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Human development and climate affect hibernation in a large carnivore with implications for human–carnivore conflicts

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Abstract

1. Expanding human development and climate change are dramatically altering habitat conditions for wildlife. While the initial response of wildlife to changing environmental conditions is typically a shift in behaviour, little is known about the effects of these stressors on hibernation behaviour, an important life-history trait that can subsequently affect animal physiology, demography, interspecific interactions and human-wildlife interactions. Given future trajectories of land use and climate change, it is important that wildlife professionals understand how animals that hibernate are adapting to altered landscape conditions so that management activities can be appropriately tailored.
2. We investigated the influence of human development and weather on hibernation in black bears (*Ursus americanus*), a species of high management concern, whose behaviour is strongly tied to natural food availability, anthropogenic foods around development and variation in annual weather conditions. Using GPS collar data from 131 den events of adult female bears ($n = 51$), we employed fine-scale, animal-specific habitat information to evaluate the relative and cumulative influence of natural food availability, anthropogenic food and weather on the start, duration and end of hibernation.
3. We found that weather and food availability (both natural and human) additively shaped black bear hibernation behaviour. Of the habitat variables we examined, warmer temperatures were most strongly associated with denning chronology, reducing the duration of hibernation and expediting emergence in the spring. Bears appeared to respond to natural and anthropogenic foods similarly, as more natural foods, and greater use of human foods around development, both postponed hibernation in the fall and decreased its duration.
4. *Synthesis and applications.* Warmer temperatures and use of anthropogenic food subsidies additively reduced black bear hibernation, suggesting that future changes in climate and land use may further alter bear behaviour and increase the length of their active season. We speculate that longer active periods for bears will result in subsequent increases in human–bear conflicts and human-caused bear mortalities. These metrics are commonly used by wildlife agencies to index trends in bear populations, but have the potential to be misleading when bear behaviour dynamically

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adapts to changing environmental conditions, and should be substituted with reliable demographic methods.

KEYWORDS

behaviour, black bear, climate, Colorado, denning chronology, food availability, hibernation, human–bear conflict, residential development, *Ursus americanus*

1 | INTRODUCTION

Human development and climate change are arguably the most significant factors altering habitat conditions for wildlife world-wide (Parmesan & Yohe, 2003; Vitousek, Mooney, Lubchenco, & Melillo, 1997). These factors have transformed landscapes across the globe with ensuing effects on animal behaviour, distributions, population dynamics and interspecific interactions (Parmesan, 2006; Selwood, McGeoch, & Nally, 2015). While the influences of land use and climate change on wildlife and their habitats are well recognized, there is growing recognition that these factors can also significantly increase human–wildlife conflicts (Aryal, Brunton, & Raubenheimer, 2014; Stirling & Derocher, 2012). Indeed, shifts in both human and animal behaviours can increase their rates of interaction, resulting in consequences that generate significant challenges for wildlife management agencies (Treves & Karanth, 2003). Given the expected trajectories of land use and climate, there is a critical need to understand how animals are adapting to these changes, and the associated implications for management and conservation.

For many species, hibernation is an important life-history strategy that is likely to be influenced by changing patterns of land use and climate. Hibernation is a state of inactivity that enables animals to conserve energy during seasonal food shortages or severe weather (Ruf & Geiser, 2015), a need that may decline in response to changing environmental conditions. For example, expanding development is providing consistent anthropogenic food subsidies for many wildlife species in the form of crops, garbage, livestock and other resources (Oro, Genovart, Tavecchia, Fowler, & Martinez-Abraín, 2013). For animals that hibernate in response to resource limitation, the availability of these foods has the potential to alter seasonal patterns of behaviour with subsequent effects on physiology, demography and even human–wildlife conflicts. Meanwhile, the long-term trend of warmer winter weather (Williams, Henry, & Sinclair, 2015) has been associated with earlier emergence from hibernation for some animals (Inouye, Barr, Armitage, & Inouye, 2000). Investigators have found that early emergence can result in trophic mismatches when spring food resources are unavailable (Inouye et al., 2000), and that weather-induced changes in hibernation can subsequently affect individual and population fitness (Lane, Kruuk, Charmantier, Murie, & Dobson, 2012).

