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Source: Wildlife Biology, 12(4) : 367-373

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2006)12[367:COBBUA]2.0.CO;2

Courtship of brown bears *Ursus arctos* in northern Spain: phenology, weather, habitat and durable mating areas

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Fernández-Gil, A., Naves, J. & Delibes, M. 2006: Courtship of brown bears *Ursus arctos* in northern Spain: phenology, weather, habitat and durable mating areas. - Wildl. Biol. 12: 367-373.

During 1988-2004 we made 297 non-systematic direct observations of free-ranging brown bears *Ursus arctos* in the Cantabrian Range of Spain, one of the southernmost and most endangered populations in Europe. Observations were distributed over the whole calendar year, with records in every month. We classified 23 observations as breeding behaviour (male-female close interactions). They occurred between 17 April and 12 June, but mainly from the second week of May to the first week of June, both included. Matings (N = 12) took place between 25 April and 12 June, with one in April, nine in May and two in June. These dates indicated that the mating season started earlier in the Cantabrian bear population than in other Euroasiatic and American bear populations. Breeding bears showed greater diurnal activity in cloudy and rainy weather than did non-breeding bears in the same period. Also, breeding bears used brush more often than forests and grasslands when compared with other bears in the same areas and periods. Some mating areas were used repeatedly in different breeding seasons (up to five years). The observed behaviour could be related to the small size of the bear population, the reduced and fragmented forest habitat and the high level of human disturbance characteristic of the Cantabrian Mountains. Reproductive strategies and mating systems, including the spatial and temporal patterns of breeding activities, are considered important scientific topics with implications for the implementation of suitable conservation measures, for the bears as well as for their habitat.

Key words: brown bear, breeding behaviour, habitat, mating areas, phenology, Ursus arctos, weather

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Received 1 November 2004, accepted 24 February 2006

Associate Editor: Andrew E. Derocher

The fate of any animal population is explicitly linked to demographic features such as reproduction and mortality (Begon & Mortimer 1986, Stearns 1992, Naves et al. 2003). To be successful, reproduction demands the temporal optimisation of gamete production, courtship activities, production of embryos and rearing of young, in relation to the seasonal availability of environmental resources (Lack 1954). Also, in sexual species the male and the female must synchronise their cycles and find each other at the suitable place and time (e.g. Bronson 1989, Clutton-Brock 1989, Dahle & Swenson 2003b). On the other hand, courtship and breeding activities usually imply increased risks, as animals become less cautious and thus are more easily detected. For all these reasons, reproductive strategies and mating systems, including the spatial and temporal patterns of breeding activities, are considered important scientific topics with conservation implications in the case of endangered species (Reed & Shine 2002, Brashares 2003, Morrow & Pitcher 2003).

The brown or grizzly bear *Ursus arctos* is the most widespread bear in the world. Formerly it had an almost continuous Holartic distribution in Europe, Asia and North America, ranging from northern arctic tundra to dry southern desert habitats; at present its range is fragmented and reduced, especially in Europe (Swenson et al. 2000). Plasticity has been considered one characteristic of brown bear mating behaviour (Herrero & Hamer 1977, LeFranc et al. 1987). However, there are few published reports on courtship and mating activities of free-ranging brown bears and most of them are based on observations of grizzly bears in North America (Herrero & Hamer 1977, Brady & Hamer 1992, Hamer & Herrero 1990, Murie 1985, Craighead & Mitchell 1982, Craighead et al. 1995). The only instances in Eurasia originate from the former Soviet Union (Vaisfeld & Chestin 1993) and one record originates from the Cantabrian Mountains of northern Spain (Clevenger et al. 1992). In spite of this, some behavioural aspects of the mating system can only be properly known and evaluated through direct observation of breeding individuals during the mating season.

Based on direct observations of free-ranging bears, we describe the period of the year, the weather conditions and the habitat used by courting and mating bears in the Cantabrian mountains in this paper. The Cantabrian brown bear population is the most western and one of the smallest in Europe, highly threatened with extinction (Wiegand et al. 1998, Swenson et al. 2000). A more complete knowledge of the breeding biology of this small and isolated population will be useful for a better understanding of the biology of the species, but may also improve the implementation of suitable conservation measures, for the bears and for their habitat (see Dayton 2003).

