason the Chao estimator was used as a complementary effort to evaluate if the minimum number of F_{CUB} was far from the theoretical value.

Beginning in 1989, monitoring was standardized, with one coordinator, the use of criteria to differentiate F_{CUB} , and financial support for monitoring. Between 1989 and 1993, monitoring efforts of F_{CUB} was moderate. Even if effort in both populations was applied, there was no coordinated monitoring program for all bear range that used experienced rangers. During this period, greater effort in the EP resulted in more data than in the WP. Beginning in 1994, monitoring effort increased as a coordinated network of well trained rangers formed, allowing a better definition of each F_{CUB} and a sufficient effort for the following years, so we assumed constant observation probability for all F_{CUB} . For this reason, the analysis of trends in the EP includes data since 1989 but only since 1994 for the WP. All

other analyses include data from 1989 through 2004. An observation was considered valid if it came from the monitoring network (WP = 90.1%; EP = 87.7%), or if a personal interview of the observer was conducted by a member of the monitoring network who could vet the observation.

WP data came from rangers and technicians of the FOP (55.6%), other rangers of the Autonomous Communities (27.8%), the Asturian Foundation for the Conservation of Wildlife (FAPAS; 6.7%), and other people (9.9%). EP data came from FOP (60.7%), other rangers of the Autonomous Communities (27%), and other people (12.3%).

Demographic analysis

To analyze the temporal dynamics of the Cantabrian brown bear populations, we used the annual \hat{N}_{Obs} as an index. To assess changes in \hat{N}_{Obs} , we evaluated the goodness-of-fit of exponential and linear growth models (Caughley and Sinclair 1994). Changes in the annual \hat{N}_{Obs} as a function of time were analyzed using Poisson regression (Kleinbaum et al. 1988, Doménech and Navarro 2005), which is similar to standard multiple regression except the dependent variable is a count that follows the Poisson distribution. We defined a generalized linear model fit with the GENMOD procedure of SAS (SAS Institute, Inc. 2004) with the response variable given by the annual count of \hat{N}_{Obs} , a Poisson error distribution, and an identity link function (for the linear growth model) or a natural log link function for the exponential growth model (for which the parameter b can be interpreted as the intrinsic rate of increase). To detect statistically significant trends, we used likelihood ratio tests.

Table 2. Number of sightings by year for female brown bears with cubs-of-the-year for the Western Cantabrian population (WP) and Eastern Cantabrian population (EP), Spain, where f_j is the number of unique females with cubs-of-the-year seen j times that year. Total number of observations is given by $n = \sum_{j=1} jf_j$.

| Year | Observation frequency | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|------|-----------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|---|---|---|
| | n | f_1 | f_2 | f_3 | f_4 | f_5 | f_6 | f_7 | f_8 | f_9 | f_{10} | f_{11} | f_{12} | f_{13} | f_{14} | f_{15} | f_{16} | f_{17} | f_{18} | f_{19} | f_{20} | f_{22} | f_{23} | f_{24} | f_{25} | f_{27} | f_{30} | f_{33} | f_{37} | f_{41} | f_{44} | f_{45} | f_{47} | f_{64} | | | |
| WP | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1989 | 21 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1990 | 40 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1991 | 31 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1992 | 23 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1993 | 17 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1994 | 14 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1995 | 41 | 1 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1996 | 40 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1997 | 46 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1998 | 62 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1999 | 130 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | |
| 2000 | 72 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2001 | 86 | 0 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | |
| 2002 | 77 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2003 | 39 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2004 | 119 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EP | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1989 | 20 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| 1991 | 56 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | |
| 1993 | 43 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1995 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | |
| 1996 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 1997 | 41 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | | |
| 1999 | 53 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2000 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2001 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2002 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2003 | 59 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 2004 | 34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |

Spatial analysis

Typically, each F_{CUB} sighting or track was assigned to a 100 x 100 m grid; however, when possible the precision was 10 x 10 m. To obtain the UTM coordinates of locations, we used the Spanish National Topographical Map (1:25,000) and GPS when possible. Locations were added as a point shape file in a geographical information system developed with ArcView (ESRI, Redlands, California, USA).

To reduce the effect of detectability on the spatial analysis (more direct sightings in the WP, more tracks in the EP and variation in the number of sightings of each F_{CUB}), each F_{CUB} was represented by her central point (barycenter), which was the arithmetical average of the X and Y coordinates of all the observations of the F_{CUB} .

To detect changes in the spatial distributions, we represented the reproductive area (RA) of each population during each of the four 4-year periods

of the study, as the area covered by the sum of the central points of each F_{CUB} with a 7.25-km buffer.

To detect changes in the distance between the RA of the 2 populations, we measured the linear distance between the 2 closest inter-population F_{CUB} in each 4-year period. All spatial values were calculated using the animal movement extension in ArcView (Hooge and Eichenlaub 1997).

