Characterization of a brown bear aggregation during the hyperphagia period in the Cantabrian Mountains, NW Spain

Héctor Ruiz-Villar[1,*,†], Ana Morales-González[1,*], Giulia Bombieri[2], Alejandra Zarzo-Arias[2], and Vincenzo Penteriani[2,3,‡]

[1] *Scottish Wildcat Action, Scottish Natural Heritage, Great Glen House, Leachkin Road, IV3 8NW, Inverness, Scotland, UK*
[2] *Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University - Campus Mieres, 33600 Mieres, Spain*
[3] *Pyrenean Institute of Ecology (IPE), CSIC, Avda. Montañana 1005, 50059 Zaragoza, Spain*

Abstract: We characterized a brown bear (*Ursus arctos*) feeding aggregation that occurred in an oak (*Quercus* spp.) forest in the Cantabrian Mountains (NW Spain), during the hyperphagia period 2017 (Sep to Dec), which was an atypical year in terms of low fructification success due to late frost events and drought. We described (1) number, sex, and age class of aggregated bears; (2) temporal use of the area; and (3) bear interactions. We identified a minimum of 31 individuals, representing 10% of the estimated Cantabrian bear population. The number of adults increased during the study period, whereas the number of subadults decreased, which could be related to a displacement of subadults by dominant adults. The proximity of the aggregation site to a public road attracted numerous people to observe the bears. To minimize adverse bear–human interactions, we recommend providing educational material on best bear-viewing practices as well as on-site staffing.

Key words: bear interactions, brown bear, Cantabrian Mountains, feeding aggregation, hyperphagia, *Ursus arctos*

DOI: 10.2192/URSU-D-29-1.1
Ursus 29(2):93–100 (2019)

Solitary animals can aggregate temporarily for various biological reasons, including mating (Sadovy et al. 2008), nesting (Bass et al. 2006), migrating (Taylor and Taylor 1977), and feeding (Peirce and Van Daele 2006). Feeding aggregations of solitary animals generally occur as a response to natural events, such as predictable seasonal peaks in the availability of food resources, as observed in Bryde's whales (*Balaenoptera brydei;* Penry et al. 2011) and large vertebrates (Shardlow and Hyatt 2013). However, there has been an increase in the frequency of feeding aggregations produced by anthropogenic food resources (e.g., garden birds; Robb et al. 2008) and food shortages caused by climate change (e.g., polar bears [*Ursus maritimus;* Schliebe et al. 2008]).

The brown bear (*U. arctos*) is a solitary species, but aggregations may occur in areas where food is abundant, profitable, and reliable because bears generally use the most productive foraging habitats to maximize nutrition (Schoen 1990). Bear congregations around feeding resources have been reported primarily in North America (e.g., in garbage dumps [Peirce and Van Daele 2006], insect aggregation sites [White et al. 1998], salmon [Salmonidae] spawning sites [Egbert and Stokes 1976, Ben-David et al. 2004], and humpback whale [*Megaptera novaeangliae*] carcasses [Lewis and Lafferty 2014]), as well as in Eastern Europe (Eastern Carpathians) around supplementary food sites (Štofík et al. 2016).

The Cantabrian Mountains (northwestern Spain) are inhabited by a small, isolated, and endangered population of brown bears, which is distributed in 2 partly connected subpopulations (Gonzalez et al. 2016), with approximately 200 individuals in the western subpopulation (95% CI = 168–260 individuals) and 20 individuals in the eastern subpopulation (95% CI = 12–40 individuals; Pérez et al. 2014). Bear aggregations are rare in this population and the few available records are related to the mating period, when several males and/or females stay together for some hours engaging in multiple mating episodes (Fernández-Gil et al. 2006).