The influences of land use and climate change are expected to be particularly pronounced in hibernation of the American black bear (*Ursus americanus*). Like many other species, black bears hibernate in response to seasonal food shortages (Johnson & Pelton, 1980; Schooley, McLaughlin, Matula, & Krohn, 1994). As residential and

agricultural development expands, however, some bears have learned to utilize anthropogenic foods (e.g. garbage, fruit trees, birdfeeders) for subsidy (Kirby, Alldredge, & Pauli, 2016; Lewis et al., 2015). Limited research suggests that black bears foraging on anthropogenic foods hibernate for shorter periods (Baldwin & Bender, 2010; Beckmann & Berger, 2003), or even forgo hibernation altogether (Beckmann & Berger, 2003), presumably as their dependence on seasonal native foods declines. Investigators have also found that bear hibernation is correlated with various weather patterns, with individuals entering dens when temperatures drop and snow accumulates and exiting once temperatures increase and snow has melted (Johnson & Pelton, 1980; Schooley et al., 1994). Although investigators have speculated that warming climate conditions will reduce brown bear (*Ursus arctos*) hibernation (Pigeon, Stenhouse, & Côté, 2016), there is uncertainty about the effects of changing weather patterns on black bears, the specific conditions that trigger hibernation cues, and the magnitude of weather effects. Inferences from past studies suggest that changes in land use and climate are both likely to reduce black bear hibernation, but prior investigations assessed only the individual influence of these factors on den chronology, often in the absence of corresponding information on natural food conditions, which may confound both effects. As a result, information about the relative and cumulative effects of human development, weather and natural food availability is currently unknown, despite concurrent changes in all these factors for bear populations across much of their range.

Reduced hibernation in bears, due to expanding development and/or a warming climate, may have implications for human–bear conflicts (Krofel, Špacapan, & Jerina, 2017; Pigeon et al., 2016). Human–black bear conflicts (*hereafter* “human–bear conflicts”) have been rising throughout the United States, becoming a major management challenge for many wildlife agencies (Hristienko & McDonald, 2007). Conflicts are particularly high along the urban–wildland interface as bears increase their use of development, especially when natural foods are scarce (Baruch-Mordo et al., 2014; Johnson et al., 2015). For people, the primary consequences of these conflicts are public safety concerns, property damage and high management costs (Treves, Kapp, & MacFarland, 2010), while for bears, the primary consequence is high mortality (e.g. vehicle collisions, lethal removal; Beckmann & Berger, 2003; Hostetler et al., 2009). If changes in land use and climate increase the “active” period for bears, conflicts incurred by people, and mortalities incurred by bears, may both increase accordingly.

To better understand the influences of human development and weather on hibernation in black bears, we examined factors associated with the start, duration and end of hibernation. While previous studies

of bear hibernation have been limited by small sample sizes and coarse, population-level indices of habitat conditions, we were able to use an extensive dataset on 131 ($n = 51$) den events of adult female bears monitored with global positioning system (GPS) collars near Durango, CO, USA. As a result, we were uniquely able to assess annual patterns in hibernation in response to fine-scale, animal-specific habitat conditions, capitalizing on considerable spatial variation experienced by individual bears with respect to use of human development, weather and natural food conditions. While our primary interest was to evaluate the role of these habitat factors on bear hibernation, we also accounted for the effects of individual attributes (i.e. age, reproductive status), as previous studies have shown them to strongly influence den chronology (Johnson & Pelton, 1980; Schooley et al., 1994). Thus, our research objective was to assess the relative and cumulative influence of anthropogenic food use, weather, natural food availability and individual bear attributes on the start, duration and end of hibernation. This resulted in a comprehensive evaluation of factors associated with hibernation behaviour, with key implications for how future changes in human development and climate may continue to shape denning chronology of black bears, and their interactions with people.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study occurred near Durango, a town consisting of ~18,000 residents (US Census Bureau, 2015) in south-west CO, USA (37.2753°N, 107.8801°W; Figure 1). Lands surrounding Durango range between 1,930 and 3,600 m in elevation and are largely owned and managed by city, state and federal agencies. The area is considered high-quality bear habitat and is dominated by ponderosa pine (*Pinus ponderosa*), Gambel oak (*Quercus gambelii*), aspen (*Populus tremuloides*), pinyon pine (*Pinus edulis*), juniper (*Juniperus* spp) and mountain shrubs such as chokecherry (*Prunus virginiana*) and serviceberry (*Amelanchier alnifolia*).