Results

Spatial and temporal distribution of observations

During 1989–2004, we recorded 1,388 locations of F_{CUB} (917 in the WP and 471 in the EP), 94.4% of which we assigned to a specific F_{CUB} . In the WP and the EP, there were 106 and 22 F_{CUB} , respectively. We recorded 8.1 locations per F_{CUB} (SD = 9.2; range = 1–64) in the WP and 20.6 (SD = 12.7; range = 4–49) in the EP (Table 2).

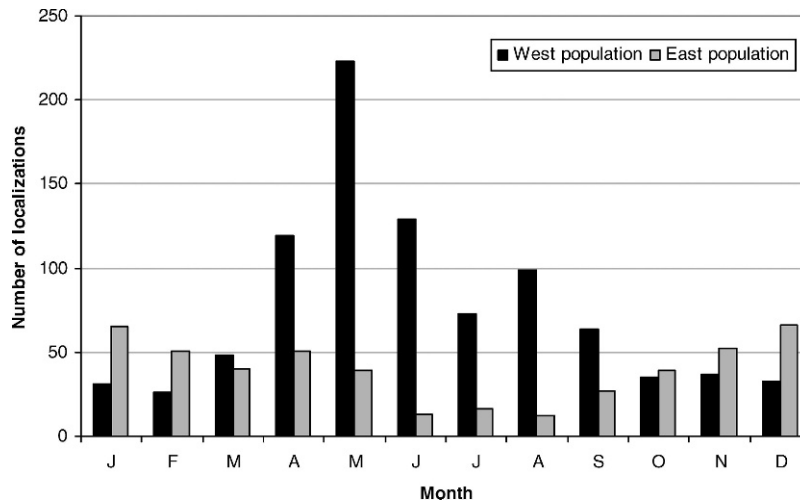


Fig. 1. Monthly distribution of the locations of F_{CUB} in 2 populations of brown bears in the Cantabrian Mountains, Spain, 1989–2004 (West population: $n = 917$; East population: $n = 471$).

In the WP, locations (mainly direct sightings) were concentrated in spring and summer, whereas in the EP, locations (mainly footprints) were most frequent in autumn and winter (Fig. 1). All F_{CUB} in the EP and 94.3% of the F_{CUB} in the WP were first observed during the first year of life of the cubs. The earliest locations of F_{CUB} were in April, and the maximum numbers were recorded in May (Fig. 2). Some F_{CUB} were active all year (G. Palomero et al. unpublished data).

\hat{N}_{Obs} and litter sizes

In the WP, the mean litter size was 1.8 (SD = 0.6; $n = 106$); 28 (26.4%) females had 1 cub, 68 (64.2%) had 2, and 10 (9.4%) had 3 (Table 3). Overall, at least 194 cubs were born in the WP, and mean cubs/year was 12.1 (SD = 4.5; range = 6–23; $n = 16$). In the EP, the mean litter size was 1.5 (SD = 0.5, $n = 22$); 12 (54.5%) females had 1 cub and 10 (45.5%) had 2 cubs. In the EP, at least 32 cubs were born,

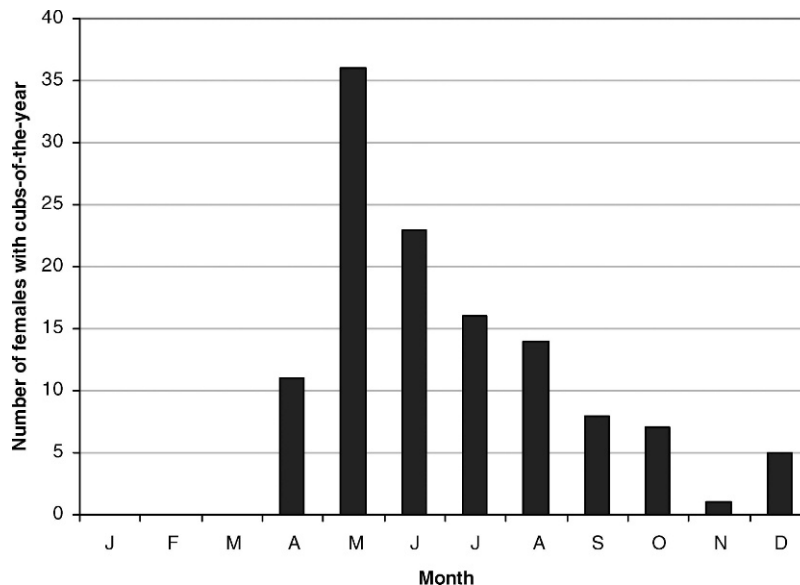


Fig. 2. Monthly distribution of the first detection of individual F_{CUB} in 2 populations of brown bears in the Cantabrian Mountains, Spain, 1989–2004 ($n = 122$).

