



Phenology of brown bear breeding season and related geographical cues

A. García-Rodríguez , R. Rigg , I. Elguero-Claramunt , K. Bojarska , M. Krofel , J. Parchizadeh , T. Pataky , I. Seryodkin , M. Skuban , P. Wabakken , F. Zięba , T. Zwijacz-Kozica & N. Selva

To cite this article: A. García-Rodríguez , R. Rigg , I. Elguero-Claramunt , K. Bojarska , M. Krofel , J. Parchizadeh , T. Pataky , I. Seryodkin , M. Skuban , P. Wabakken , F. Zięba , T. Zwijacz-Kozica & N. Selva (2020) Phenology of brown bear breeding season and related geographical cues, The European Zoological Journal, 87:1, 552-558, DOI: [10.1080/24750263.2020.1801866](https://doi.org/10.1080/24750263.2020.1801866)

To link to this article: <https://doi.org/10.1080/24750263.2020.1801866>



© 2020 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.



Published online: 17 Sep 2020.



[Submit your article to this journal](#)



Article views: 690












[View related articles](#)



[View Crossmark data](#)



Phenology of brown bear breeding season and related geographical cues

A. GARCÍA-RODRÍGUEZ ^{1*}, R. RIGG², I. ELGUERO-CLARAMUNT³, K. BOJARSKA ¹,
M. KROFEL ⁴, J. PARCHIZADEH ⁵, T. PATAKY⁶, I. SERYODKIN ^{7,8}, M. SKUBAN ⁹,
P. WABAKKEN ¹⁰, F. ZIĘBA¹¹, T. ZWIJACZ-KOZICA ¹¹, & N. SELVA ¹

¹Polish Academy of Sciences, Institute of Nature Conservation, Kraków, Poland, ²Slovak Wildlife Society, Liptovský Hrádok, Slovakia, ³Madrid, Spain, ⁴Department of Forestry, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia, ⁵City of Tehran, Iran, ⁶Department of Applied Zoology and Wildlife Management, Faculty of Forestry, Technical University in Zvolen, Zvolen, Slovakia, ⁷Laboratory of Ecology and Conservation of Animals, Pacific Institute of Geography of Far East Branch of Russian Academy of Sciences, Vladivostok, Russia, ⁸Far Eastern Federal University, Vladivostok, Russia, ⁹Carpathian Wildlife Society, Zvolen, Slovakia, ¹⁰Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences, Koppang, Norway, and ¹¹Tatra National Park, Zakopane, Poland

(Received 28 October 2019; accepted 20 July 2020)

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

*Correspondence: A. García-Rodríguez, Institute of Nature Conservation, Polish Academy of Sciences, Kraków 31-120, Poland.
Email: albertogarciarodriguez1985@gmail.com