Bears in Europe usually mate between mid-May and early July (Swenson et al. 2000), but the period of copulation can be affected by physiological and climatic conditions (Tumanov 1998). Given the low latitude and the corresponding warm climatic conditions of the Cantabrian Mountains, we suspect that breeding dates could be advanced in this area compared to more northern localities. Furthermore, brown bears of some populations in North America seem to choose small mating areas in unproductive summit ridges above the treeline (Hamer & Herrero 1990, Brady & Hamer 1992). Here we also test the hypothesis that habitat and weather conditions for breeding activity of Cantabrian bears will be different from those chosen by non-breeding bears in the same period. Finally, we will describe the reiterative use by bears in subsequent breeding seasons (different years) of definite mating locations. To our knowledge, only Hamer & Herrero (1990) have suggested the existence of durable mating areas in which bears meet for courtship behaviour in two or more separate years.

Study area and methods

The Cantabrian Mountains run east-west along the Atlantic coast in northern Spain, with a maximum elevation of 2,648 m a.s.l. and average elevations and gradients of north- and south-facing slopes of 700 m and 34% and 1,300 m and 21%, respectively. Proximity to the ocean and the geographic orientation of the mountain chain result in heavy rainfall (about 900-1,900 mm per year) on the north-facing slopes and a rain shadow (400-700 mm) on southern slopes. Forest cover is rather varied on north-facing slopes, with oak *Quercus petraea*, *Q. pyrenaica* and *Q. rotundifolia*, beech *Fagus sylvatica*, birch *Betula alba*, and chestnut *Castanea sativa* trees, whereas oak forest dominates the south-facing slopes. In total, forests cover around 25% of the landscape (the lowest value for all the bear ranges in Europe) and are interspersed in a matrix of grasslands and shrub of broom *Cytisus scoparius*, *C. purgans*, *C. cantabrica*, *Genista florida*, *G. obtusirramea* and heather *Erica aragonensis*, *E. arborea*, *Calluna vulgaris*. A subalpine shrub of bilberry *Vaccinium myrtillus*, *V. uliginosum*, juniper *Juniperus communis* and bearberry *Arctostaphilos uva-ursi* predominates above 1,700-2,300 m, where climatic conditions prevent forest growth.

The Cantabrian bear population includes about 80-90 individuals in two subpopulations (western and eastern) separated by physical barriers (e.g. motorways and rail-

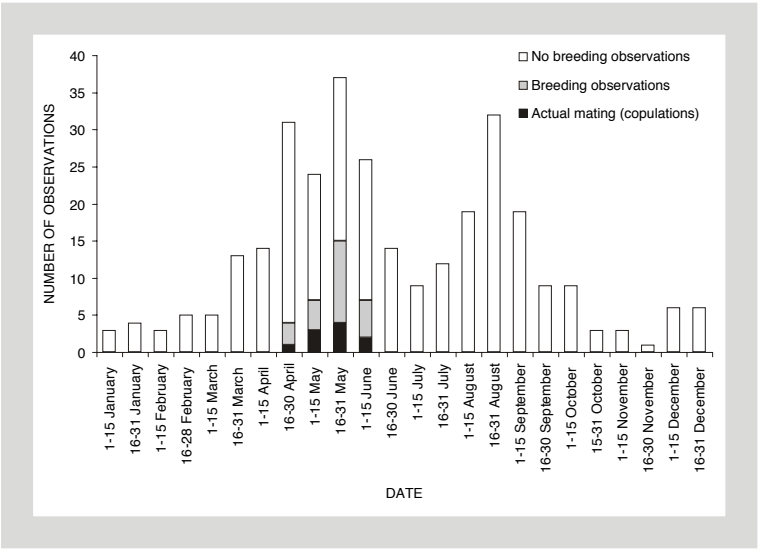

Figure 1. Distribution of dates of 297 direct observations on bears in the western Cantabrians, including observations of no breeding behaviour (N = 264), of breeding behaviour (N = 23) and of actual matings (N = 10).

ways) and unsuitable habitat (Palomero et al. 1997, Naves et al. 2003). Human densities are 12.1 and 6.1 inhabitants/km^2 for the western and eastern nuclei, respectively. The main economic activity is livestock raising, mainly cattle, but mining, tourism, hunting, agriculture and timber harvest are of local importance.

During 1988-2004, we made 297 non-systematic direct observations of free-ranging bears throughout the whole year, with observations in every month (Fig. 1). All observations were made directly by the authors and exclusively in the western subpopulation, which includes 6-9 females with cubs each year (Wiegand et al. 1998). All observations but one were made using spotting scopes, usually at distances of 0.8-2 km, and bears were followed for as long as weather, light or vegetation cover permitted. Only observations that lasted > 10 minutes were considered. We assigned to breeding behaviour all the records that included adult male-female close interactions (such as following close behind, playing, genital smelling, physical contact and mutual rubbing) and attempts of copulation, whether successful or not. The sex of each individual was inferred from its physical characteristics and behaviour. Lone bears, juvenile groups and females with cubs or yearlings were considered as non-breeding bears.