Table 3. Demographics of 2 populations of brown bears in the Cantabrian Mountains, Spain, 1989–2004. Averages are based on 4-year periods and are presented as mean (standard deviation). \hat{N}_{Chao} were estimated using \hat{N}_{Chao1} .

| Year | West population | | | | | | East population | | | | | | | |
|-------|---|--|-----------------|-------------------------------------|----------------|--------------------------|------------------------------|---|--|-------------------|-------------------------------------|----------------|--------------------------|------------------------------|
| | Four-year average | | | Four-year average | | | Four-year average | | | Four-year average | | | | |
| | \hat{N}_{Obs}^a (\hat{N}_{Chao}) | Number of cubs (1,2,3) ^b | \hat{N}_{Obs} | Average annual \hat{N}_{Obs} (SD) | Number of cubs | Average annual cubs (SD) | Average cubs per female (SD) | \hat{N}_{Obs}^a (\hat{N}_{Chao}) | Number of cubs (1,2,3) ^b | \hat{N}_{Obs} | Average annual \hat{N}_{Obs} (SD) | Number of cubs | Average annual cubs (SD) | Average cubs per female (SD) |
| 1989 | 4 (4) ^c | 8 (1,2,1) | 22 | 5.50 (1.3) | 43 | 10.75 (3.4) | 1.95 (0.7) | 2 (2) ^c | 3 (1,1,0) | 5 | 1.25 (1.5) | 8 | 2.00 (2.4) | 1.60 (0.5) |
| 1990 | 7 (7.5) | 15 (1,4,2) | | | | | | 0 (0) | 0 | | | | | |
| 1991 | 6 (6) | 12 (2,2,2) | | | | | | 3 (3) ^c | 5 (1,2,0) | | | | | |
| 1992 | 5 (5.5) | 8 (2,3,0) | | | | | | 0 (0) | 0 | | | | | |
| 1993 | 4 (4.5) | 6 (2,2,0) | 19 | 4.75 (2.2) | 32 | 8.00 (4.0) | 1.68 (0.5) | 3 (3) ^c | 4 (2,1,0) | 5 | 1.25 (1.3) | 6 | 1.50 (1.7) | 1.20 (0.4) |
| 1994 | 3 (3.5) | 6 (0,3,0) | | | | | | 0 (0) | 0 | | | | | |
| 1995 | 8 (8) ^c | 14 (2,6,0) | | | | | | 1 (1) ^c | 1 (1,0,0) | | | | | |
| 1996 | 4 (4) | 6 (2,2,0) | | | | | | 1 (1) ^c | 1 (1,0,0) | | | | | |
| 1997 | 7 (7.5) | 12 (2,5,0) | 30 | 7.50 (1.3) | 54 | 13.50 (1.9) | 1.80 (0.6) | 1 (1) ^c | 1 (1,0,0) | 4 | 1.00 (0.8) | 5 | 1.25 (1.3) | 1.25 (0.50) |
| 1998 | 6 (7) ^c | 12 (1,4,1) | | | | | | 0 (0) | 0 | | | | | |
| 1999 | 8 (8) | 14 (2,6,0) | | | | | | 2 (2) ^c | 3 (1,1,0) | | | | | |
| 2000 | 9 (9.25) | 16 (3,5,1) | | | | | | 1 (1) ^c | 1 (1,0,0) | | | | | |
| 2001 | 8 (8) ^c | 13 (3,5,0) | 35 | 8.75 (1.5) | 65 | 16.25 (4.6) | 1.86 (0.6) | 2 (2) ^c | 3 (1,1,0) | 8 | 2.00 (0.8) | 13 | 3.25 (1.3) | 1.63 (0.5) |
| 2002 | 8 (8.5) | 14 (2,6,0) | | | | | | 1 (1) ^c | 2 (0,1,0) | | | | | |
| 2003 | 8 (8.25) | 15 (2,5,1) | | | | | | 3 (3) ^c | 5 (1,2,0) | | | | | |
| 2004 | 11 (11.5) | 23 (1,8,2) | | | | | | 2 (2) ^c | 3 (1,1,0) | | | | | |
| Total | 106 | 194(28,68,10) | 106 | 6.63 (2.2) | 194 | 12.13 (4.5) | 1.83 (0.6) | 22 | 32(12,10,0) | 22 | 1.38 (1.1) | 32 | 2.00 (1.8) | 1.45 (0.5) |

^a \hat{N}_{Obs} : number of F_{CUB} obtained using protocols to distinguish unique animals.

^b \hat{N}_{Chao} : number of F_{CUB} using Chao's non-parametric procedure.

^c \hat{N}_{Obs} with litter size 1, 2, and 3.

^dEstimated using \hat{N}_{Chao2} , because $f_2 = 0$.

