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Phenology of brown bear breeding season and related geographical cues

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Abstract

Knowledge about breeding biology is often incomplete in species with complex reproductive strategies. The brown bear *Ursus arctos* is a polygamous seasonal breeder inhabiting a wide variety of habitats and environmental conditions. We compiled information about brown bear breeding season dates from 36 study areas across their distribution range in the Palearctic and Nearctic regions and investigated how their breeding phenology relates to geographical factors (latitude, photoperiod, altitude and region). Brown bear matings were observed for 8 months, from April to November, with a peak in May–July. We found a 59-day difference in the onset of bear breeding season among study areas, with an average 2.3 days delay for each degree of latitude northwards. The onset of the breeding season showed a strong relationship with photoperiod and latitude, but not with region (i.e. Palearctic vs Nearctic) and altitude. First observations of bear mating occurred earlier in areas at lower latitudes. Photoperiod ranged between 14 and 18 hours at the beginning of the season for most of the study areas. The duration of the breeding season ranged from 25 to 138 days among study areas. None of the investigated factors was related to the length of the breeding season. Our results support the relevance of photoperiod to the onset of breeding, as found in other ursids, but not a shorter breeding season at higher latitudes, a pattern reported in other mammals. Our findings suggest a marked seasonality of bear reproductive behaviour, but also certain level of plasticity. Systematic field observations of breeding behaviour are needed to increase our knowledge on the factors determining mating behaviour in species with complex systems and how these species may adapt to climate change.

Keywords: Latitude, mating, photoperiod, season, *Ursus arctos*

Introduction

Seasonal reproduction is widespread among mammals and has probably evolved as an adaptation to increase juvenile survival rates in temperate and polar areas (Bronson 2009; Zerbe et al. 2012). This seasonality has been found to relate to several factors, but latitude has traditionally been considered the most important,

with shorter reproductive periods observed at higher latitudes (e.g. in ruminant species, Zerbe et al. 2012). Photoperiod (i.e. day length), which is directly related to latitude, has been identified as an important cue in the breeding seasonality of both birds and mammals (Bronson 2009). Increasing altitude may shorten the duration of favourable conditions and, therefore, can also affect species' reproductive seasonality (Zerbe

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et al. 2012). It has been hypothesized that long-lived mammals at mid- and higher latitudes, whose reproduction is strongly regulated by photoperiod, will not easily adapt to new climatic conditions (Bronson 2009). In this context, characterizing the breeding phenology and related factors in mammals is crucial to understand reproductive strategies and how they could be affected by climate change (Bronson 2009).

The brown bear *Ursus arctos* is one of the world's most widely distributed terrestrial carnivores (Figure 1). It is a seasonal breeder throughout its range (Spady et al. 2007), usually mating in late spring to early summer. Females have delayed implantation and cubs are born during the winter denning period, between January and March (Steyaert et al. 2012). Due to the difficulty of observing copulations in the wild, the phenology of the breeding season is insufficiently known. Most studies are local and have been conducted either in captivity (Tumanov 1998; Spady et al. 2007) or in North American wild populations (see review in Lefranc et al. 1987). Published data from wild populations in Europe, where observations of wild bears are more difficult than in North America, are scarce and restricted to Scandinavia and Spain (Dahle & Swenson 2003; Fernández-Gil et al. 2006). Some authors have suggested photoperiod as the main factor triggering the onset of bear breeding season (Fernández-Gil et al. 2006; Spady et al. 2007), but there is a general shortage of information about the factors related to the duration of the bear breeding season; e.g. only a few studies have highlighted the importance of density-dependent mechanisms (Ishikawa et al. 2003; Steyaert et al. 2012).

Here, we aim to improve our understanding on the phenology of brown bear mating and the

geographical factors related to its onset and duration. First, we describe the phenology of the breeding season by compiling dates of bear copulations observed in 36 different study areas across the brown bear range. Secondly, we explore how geographical factors, namely latitude, altitude, photoperiod and region (Palearctic vs Nearctic), relate to breeding season onset, and duration.