Bears belonging to the Cantabrian population have a well-defined seasonal diet consisting mainly of plants and fruits available during different times of the year (Fernández-Gil 2013). During the hyperphagia period (Jul–Dec; Martínez Cano et al. 2016), acorns (*Quercus pyrenaica, Q. robur,* and *Q. ilex*) are prevalent items in their diet (Fernández-Gil 2013). However, the combination of atypical weather conditions—such as high temperatures at the end of winter, late snowfall and frost, and low rainfall—affect fructification success of

* These authors equally contributed to this work and should be considered as co-first authors.
†email: hector.ruiz.villar@gmail.com
‡ email: penteriani@ipe.csic.es

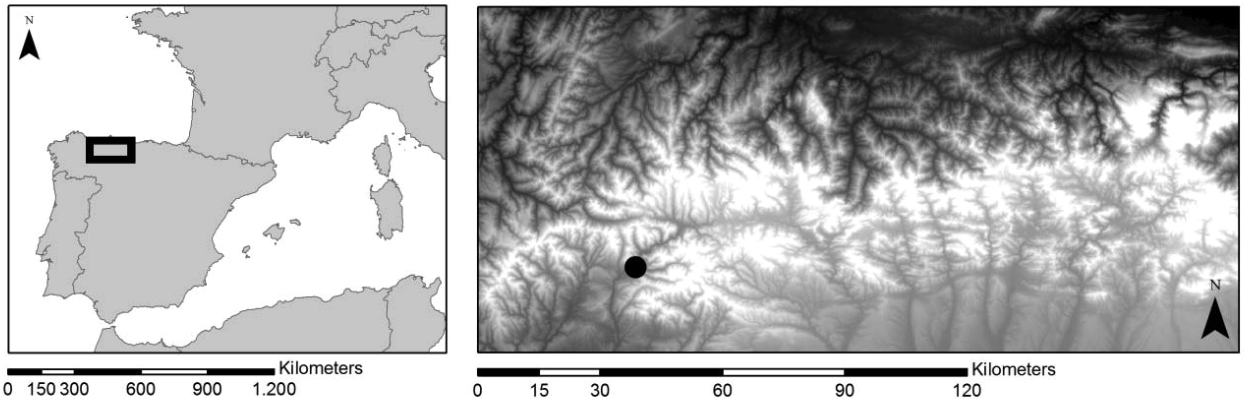

Fig. 1. Study area location of the brown bear (*Ursus arctos*) aggregation in the western Cantabrian Mountains (León Province, Spain) during 2017.

several plant species, including oaks (*Quercus* spp.; Inouye 2000, Sanchez-Humanes and Espelta 2011). The effect of frost on food availability and its impact on fruit consumer populations has been studied for several mammal species (e.g., montane voles [*Microtus montanus;* Murray 1965] and grey squirrels [*Sciurus carolinensis;* Nixon and McClain 1969]) and has been suggested for other acorn consumers, including bears (Inouye 2000).

During 2017, the Cantabrian Mountains suffered the weather conditions mentioned above, which affected the fruiting process of multiple plant species used by brown bears during summer and autumn (Servicio de Aplicaciones Agricolas e Hidrológicas de la Agencia Estatal de Meterología 2017). However, areas at low altitudes are usually less affected by frost and fructification is generally successful (Dittmar et al. 2006).

This scenario may have precipitated the occurrence of an unusual situation of bears congregating in a *Quercus* spp. forest at low altitude in order to exploit a locally abundant food resource. To our knowledge, the guards of the local Administration, who have been working in the area during the past 20 years, have not experienced or heard of such an event in the Cantabrian Mountains. The bear aggregation occurred in a relatively open area at a distance of 150 m from a main road, which caused many people (attracted by the real possibility of observing bears) to gather nearby and sometimes adopt inappropriate behaviors. These kinds of situations may lead to bear disturbance and human–bear conflicts (Penteriani et al. 2017). Therefore, it is important to understand the causes and consequences of these aggregations, which may occur again in future years with similar atypical weather conditions. Indeed, by being able to predict these situations, we could better manage human activities in order to avoid human–bear conflicts in a human-modified landscape (Penteriani et al. 2018; Penteriani et al., unpublished data).

The objectives of this paper were to describe (1) number, sex, and age class of the bears using the aggregation area; (2) temporal use of the area by bears; and (3) interactions among the bears. Finally, we recommend actions for minimizing adverse bear–human interactions when aggregations occur.