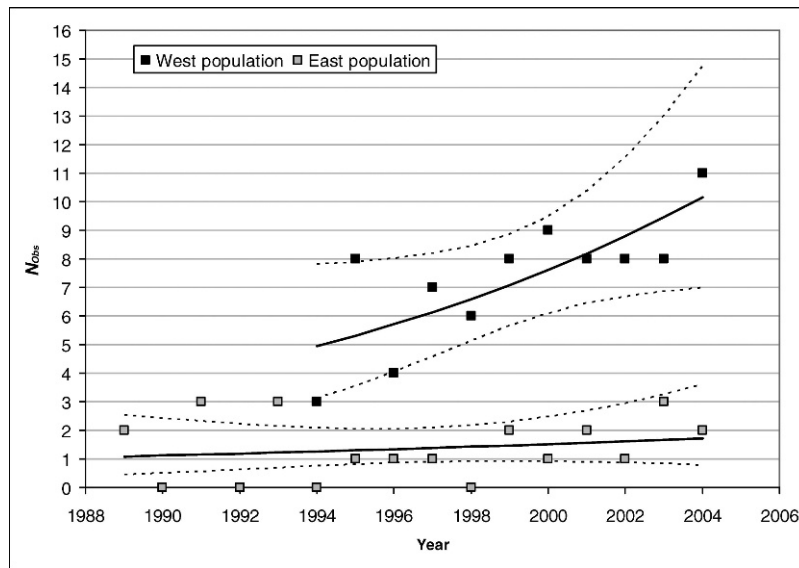


Fig. 3. Number of F_{CUB} observed (\hat{N}_{Obs}) and fitted by Poisson regression (lines) of 2 populations of brown bears in the Cantabrian Mountains, Spain (1989–2004 and 1994–2004); 95% confidence limits are dashed lines.

and the mean/year was 2.0 ($SD = 1.8$, range = 0–5, $n = 16$). The mean litter size was significantly higher in the WP than in the EP (Mann-Whitney test $Z = -2.77$, $P = 0.006$, $n = 128$).

Yearly \hat{N}_{Chao} were only slightly greater than \hat{N}_{Obs} (Table 3). In the EP, all F_{CUB} were identified more than twice, so \hat{N}_{Chao} and \hat{N}_{Obs} were identical in all cases.

Trends in the \hat{N}_{Obs} index

In the WP, \hat{N}_{Obs} decreased from 22 (1989–92) to 19 (1993–96) before increasing to 30 (1997–2000) and 35 (2001–04). In the EP, after a long period when \hat{N}_{Obs} was very low (5 during 1989–92 and 1993–96; 4 during 1997–2000), the number increased (8 during 2001–04), when reproduction occurred annually and at least 1 female reproduced every year (Table 3).

In both populations, linear and exponential growth models had similar goodness-of-fit, so we used the exponential growth model to estimate the annual rate of increase (Fig. 3). In the WP, the estimated rate of exponential growth was 0.072 (SE = 0.036), equivalent to an annual increase of 7.5% ($P = 0.043$). In the EP, the estimated rate of exponential growth was 0.0301 (SE = 0.046), equivalent to an annual increase of 3%, but this rate was not significantly different from zero ($P = 0.517$).

Spatial distribution of the brown bear populations

The RA of the WP had 3 nuclei or female concentration areas in 1989–92 (Fig. 4). \hat{N}_{Obs} in the 3 nuclei were 4, 9, and 9. During 1993–96, \hat{N}_{Obs} in the first and second nuclei decreased (1 and 4 respectively) and in the third nucleus increased (13). In 1997–2000, the first nucleus completely disappeared, but the second nucleus began recovering (8), the third nucleus increased in density and number (22), and the population expanded to the south and the southeast. During 2001–04, the increase continued, although the expansion was less than in the previous period. The first nucleus was reoccupied (1), the second remained stable (9), and the third nucleus continued its expansion (25).

In the EP during 1989–92, F_{CUB} occupied the population's entire distribution area and existed within 2 nuclei (one with 3 \hat{N}_{Obs} and another with 2 \hat{N}_{Obs}). During 1993–96, the RA was similar but F_{CUB} began to concentrate in the eastern part. In 1997–2000, there was a retraction of RA and loss of peripheral areas, and only 1 nucleus remained, with a \hat{N}_{Obs} of 4. In 2001–04, a significant recovery occurred associated with an expansion to northwest, which increased the \hat{N}_{Obs} to 8.