Material and methods

Data collection

We defined the breeding (or mating) season in brown bears as the period when copulations were recorded and/or when males and females were observed consorting together or displaying pre- and post-copulatory behaviour (Lefranc et al. 1987). We compiled all available information about the earliest and latest dates of observed breeding behaviour in 36 brown bear study areas from Europe ($n = 4$), Asia ($n = 15$) and North America ($n = 17$, Table I, Figure 1) by contacting a wide network of bear researchers and from the available literature. We searched Google Scholar and Scopus databases for articles containing data on brown bear mating using different combinations of the following terms: “brown bear”, “grizzly bear”, “mating”, “courtship”, “association”, “breeding” and “copulation”. We also checked all volumes of the specialized journal “Ursus”, as well as the references provided in the retrieved articles. Additionally, we collected unpublished field records from researchers, hunters, rangers and photographers (both direct observations and with the help of remote cameras) and gathered information about the date, number of bears

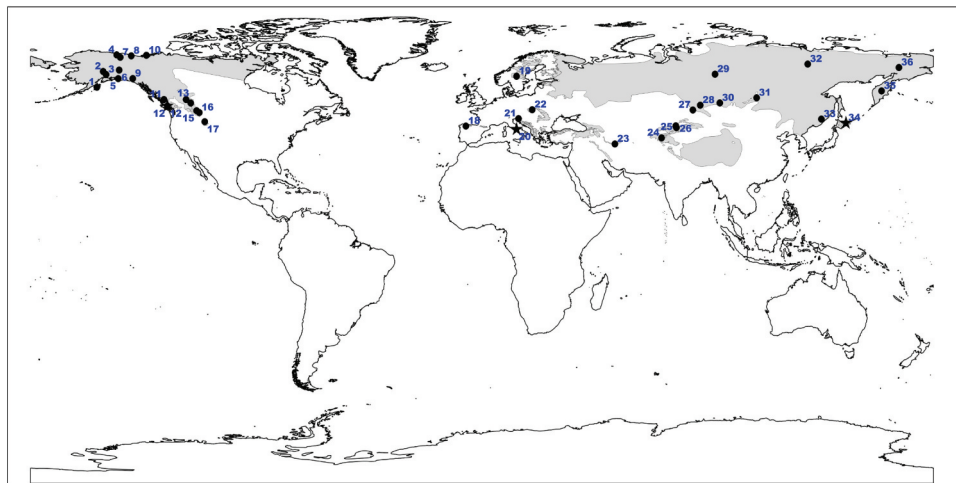


Figure 1. Map showing the study areas in the Nearctic ($n = 17$) and Palearctic regions ($n = 19$) where data on brown bear breeding phenology were gathered. Species distribution is shown in grey. Black stars represent study areas with a single observation of brown bear mating (i.e. study areas 20 and 34).

Table 1. Location and phenology of the brown bear breeding season in 36 study areas from the Nearctic and Palearctic regions. Areas with a single observation are marked with †. Positive values represent the Eastern Hemisphere for longitude. Start date and end date correspond to the dates when the earliest and the latest observations of brown bear breeding behaviour were recorded for each of the study areas. Study areas are ordered according to longitude (see Fig. 1).