Study area

The study area is located in the western part of the Cantabrian Mountains (León Province) in northern Spain (Fig. 1), near the Eurosiberian–Mediterranean climatic boundary (Moreno et al. 1990). Predominant vegetation is characterized by common oaks (*Quercus robur*), Pyrenean oaks (*Q. pyrenaica*), common broom (*Cytisus scoparius*), and *Genista florida polygaliphylla* (Moreno et al. 1990, García and Jimenez Mejías 2009). The area consists of an approximately 44-ha wooded siliceous rocky mountain slope with open zones composed of rock deposits, with an altitude range from 800 to 1,264 m above sea level. A main road is at the bottom of the frequented slope, 150 m across from the aggregation area.

Methods

Data collection

We opportunistically visited the area to observe bears ≥2 times/week from 16 September 2017, coinciding with the start of the bear aggregation, to 4 December 2017. We conducted observation sessions from 1 hour before to 30 minutes after sunset, when bears are generally more active, especially in human-modified landscapes such as the Cantabrian Mountains (Ordiz et al. 2014). We used telescopes (Swarovski ATS 80 HD; Swarovski Optik, Absam, Austria) and binoculars (Swarovski Habicht 10 × 40; Swarovski Optik) to locate the individuals, always from the same spot, at an average distance of 400 m from the area frequented by bears. We used a Canon s×540 camera (Canon Inc., Ōta, Tokyo, Japan) and a Swarovski telescope coupled with a Nikon D7000 camera (Nikon Corporation, Shinagawa, Tokyo, Japan) to record videos of the sightings, with the aim of individually recognizing the different bears in the aggregation area.

Bear number, sex, and age class estimation

To individually recognize all the bears, we compared all the video footage we recorded. Specific characters of each animal, such as fur marks and body morphology, allowed individual identification (Fagen and Fagen 1996, Higashide et al. 2012). This made it possible to estimate the minimum number of individuals that congregated in this area (O'Brien and Lindzey 1995). Video analyses also allowed confirmation, when possible, of field estimations of the age and sex of observed bears. We adapted the age classification system described by Peirce and Van Daele (2006) for a bear aggregation in a garbage dump in Alaska as follows: adults (males and single females), females with cubs (both females with cubs-of-the-year and with yearlings), and subadults (2–4-yr-old individuals). We estimated the age of bears by observing body size and morphology (Herrero 1983). For all analyses we considered family units as one individual, given their spatial requirements, because mothers and cubs forage close to each other whereas solitary bears need more space to forage (Peirce and Van Daele 2006). Field observations did not allow sex identification, except when females were accompanied by cubs.

Determination of the temporal use of the aggregation site

We assessed temporal patterns of bear use of the aggregation area by examining (1) variation in the number of bears observed during each session over the sampling period, and (2) individual bear presence or absence during each session over the sampling period.

We determined the temporal use of the area by all the observed bears by summing the minimum number of different individuals that used the area in each session during the study period. We fitted 2 Poisson generalized linear models to analyze the effect of successive observation sessions (hereafter, referred to 'as time') over the study period on the number of adult (including females with cubs) and subadult bears observed per session. We excluded from analysis any sample days when age class determination was not possible for all the individuals observed per session because of poor light, bad weather conditions, or short length of the sighting. We conducted statistical analyses in Program R 3.4.2 statistical software (R Core Team 2017). We set statistical significance levels at $\alpha < 0.05$. We performed the statistical models with the package 'stats' and tested autocorrelation to ensure that model residuals were independent of each other (R Core Team 2017).

We classified individuals from each age class (categorical variable 'age class': adults, females with cubs, and subadults) according to the number of observation days on which they were spotted (categorical variable 'number of sightings': 1 sighting vs. 2–3 sightings vs. >3 sightings) over the study period.

Bear interaction analysis

We recorded all the interactions that occurred between all age classes. We classified the interactions as aggressive versus nonaggressive; and, following the classification of Peirce and Van Daele (2006), we considered lunges, direct stares, chases, and charges as aggressive interactions. We classified bears involved in aggressive interactions as winners versus losers; winners caused another bear (the loser) to move away from the disputed area (Herrero 1983). We considered play-fight and seen-ignored as nonaggressive interactions.

Results

We visited the study area for 22 days and recorded 33 hours of observations. We collected 85 bear sightings during the sample period and recorded ≥1 video for 69 of them, with an average length of 2 minutes. We did not record the individuals for 16 sightings because of the poor light, bad weather conditions, or short length of the sighting.