2.2 | Field data collection on black bears

Between May and September 2011–2015, black bears were captured within 10 km of Durango using cage traps and Aldrich foot snares (Colorado Parks and Wildlife [CPW] Animal Care and Use Protocol #01-2011; Johnson et al., 2011). Female bears estimated to be ≥ 3 years old were immobilized and fit with Vectronics Globalstar collars (Vectronic Aerospace GmbH, Berlin) programmed to collect a GPS location every hour and activity data at 5-min intervals. A premolar tooth was removed to determine age by cementum annuli ($n = 45$; Willey, 1974), and on occasions where tooth samples were not collected ($n = 6$), age was estimated by assessing tooth wear, bear size and evidence of previous lactation.

We used GPS collars to track female bears to their dens each winter (January–March) to collect data on reproductive status and body mass. Based on the presence of offspring in the den, bears were categorized as being barren (barren), having newborn cubs (cubs) or having yearlings (yearlings). During most den visits bears could be extracted

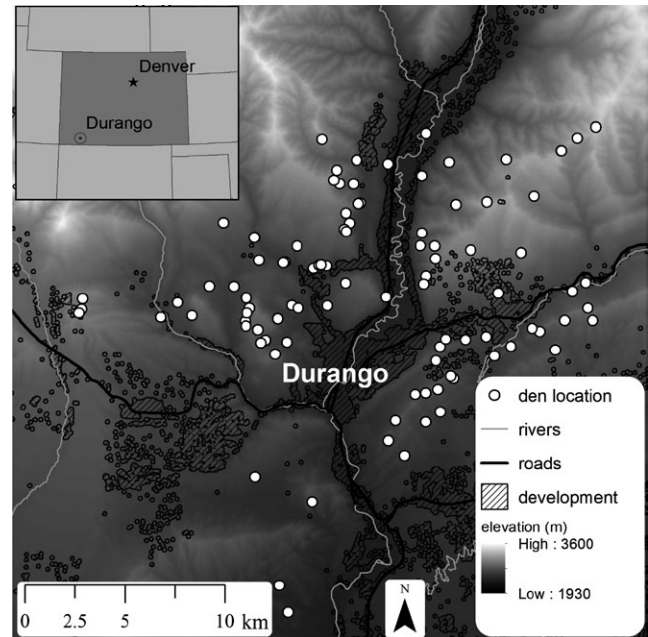


FIGURE 1 Winter den locations of female black bears (white dots) near Durango, CO, USA (2012–2016)

from their dens to record exact mass (kg; $n = 96$). In instances where bears could not be removed from their dens but body measurements were collected ($n = 21$), we estimated mass using chest girth. Mass and chest girth are strongly correlated in black bears, so we used a Bayesian linear regression model (based on female capture measurements within our study area; $n = 265$) to estimate mass from chest girth ($\text{mass} = (1.53 \times \text{chest girth}) - 59.24$; Bayesian $R^2 = 0.90$; Kéry & Royle, 2016). Data were not available on either mass or chest girth for 14 den events. Because captures during hibernation occurred over 8 weeks, when bear condition declines, we back-calculated body mass measurements to their predicted values on 20 January (when winter captures commenced; see Appendix S1 in supporting information). To account for topographical differences in den locations, we also recorded the elevation of each den site using a USGS digital elevation model (30 m).

2.3 | Defining den entry and exit dates

We calculated hibernation start and end dates using activity data from GPS collars (Friebe et al., 2014; Gervasi, Brunberg, & Swenson, 2006; Laske, Garshelis, & Laizzo, 2011; Sahlén, Friebe, Sæbø, Swenson, & Støen, 2015). When we successfully determined both dates for a bear over a winter, we also calculated the duration of hibernation. Activity data were collected using acceleration sensors that summed the number of head tilt movements during 5-min intervals over three orthogonal axes, values which we then used to calculate an hourly average. We defined the start of hibernation as the first day between 1 September and 30 December when a bear's average hourly activity levels were < 23 (based on observations of collared captive bears from Gervasi et al., 2006) for ≥ 22 hr/day (≤ 3 "active" hr/day), with the added constraint that the bear remain in this state for ≥ 7 days (Laske et al., 2011; Figure 2a). Conversely, we