| Id | Study area | Region | Latitude (degrees) | Longitude (degrees) | Start date | End date | Length (days) | References |
|-----|-----------------------------|------------|--------------------|---------------------|------------|-------------|---------------|--|
| 1 | Kodiak Island | Nearctic | 57.42 | -153.56 | 15-May | 15-July | 71 | Lefranc et al. (1987) |
| 2 | Denali National Park | Nearctic | 63.28 | -151.05 | 14-May | 17-July | 64 | Lefranc et al. (1987) |
| 3 | Upper Susitna | Nearctic | 62.15 | -149.88 | 25-May | 25-June | 31 | Lefranc et al. (1987) |
| 4 | Canning River | Nearctic | 69.48 | -145.65 | 2-June | 30-June | 28 | Lefranc et al. (1987) |
| 5 | Copper River Delta | Nearctic | 60.63 | -145.04 | 14-May | 18-June | 35 | Lefranc et al. (1987) |
| 6 | Black Lake area | Nearctic | 63.80 | -144.68 | 5-May | 5-August | 88 | Lefranc et al. (1987) |
| 7 | Arctic Nat. Wildlife Refuge | Nearctic | 68.57 | -144.23 | 13-June | 8-July | 25 | Lefranc et al. (1987) |
| 8 | Northern Yukon | Nearctic | 69.10 | -139.84 | 5-May | 15-July | 71 | Lefranc et al. (1987) |
| 9 | Kluane National Park | Nearctic | 60.65 | -139.24 | 21-May | 16-July | 56 | Lefranc et al. (1987) |
| 10 | Richard Islands | Nearctic | 69.31 | -133.92 | 21-May | 23-July | 63 | Lefranc et al. (1987) |
| 11 | Kimsquit River Valley | Nearctic | 52.85 | -126.81 | 19-May | 21-June | 33 | Lefranc et al. (1987) |
| 12 | British Columbia | Nearctic | 50.42 | -125.46 | 15-May | 5-October | 143 | Nevin and Gilbert (2005) |
| 13 | Jasper National Park | Nearctic | 52.85 | -117.98 | 15-May | 5-July | 51 | Lefranc et al. (1987) |
| 14 | Banff National Park | Nearctic | 51.54 | -116.12 | 13-May | 21-June | 39 | Hamer and Herrero (1990), Lefranc et al. (1987) |
| 15 | Glacier National Park | Nearctic | 48.68 | -113.80 | 30-April | 25-June | 56 | Lefranc et al. (1987) |
| 16 | Rocky Mountains East Front | Nearctic | 47.99 | -112.72 | 21-April | 28-June | 68 | Lefranc et al. (1987) |
| 17 | Yellowstone National Park | Nearctic | 44.59 | -110.55 | 14-May | 15-July | 62 | Lefranc et al. (1987), Craighead et al. (1995) |
| 18 | Cantabrian Mountains | Palearctic | 42.97 | -6.43 | 17-April | 1-July | 75 | Clevenger et al. (1992), Fernández-Gil et al. (2006) |
| 19 | Southern Sweden | Palearctic | 61.50 | 13.77 | 3-May | 9-June | 37 | Wabakken et al. (1992) |
| 20† | Apennine Mountains | Palearctic | 41.80 | 13.78 | NA | 3-November | NA | Tosoni et al. (2011) |
| 21 | Dinaric - Slovenia | Palearctic | 45.73 | 14.56 | 25-April | 2-September | 130 | This study |
| 22 | Northern Carpathians | Palearctic | 49.04 | 20.01 | 1-May | 25-June | 55 | This study |
| 23 | Northern Iran | Palearctic | 36.30 | 52.99 | 20-April | 29-June | 70 | This study |
| 24 | Pamir-Altai Mountains | Palearctic | 38.56 | 71.61 | 20-May | 23-June | 34 | Sokov (1969) |
| 25 | Trans-Ili Mountains | Palearctic | 43.06 | 77.28 | 16-May | 25-July | 70 | Zhiryakov (1991) |
| 26 | Tian Shan Mountains | Palearctic | 42.37 | 77.51 | 2-May | 23-June | 52 | Vaisfeld and Chestin (1993) |
| 27 | East Kazakhstan | Palearctic | 48.96 | 84.07 | 5-June | 25-July | 50 | Chestin and Uspensky (1993) |
| 28 | Altai Republic | Palearctic | 50.73 | 87.01 | 15-May | 5-July | 51 | Sobanskiy (2008) |
| 29 | Middle Siberia | Palearctic | 62.27 | 92.90 | 5-June | 25-July | 50 | Vaisfeld and Chestin (1993) |
| 30 | Tuva Republic | Palearctic | 51.58 | 94.82 | 5-June | 25-July | 50 | Smirnov and Shurygin (1991) |
| 31 | Buryatia Republic | Palearctic | 53.47 | 109.50 | 20-May | 10-August | 82 | Smirnov et al. (1987) |
| 32 | Yakutia - Sakha Republic | Palearctic | 66.04 | 129.87 | 15-June | 15-July | 30 | Chestin and Uspensky (1993). |
| 33 | Sikhote Alin Mountains | Palearctic | 45.55 | 135.31 | 5-June | 10-August | 66 | Bromley (1965) |
| 34† | Hokkaido Island | Palearctic | 44.12 | 145.12 | NA | 11-October | NA | Kohira and Mori (2010) |
| 35 | Kamchatka Peninsula | Palearctic | 56.05 | 159.32 | 25-May | 26-July | 62 | Vaisfeld and Chestin (1993) Nikolaenko (2003) |
| 36 | Russian North Far East | Palearctic | 64.77 | 166.23 | 5-Jun | 25-July | 50 | Vaisfeld and Chestin (1993) |