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

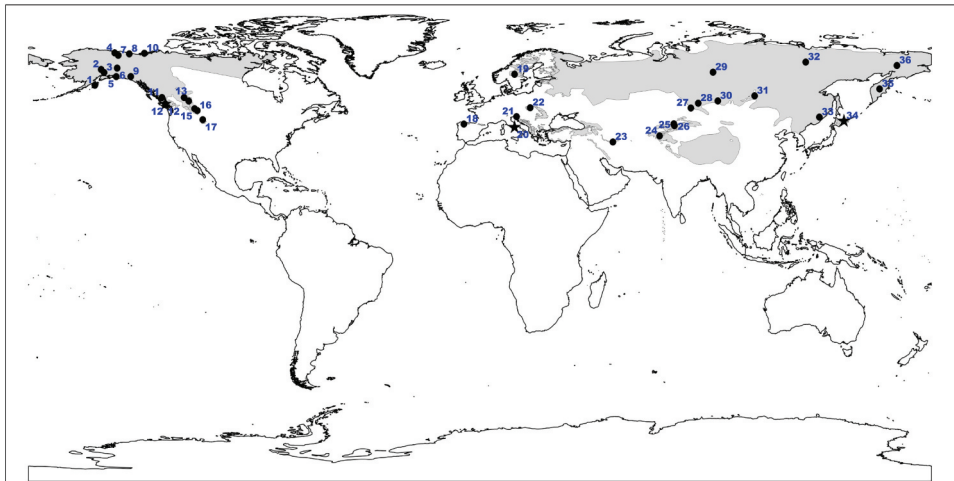


Figure 1. Map showing the study areas in the Nearctic ($n = 17$) and Palearctic regions ($n = 19$) where data on brown bear breeding phenology were gathered. Species distribution is shown in grey. Black stars represent study areas with a single observation of brown bear mating (i.e. study areas 20 and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

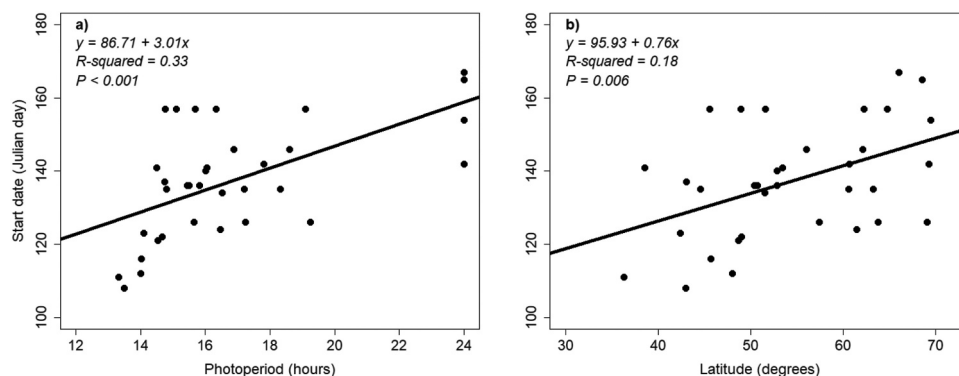


Figure 2. Onset of the breeding season in 34 brown bear study areas across the species distribution range in relation to a) photoperiod (hours) and b) latitude (°). Data sources cited in Table I. Study areas with a single observation of brown bear mating were excluded (n = 2).

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.

Acknowledgements

We thank Marjan Artnak, Peter Bajc, Matic Brenk, Tomáš Flajs, Uroš Grželj, Robert Hlavica, Aleš Jagodnik, Peter Klančar, Anton Marinčič, Mariusz Nędzyński, Borut Semenič and Vladimir Vician for providing information about their observations of bear mating. Robert Gatzka assisted with data collection in the Bieszczady Mountains. We thank Jon Swenson and Jumpei Tomiyasu for their help in the literature search. AGR and NS were supported by the BearConnect project funded by the National Science Centre in Poland (2016/22/Z/NZ8/00121) through the 2015-2016 BiodivERsA COFUND call for research proposals, with the national funders ANR/DLR-PT/UEFISCDI/NCN/RCN.

Additional funding from the Polish Ministry of Science and Higher Education (project NN304-294037, NS, IEC, KB), the National Science Centre in Poland (project DEC-2013/08/M/NZ9/00469, NS), the National Centre for Research and Development (GLOBE, POL-NOR/198352/85/2013, NS, TZK, FZ) and Slovenian Research Agency (P4-0059, MK) is acknowledged. AGR and NS conceived the study and wrote a first draft of the paper; AGR and NS compiled the data, AGR analyzed the data; all authors provided data and comments that improved the manuscript. We thank two anonymous reviewers for useful comments on the previous versions of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