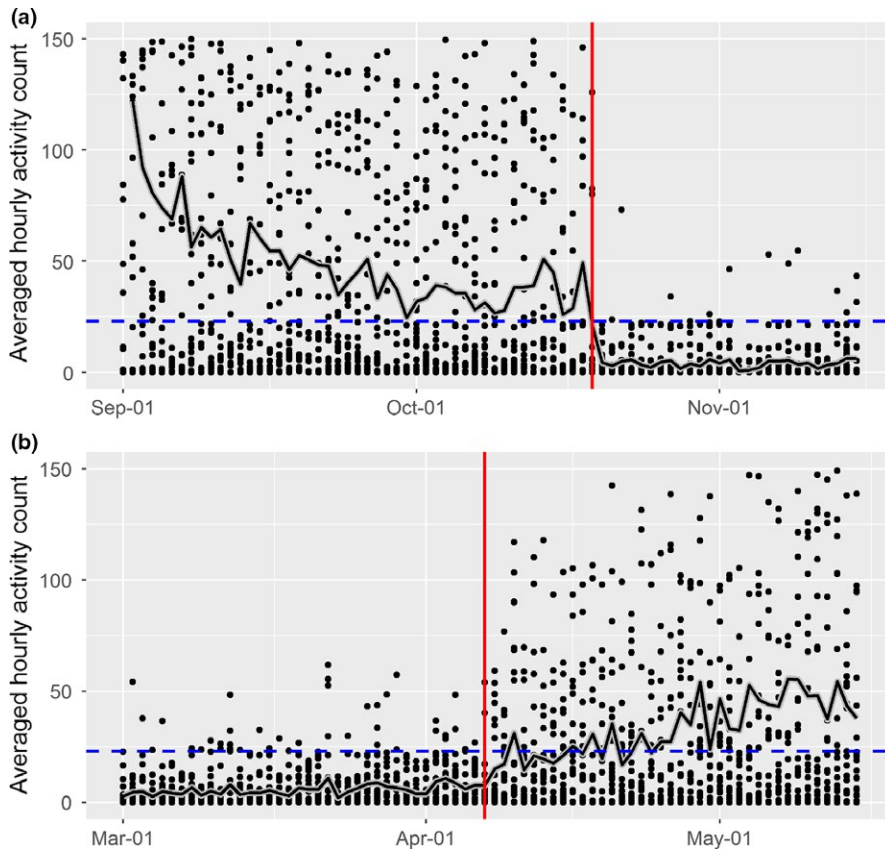


FIGURE 2 Red vertical lines depict the start (a) and end (b) of hibernation for a GPS collared adult female black bear (B52) using activity data during winter (2013–2014) near Durango, CO, USA. The dots represent B52's hourly activity values, the black lines depict daily average activity values, and the blue dashed line depicts the threshold for inactivity. Based on activity criteria, B52 started hibernation on 18 October (a) and ended hibernation on 7 April (b)

defined the end of hibernation as the first day that a bear's activity levels remained >23 for ≥ 3 hr/day and was sustained for ≥ 7 days (Figure 2b).

2.4 | Covariates associated with food resources and weather

To examine the relative and cumulative influence of use of human development, weather and natural food availability on black bear hibernation, we estimated several covariates associated with each den event. To estimate human food use for each bear/year, we first obtained point data of all human structures within La Plata County. We buffered those structures by 100 m to depict the spatial footprint of human development. We then calculated the proportion of an individual bear's year-specific hyperphagia range that overlapped with development (hereafter "development"). A bear's hyperphagia range was defined as the 95% kernel utilization distribution of hourly locations collected 15 July–15 October. To minimize the effects of over-smoothing, we calculated the utilization distribution based on 80% of the reference bandwidth (h_{ref} ; Kie et al., 2010) using the `r` package `adehabitatHR` (Calenge, 2006). The proportion of a bear's annual hyperphagia range that overlapped development became our annual metric of their human food use, as we assumed that bears using human development were foraging on anthropogenic resources (Lewis et al., 2015).

To examine annual weather conditions associated with bear hibernation, we used daily PRISM temperature and precipitation data

(800 m; <http://www.prism.oregonstate.edu/>), and SNOWDAS snow depth data (1 km; <http://nsidc.org>). We investigated weather factors associated with the start of hibernation by calculating the average minimum daily temperature ($^{\circ}\text{C}$) and total precipitation (mm) for the annual fall range of each bear. Fall ranges were estimated using 95% kernel density estimates from hourly collar locations collected 15 September–15 November. To assess the influence of winter weather on the duration of hibernation, we calculated the average daily minimum temperature ($^{\circ}\text{C}$) and snow depth (mm) at each den site from 15 November–1 April. Finally, to assess spring weather associated with the end of hibernation, we calculated the average daily minimum temperature ($^{\circ}\text{C}$) and snow depth (mm) at each den site from 15 February–1 April. PRISM data were not yet available for 2016, so observations for the end of hibernation in 2016 were missing temperature information ($n = 30$).