observed and presence of artificial feeding sites from 37 observations in the Dinaric-Pindos ($n = 12$), Carpathian ($n = 14$) and Northern Iran ($n = 11$) brown bear populations (Table S1). We excluded from the statistical analysis areas with only one observation of bear mating ($n = 2$).

Factors affecting brown bear breeding phenology

We calculated the latitude (in degrees) of each study area as the centroid of the polygon with 0.1° resolution. Data on altitude (metres above sea level, m.a.s.l.) of the centroid of each study area were obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer database (<https://asterweb.jpl.nasa.gov/gdem.asp>) with a 1 degree resolution. The photoperiod at the beginning of the breeding season for each centroid was calculated using the Sunrise/Sunset calculator of the National Oceanic and Atmospheric Administration – U.S. Department of Commerce (NOAA) (<https://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html>).

Statistical analysis

To investigate the relationships among geographical factors (latitude, altitude, photoperiod, and biogeographical region) and both onset (Julian calendar) and duration (in days) of the breeding season we examined a set of *a priori* univariate models. We defined duration as the difference in days between the first and the last observation of breeding behaviour for each study area. In eleven cases the precise dates of either the first or the last mating observation were not available, so we treated those dates described as “early”, “mid” and “late” as the 5th, 15th and 25th days of the month, respectively (e.g. an observation reported as “late June” was analysed as June 25th, Table I). We considered two biogeographical regions, Palearctic and Nearctic. We tested the relationship between each dependent and independent variable with a simple linear regression. We did not test factors together due to the small sample size and that some of them were strongly correlated. We applied the Bonferroni correction, i.e. we divided the alpha value of 0.05 among the number of studied variables and established a new alpha value of 0.0125 as the threshold for significant differences, to counteract the probability of finding significant relationships by chance in multiple comparisons. All geospatial analyses were performed in QGIS 2.14.22 and all statistical analyses in R (version 3.4.0, R Development Core Team 2017).

Results

We found a difference of 59 days in the start of the breeding season between northern and southern study areas (Figure 2). On average, the breeding season started 2.3 days later for each degree of latitude northwards. Most recorded matings took place between spring and early summer. The first breeding observation was recorded in the Cantabrian Mountains (43°N , Spain) on April 17th, while the latest starting date of the breeding season was noted in Yakutia (66°N , Russia) on June 15th. The last observation of breeding behaviour was recorded as early as June 9th in Southern Sweden (61°N) and as late as November 3rd in the Apennine Mountains, Italy (41°N). The duration of the breeding season, as documented by the observations compiled, ranged from 25 days in the Arctic National Wildlife Refuge to 139 days in British Columbia, Canada (Table I).