During 1989–92 and 1993–96, the linear distance between the populations decreased from 88 km to

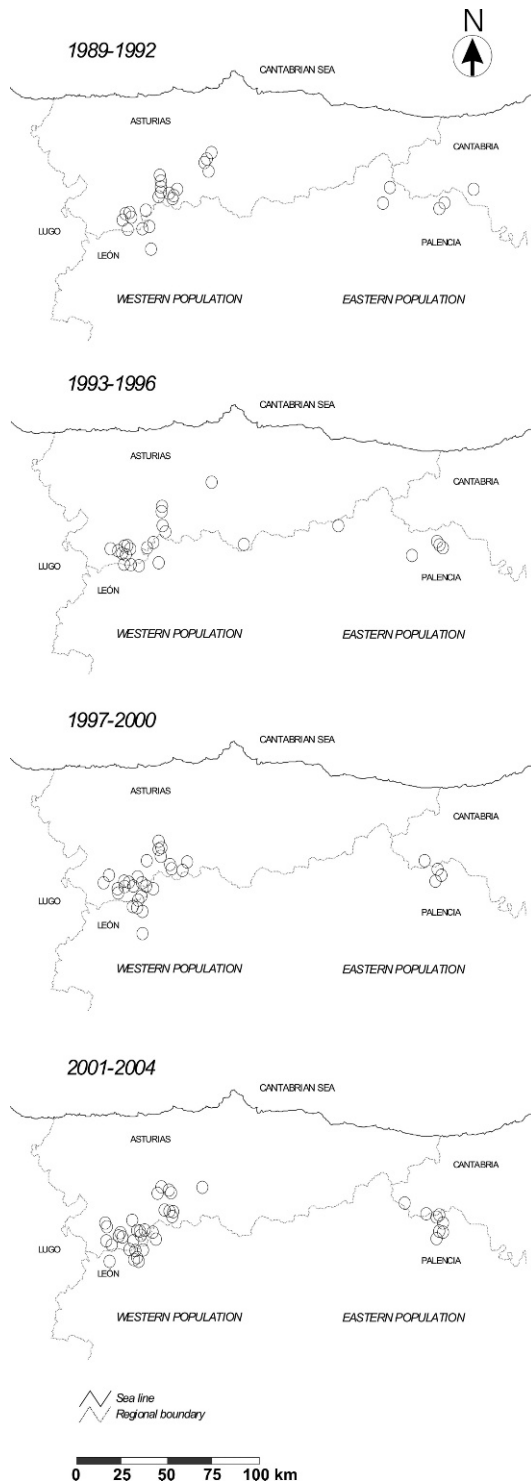


Fig. 4. Distribution of reproductive areas within 2 populations of brown bears in the Cantabrian Mountains, Spain, 1989–2004.

43 km because of the presence of 2 peripheral F_{CUB} in each RA during 1994 and 1995. The lack of continuity in those peripheral areas led to a significant increase in the distance between these 2 populations in the third period 1997–2000 (106.7 km). In the fourth period, 2001–04, the distance between the populations declined to 97 km as a consequence of a slight expansion to the northwest of the EP and the recovery of the first nucleus in the WP.

Discussion

Monitoring reproductive individuals, specifically F_{CUB} , provides some advantages over methods such as radiotracking as a means of monitoring populations (Knight et al. 1995, Servheen et al. 1999, Keating et al. 2002). First, F_{CUB} are an important proportion of the population and are the most important demographic component. Second, F_{CUB} , particularly when the cubs are young, are more easily detected and identified than other segments of the population because they tend not to range as far as solitary bears and they can be more active during the day than other bears (Knight et al. 1995). Third, direct observations of F_{CUB} make it easier to differentiate groups based on their composition and physical characteristics (Servheen 1989). Monitoring F_{CUB} provides information about demography and ecology and the factors that threaten them and contributes to their surveillance and protection during a sensitive phase of the annual cycle, which is a key aspect of population recovery (Knight and Eberhardt 1985, Knight et al. 1995, Wiegand et al. 1998).

In recent years, counting F_{CUB} to monitor bear populations has faced criticism. Mattson (1997) argued that unreplicated counts of females with cubs might vary because of differences in search effort and sightability of this class. While he recognized that managers might have to rely on indices (such as unduplicated F_{CUB}) as the basis for population assessments, he emphasized the uncertainty of the method, particularly when calculating maximum allowable mortality. Keating et al. (2002) developed a method to avoid incomplete counts, based on application of the Chao non-parametric estimator, robust enough to allow calculating how many F_{CUB} exist in the sampled area, which also solved the problem of the dependence on the number of observed F_{CUB} on sampling effort. Whereas Keating

et al. (2002) observed substantial differences between \hat{N}_{Obs} and \hat{N}_{Chao} , we found very small differences in the Cantabrian Mountains (none at all in the EP). This difference can be explained by the smaller area and real number of F_{CUB} in the Cantabrian Mountains, allowing a more exhaustive population monitoring and thus a larger number of detections per F_{CUB} (Monte Carlo methods have shown that increasing the relative sample size, total observations (n)/ \hat{N}_{Obs} , diminishes the estimate's bias). Relative sample size varied between 4.25 and 15.7 in the Cantabrian Mountains and 0.5 and 2.6 in the Greater Yellowstone Ecosystem (Keating et al. 2002). In our case, we recognize possible biases of the Chao estimator. However, because differences between \hat{N}_{Obs} and \hat{N}_{Chao} were small, we are more confident that \hat{N}_{Obs} can be used as a minimum index that underestimates only slightly the true number of F_{CUB} . Even if some F_{CUB} are not detected in a given year, we believe it likely these animals would be detected the subsequent year due to our intensity of field work.