To account for annual variation in natural food availability (hereafter "natural food"), we assessed the abundance of fall mast on Gambel oak, chokecherry, serviceberry and pinyon pine shrubs and trees (Johnson et al., 2015). Each year, 15 transects 1 km in length were surveyed every two weeks throughout August and September. During each survey, on each transect, the abundance of fruit or nuts for each species was estimated as the percentage of plants with no mast (value = 0), scarce mast (value = 25), moderate mast (value = 50), abundant mast (value = 75) or a bumper crop (value = 100). We then multiplied the percentage of plants in each category by their assigned value (i.e. 0, 25, 50, 75 or 100) to estimate an index of mast abundance for each transect. Each year, we averaged the highest abundance score

for each forage species across all 15 transects to calculate an annual mean abundance for each species across the study area.

We used annual mast abundance indices to calculate the relative amount of natural food available for each bear based on their annual hyperphagia range (see previous description). We used the USDA/USDOJ LANDFIRE existing vegetation type coverage (www.landfire.gov/NationalProductDescriptions21.php) to calculate the proportion of Gambel oak, mountain shrub (chokecherry and serviceberry plants) and pinyon pine landcover types within each bear's annual hyperphagia range, corresponding to our mast surveys. We multiplied these proportions by the annual abundance index for each species (using the mean of chokecherry and serviceberry values for the "mountain shrub" category) to estimate the relative annual availability of natural food within each bear's hyperphagia range.

2.5 | Modelling factors associated with hibernation

We examined the influence of development, weather, natural food and individual bear attributes on the start, duration and end of bear hibernation. To conduct this investigation, we first tested for pairwise correlations among covariates associated with each response variable (start, duration and end). When covariates were highly correlated (correlation coefficients $>|0.6|$), we retained the covariate that had a stronger univariate relationship with the response variable. For the start of hibernation, natural food and precipitation were correlated ($R = 0.66$) and we retained natural food in our models. For both the duration and end of hibernation, snow depth was correlated with elevation ($R \geq 0.78$) and we retained snow depth for further modelling.

Given these decisions, we assessed relationships between the start, duration and end of hibernation with the following covariates: development, minimum temperatures, elevation (for "start" only), snow depth (for "duration" and "end" only), natural food, reproductive status (reference class = barren), age and mass. For each response variable, we fit a single Bayesian linear mixed model with all covariates. For observations that were missing data on mass or temperature, we included priors on those covariates that were normally distributed with a mean equal to the sample mean and a standard deviation that was twice the sample value. In all models, we included a random intercept for each unique bear to account for multiple observations of the same individual across years. We used uninformative priors on all regression coefficients and random intercepts so that parameters were normally distributed with a mean of 0 and precision of 0.0001. We used random starting values for all parameters.

We used posterior distributions from Markov Chain Monte Carlo simulations to assess model results, calling OPENBUGS 3.2.3 (Spiegelhalter, Thomas, Best, & Lunn, 2007) from R 3.2.3 (R Core Team, 2015). We generated three chains for each model, running 5,00,000 iterations/chain, discarding the first 1,00,000 as "burn-in," and sampling one of every 10 iterations thereafter. We ran models based on both standardized and unstandardized covariate values to allow us to compare the relative effects of different factors on hibernation behaviour, and to facilitate interpretation of model results. Covariates were standardized to have a mean of 0 and a standard deviation of 1.

TABLE 1 Median covariate values for continuous variables used in Bayesian linear mixed models associated with the start, duration and end of black bear hibernation near Durango, CO, USA

Covariate	Median	SD	Range
Age (years)	8.0	6.0	2.0–28.0
Mass (kg)	94.6	20.7	46.2–156.3
Fall minimum temperature (°C)	2.1	1.4	–1.5 to 4.5
Fall precipitation (mm)	131.8	46.0	20.8–206.9
Winter minimum temperature (°C)	–6.7	1.4	–9.9 to –3.8
Winter snow depth (mm)	123.2	192.7	13.5–1147.0
Spring minimum temperature (°C)	–4.3	1.6	–10.0 to –2.1
Spring snow depth (mm)	84.5	237.1	0.0–1084.1
Natural food (derived index)	15.6	6.4	3.2–30.1
Development (% overlap)	15.0	14.2	0.0–80.7
Elevation (m)	2340.1	292.2	1955.4–3414.1

We assessed model convergence based on trace plots and Gelman–Rubin statistics ($R_{\text{hat}} < 1.1$). Additionally, we calculated the proportion of total variation explained by each full model (including random effects) and by the fixed effects portion of each model (Kéry & Royle, 2016).

