The role of spring temperatures in the den exit of female brown bears with cubs in southwestern Europe

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Abstract: Hibernation represents the most refined adaptation of endothermic species to overcome unfavorable periods when food is scarce. Thus, hibernation should take place within specific time frames with respect to environmental factors. Flexibility in the timing of biological events is thus central to how well mammals can deal with varying climatic conditions. For brown bears (*Ursus arctos*), hibernation is not only a critical period that allows them to save vital energy reserves for times of food shortage, but also the period during which pregnant females give birth to cubs. Here, we analyzed the relationship between 74 den exit dates of females with cubs, recorded from 1995 to 2018 in the Cantabrian Mountains in northwestern Spain, with (1) average daily precipitation and (2) average maximum temperature during the 30 days before den exit, as well as with (3) the number of cubs. The bears exited from 1 April to 16 May, and the mean date was 28 April. Our results, which are consistent with the general latitudinal pattern of den emergence reported in other studies, suggested that in years with higher maximum temperatures, exit dates tended to be earlier, whereas the number of cubs and the average rainfall for the 30 days prior to den exit did not seem to determine the variation in den exit dates. Considering the relationship between spring temperatures and den exit dates of females with cubs, it is important to take into account the repercussions that current global warming may have on the reproduction of brown bears. Current trends of climate change might trigger earlier den exit dates than in the past, which may have negative consequences on the population dynamics of brown bear populations. For example, a mismatch between the chronology of hibernation and food availability might reduce cub survival and, consequently, the fitness of females.

Key words: Cantabrian Mountains, climate change, cubs, den exit, drivers of hibernation, hibernation, spring temperatures, *Ursus arctos*

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Hibernation is a vital strategy to survive unfavorable periods, such as times of food shortage and the adverse weather conditions of winter. In mammals, hibernation manifests as a temporary reduction in metabolism and physiological processes (Geiser 2004, Ruf and Geiser 2015, González-Bernardo et al. 2020). Thus, this mechanism represents the most refined adaptation of endothermic species to overcome the cold season when food is scarce (Geiser 2013, Ruf and Geiser 2015). To be an adaptively efficient strategy, however, hibernation should be initiated and terminated within specific time frames in accordance with environmental factors. Flexibility in the timing of biological events is thus central to how well mammals can deal with varying climatic conditions (McCain and King 2014, Gallinat et al. 2015).

For brown bears (*Ursus arctos*), hibernation is not only a critical period that allows them to save vital energy reserves for times of food shortage (Geiser 2004, Pigeon et al. 2016), but also is the period during which pregnant females give birth to cubs in breeding dens and raise them during their first weeks of life (Ciarniello et al. 2005, Steyaert et al. 2012). In brown bears, gestation lasts an average of 56 days, with cubs born at the end of January (mean date: 26 Jan in Sweden; Friebe et al. 2014). Pregnant females are the cohort with the longest hibernation period among bears (Judd et al. 1986, Schoen et al. 1987, Miller 1990, Van Daele et al. 1990, Friebe et al. 2001, Haroldson et al. 2002, Ciarniello et al. 2005, Graham and

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Stenhouse 2014, Krofel et al. 2017). Accordingly, pregnant females, on average, tend to exhibit earlier den entry dates (Judd et al. 1986; Schoen et al. 1987; Friebe et al. 2001, 2014; Haroldson et al. 2002; Krofel et al. 2017) and later den exit dates than other bears (Van Daele et al. 1990, Friebe et al. 2001). It has also been suggested that females with cubs (hereafter, FCOYs) could also delay their exit from the den so that the cubs are better developed when they leave the den (Mcloughlin et al. 2002).