We identified a minimum of 31 bears: 14 adults, 6 subadults, and 5 females with 6 cubs. Three family groups contained cubs-of-the-year (1, 1, and 2 cubs), and 2 females were accompanied by 1 yearling each. We recorded 63 sightings of identified individuals and 22 sightings of unidentified individuals. Considering that these 22 sightings could belong to 22 different individuals, there could have been a maximum of 53 individual bears using the study area.

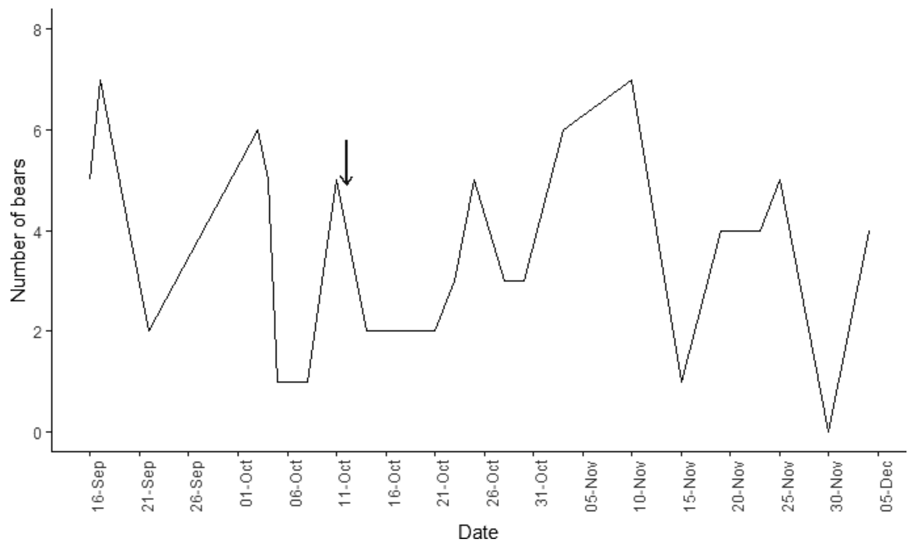

Fig. 2. Variation in the number of brown bears (*Ursus arctos*) at the study area from 16 September to 4 December ($n = 22$), western Cantabrian Mountains (Spain), 2017. The arrow indicates a fire event that occurred in the study area.

The number of bears that used the study area each evening varied from 1 to 7 individuals and showed no clear trends (Fig. 2). There was a fire event on the area from 12 to 18 October 2017, which burned approximately 350 ha. Immediately after the fire started, we observed a drop in the number of individuals observed per session (from 5 individuals on 11 Oct to 2 individuals on 14 Oct). However, the numbers recovered quickly (to 5 individuals on 25 Oct) after the fire had been put out.

The number of adult and subadult bears that used the area varied with time over the study period (Table 1; Fig. 3). The number of adult bears increased with time (estimate = 0.018, $P = 0.007$; Fig. 3), whereas the number of subadults decreased (estimate = -0.053, $P < 0.001$; Fig. 3).

Adult bears showed the greatest proportion of individuals (4 adults out of 14 adult bears) observed in >3 sessions (Table 2). Subadults comprised the greatest proportion of individuals (3 subadults out of 6 subadult bears) observed in 2 or 3 sessions, and females with cubs showed the greatest proportion of individuals (3 females with cubs out of 5 female bears with cubs) observed in only 1 session and none of them was observed in >3 sessions (Table 2).

We recorded 7 aggressive interactions: 5 adult versus adult and 2 adult versus subadult, which were all won by adults. We also recorded 5 nonaggressive interactions: 1 adult versus subadult, 1 adult versus female with cubs, 1 subadult versus female with cubs, and 2 adult versus adult.

Table 1. Details of the 2 Poisson generalized linear models investigating the effect of time (i.e., successive observation sessions) over the number of adult (modelAd) and subadult (modelSubAd) individual brown bears (*Ursus arctos*) observed per session in the Cantabrian Mountains in Spain during 16 September to 4 December 2017. Sample size for both models is 17 after excluding the sample days when age class determination was not possible for all the individuals observed per session.