We found a significant effect of photoperiod and latitude on the onset of the breeding season (Figure 2, Table II). Bear mating started earlier in areas at lower latitudes, and, therefore, with shorter photoperiod at the beginning of the breeding season. In 25 out of 34 study areas, brown bears started mating when day length was between 14 and 18 hours. However, in three locations in Alaska and one in northern Russia, the breeding season started when day length was 24 hours (Figure 2). Altitude and biogeographical region did not affect the start of the brown bear breeding season. None of the studied geographical factors influenced the length of the breeding season (Table II).

Discussion

Brown bear matings were observed for at least 8 months, from April to November and peaked in May–July. This suggests a marked seasonality of bear reproductive behaviour, but also certain level of plasticity. This pattern is in line with male–female associations reported from telemetry in Canada, which mostly occurred (79%) in May–July, peaking in mid-June, and extending to autumn (Stenhouse et al. 2005). Matings in wild brown bear populations have been observed during autumn at latitudes of 50° or below, although rarely (Nevin & Gilbert 2005; Kohira & Mori 2010; Tosoni et al. 2011). Due to delayed implantation, matings during late summer and autumn can still result in parturition in normal period and be successful, therefore the breeding season could be extended for females that lose their cubs in late summer, for instance (Steyaert et al. 2012). A prolonged breeding season also allows females to have multiple oestruses (Craighead et al. 1995) and, thus, multiple paternity within a litter (Bellemain et al. 2005), which might reduce the risk of

infanticide (Steyaert et al. 2012). Late or prolonged breeding might potentially increase the chances of reproduction of the less competitive segment of the population for both males and females and affect population dynamics, particularly in small bear populations (Tosoni et al. 2011).

Photoperiod is the main cue for endocrine rhythms and influences the timing of annual cycles of reproduction in many mammals (Bronson 2009). Our results support the relevance of photoperiod to the onset of breeding for brown bears, as already proposed previously (Fernández-Gil et al. 2006; Spady et al. 2007). Bear species inhabiting areas near the equator (e.g. sloth bear *Melursus ursinus*, Shaw 1971, and spectacled bear *Tremarctos ornatus*, Cuvier 1825) may copulate throughout the year in the wild, but show a seasonal pattern when kept in captivity at higher latitudes (Spady et al. 2007; Appleton et al. 2018), which supports the relevant role of the photoperiod in breeding season phenology in ursids. However, we did not find a similar day length across study areas at the start of the breeding season, as expected, but instead a longer day length in northern areas. This is likely related to the fact that day length changes rapidly at high latitudes.

We found that geographical variables were related to the onset of the brown bear breeding season, but they did not determine its length. Our results did not support previous findings of shorter breeding season at higher latitudes found in other mammals (Zerbe et al. 2012). In this sense, non-geographical variables may play a more relevant role in the duration of the mating season, while geographical cues may be more important to trigger the onset. Social factors, metabolic state, and nutrition may modify the status of reproductive hormones, originally regulated by photoperiod (Spady et al. 2007), and influence the duration of the breeding season.

Reproduction and maternal care have substantial energetic costs for female mammals, so births mostly coincide with periods of favourable environmental conditions (Bronson 2009). In this line, food availability can play an important role in determining the length of the mating season in brown bears. More stable conditions of both weather and food availability may be related to the matings reported in autumn at latitudes of 50° and below. We also found that about 42% of the matings observed in the Dinaric and Carpathian Mountains, including the latest one (in early September), occurred at artificial feeding sites. Although this result is likely to be influenced by observer bias (bears are observed more frequently at feeding sites than elsewhere), it is known that anthropogenic food resources affect brown bear denning behaviour (Krofel et al. 2017), habitat selection (Skuban et al. 2016) and movement (Selva et al. 2017); thus, it is reasonable to think that they could also influence mating patterns.