3 | RESULTS

Over the course of the study, we were able to identify den chronology dates from activity data for 131 black bear dens used by 51 different females (Figure 1). On average, we collected data during 3 winters/bear (range = 1–5 years/bear). The median date for the start of hibernation was 20 October ($n = 120$; range 21 September–11 December), the median date for the end of hibernation was 11 April ($n = 108$; range 11 March–17 May), and the median duration of hibernation was 170 days ($n = 97$; range 112–228 days). Across years, we collected den data on 52 females with cubs, 36 with yearlings and 43 that were barren; information on median values of continuous covariates is provided in Table 1.

We found that the start of hibernation was most strongly associated with individual bear attributes (reproductive status, age and mass), followed by natural food, fall minimum temperatures and development (90% CIs non-overlapping 0; Figure 3; Table S1). Compared to barren females, bears with cubs denned 7 days earlier, while bears with yearlings denned 13 days later. For every year a bear aged, hibernation started approximately 1 day earlier, and for every additional 10 kg a bear weighed, hibernation started 2 days later. Both natural food and development delayed hibernation, although the effect of natural food was stronger (Figure 3). A proportionate 20% increase in natural food (based on the observed range of variation) was associated with a 3.8-day delay in hibernation,

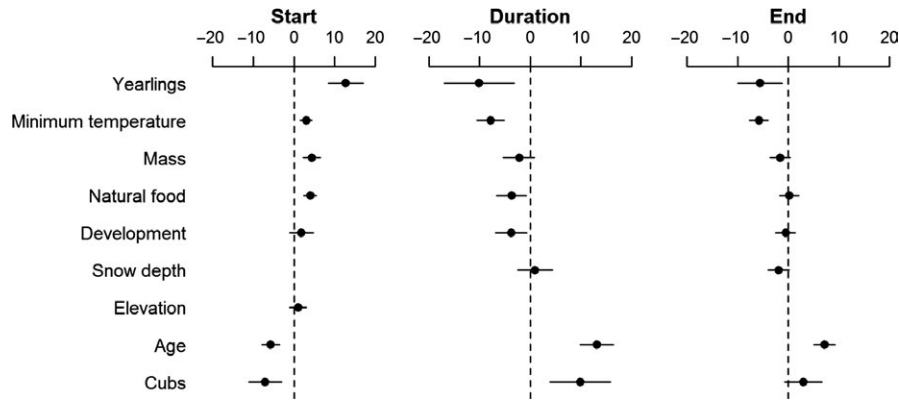


FIGURE 3 Mean and 90% credible intervals of standardized covariates associated with the start, duration and end (in days) of hibernation in female black bears near Durango, CO, USA (2011–2016). Covariates are ordered by the direction and magnitude of coefficients associated with “start.” Modelled effects depict changes in hibernation length given an increase in the covariate (except for “cubs” and “yearlings” which signifies the presence of those offspring types). Elevation was only included in the hibernation “start” model, while snow depth was only included in “duration” and “end” models

while a proportionate 20% increase in development resulted in a 2.2-day delay. For each 1°C increase in the average fall minimum temperature, hibernation was postponed 2.3 days. The only variable that was not associated with the start of hibernation was elevation, as this had little effect after accounting for fall temperatures (Figure 3).

The duration of hibernation was most strongly associated with bear age, offspring status, winter minimum temperatures, development and natural food (90% CIs non-overlapping 0; Table S1; Figures 3 and 4); minimum temperatures had approximately twice the magnitude of effect as natural food or development. For every year a bear aged, den duration increased by 2.1 days. Compared to barren females, bears with cubs denned 10 days longer, while bears with yearlings denned 10 days less. For every 1°C increase in winter minimum temperatures, bears reduced hibernation by an average of 6 days. Increases in natural food and development had similar effects on reducing hibernation. A proportionate 20% increase in natural food was associated with a reduction in hibernation of 3.0 days, while a proportionate 20% increase in development was associated with reduction of 4.1 days. Duration of hibernation was not associated with bear mass or snow depth (Figure 3; Table S1).