For each observation we registered the place, the date, the hour and the duration of the sighting, the weather conditions, the habitat characteristics and the behaviour of the bears, noting the time devoted to different activities (e.g. feeding, travelling and resting). We classified our weather observations into four classes: fog, rain, overcast and cloudless. We compared weather conditions when breeding bears were observed with a random sample of observations of non-breeding bears in the same period (mid-April to mid-June) and the same years. Sightings of breeding bears in a given mating area during one season were considered a different event when the number of participants varied. The term 'individual bears' indicates individuals identified by their physical characteristics or neck marks, present in a given mating area in one season.

Habitat analysis was made on the basis of a grid of 0.5 × 0.5 km squares, from a GIS database (Consejería de Medio Ambiente, Principado de Asturias) which is a thematic cartography (vegetation, human infrastructures, geomorphologic) composed of Arc-Info vectorial layers and based on the Spanish National Topographic Map 1:25,000. Most of it is derived from orthophotos (scale 1:25,000), completed with aerial pictures (scales ranging within 1:18,000-1:33,000), and fine-tuned with field observations. The polygons were delimited at a resolution of 25 × 25 m. At the original vegetation layer, 138 vegetation classes were distinguished. To obtain topographic information (slope and elevation) we built a digital elevation model (DEM) with a cell size of 125 m from digital elevation contours (50-m elevation interval). We calculated the average values of elevation and slope from 16 topography data points at each cell of the original grid (0.5 × 0.5 km).

We measured the following variables using a GIS: paved roads (m/cell), average altitude (m a.s.l.), average slope (%), brushwood cover (%), forest cover (%), grassland cover (%) and rocky outcrops cover (%). We compared the habitat features of the cells used by bears displaying breeding behaviour (N = 15) and those of the cells used by other bears not attempting to breed in the same period (mid-April to mid-June; N = 31). For comparison we also described the average habitat values for a polygon including all observations (N = 1,561 cells), in a core area of 390 km^2 out of the total occupied range of around 3,700 km^2 of the western population (Naves et al. 2003).

Comparisons of means were made using Mann-Whitney U-test, and significance was defined at $P < 0.05$.

Table 1. Dates of observation, durable mating areas, weather conditions, length of copulation (in minutes) and effective time of observation (in minutes) from events (N = 23) of bears displaying breeding behaviour in the western Cantabrian bear range.

Date	Durable mating areas	Weather	Copulation length	Observation length
17 April 2001		Fog		20
25 April 1999	1	Fog, rain	11	47
27 April 1999	1	Fog		19
10 May 1993	1	Fog, rain	50	158
12 May 1993	1	Fog, rain	35	122
13 May 1993	1	Fog, rain	10; 5	153
14 May 2001		Rain		25
16 May 1994	2	Rain	25; 3	72
18 May 2000	3	Fog	5	55
18 May 2004		Rain	19	205
19 May 1998	2	Cloudless		12
20 May 2004		Overcast		56
22 May 2002		Fog, rain		55
23 May 1995	2	Overcast		50
25 May 2000	3	Fog, rain		47
26 May 1999		Cloudless		21
26 May 2000	3	Rain		175
31 May 1994	3	Fog	6	78
1 June 2001		Cloudless		25
3 June 1999	3	Overcast		58
6 June 1995	3	Fog		16
7 June 1996	3	Cloudless	4	83
12 June 2001		Overcast	30	90

Results

We registered 23 observations (7.7% of the total) during 1993-2004 (no breeding events were observed between 1988 and 1992) that could be assigned to breeding behaviour. All of them occurred between 17 April and 12 June, but 83% (19 of 23) occurred in just one month, between the second week of May and the first week of June. Matings (N = 12) took place between 25 April and 12 June), with one in April, nine in May and two in June (see Fig. 1, Table 1). On two occasions we were able to see two copulations of the same individuals during a single observation. Copulation length varied between three and 50 minutes and averaged 17 minutes (see Table 1).

Only four of 23 (17.4%) observations of breeding bears were made in cloudless weather, whereas 10 (43.5%) of a random sample of 23 observations of non-breeding bears were made in cloudless weather. The differences were marginally significant ($\chi^2 = 3.70$, P = 0.055).

Breeding behaviour was observed in cells with less forest and grassland and more brushwood than in cells used during the same period by non-breeding bears, but the differences tended to be only marginally significant (Table 2). In relation to the whole available habitat, breeding and non-breeding bears seemed to prefer areas with more rocky outcrops, less grassland and less roads (see Table 2).