Model	RV[a]	EV[a]	EST[a]	SE[a]	*Z*[a]	*P*-VAL[a]	DEV (%)[a]
ModelAd	No. of adults	Time	0.018	0.007	2.694	0.007	37.6
ModelSubAd	No. of subadults	Time	−0.053	0.014	−3.711	<0.001	47.5

[a]RV = response variable; EV = explanatory variable; EST = model estimate; SE = standard error of model estimate; Z = test statistic for assessing the significance of the model curve (i.e., slope); P-VAL = P-value for the null hypotheses that the curve is zero; DEV (%) = proportion of explained deviance (i.e., proportion of the variation in the response variable that is explained by the explanatory variable).

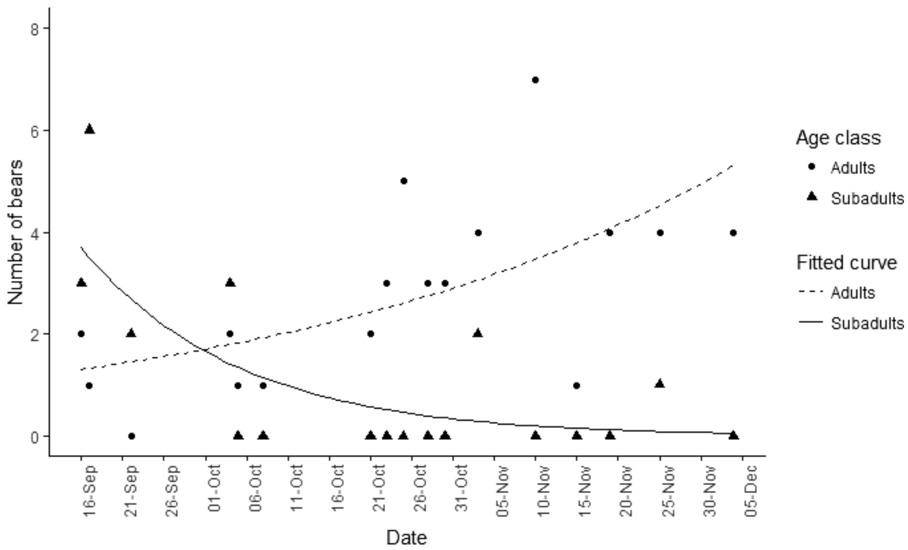

Fig. 3. Scatterplot of the number of adult and subadult brown bears ([*Ursus arctos*] response variables; circles and triangles, respectively) observed in the Cantabrian Mountains in Spain during 16 September to 4 December 2017 (explanatory variable), and the fitted curve for each Poisson generalized linear models model (broken and solid line for models with no. of adults and subadults, respectively, as response variables). Sample size for the estimation of both curves is 17 after excluding the sample days when age class determination was not possible for all the individuals observed per session.

Number of observers in the area was usually low from Monday to Friday (<10 people). But during weekends and public holidays, up to 50 people were present. People were generally on the road and its surroundings, at a distance of 150 m from the bear area. However, the distance was considerably shorter under some situations, which implied potential conflicts with bears. For instance, one evening one bear came down to the river to drink and approximately 30 people crossed the guardrails to get closer and take pictures of it from a distance of approximately 40 m. The bear stared at the people and walked along the riverside away from them. On a different occasion, 12 people stood on the road 20 m away from a subadult bear that was trying to cross it (https://www.youtube.com/watch?v=jRi1Ql-w4as, last accessed May 2018).

Table 2. Number, age class, and frequency of sightings of individually identified brown bears (*Ursus arctos*) in the Cantabrian Mountains in Spain during 16 September to 4 December 2017.

Age class	1 sighting	2–3 sightings	>3 sightings	Total
Adults	6	4	4	14
Subadults	2	3	1	6
Females + cubs	3	2	0	5
Total	11	9	5	25

Discussion

Bear number, sex, and age class estimation

A remarkable number of bears (31–53) congregated at this site, especially when considering the estimated size of this bear population. Indeed, the minimum number of bears we were able to identify represented 10% of the entire Cantabrian population, which is estimated to be a maximum number of 300 individuals (Pérez et al. 2014). This aggregation occurred during the hyperphagia period (a critical period for bears), when individuals spend most of their active time foraging to store fat, which is essential for successful hibernation and cub production (Farley and Robbins 1995, Fernández-Gil 2013). Acorns are bears' main food item in the Cantabrian Mountains during this period (Fernández-Gil 2013), and acorn production locally may have been low in 2017. The damage caused by a late snowfall and frost event on prematurely developed flower buds caused by a mild winter, as well as a severe drought, may have affected fructification success in this and several other species (Servicio de Aplicaciones Agricolas e Hidrológicas de la Agencia Estatal de