The end of hibernation was strongly related to bear age, minimum spring temperatures and reproductive status. The effect of age on the termination of hibernation was nearly equal and opposite of its effect on the start of hibernation, where each additional year increased denning length by a day. Spring temperatures had the second strongest effect on the end of hibernation, such that for every 1°C increase, bears emerged from hibernation 3.5 days earlier. Bears with cubs ended hibernation 2.8 days later than barren females, while bears with yearlings ended 5.7 days earlier. Other covariates had 90% credible intervals overlapping zero (Table S1).

The total proportion of variation explained by covariates associated with the start, duration and end of hibernation was 0.61, 0.66 and 0.62, respectively (fixed and random effects), whereas the variation explained by only the fixed effects was 0.34, 0.23 and 0.32, respectively.

4 | DISCUSSION

As changes in land use and climate dramatically alter landscapes for wildlife, there is a critical need for managers and conservation practitioners to understand how animals are adapting. While the initial response of animals to a new environmental stressor is typically a shift in behaviour (Wong & Candolin, 2015), little is known about the effects of human-induced environmental change on hibernation, an important life-history strategy for many species. By examining individual-level variation associated with 131 den events from black bears utilizing a wide range of habitat conditions, we found that hibernation was strongly related to weather conditions and food availability (natural and human), even after accounting for individual bear attributes (Figures 3 and 4). Of the habitat conditions we evaluated, warmer temperatures tended to be most influential, delaying the onset of hibernation in the fall, expediting emergence from hibernation in the spring and reducing the overall duration of hibernation. The increased availability of natural and human foods had similar effects, as good natural food conditions and high use of anthropogenic subsidies both delayed the start of hibernation and reduced its duration. Given that warmer temperatures and human development both reduced hibernation in our study, we predict that future trajectories of climate and land use change may increase the length of the active bear season, with the potential to cause subsequent increases in human–bear conflicts and bear mortalities.

After accounting for individual attributes, we found that the duration and end of black bear hibernation was most strongly associated with temperature (Figure 3, Table S1). Indeed, temperature had twice the magnitude of effect of either natural or human food availability in decreasing the overall length of hibernation. Our results suggest that ambient temperature serves as an important trigger of hibernation behaviour in bears, and corroborates studies on marmots (*Marmota flaviventris*) and brown bears that temperature is more influential at driving changes in hibernation than snowpack (Evans et al., 2016; Inouye et al., 2000). Climate models project widespread increases

in winter temperatures, while winter precipitation is predicted to be more variable, depending on location (Williams et al., 2015). Indeed, the long-term climate prediction for Colorado is that of substantially warmer temperatures but potentially greater winter precipitation (Gordon & Ojima, 2015). For hibernators sensitive to temperature, trends in warmer weather are likely to reduce the duration of hibernation, while disparate patterns in the snowpack could create trophic mismatches for animals that emerge prior to the onset of spring food resources (Inouye et al., 2000). By 2050, Colorado climate models project that the average temperature will have increased by 2.5 to 5°C under medium–low emissions scenarios and by 3.5 to 6.5°C under high emissions scenarios (Gordon & Ojima, 2015). Assuming that the relationship we observed between temperature and hibernation length is temporally consistent, where a 1°C increase in the winter minimum temperature is associated with a 6-day reduction in black bear hibernation; by 2050, the average length of bear hibernation in our study area could decline by 15 to 39 days.