Regarding the observations of feeding activity in breeding vs non-breeding bears, we found a significant difference: 46 breeding bears devoted a mean of 9.6% of their time to feeding, while 52 non-breeding bears devoted a mean of 40.0% of their time to feeding during the same period (Mann-Whitney U-test: P < 0,001; A. Fernández-Gil, J. Naves & M. Delibes, unpubl. data).

We observed breeding behaviour at three places in different years (areas 1, 2 and 3 in Table 1, with observations in two, three and five years, respectively). We considered these three locations as 'durable mating areas' (*sensu* Hamer & Herrero 1990). Breeding bears in mating area 1 were observed in 1993 and 1999 in an area of < 4 ha; in area 2 in 1994, 1995 and 1998 in an area of 2.4 ha, and in area 3 in 1994, 1995, 1996, 1999 and 2000, in an area of 125 ha. As our data come from casual observations and the effort of field research was not evenly distributed over time, we do not know if breeding occurred in other years in the same areas. Moreover, breeding activity may extend over several weeks, so it is possible to miss or overlook mating bears, even when looking for them. For instance, we did not record any evi-

Table 2. Comparison of the habitat variables roads (m/0.25 km^2), elevation (in m a.s.l.) and slope (in %) expressed as means and SD between breeding (N = 15) and non-breeding (N = 31) cells of 0.5 × 0.5 km. The values for the study area enclose all cells (N = 1,561).

				% cover (0.25 km^2) [1]			
	Roads (m/0.25 km^2)	Elevation (m)	Slope (%)	Brushwood	Forest	Grassland	Rocky outcrops
Breeding cells	4 (17)	1,213 (255)	58 (17)	63.2 (27.1)	25.8 (25.5)	1.2 (4.2)	28.4 (26.1)
No breeding cells	120 (254)	1,255 (275)	61 (19)	46.7 (28.7)	37.0 (25.1)	5.8 (11.1)	21.1 (16.1)
P-values [2]	0.22	0.82	0.78	0.068	0.146	0.036	0.542
Study area	228(388)	1,278 (285)	58 (26)	51.1 (32.0)	33.2 (30.1)	11.2 (18.1)	8.7 (14.9)

[1] Rocky outcrops data were measured from a geomorphologic map; brushwood, forest and grassland were measured from a vegetation map.
[2] Mann-Whitney U-test results.

dence that area 1 was used by mating bears (only by other bears) after 1999, despite looking for mating behaviour several times each year. Nevertheless, we obtained indirect evidence of use in other years (in June 2003 we recorded a track set of two bears, probably a male and a female, within 1 km of area 1). Similarly, in May 1998 we recorded tracks of a pair in area 3.

Discussion

To compare our results with results obtained in other areas, we considered the breeding season as either the period when copulations occur or when consorting and breeding displays are observed (LeFranc et al. 1987). The breeding season of European brown bears is thought to occur between mid-May and early July (Swenson et al. 2000). A compendium by LeFranc et al. (1987) refers to 20 studies in which dates of the breeding season are reported from North America. The breeding season starts in April (two cases), May (15 cases) and June (three cases), and it ends in June (two cases), July (11 cases) and August (two cases). Extreme dates in North America are 21 April and 12 August. In Sweden, Dahle & Swenson (2003a) recorded the mating season (defined as the period when radio-marked males and females were seen together) between early May and mid-July, but > 75% (N = 50) occurred between mid-May and early June. According to our prediction which is based on these data and other data from the literature (Pearson 1975, Murie 1985, Craighead & Mitchell 1982, Vaisfeld & Chestin 1993), breeding takes place earlier in the Cantabrian Mountains than elsewhere, though the only previously published dates for the eastern Cantabrian nucleus was in late June and early July (Clevenger et al. 1992). Because the period of copulation could be regulated by the physiological condition of bears and climatic conditions (Tumanov 1998; though one is probably an effect of the other), benign climatic conditions at low latitudes (probably related to a shorter hibernation period; see Naves & Palomero 1993, Naves et al. 2001) could explain an early breeding season in the Cantabrian range.

Some breeding activity of bears likely occurs at night, but our observations were made only in daylight. From our data on weather conditions, it appears that bears are less prone to copulate, at least during daytime, when the sky is cloudless. We have not found any report about a potential relation between weather conditions and breeding activity elsewhere in the literature. This preference could be related to the shy behaviour of the breeding bears inhabiting a highly humanised landscape. The observed greater breeding activity during 'bad' weather could be an adaptive decision by bears to avoid human disturbance during the risky breeding period. In fact, human related mortality is the most important factor affecting bear demography in the western Cantabrian subpopulation (Wiegand et al. 1998, Naves et al. 2003). Nevertheless, we have not found significant differences between breeding vs non-breeding bears regarding distances to paved roads, the only metric of human disturbance we used (see Table 2).