Meterología 2017). Acorn production has been recorded to decrease under similar conditions in other parts of the world (Inouye 2000, Sanchez-Humanes and Espelta 2011). A localized abundance of acorns in a low-altitude oak forest, where plants are generally less affected by extreme weather (Dittmar et al. 2006), could have promoted this bear aggregation. Even though brown bears are known to aggregate at concentrated food resources (White et al. 1998, Peirce and Van Daele 2006), this is the first time that a feeding aggregation has been recorded for the Cantabrian brown bear population. This small and isolated population is located in the southwestern periphery of the European distribution of the brown bear, making it especially vulnerable to unpredictable meteorological events caused by climate change (Vucetich and Waite 2003).

Determination of the temporal use of the aggregation site

Subadults decreased and adults increased in the area over time, suggesting that they avoided conflicts with adults. In other brown bear aggregations, subadults were the least dominant individuals and actively avoided encounters with adult individuals to reduce risk of aggressive fights and predation (Egbert and Stokes 1976, Peirce and Van Daele 2006). Therefore, adults may have progressively increased in number over the course of the study period, displacing subadults, which may have either left the area or remained in peripheral areas.

When analyzing individual frequency in adults versus subadults versus females with cubs, adults showed a greater proportion of frequent visitors than subadults, which could be due to dominance of adult bears over subadults explained above. However, females with cubs had the lowest proportion of frequent visitors, perhaps because females with cubs of the year usually avoid encounters with adult males (Egbert and Stokes 1976).

Management implications

Bear-viewing practices have been shown to cause both negative and positive impacts on bears, people, and ecosystems, and are highly context-dependent; thus, each situation should be managed at a local scale (Penteriani et al. 2017). In the case of the bear aggregation site in the Cantabrian Mountains, its location close to a public road facilitated the presence of many people who were attracted by the strong possibility of observing bears. Several of these people did not behave in an appropriate way while observing the bears (e.g., closely approaching the bears to take photos or speaking loudly). It is well-known that these behaviors can induce bears to leave the area (Nevin and Gilbert 2005) or become habituated to human presence, which may represent a serious source of human–bear conflict (Herrero et al. 2005, Smith et al. 2005).

Therefore, we recommend providing bear viewers with educational material on bear behavior and best bear-viewing practices to minimize adverse bear–human interactions in future similar situations. It would also be valuable to have on-site staff available to provide instruction and enforcement of guidelines for safe viewing. Finally, specific research should be done to detect areas with similar environmental and vegetation characteristics as the bear aggregation spot, in order to predict potential areas of bear feeding aggregation during years with low fructification success. The location of such areas may also help limit human activities that may affect these potential food reservoirs for brown bears.

Acknowledgments

The suggestions of J. Swenson, the Associate Editor S. Miller, and 2 anonymous referees greatly improved the first draft of the manuscript. VP was financially supported by the Excellence Project CGL2017-82782-P financed by the Spanish Ministry of Science, Innovation and Universities, the Agencia Estatal de Investigación (AEI), and the Fondo Europeo de Desarrollo Regional (FEDER, EU).

Literature cited

BASS, A.L., S.P. EPPERLY, AND J. BRAUN-MCNEILL. 2006. Green turtle (*Chelonia mydas*) foraging and nesting aggregations in the Caribbean and Atlantic: Impact of currents and behavior on dispersal. Journal of Heredity 97:346–354.

BEN-DAVID, M., K. TITUS, AND L.V.R. BEIER. 2004. Consumption of salmon by Alaskan brown bears: A trade-off between nutritional requirements and the risk of infanticide? Oecologia 138:465–474.

DITTMAR, C., W. FRICKE, AND W. ELLING. 2006. Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. European Journal of Forest Research 125:249–259.