Brown bear copulations in the wild are difficult to observe, especially in Europe, where bears are more elusive and reports of copulations are very limited. European brown bears have become largely nocturnal forest dwellers, probably as a result of a more humanized landscape (Ordiz et al. 2014). In this context, it is relevant to present here an updated compilation of available observations of brown bear copulations worldwide. Although most of the observations analysed here were opportunistically collected (the only option available nowadays), and we are aware that a lack of observation does not mean absence of mating and that the number of observations may influence the length of the mating season reported, this study represents a first step to characterize the phenology and plasticity of the brown bear breeding season at a large spatial scale. There is a need for systematic compilation of field

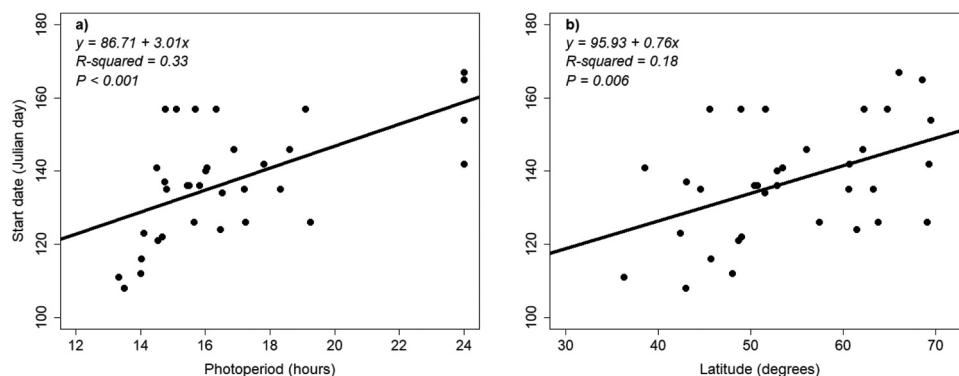


Figure 2. Onset of the breeding season in 34 brown bear study areas across the species distribution range in relation to a) photoperiod (hours) and b) latitude (°). Data sources cited in Table I. Study areas with a single observation of brown bear mating were excluded (n = 2).

Table II. Summary statistics of the simple linear regressions built to test relationships between brown bear breeding season variables, namely onset (Julian dates) and duration (no. days) and geographical factors (photoperiod, latitude, region and altitude) for 34 study areas worldwide. Following Bonferroni correction, p-values are considered significant (*, in bold) if smaller than 0.0125.

| | Onset breeding season | | | | Length breeding season | | | |
|-------------|-----------------------|-------|----------------|---------|------------------------|-------|----------------|---------|
| | Estimate | SE | R ² | p-value | Estimate | SE | R ² | p-value |
| Intercept | 86.71 | 12.41 | 0.33 | <0.001* | NA | NA | NA | NA |
| Photoperiod | 3.01 | 0.73 | | | | | | |
| Intercept | 95.93 | 14.31 | 0.18 | 0.006* | 101.29 | 25.15 | 0.05 | 0.11 |
| Latitude | 0.76 | 0.26 | | | -0.75 | 0.46 | | |
| Intercept | 137.47 | 3.73 | -0.03 | 0.67 | 62.23 | 6.23 | -0.02 | 0.64 |
| Neoarctic | -2.23 | 5.28 | | | -4.12 | 8.81 | | |
| Intercept | 130.17 | 8.14 | -0.01 | 0.43 | 76.71 | 13.39 | 0.02 | 0.20 |
| Altitude | 0.04 | 0.04 | | | -0.10 | 0.07 | | |

observations and long-term monitoring of mating behaviours, particularly in the Palearctic, in order to increase our knowledge of basic aspects of ursid mating systems and their adaptation to changing environmental conditions. Video-cameras attached to GPS collars, which are quickly improving, could help to fill this knowledge gap in future.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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