Dates of den entry and exit vary between different brown bear populations across the Northern Hemisphere because winters vary in duration and harshness according to latitude. Indeed, hibernation length generally shows a positive relationship with latitude (Haroldson et al. 2002, Manchi and Swenson 2005, Krofel et al. 2017), and brown bears have adapted their hibernation chronology to a series of environmental factors (Delgado et al. 2018, Fowler et al. 2019). Many studies have tried to identify the factors that might affect the chronology and duration of brown bear hibernation, evaluating possible climatic, physiological, and food availability factors (Evans et al. 2016, Pigeon et al. 2016, Delgado et al. 2018, Bojarska et al. 2019, Fowler et al. 2019). However, different drivers have been suggested for different bear populations; they appear to be area- or population-specific or both. Whereas some authors link the beginning of hibernation with food shortages (Schoen et al. 1987, Van Daele et al. 1990, Ciarniello et al. 2005, Pigeon et al. 2016), others point to environmental factors, such as the first snowfall (Craighead and Craighead 1972, Manchi and Swenson 2005, Friebe et al. 2014, Evans et al. 2016, Delgado et al. 2018) or the temperature in autumn (Evans et al. 2016). Factors that determine den exit include negative relationships with both winter (Evans et al. 2016) and spring (Miller 1990, Mcloughlin et al. 2002, Manchi and Swenson 2005, Pigeon et al. 2016, Delgado et al. 2018) temperature, in addition to positive relationships with snow depth and date of snowmelt (Schoen et al. 1987, Fowler et al. 2019) as well as spring precipitation (Pigeon et al. 2016). Additionally, human disturbances can force the change or premature abandonment of dens (Swenson et al. 1997, Linnell et al. 2000). Premature den abandonment can compromise population viability because it increases the risk of cub loss in pregnant females (Swenson et al. 1997) and decreases survival rate of neonates (Linnell et al. 2000).

Not all brown bears hibernate if they have food in winter (Van Daele et al. 1990); this phenomenon is more commonly described in low latitudes, where winters are milder and snow cover less or ephemeral (Huber and Roth 1997, Nores et al. 2010). Likewise, a higher probability of observing brown bears during the winter has been reported as ambient temperature rises (Bojarska et al. 2019). Therefore, factors that trigger den exit of FCOYs might be more complex than those that trigger den exit in other sex and age categories of brown bears because pregnant females do not hibernate only in response to food shortage. Understanding such factors is also important in the context of global warming, with current forecasts of several degrees Celsius increase by the end of the century at a global level (IPCC 2013, Raftery et al. 2017). The rise of mean temperatures (IPCC 2013), as well as the increase in temperature and precipitation variability (Giorgi et al. 2004, Pendergrass et al. 2017), has affected biological systems in part by altering the phenology of seasonal processes such as hibernation (Root et al. 2003). Changes in climate could reduce the duration of hibernation in bears and lead to earlier den exit (Pigeon et al. 2016, Johnson et al. 2017). For other hibernating mammals, such as rodents, duration of hibernation (Inouye et al. 2000, Ozgul et al. 2010), as well as fitness or survival rate of individuals (Turbill and Prior 2016), has been reduced in recent decades as a result of climate change. Climate change might also have negative consequences on cub survival in particular (Miller 1990, Pigeon et al. 2016, Johnson et al. 2017), because an earlier den exit caused by warmer temperatures implies possible mismatches with trophic resources (Inouye et al. 2000, Rodríguez et al. 2007, Bojarska and Selva 2012), as well as younger and smaller cubs that might be more vulnerable to predation and infanticide (Sahlén al. 2015, Pigeon et al. 2016). Finally, an increase in winter temperatures has been shown to negatively affect reproduction of brown bears (Albrecht et al. 2017). On the other hand, a general increase in spring temperatures or rainfall could result in earlier availability of some foods, and an early den exit could thus be advantageous for brown bears to access these food resources (Fowler et al. 2019). In addition to the general trend toward an increase in temperature, interannual fluctuations in the chronology of hibernation may also be important. These fluctuations may be caused by both interannual variations in climatic variables resulting from climate change and extreme climatic events and temperature anomalies, which have been predicted for southwestern Europe (Giorgi et al. 2004, Castro et al. 2005, Pendergrass et al. 2017). Such year-to-year changes in hibernation length have already been reported in American black bears (*U. americanus;* Miller et al. 2017) and even in brown bears, where these changes depend on temperatures or precipitation during winter and spring (Miller 1990, Mcloughlin et al. 2002, Friebe et al. 2014, Evans et al. 2016, Pigeon et al. 2016, Johnson

et al. 2017, Delgado et al. 2018). Therefore, identifying triggers of den exit of FCOYs and their adjustment to climatic factors is of great importance and would allow for better prediction of the effect of climate change on this vulnerable brown bear population.