In the Cantabrian Mountains, the inter-population differences in the seasonal patterns of locations of F_{CUB} (Fig. 1) were an artifact of the different methods used to locate bears (primarily direct sightings in the WP and tracks in the EP). In the WP, the higher concentration of observations in spring and summer was because the bears were more active in open habitats at that time and, consequently, the likelihood of detection by direct sighting was higher. In the EP, the number of locations was higher in autumn and winter than at other times because detectability increased when mud and snow were present. Another interesting aspect derived from 16 years of monitoring the population is that some F_{CUB} were active year-round, which is probably true in other southern European brown bear populations (Huber and Roth 1993).

Our study confirmed that the \hat{N}_{Obs} in the Cantabrian Mountains was low. During 2001–04, mean \hat{N}_{Obs} per year was 8.75 and 2.0 in the WP and the EP, respectively, indicating that they are among the most threatened brown bear populations in the world. In Europe, only the Pyrenean (Chapron et al. 2003) and the Trentinian (Genovesi et al. 2000) populations have fewer adult bears, and both of these populations have been the subjects of restocking and re-introduction programs, respectively. Nevertheless, after the WP decrease of 1982–95 (Wiegand et al. 1998), the population index experi-

enced an annual increase of 7.5%, which although slower than the growth rate reported for the brown bear population in Sweden (Saether et al. 1998), is still a positive trend. The populations in the Cantabrian Mountains are isolated from other bear populations; therefore, natality and mortality are the only factors that influence population trends. In our study, litter size did not increase; therefore, we hypothesize that mortality decreased. Poaching, snares, and poison set to capture wild boar (*Sus scrofa*) and wolf (*Canis lupus*) were the main human-induced causes of brown bear mortality (Palomero et al. 1993). The possible decrease in bear mortality appears to have resulted from the conservation efforts implemented in the Cantabrian Mountains over the last 20 years, and the number of rangers involved in the control and surveys of bears are the main reason for this initial recovery. We do not have evidence of other reasons for this increase, such as changes in reproductive characteristics like a decrease in litter interval or age of first reproduction.

During 2001–04, the WP was within the range of what most authors believe is a viable brown bear population (Shaffer 1983, Suchy et al. 1985, Eberhardt et al. 1986, Mysterud and Muus Flack 1989, Schroeder 1992, Saether et al. 1998, Wiegand et al. 1998). In addition, the recent trend toward an increase in the size of the WP gives reason to be optimistic about the long-term viability of the population. Unfortunately, the current size of the EP is too small to be viable. Nevertheless, the major aim of future monitoring programs should be to determine whether the positive trend toward increased size and range of the populations persists.

Mean litter size of Cantabrian Mountains bears are among the lowest reported (Le Franc et al. 1987) and are similar to those recorded in the Pyrenees and Trentino populations prior to the introduction of brown bears from Slovenia (Camarra 1990, Osti 1991). Litter sizes in the WP were higher than those in the EP, which might have been due to greater genetic variability and, consequently, better genetic fitness (Laikre et al. 1996, Liberg et al. 2005) or to higher habitat quality (food diversity and abundance) in the WP than in the EP (Palomero et al. 1993, Naves et al. 2003). Detectability and seasonality could have also played a role in this difference.

The considerable temporal variation in the spatial distribution of F_{CUB} during the course of our study has important consequences for the conservation of these populations. The loss of a F_{CUB} led to an

immediate reduction in the size of the RA, particularly on the periphery of the population. The addition of a F_{CUB} resulted in an increase in the RA, but the expansion was much slower than the contraction, possibly because of female philopatry and fidelity to reproductive areas. Following the recovery of the Cantabrian populations, the RA of the new F_{CUB} was clumped, which changed the structure of spatial nuclei. That type of change occurred also in the Scandinavian brown bear population, where areas of concentration of females were surrounded by wide areas of dispersal and communication, in which mainly males were found (Swenson et al. 1998). Typically, in brown bear populations, dispersal and genetic flow is by males; however, in saturated or presaturated but increasing populations, some young females disperse from their natal area, which favors an expansion of the RA (Swenson et al. 1998, Kojola and Laitala 2000). Although we did not study dispersal in the populations in the Cantabrian Mountains, field data indicated high mobility of males and their role as the dispersing sex (Clevenger and Purroy 1991). Dispersal by females might explain the presence of new F_{CUB} in abandoned areas. Currently, RA are concentrated on the opposite sides of the WP and EP, which increases the difficulty of establishing a connection between them. The RA of the populations are separated by about 90 km, crossed by important transportation routes (roads, highways, railways), and have centers of human activity such as mining operations and ski resorts. Additional developments are under construction or projected that will increase the difficulty of bear movements in the near future. Studies of the habitat between the populations confirmed that there are no problems with the food or cover availability, but there is a shortage of winter refuges for den sites (J. Marquinez, P. García-Manteca, C. Nores, and M.V. Varela de Seijas, 2002, Delimitación de áreas críticas para el oso pardo, INDUROT, Principado de Asturias, Spain).