EGBERT, A.L., AND A.W. STOKES. 1976. The social behaviour of brown bears on an Alaskan salmon stream. Pages 41–56 in M.R. Pelton, J.W. Lentfer, and G.E. Folk, editors. Bears—Their biology and management: Proceedings of the 3rd International Conference on Bear Research and Management. International Union for the Conservation of Nature and Natural Resources, Morges, Switzer-land; Binghamton, New York, USA; and Moscow, Russia.

FAGEN, R., AND J.M. FAGEN. 1996. Individual distinctiveness in brown bears, *Ursus arctos* L. Ethology 102:212–226.

FARLEY, S.D., AND C.T. ROBBINS. 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Canadian Journal of Zoology 73:2216–2222.

FERNÁNDEZ-GIL, A. 2013. Behavior and conservation of large carnivores in human-dominated landscapes. Brown bears and wolves in the Cantabrian Mountains. Dissertation, Oviedo University, Asturias, Spain.

———, J. NAVES, AND M. DELIBES. 2006. Courtship of brown bears *Ursus arctos* in northern Spain: Phenology, weather, habitat and durable mating areas. Wildlife Biology 12:367–373.

GARCÍA, I., AND P. JIMENEZ MEJÍAS. 2009. Robledales de *Quercus pyrenaica* y robledales de *Quercus robur* y *Quercus pyrenaica* en el noroeste ibérico. Pages 1–66 in Ministerio de Medio Ambiente, y Medio Rural y Marino, editor. Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España. Spanish Ministry of the Environment Rural and Marine Affairs, Madrid, Spain. [In Spanish.]

GONZALEZ, E.G., J.C. BLANCO, F. BALLESTEROS, L. ALCARAZ, G. PALOMERO, AND I. DOADRIO. 2016. Genetic and demographic recovery of an isolated population of brown bear *Ursus arctos* L., 1758. PeerJ 4:e1928.

HERRERO, S. 1983. Social behaviour of black bears at a garbage dump in Jasper National Park. International Conference on Bear Research and Management 5:54–70.

———, T. SMITH, T.D. DEBRUYN, K. GUNTHER, AND C.A. MATT. 2005. Brown bear habituation to people—Safety, risks, and benefits. Wildlife Society Bulletin 33:362–373.

HIGASHIDE, D., S. MIURA, AND H. MIGUCHI. 2012. Are chest marks unique to Asiatic black bear individuals? Journal of Zoology 288:199–206.

INOUYE, D.W. 2000. The ecological and evolutionary significance of frost in the context of climate change. Ecology Letters 3:457–463.

LEWIS, T.M., AND D.J.R. LAFFERTY. 2014. Brown bears and wolves scavenge humpback whale carcass in Alaska. Ursus 25:8–13.

MARTÍNEZ CANO, I., F.G. TABOADA, J. NAVES, A. FERNÁNDEZ-GIL, AND T. WIEGAND. 2016. Decline and recovery of a large carnivore: Environmental change and long-term trends in an endangered brown bear population. Proceedings of the Royal Society B: Biological Sciences 283:20161832. DOI: 10.1098/rspb.2016.1832.

MORENO, J.M., F.D. PINEDA, AND S. RIVAS-MARTINEZ. 1990. Climate and vegetation at the Eurosiberian–Mediterranean boundary in the Iberian Peninsula. Journal of Vegetation Science 1:233–244.

MURRAY, K.F. 1965. Population changes during the 1957–1958 vole (*Microtus*) outbreak in California. Ecology 46:163–171.

NEVIN, O.T., AND B.K. GILBERT. 2005. Perceived risk, displacement and refuging in brown bears: Positive impacts of ecotourism? Biological Conservation 121: 611–622.

NIXON, C.M., AND M.W. MCCLAIN. 1969. Squirrel population decline following a late spring frost. Journal of Wildlife Management 33:353–357.

O'BRIEN, S.L., AND F.G. LINDZEY. 1995. Aerial sightability and classification of grizzly bears at moth aggregation sites in the Absaroka Mountains, Wyoming. Ursus 10:427–435.

ORDIZ, A., J. KINDBERG, S. SÆBØ, J.E. SWENSON, AND O.-G. STØEN. 2014. Brown bear circadian behavior reveals human environmental encroachment. Biological Conservation 173:1–9.

PEIRCE, K.N., AND L.J. VAN DAELE. 2006. Use of a garbage dump by brown bears in Dillingham, Alaska. Ursus 17:165–177.