Here, we analyzed data on den exit dates of FCOYs collected over 19 years (from 1995 to 2018) for the small and isolated brown bear population inhabiting the Cantabrian Mountains (northwestern Spain), with the aim of exploring the attempt of bears to adjust their den exit to short-term variation in climatic conditions (which may be at least partially extracted from year-to-year variation), and assess the potential role of (1) temperature and rainfall, as well as (2) the number of cubs, in den exit dates. We also compared exit dates of the Cantabrian population with other studies carried out across the brown bear distribution area. Thus, we tested 3 main hypotheses: (1) higher temperatures in the month prior to den exit (when hibernating brown bears seem to be most sensitive to changes in temp; Delgado et al. 2018) will lead to earlier exit dates; (2) den exit will occur later if there are heavy rainfalls, which may represent harsh weather conditions for cubs; and (3) more cubs per litter will require greater energy demands that can be satisfied by an earlier den exit. To our knowledge, this is the first long-term study on den exit chronology carried out on FCOYs of one of the southernmost (42–43°N latitude) populations of brown bears.

Study area

In this study, we considered most of the range currently occupied by brown bears in the Cantabrian Mountains (Fig. 1), which consists of approximately 4,476 km^2 across parts of Asturias, León, and Palencia provinces (northwestern Spain; Penteriani et al. 2019). The Cantabrian Mountains are one of the main mountain systems in Spain and extend for approximately 300 km parallel to the Atlantic coast. Average altitude is approximately 1,100 m above sea level (asl), with the highest peak reaching 2,648 m asl (Martínez Cano et al. 2016). The region is characterized by an oceanic climate, with remarkable differences between northern slopes (oceanic climate with greater rainfall and more constant temperature) and southern slopes (continentalized and drier climate, with greater thermal amplitude, cold winters, and warmer summers; Ortega and Morales 2015). The landscape is mainly composed of forests (39%), shrubs (24%), and croplands (22%; Mateo-Sánchez et al. 2016), and the region is home to the largest extent of deciduous Atlantic forest in the Iberian Peninsula (Polunin and Walters 1985). Southern slopes are dominated by forests of semi-deciduous oaks and evergreen oaks (*Quercus pyrenaica* and *Q. ilex;* Mateo-Sánchez et al. 2016), whereas northern slopes are primarily occupied by deciduous forests of beeches (*Fagus sylvatica*), deciduous oaks (*Q. robur* and *Q. petraea*), birches (*Betula* spp.), and chestnuts (*Castanea sativa;* Mateo-Sánchez et al. 2016) with an understory mainly consisting of bilberry (*Vaccinium myrtillus;* Pato and Obeso 2012). Shrubs occur in degraded or non-forest areas, where several species of heather (*Erica, Calluna*) and brooms (*Genista, Cytisus*) predominate, among others (Fernández-Gil et al. 2006, Mateo-Sánchez et al. 2016). Above the tree line, around 1,500–1,700 m asl, bilberries (*V. myrtillus V. uliginosum*), bearberries (*Arctostaphylos uva-ursi*), subalpine juniper (*Juniperus communis*), and buckthorns (*Rhamnus alpina*) are common (Pato and Obeso 2012, Martínez Cano et al. 2016). In general, the study area is characterized by a human-modified landscape, with core areas of optimal habitat inhabited by bears surrounded by a matrix of urbanized and cultivated areas with a high density of transport routes (Mateo-Sánchez et al. 2016; Zarzo-Arias et al. 2018, 2019). The predominant economic activity is the extensive breeding of livestock, followed by mining, timber harvest, and recreational activities such as tourism and hunting (Fernández-Gil et al. 2006).