Isolation can be increased by conspecific attraction (Stamps 1988), which can cause juveniles to disperse into deserted areas because females and males might prefer occupied over unoccupied areas (as observed in birds; Alonso et al. 2004). The large distance between the closest breeding areas in the populations remains the major impediment to the recovery of a single large population, and the EP is too small to survive in isolation. Reducing the

distance between the populations will require a concerted effort to conserve habitat between their RA. If the populations continue to increase, the conservation of shared, unused habitat might favor an increase in distribution areas and the exchange of individuals between the WP and EP, ultimately leading to a single, less endangered Cantabrian brown bear population.

Brown bear populations in the Cantabrian Mountains, Spain, are recovering, but the isolation of the 2 populations is jeopardizing this process. Habitat quality has not changed dramatically in areas that have not been re-occupied, so female philopatry might be the main cause of the slow rate of recolonization. Both populations, but particularly the EP (0–3 breeding females per year), remain severely endangered. Conservation priorities should include recovering the range previously occupied by breeding females and promoting the exchange of individuals between populations.

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Literature cited

- ALONSO, J.C., C. MARTÍN, J.A. ALONSO, C. PALACÍN, M. MAGAÑA, AND S.J. LANE. 2004. Distribution dynamics of a great bustard metapopulation throughout a decade: Influence of specific attraction and recruitment. *Biodiversity and Conservation* 13:1659–1674.
- CAMARRA, J.J. 1990. L'Ours dans les Pyrénées: Suivi de la population de 1979 a 1988. *Bulletin Mensuel de l'Office National de la Chasse* 142:18–22. (In French.)
- CAUGHLEY, G., AND A.R.E. SINCLAIR. 1994. *Wildlife ecology and management*. Blackwell Science, Cambridge, Massachusetts, USA.
- CHAPRON, G., P.-Y. QUENETTE, S. LEGENDRE, AND J. CLOBERT. 2003. Which future for the French Pyrenean