A. García-Rodríguez  <http://orcid.org/0000-0002-9776-8037>

K. Bojarska  <http://orcid.org/0000-0001-7872-5763>

M. Krofel  <http://orcid.org/0000-0002-2010-5219>

J. Parchizadeh  <http://orcid.org/0000-0001-8184-9142>

I. Seryodkin  <http://orcid.org/0000-0003-4054-9236>

M. Skuban  <http://orcid.org/0000-0002-5352-7901>

P. Wabakken  <http://orcid.org/0000-0002-3882-924X>

T. Zwijacz-Kozica  <http://orcid.org/0000-0002-7488-975X>

N. Selva  <http://orcid.org/0000-0003-3389-201X>

References

- Appleton RD, Van Horn RC, Noyce KV, Spady TJ, Swaisgood RR, Arcese P. 2018. Phenotypic plasticity in the timing of reproduction in Andean bears. *Journal of Zoology* 305(3):196–202. DOI:10.1111/JZO.12553.
- Bellemain E, Swenson JE, Tallmon D, Brunberg S, Taberlet P. 2005. Estimating population size of elusive animals with DNA from hunter-collected feces: Four methods for brown bears. *Conservation Biology* 19(1):150–161. DOI:10.1111/J.1523-1739.2005.00549.X.
- Bromley GF. 1965. Bears of the south far eastern USSR. 1st. Moscow-Leningrad: Nauka press. In Russian.
- Bronson FH. 2009. Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364(1534):3331–3340. DOI:10.1098/RSTB.2009.0140.
- Chestin IE, Uspensky SM. 1993. Bears of Russia and adjacent countries - state of populations. 1st. Moscow: Argus press. In Russian with English summaries.
- Clevenger AP, Purroy FJ, De Buruaga MS. 1992. Copulation of wild European brown bears (*Ursus arctos*), with comments on the breeding behavior of the one adult male. *Mammalia* 56(1):3–8. DOI:10.1515/MAMM.1992.56.1.3.
- Craighead JJ, Summer JS, Mitchell JA. 1995. The grizzly bears of Yellowstone: Their ecology in the Yellowstone ecosystem, 1959–1992. 1st ed. Washington, DC: Island Press.