Methods

Brown bear data

We used information on the approximate date of 74 den exit events (defined as the first observation of a FCOY around the breeding den), number of cubs per den exit event, and den location in the Cantabrian Mountains collected from 1995 to 2018. We define den exit or den emergence as the time when the female leaves the winter den accompanied by cubs. The approximate date of den exit was obtained from (1) almost daily direct observations of den areas by rangers of the regional administrations (Principado de Asturias and Castilla y León, principally by the Patrulla Oso; i.e., Bear Patrol, in both regions), as well as by personnel of the Asturian Foundation for the Conservation of Wildlife (Fondo para la Protección de los Animales Salvajes), the Fundación Oso de Asturias, and the Brown Bear Foundation (Fundación Oso Pardo); and (2) almost daily personal observations by the authors. Indeed, every year, known reproductive den areas are intensively monitored from the beginning of spring (late Mar–beginning of Apr). Continuous and early monitoring of known breeding dens and their visibility (breeding dens in the Cantabrian Mountains are generally located in rocky areas with sparse vegetation, where bear families

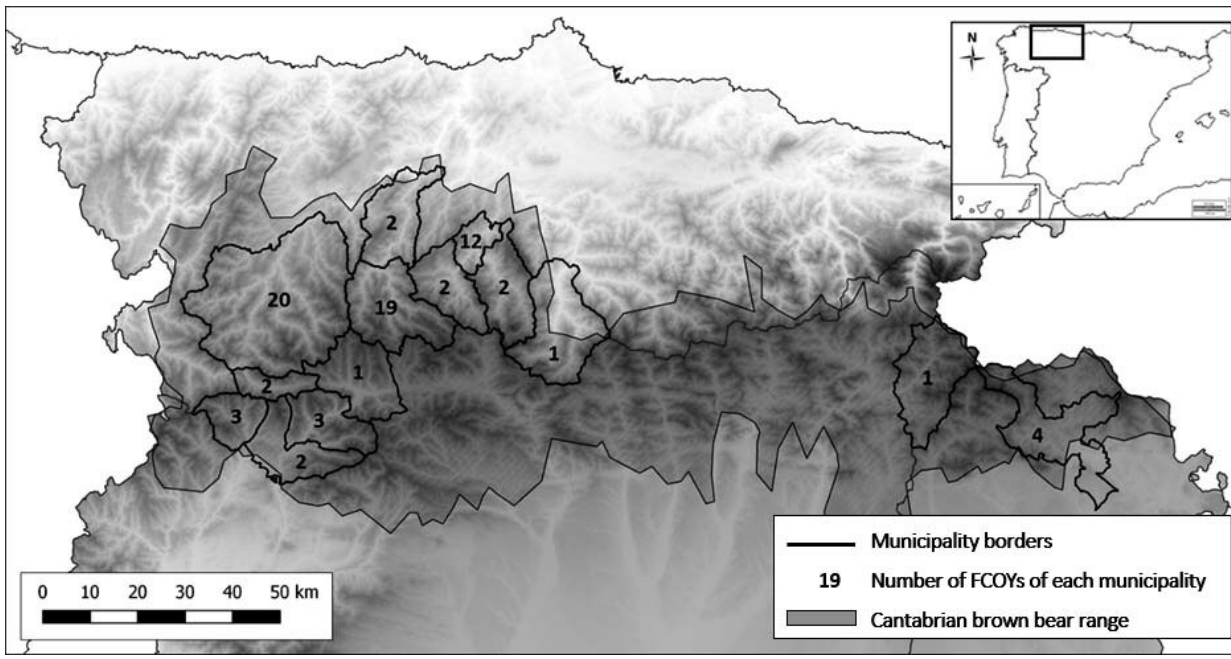

Fig. 1. The distribution range of brown bears (*Ursus arctos*) in the Cantabrian Mountains (northwestern Spain; shaded area), together with the number of recorded dates of den exit ($n = 74$) of females with cubs (FCOYs) per municipality. The grey scale of the base map indicates the altitude of the terrain, with the darkest tones corresponding to areas of higher altitude.

are visible; Zarzo-Arias et al. 2019, Penteriani et al. 2020 and Supplemental Material) reduced the risk of considerable delay in the observation of FCOYs after den exit. Moreover, monitoring generally occurred during the 3 peaks of activity of females with cubs (i.e., around sunrise, between 1200 and 1500 hr, and at sunset [authors' unpublished data]). We considered 16 May to be the last occurrence of den exit of a FCOY. After this date, the following first observations of females with cubs were too late (end of May–beginning of Jun) to be included as real den exits. However, this does not mean that some later den exits by FCOYs might not occur sporadically in the Cantabrian Mountains.