- bear (*Ursus arctos*) population? An approach using stage-structured deterministic and stochastic models. *Comptes Rendus Biologies* 326:174–182.
- CLEVENGER, A.P., AND F.J. PURROY. 1991. Ecología del oso pardo en España. Museo Nacional de Ciencias Naturales, Monografías 4, CSIC, Madrid. (In Spanish.)
- , ———, AND M.R. PELTON. 1992. Brown bear (*Ursus arctos* L.) habitat use in the Cantabrian Mountains, Spain. *Mammalia* 56:203–213.
- CURRY-LINDAHL, K. 1972. The brown bear (*Ursus arctos*) in Europe: decline, present distribution, biology and ecology. Bears—their biology and management. IUCN, Gland, Switzerland.
- DOMÉNECH, J.M., AND J.B. NAVARRO. 2005. Regresión logística binaria, multinomial y de Poisson. Signo, Barcelona, Spain. (In Spanish.)
- EBERHARDT, L.L., R.R. KNIGHT, AND B.M. BLANCHARD. 1986. Monitoring grizzly bear population trends. *Journal of Wildlife Management* 50:613–618.
- GENOVESI, P., E. DUPRÉ, AND L. PEDROTTI. 2000. Feasibility study for the re-introduction of the brown bear in the Italian Central Alps. Pages 51–80 in J.F. Layna, B. Heredia, G. Palomero, and E.I. Doadrio, editors. La conservación del oso pardo en Europa: un reto de cara al siglo XXI. Fundación Biodiversidad, Madrid, España. (In Spanish.)
- HOOGE, P.N., AND B. EICHENLAUB. 1997. Animal movement extension to Arcview, Version 1.1. US Geological Survey, Biological Science Office, Alaska Science Center, Anchorage, Alaska, USA.
- HUBER, D., AND H.U. ROTH. 1993. Movements of European brown bears in Croatia. *Acta Theriologica* 38:151–159.
- KEATING, K.A., C.C. SCHWARTZ, M.A. HAROLDSON, AND D. MOODY. 2002. Estimating numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Ursus* 13:161–174.
- KLEINBAUM, D.G., K.L. LAWRENCE, AND M.E. KEITH. 1988. Applied regression analysis and other multivariable methods. Second edition. The Duxbury Series in Statistics and Decision Sciences. PWS-KENT Publishing Co., Boston, Massachusetts, USA.
- KNIGHT, R.R., AND L.L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology* 66:323–334.
- , B.M. BLANCHARD, AND L.L. EBERHARDT. 1995. Appraising status of Yellowstone grizzly bear population by counting females with cubs-of-the-year. *Wildlife Society Bulletin* 23:245–248.
- KOJOLA, I., AND H.M. LAITALA. 2000. Changes in the structure of an increasing brown bear with distance from core areas: another example of presaturation female dispersal? *Annales Zoologici Fennici* 37:59–64.
- LAIKRE, L., R. ANDRÉN, H. LARSSON, AND N. RYMAN. 1996. Inbreeding depression in brown bear. *Biological Conservation* 76:69–72.
- LE FRANC, M.N., M.B. MOSS, K.A. PATNODE, AND W.C. SUGG. 1987. Grizzly bear compendium. Fish and Wildlife Service, Missoula, Montana, USA.
- LIBERG, O., H. ANDRÉN, H-C. PEDERSEN, H. SAND, D. SEIBERG, P. WABAKKEN, M. AKESSON, AND S. BENSCH. 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biology Letters* 1:17–20.
- MATTSON, D.J. 1997. Sustainable grizzly bear mortality calculated from counts of females with cubs-of-the-year: An evaluation. *Biological Conservation* 81:103–111.
- MYSTERUD, I., AND M. MUUS FALCK. 1989. The brown bear in Norway. I. Subpopulation ranking and conservation status. *Biological Conservation* 48:21–29.
- NATIONAL TOPOGRAPHICAL MAP. National Geographical Institute, Ministry of Public Works, Madrid, Spain.
- NAVES, J., AND G. PALOMERO. 1993. El oso pardo (*Ursus arctos*) en España. ICONA, Madrid. (In Spanish.)
- , A. FERNÁNDEZ, AND DELIBES. 2001. Effects of recreation activities on a brown bear family group in Spain. *Ursus* 12:135–139.
- , T. WIEGAND, E. REVILLA, AND M. DELIBES. 2003. Endangered species constrained by natural and human factors: the case of brown bears in Northern Spain. *Conservation Biology* 17:1276–1289.
- NORES, C., AND J. NAVES. 1993. Distribución histórica del oso pardo en la Península Ibérica. Pages 13–33 in J. Naves and G. Palomero, editors. El oso pardo (*Ursus arctos*) en España. ICONA, Madrid. (In Spanish.)
- OSTI, F. 1991. L'Orso bruno nel Trentino. Editoriale Arca, Trento, Italia. (In Italian.)
- PALOMERO, G., A. FERNÁNDEZ, AND J. NAVES. 1993. Demografía del oso pardo en la Cordillera Cantábrica. In El oso pardo (*Ursus arctos*) en España. J. Naves and G. Palomero, editors. ICONA, Madrid. (In Spanish.)
- REQUES, P. 1993. Antropogeografía del área de distribución del oso pardo en la Cordillera Cantábrica. Pages 223–264 in El oso pardo (*Ursus arctos*) en España. J. Naves and G. Palomero, editors. ICONA, Madrid. (In Spanish.)
- SAETHER, B-E., S. ENGEN, J.E. SWENSON, O. BAKKE, AND F. SANDEGREN. 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. *Oikos* 83:403–416.
- SAS INSTITUTE, INC. 2004. SAS 9.1.3. Cary, North Carolina, USA.
- SCHROEDER, W. 1992. Piano di recupero dell'orso bruno. Wildbiologische Gesellschaft Oberammergau, München, Germany. (In Italian.)
- SERVHEEN, C. 1989. Monitoring of bear populations. Environmental encounters series. Council of Europe 6:39–45.

- , S. HERRERO, AND B. PEYTON. 1999. Bears. Status survey and Conservation Action Plan. IUCN/SSC Bear and Polar Bear Specialist Groups. IUCN, Gland, Switzerland.
- SHAFFER, M.L. 1983. Determining minimum viable population sizes for the grizzly bear. *International Conference Bear Research and Management* 5:133–139.
- STAMPS, J.A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329–347.
- SUCHY, W.J., L. McDONALD, M.D. STRICKLAND, AND S. ANDERSON. 1985. New estimates on minimum viable population size for grizzly bear of the Yellowstone ecosystem. *Wildlife Society Bulletin* 13:223–228.
- SWENSON, J.E., F. SANDEGREN, AND A. SÖDERBERG. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67:819–82.
- WIEGAND, T., J. NAVES, T. STEPHAN, AND A. FERNÁNDEZ. 1998. Assessing the risk of extinction from the brown bear (*Ursus arctos*) in the Cordillera Cantabria, Spain. *Ecological Monographs* 68:539–570.

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