- Dahle B, Swenson JE. 2003. Family breakup in brown bears: Are young forced to leave? *Journal of Mammalogy* 84(2):536–540. DOI:10.1644/1545-1542(2003)084<0536:FBIBBA>2.0.CO;2.
- Fernández-Gil A, Naves J, Delibes M. 2006. Courtship of brown bears *Ursus arctos* in northern Spain: Phenology, weather, habitat and durable mating areas. *Wildlife Biology* 12(4):367–373. DOI:10.2981/0909-6396(2006)12[367:COBBUA]2.0.CO;2.
- Hamer D, Herrero S. 1990. Courtship and use of mating areas by grizzly bears in the front ranges of Banff National Park, Alberta. *Canadian Journal of Zoology* 68:2695–2697.
- Ishikawa A, Sakamoto H, Katagiri S, Takahashi Y. 2003. Changes in sexual behavior and fecal steroid hormone concentrations during the breeding season in female Hokkaido brown bears (*Ursus arctos yesoensis*) under captive condition. *The Journal of Veterinary Medical Science* 65(1):99–102. DOI:10.1292/JVMS.65.99.
- Kohira M, Mori S. 2010. Reported mating of Hokkaido brown bear in autumn. *Ursus* 21(2):192–194. DOI:10.2192/09SC030.1.
- Krofel M, Špacapan M, Jerina K. 2017. Winter sleep with room service: Denning behaviour of brown bears with access to anthropogenic food. *Journal of Zoology* 302(1):8–14. DOI:10.1111/JZO.12421.
- Lefranc MN, Moss MB, Patnoda KA, Sugg WC. 1987. Grizzly bear compendium. 1st ed. Washington, DC: Interagency Grizzly Bear Committee.
- Nevin OT, Gilbert BK. 2005. Observations of autumn courtship and breeding in Brown Bears, *Ursus arctos*, from coastal British Columbia. *The Canadian Field-Naturalist* 119(3):449–450. DOI:10.22621/CFN.V119I3.159.
- Nikolaenko V. 2003. Kamchatka bear. 1st. Moscow: Logata press. In Russian.
- Ordiz A, Kindberg J, Sæbø S, Swenson JE, Støen O-G. 2014. Brown bear circadian behavior reveals human environmental encroachment. *Biological Conservation* 173:1–9.
- R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria. Retrieved from <https://www.r-project.org/>
- Selva N, Teitelbaum CS, Sergiel A, Zwijacz-Kozica T, Zięba F, Bojarska K, Mueller T. 2017. Supplementary ungulate feeding affects movement behaviour of brown bears. *Basic and Applied Ecology* 24:68–76.
- Skuban M, Find'o S, Kajba M. 2016. Human impacts on bear feeding and habitat selection in the Pol'ana Mountains, Slovakia. *European Journal of Wildlife Research* 62:353–364.
- Smirnov MN, Noskov VT, Kelberg GV. 1987. Ecology and economic importance of a brown bear in Buryatia. In: Bears ecology. 1st (pp. 60–76). Novosibirsk: Nauka press. In Russian.
- Smirnov MN, Shurygin VV. 1991. The brown bear in Tuva. In: Bears in the USSR. 1st (pp. 162–170). Novosibirsk: Nauka press. In Russian.
- Sobanskiy. 2008. Mammals of Altai – Part 1. Large carnivores and ungulates. 1st. Moscow: KMK Scientific Press Ltd. In Russian.
- Sokov AI. 1969. Bear research in Tajikistan. In: *Voprosy povysheniya produktivnosti okhotnich'ikh ugodii* (Problems in improving productivity of hunting grounds). 1st (pp. 185–189). Moscow. In Russian.
- Spady TJ, Lindburg DG, Durrant BS. 2007. Evolution of reproductive seasonality in bears. *Mammal Review* 37(1):21–53. DOI:10.1111/J.1365-2907.2007.00096.X.
- Stenhouse G, Boulanger J, Lee J, Graham K, Duval J, Cranston J. 2005. Grizzly bear associations along the eastern slopes of Alberta. *Ursus* 16(1):31–40. DOI:10.2192/1537-6176(2005)016[0031:GBAATE]2.0.CO;2.
- Steyaert SMJG, Endrestol A, Hacklander K, Swenson JE, Zedrosser A. 2012. The mating system of the brown bear *Ursus arctos*. *Mammal Review* 42:12–34.
- Tosoni E, Palozzi G, Trella E, Boitani L, Ciucci P. 2011. A case of autumn mating in the apennine brown bear (*Ursus arctos marsicanus*). *Hystrix* 22:349–353.
- Tumanov IL. 1998. Reproductive characteristics of captive European brown bears and growth rates of their cubs in Russia. *Ursus* 10:63–65.
- Vaisfeld MA, Chestin IE. 1993. Bears: Brown bear, polar bear, Asian black bear. 1st. Moscow: Nauka press. In Russian with English summaries.
- Wabakken P, Björvall AR, Maartmann E, Sandegren F, Söderberg A. 1992. The Swedish-Norwegian brown bear project, 1984-1992. Norwegian institute for nature research, Report on commission no 146. In Norwegian with English summary.
- Zerbe P, Clauss M, Codron D, Lackey LB, Rensch E, Streich JW, Hatt J-M, Müller WH. 2012. Reproductive seasonality in captive wild ruminants: Implications for biogeographical adaptation, photoperiodic control, and life history. *Biological Reviews of the Cambridge Philosophical Society* 87(4):965–990. DOI:10.1111/J.1469-185X.2012.00238.X.
- Zhiryakov VA. 1991. Tien Shan brown bear in Zailiysky Alatau (Northern Tien Shan). In: Bears of the USSR - the state of populations Pazhetnov VS, editor, 98–102. Rzhhev. In Russian.