Meteorological data

We collected data on average (1) daily precipitation and (2) maximum temperature for the 30 days before the first observation of each FCOY after den exit (i.e., when hibernating brown bears seem most sensitive to changes in temperature [Delgado et al. 2018]). We did this for all FCOYs and for each of the years studied. This information was collected at the meteorological station closest to the den area (1–30 km) among the available stations administered by the Spanish State Meteorological Agency (Agencia Estatal de Meteorología) spread across the Cantabrian Range. We then calculated the mean of the collected maximum temperature and mean precipitation data. Similar studies carried out in other regions of the world (Evans et al. 2016, Pigeon et al. 2016, Delgado et al. 2018) also included depth and permanence of snow cover, but we did not collect this information because snow cover is scarce or absent around breeding dens, especially in the month prior to first observations of FCOYs. Snowfall in the study area averages 38 days, concentrated from December to March (Nores et al. 2010).

Statistical analyses

Our sample size was relatively small to allow us to include all predictors into a single model, and we had, a priori, clearly distinct hypotheses. Therefore, we ran 2 separate statistical analyses. First, we were interested in assessing whether the number of cubs of the year affected the den exit date of mother bears. To this end, we built a linear mixed model (LMM) with a normal distribution with Julian exit date as the response variable and the number of cubs as the explanatory variable. Second, we assessed which climatic factors were the most relevant for bear den exit. Such information may be

at least partially extracted from year-to-year variation, which is likely to reflect bears' attempts to adjust their phenology to short-term variation in climatic conditions. With such an aim, we employed a 2-step approach. First, we built 3 different LMMs using (1) den exit date (Julian date), (2) maximum temperature, or (3) precipitation for the 30 days before den exit as the response variable and year as the explanatory variable. We extracted the residuals of these models, which respectively represent shift-corrected phenological and shift-corrected climatic variables. We then built linear models to explain shift-corrected dates by shift-corrected climatic variables. There was no correlation between the 2 explanatory climatic variables ($r = 0.38$, variance inflation factor, VIF = 1.17). In all models, we included the council in which each FCOY was located as a random factor to account for the fact that different bears were observed over different years in the same councils (i.e., repeated measurements) and the fact that the number of observed bears across years in the different councils differed (i.e., unbalanced data). We selected the best competing model or set of models based on Akaike's Information Criterion (AIC_c) and considered models with a ΔAIC_c value <2 as equally competitive. We also calculated values of ΔAIC_c and weighted AIC_c of each competing model (Table 1). We ran all statistical analyses in Program R v. 3.5.1 statistical software (R Core Team 2018). We built linear models using the "lme4" package (Bates et al. 2015). We generated models and calculated AIC_c values using the "dredge" function in the "MuMIn" package (Bartoń 2013).

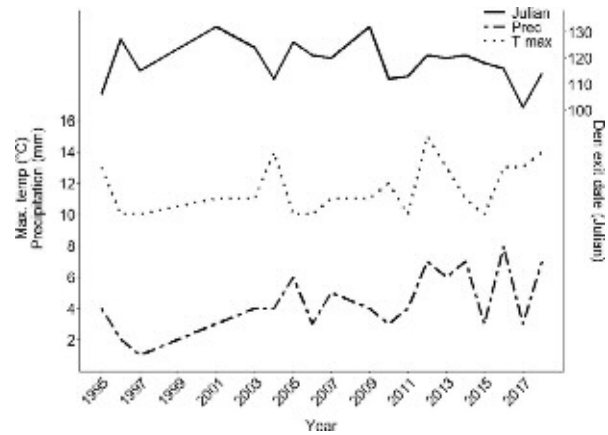

Fig. 2. Annual variation in den exit dates (Julian dates, $n = 74$) of female brown bears (*Ursus arctos*) with cubs in the Cantabrian Mountains, northwestern Spain, recorded from 1995 to 2018. Annual patterns of maximum temperature (T max) and precipitation (Prec) in the 30 days prior to den exit are also shown.