The apparent increased use of brushwood (and decreased use of forests and grassland) by bears while breeding could favour the meeting of mating bears, while keeping away other bears that eat grasses and forbs in grassland habitats in the same period or remain inside the forest. We found significant differences between breeding and non-breeding bears in time devoted to feeding, and several authors have noted a similar decrease in feeding activity by bears involved in mating activities. For example, Hetchel (in Lefranc et al. 1987) reported a dramatic drop in feeding from 60% to < 10%, and Phillips (in Lefranc et al. 1987) noted that mating bears devote only 6.7% of their time to feeding. Also Herrero & Hamer (1977) noted a reduction in food intake by a mating pair. On the other hand, Hamer & Herrero (1990) and Brady & Hamer (1992) described courting areas in the Canadian Rockies as summit ridges in the subalpine zone with low abundance of food resources. However, other studies have reported that breeding bears select areas with abundant foraging resources (see compendium by LeFranc et al. 1987). The selection of the spatial grain (0,25 km^2) was imposed by GIS data availability. However, habitat selection by breeding bears could operate at finer scales. So, we can not rule out that breeding areas are chosen because of some other non-structural habitat characteristics, for instance spatial overlap of home ranges.

To our knowledge, the existence of a discrete location in which bears met for courtship behaviour during two subsequent seasons has been proposed in only one area, i.e. the southern Rocky Mountains (Hamer & Herrero 1990). However, the repeated use of the same mating areas in subsequent years seems to be moderately frequent in the western Cantabrian Mountains. It is well known that small populations of solitary animals spread over a large area could have reduced breeding success, because it becomes difficult for widely dispersed individuals to find a mate (this is an aspect of the 'Allee effect', which postulates that the *per capita* birth rate declines at low densities; Allee et al. 1949; see Stephens & Sutherland 1999). Berec et al. (2001) have looked in detail at dynamical consequences of explicitly modelled sexual reproduction in a single-species population, and

showed that sufficiently sparse populations will go extinct due to the Allee effect arising via mate shortage. Hence, in small and fragmented bear populations, such as that of the Cantabrian Mountains, the selection of durable areas to mate could be advantageous to counteract the Allee effect, and would make the meeting of individuals of both sexes easier during the breeding season. In our study area these discrete mating places are used in the same year, simultaneously or successively, by more than one pair of bears, as several instances of multiple mating attempts were observed, including females copulating (or attempting to copulate) with several males, and males trying to copulate with several females (authors, unpubl. data). This finding contrasts with the mating area described by Hamer & Herrero (1990), in which only one pair of bears were involved. Our results could imply a high degree of polygamy and the existence of tenuous bonds between breeding bears, suggesting that the use of small and durable areas to mate might be only part of a complex mating system of bears in our study area.

Our findings have important implications for the conservation management of the critically endangered Cantabrian bears and maybe also for other small and isolated European bear populations. Although more studies on breeding strategies and behaviour are needed, it seems that in our study area breeding habitat could be defined and delineated, and the discrete mating areas (< 125 ha) used by several adult bears in subsequent years could probably be identified. We recorded up to seven different adult individuals in a 24-hour period in the same mating area (# 3), the greatest known concentration of adult bears in the Cantabrians, where < 100 individuals are currently living (Palomero et al. 1997). Hence, these places should be considered as critical areas in the life cycle of bears, similar to denning places or some important feeding areas. Tourism is quickly growing in the Cantabrian range, mainly as a summer activity but also during the spring, and it is an important disturbance source for bears (Naves et al. 2001). So, tourism and other human activities (such as hunting and livestock raising) should be regulated in these areas during the mating period, and the human access through paved or unpaved roads should be limited. Obviously, because mating areas could change their location or disappear through time, continuous and careful monitoring is needed.

Acknowledgements - we acknowledge Francisco Palomares, Alejandro Rodríguez, Jon E. Swenson, José Manuel Samos, Mario Quevedo and Carlos Rodríguez for their ideas and comments. We want to kindly acknowledge the comments of Andrew E. Derocher and two anonymous reviewers. This paper is a contribution to the projects Fremd F+E 0302 UFZ-CSIC and Plan Nacional de I+D+I BOS2001-2391-CO2-02 (Ministerio de Educación y Ciencia, Spain), and we acknowledge Thorsten Wiegand and José Ramón Obeso as responsible researchers of both projects, respectively.

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