PENRY, G.S., V.G. COCKCROFT, AND P.S. HAMMOND. 2011. Seasonal fluctuations in occurrence of inshore Bryde's whales in Plettenberg Bay, South Africa, with notes on feeding and multispecies associations. African Journal of Marine Science 33:403–414.

PENTERIANI, V., M.D.M. DELGADO, M. KROFEL, K. JERINA, A. ORDIZ, F. DALERUM, A. ZARZO-ARIAS, AND G. BOMBIERI. 2018. Evolutionary and ecological traps for brown bears *Ursus arctos* in human-modified landscapes. Mammal Review 48:153–228.

———, J. VICENTE LÓPEZ-BAO, C. BETTEGA, F. DALERUM, M. DEL MAR DELGADO, K. JERINA, I. KOJOLA, M. KROFEL, AND A. ORDIZ. 2017. Consequences of brown bear viewing tourism: A review. Biological Conservation 206:169–180.

PÉREZ, T., J. NAVES, J.F. VÁZQUEZ, A. FERNÁNDEZ-GIL, J. SEIJAS, J. ALBORNOZ, E. REVILLA, M. DELIBES, AND A. DOMÍNGUEZ. 2014. Estimating the population size of the endangered Cantabrian brown bear through genetic sampling. Wildlife Biology 20:300–309.

R CORE TEAM. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

ROBB, G.N., R.A. MCDONALD, D.E. CHAMBERLAIN, AND S. BEARHOP. 2008. Food for thought: Supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6:476–484.

SADOVY, Y., D. MITCHESON, A. CORNISH, M. DOMEIER, P.L. COLIN, M. RUSSELL, AND K.C. LINDEMAN. 2008. A global baseline for spawning aggregations of reef fishes. Conservation Biology 22:1233–1244.

SANCHEZ-HUMANES, B., AND J.M. ESPELTA. 2011. Increased drought reduces acorn production in *Quercus ilex* coppices: Thinning mitigates this effect but only in the short term. Forestry 84:73–82.

SCHLIEBE, S., K.D. RODE, J.S. GLEASON, J. WILDER, K. PROFFITT, T.J. EVANS, AND S. MILLER. 2008. Effects of sea ice extent and food availability on spatial and temporal distribution of polar bears during the fall open-water period in the Southern Beaufort Sea. Polar Biology 31:999–1010.

SCHOEN, J.W. 1990. Bear habitat management: A review and future perspective. Pages 143–154 in L.M. Darling and W.R. Archibald, editors. Bears: Their biology and management: A selection of papers from the 8th International Conference on Bear Research and Management. International Association for Bear Research and Management. doi:10.2307/3872914.

SERVICIO DE APLICACIONES AGRICOLAS E HIDROLÓGICAS DE LA AGENCIA ESTATAL DE METEROLOGÍA. 2017. Informe meteorofenológico de la primavera de 2017. Spanish Ministry of Agriculture and Fisheries, Food and Environment, Madrid, Spain. [In Spanish.]

SHARDLOW, T.F., AND K.D. HYATT. 2013. Quantifying associations of large vertebrates with salmon in riparian areas of British Columbia streams by means of camera-traps, bait stations, and hair samples. Ecological Indicators 27: 97–107.

SMITH, T.S., S. HERRERO, AND T.D. DEBRUYN. 2005. Alaskan brown bears, humans, and habituation. Ursus 16:1–10.

ŠTOFÍK, J., J. MERGANIČ, K. MERGANIČOVÁ, J. BUČKO, AND M. SANIGA. 2016. Brown bear winter feeding ecology in the area with supplementary feeding—Eastern Carpathians (Slovakia). Polish Journal of Ecology 64:277–288.

TAYLOR, L.R., AND R.A. TAYLOR. 1977. Aggregation, migration and population mechanics. Nature 265:415–21.

VUCETICH, J.A., AND T.A. WAITE. 2003. Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics. Conservation Genetics 4:639–645.

WHITE, D.J., K.C. KENDALL, AND H.D. PICTON. 1998. Grizzly bear feeding activity at alpine army cutworm moth aggregation sites in northwest Montana. Canadian Journal of Zoology 76:221–227.

Received: March 20, 2018
Accepted: October 10, 2018
Associate Editor: Miller