Results

Mean den exit date of FCOYs was 28 April in non-leap years (SD = 11.9 days). Most of the den exit dates were distributed toward the end of the range of dates. Only 19% ($n = 14$) of FCOYS left the den during the first half of April, and the remaining 32% ($n = 24$) and 49% ($n = 36$) of FCOYs left the den during the second half of April and the first half of May, respectively. When comparing our results with those obtained in other studies, both range and average den exit date corresponded to the period of den exit for FCOYs of brown bear populations at similar latitudes (Table 2). Our results seem to be consistent with the general latitudinal pattern of advancement of brown bear den exit date as a function of decreasing latitude (Table 2).

We did not find any relationship between den exit dates and number of cubs ($F_{1,72} = 0.25$, $P = 0.62$). Moreover, even though there was no significant trend in the exit date of FCOYs across study years, both den exit date and climatic variables (i.e., max. temperature and precipitation) showed year-to-year variability during the study period (Fig. 2). Models built to assess the effect of this year-to-year climatic variation on the year-to-year variation of den exit revealed that only maximum temperature played a role in explaining the short-term fluctuations in den exit date (conditional $R^2 = 0.18$; Table 1). Specifically, our results showed that in years with higher spring temperatures, den exit dates of FCOYs were earlier.

Discussion

Brown bears show remarkable plasticity when hibernating, being able to adjust their denning behavior to environmental factors, such as food available during hyperphagia or snow conditions during the winter (Fowler et al. 2019). In fact, the chronological variability of hibernation has been described as more intense as one moves away from the equator (Manchi and Swenson 2005, Fowler et al. 2019). In addition, previous studies that have analyzed dates of brown bear den exit (Table 2) have shown that, generally, the average duration of hibernation decreases with distance to the equator (i.e., earlier dates of den exit), probably because of the reduced harshness of climatic conditions and greater availability of food in late autumn–early winter at more southerly latitudes (Manchi and Swenson 2005). Fowler et al. (2019) attributed this pattern to a stronger effect of the factors that determine

Table 1. Comparison of the competing models built to analyze the effect of climatic variables (i.e., residuals of maximum temperature and precipitation for the 30 days before the first observation of brown bear [*Ursus arctos*] females with cubs on their den exit date in the Cantabrian Mountains, northwestern Spain, recorded from 1995 to 2018) based on values of AIC_c[a], ΔAIC_c[b], and AIC_c weights ($n = 74$ den exit events). Competitive models are ranked from the lowest (best model) to the highest AIC_c value. Summary of fitted parameters is shown for models with $\Delta AIC_c < 2$. Conditional $R^2 = 0.18$.

Competing models		β	SE	AIC_c[a]	ΔAIC_c[b]	AIC_c weights
Max. temp				576.8		0.649
	Intercept	0.147	2.141			
	Max. temp	−1.319	0.475			
Max. temp + Precipitation				579.1	2.27	0.208
NULL				580.5	3.67	0.103
Precipitation				582.4	5.58	0.040

[a] AIC_c = Akaike's Information Criterion, adjusted for small sample sizes.
[b] ΔAIC_c is the difference in AIC_c value from the minimum AIC_i model.

Table 2. Den exit dates and hibernation lengths of brown bear (*Ursus arctos*) females with cubs for populations at different latitudes. Data are sorted by decreasing latitude of the study area. '-' indicates no data.

Study area	Latitude range	Mean date of den exit	Range of den exit	Mean hibernation length (days)	*N*	Source
Norbotten (North Sweden)	67–68°N	-	-	226	15	Manchi and Swenson 2005
Talkeetna Mountains (South-central AK, USA)	62–63°N	15 May	23 Apr–2 Jun	217	16	Miller 1990
Dalarna (Central Sweden)	61–62°N	7 May	5 Apr–14 Jun	196	47	Friebe et al. 2001
Chichagof and Admiralty islands (Southeast AK, USA)	57–58°N	11 May	First week of April–Third week of June	211	18	Schoen et al. 1987
NE Kodiak Island (Southwest AK, USA)	58°N	27 May	20 Mar–13 Jul	211	15	Van Daele et al. 1990
SW Kodiak Island (Southwest AK, USA)	57°N	31 May	7 May–3 Jul	198	18	
Mountains of Parsnip River area (BC, Canada)	54–55°N	-	-	206	6	Ciarniello et al. 2005
Plateau of Parsnip River area (BC, Canada)	54–55°N	-	-	177	3	
Jasper National Park and the Wilmore Wilderness area (AB, Canada)	53–54°N	Fourth week April	Second week April–Second week May	175	17	Graham and Stenhouse 2014
Mission and Rattlesnake Mountains (MT, USA)	47–48°N	25–26 Apr	-	-	1	Servheen and Klaver 1983
Sikhote-Alin State Biosphere Zapovednik (Russian Far East)	44–45°N	9 May (mean)	25 Apr–19 May	176	3	Seryodkin et al. 2003
Greater Yellowstone Ecosystem (MT, WY, and ID, USA)	44–45°N	Third–fourth week April	Fourth week of March–Third week of May	171	35	Haroldson et al. 2002
Yellowstone National Park area (MT, WY, and ID, USA)	44–45°N	13 Apr	-	170	9	Judd et al. 1986
Dinaric Mountain Range (Slovenia)	44–45°N	11 Mar	-	94[a]	4	Krofel et al. 2017
Cantabrian Mountains (northwestern Spain)	42–43°N	28 Apr	1 Apr–16 May[b]	-	74	This study

[a] Supplementary feeding was provided to the brown bears of this study.
[b] To avoid potential bias due to late first observations of females with cubs from unknown dens, we considered 16 May to be the last den exit occurrence. However, this does not mean that some later den exits by FCOYs might not occur in the Cantabrian Mountains.

the variability in hibernation at high latitudes, and Krofel et al. (2017) calculated an increase of 3.1 days in the duration of hibernation for each degree of north latitude. The range of the Cantabrian brown bear population is between 42° and 43°N latitude (i.e., within the southern limits of brown bear populations in Europe, along with those of the Pyrenees and the Balkan Peninsula). Following the patterns observed by Manchi and Swenson (2005) and Fowler et al. (2019), the dates in den exit recorded for the Cantabrian brown bear population are among the earliest dates reported for the species.

The mean date obtained for all FCOYs (last week of April) and the range of dates on which den exit occurs (from the first week of April to the second week of May) correspond to the exit dates we would expect according to the latitude of our study area (Table 2). Comparable exit dates have been recorded in 2 areas at latitudes similar to those of the Cantabrian Mountains (Yellowstone National Park in the USA [Judd et al. 1986, Haroldson et al. 2002] and Sikhote-Alin State Biosphere Zapovednik in the Russian Far East [Seryodkin et al. 2003]). In addition, Haroldson et al. (2002; Table 2) reported (1) a range of dates for den exit very similar to ours (i.e., from the fourth week of March to the third week of May); and (2) mean den exit between the third and fourth weeks of April, a date range that includes our mean den exit date (28 Apr).

The inverse relationship between maximum temperature and den exit in brown bears was also reported by Miller (1990), McLoughlin et al. (2002), Manchi and Swenson (2005), and Delgado et al. (2018), as well as for American black bears by Miller et al. (2017) and Johnson et al. (2017). In particular, Pigeon et al. (2016) reported that for each increase of 4°C in spring temperature, den exit occurs 10 days earlier. Schoen et al. (1987) and Fowler et al. (2019) suggested that variation in the chronology of brown bear hibernation may also be due to snowpack or the timing of snowmelt; however, it has also been suggested that discerning between the effect of these variables and spring temperature can be difficult when they are correlated. In our study area, snowfall is scarce and concentrated between December and March, which is outside the period of FCOY den exit; therefore, we can discard snowfall as one of the main variables affecting the variability of den exit dates.

Although inaccessibility of den sites prevented us from recording microclimatic characteristics, we point out that the microclimate at den sites may also play a role in bear responses to environmental conditions around a den (Pigeon et al. 2016). Another factor that we did not account for in this study, but that may play a role in determining length of hibernation, is the age and/or body condition of females in dens (Robbins et al. 2012). It is reasonable to assume that the female's physical condition might affect the reserves that she has available during the hibernation period and to feed cubs, which in turn may influence date of den exit.

Given the relationship between den exit dates and spring temperatures, it is essential to consider the consequences that an increase in temperature in the current context of global climate change would have on reproductive success and cub survival after den exit of brown bear populations, as was already reported for winter temperatures (Albrecht et al. 2017). Predictions generally project increases of 2.0° to 4.9°C in global average air temperature by 2100 (IPCC 2013, Raftery et al. 2017). In southwestern Europe, where our study population is located, increases in average temperature have already been observed in recent decades (Rodríguez et al. 2007, Penteriani et al. 2019). This general increase would be especially noticeable in higher average temperatures in winter and spring (IPCC 2013). Changes in climate due to global warming, in particular those produced in colder periods such as changes in winter–early spring temperatures and snow cover, can alter the phenology of many organisms (Williams et al. 2015). For example, such changes can cause mismatches between the biological cycle of animal species and the trophic resources on which they depend. This phenomenon has been described in other species (e.g., greater snow goose [*Chen caerulescens atlantica;* Doiron et al. 2015] and caribou [*Rangifer tarandus;* Post and Forchhammer 2008]). More specifically for hibernating mammals, lower fitness and reproductive success have been reported as a consequence of climate change (Lane et al. 2012, Turbill and Prior 2016), and specific episodes of variation in the end dates of hibernation during consecutive years with very different spring temperatures have been described (e.g., Mcloughlin et al. 2002). Advancement in den exit date and a shortening of the hibernation period in brown bears would therefore be expected. Brown bear populations in the mountains of southern Europe, such as the Cantabrian Mountains, might be especially affected. Published studies suggest that (1) the effect of climate change will be more pronounced in mountainous areas (Root et al. 2003, Penteriani et al. 2019); and (2) increases in extreme climatic events, as well as anomalies in temperature and variability in precipitation, have been predicted to occur in southernmost Europe (Giorgi et al. 2004, Castro et al. 2005, Pendergrass et al. 2017). Thus, an earlier den exit date may cause possible mismatches between hibernation chronology and food availability. Moreover, it has been

suggested that a premature den exit could affect the fitness of cubs, which are smaller and thus would be more vulnerable to predation and infanticide (Bellemain et al. 2006, Pigeon et al. 2016).

Thus, understanding how climatic change might affect future den chronology is essential to predicting how the species will respond to this new human-induced challenge. This will be particularly important in our study area because (1) our population, which inhabits the southern limit of the European bear range, is small and isolated; and (2) the Cantabrian Mountains are expected to be more severely affected than other areas by climate change, which has greater effects in mountainous landscapes (Root et al. 2003, Penteriani et al. 2019). Given the demonstrated influence of spring temperature on den exit, the predicted scenarios of climate change and the potential effects on brown bear populations, long-term studies on the chronology of hibernation and its relationships with external factors such as climate seem crucial for brown bear conservation.

Finally, although most reproductive dens in the Cantabrian Mountains are natural cavities in steep slopes or rocky cliffs and, thus, far from humans and their activities (Penteriani et al. 2020), we consider it important to highlight here that, when monitoring chronology of bear hibernation, it is also necessary account for the possible interference of human activities (Evans et al. 2012). However, human-mediated den abandonment has primarily occurred in areas with topographic relief of mild or moderate roughness and where dens are generally excavated in the ground or are accessible from ground level (Swenson et al. 1997, Evans et al. 2012).

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Supplemental Material

A brown bear female and her cub at the entrance of the breeding den. Breeding dens in the Cantabrian Mountains are generally located in open areas, which allows for quick detection of first den exit after hibernation.