Our results support previous findings that hibernation in black bears is largely a response to food limitation (Johnson & Pelton, 1980; Schooley et al., 1994), as bears delayed hibernation when natural food was abundant and expedited hibernation when it was scarce. Indeed, bears in better condition (indexed by mass) denned later in the fall, as they appeared to maximize foraging opportunities as long as resources were available (Figure 3, Table S1). Interestingly, bears appeared to respond to anthropogenic foods similar to natural foods, as those individuals that foraged more extensively within development postponed hibernation, and spent significantly less time in their dens (Figures 3 and 4). For example, compared to a bear that used only natural foods, a bear with a fall home-range that overlapped residential development by 50% shortened hibernation by approximately 13 days. While the start of hibernation was more strongly influenced by natural foods than development, these different resource types had similar effects in reducing the overall duration of hibernation (Figure 3; Table S1). As the human population grows and development continues to expand, we expect that anthropogenic food subsidies could have a greater effect on bear behaviour in the future. In the intermountain west, residential housing units have increased dramatically, particularly in rural and exurban areas (Travis, Theobald, & Malanson, 2002). Indeed, within La Plata County, where our study took place, residential development has increased by 330% in the last 30 years (<http://co.laplata.co.us/>), the lifetime of our oldest collared bears. Bears appear to readily adapt to additional anthropogenic foods on the landscape (Kirby et al., 2016), increasing their use of development when native foods are limited (Baruch-Mordo et al., 2014), and as they get older and gain more experience with human subsidies (Johnson et al., 2015). Given increasing availabilities of human foods on the landscape, coupled with shifts in bear foraging behaviour, we should expect that bears could increase their reliance on anthropogenic resources in the future, with reduced hibernation as a consequence.

Our primary interest was in examining the role of habitat conditions on black bear hibernation behaviour, but we also accounted for the influence of individual bear attributes. Indeed, of all the covariates we investigated, reproductive status and age had the greatest effects

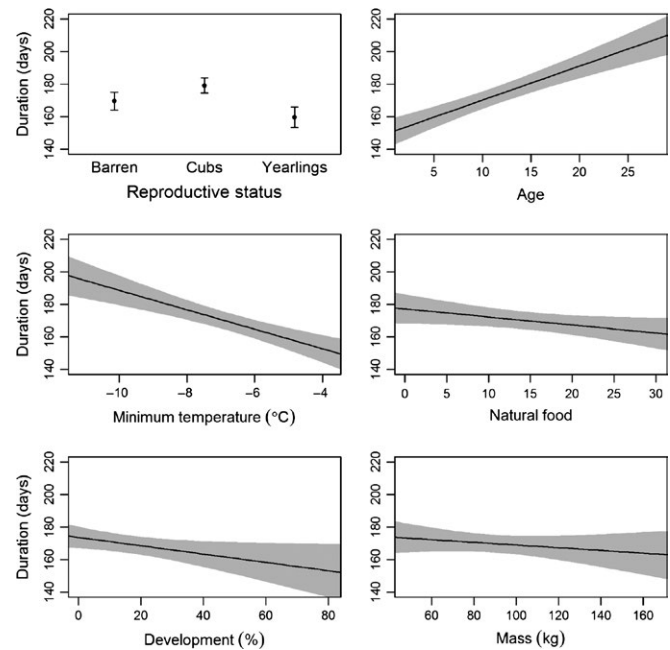


FIGURE 4 Modelled effects of reproductive status, age, winter minimum temperature, fall natural food availability (natural food), per cent overlap with human development (development) and mass on the duration (number of days) of hibernation for female black bears near Durango, Colorado, USA (2011–2016)

on denning chronology (Figure 3; Table S1). Female reproductive status is well recognized to influence the timing and duration of black bear hibernation (Johnson & Pelton, 1980; Schooley et al., 1994), and like other investigators, we found that females birthing newborn cubs entered dens earlier and exited later, while females with yearlings entered dens later and exited earlier. This pattern resulted in a difference in the length of hibernation by approximately 20 days. We suspect that pregnant females den early to conserve energy in the fall, and emerge late due to the vulnerability and limited mobility of their newborn cubs. Meanwhile, females with yearlings may delay hibernation to maximize their post-lactation condition, while their early emergence may be influenced by the desire of their smaller-bodied yearlings to forage. While previous studies have identified the influence of reproduction on hibernation, little information has been published about the exact effect of age (not age class). Sahlén et al. (2015) and Friebe et al. (2014) both reported that older brown bears arrived earlier to their dens. We also observed that older black bears initiated hibernation earlier, and also terminated hibernation later, than their younger counterparts. We hypothesize that older bears may generally be in better condition than younger bears, and more experienced in balancing energy acquisition and expenditure (Friebe et al., 2014). The effect of age on hibernation length was striking, as there was a modelled 50-day difference in hibernation between the youngest (age 2) and oldest (age 28) bears in our study. Researchers have asserted that younger bears are more likely to cause conflicts with people (Elfstöm, Zedrosser, Støen, & Swenson, 2012), which perhaps is not surprising, given how much longer these individuals are active during the year.

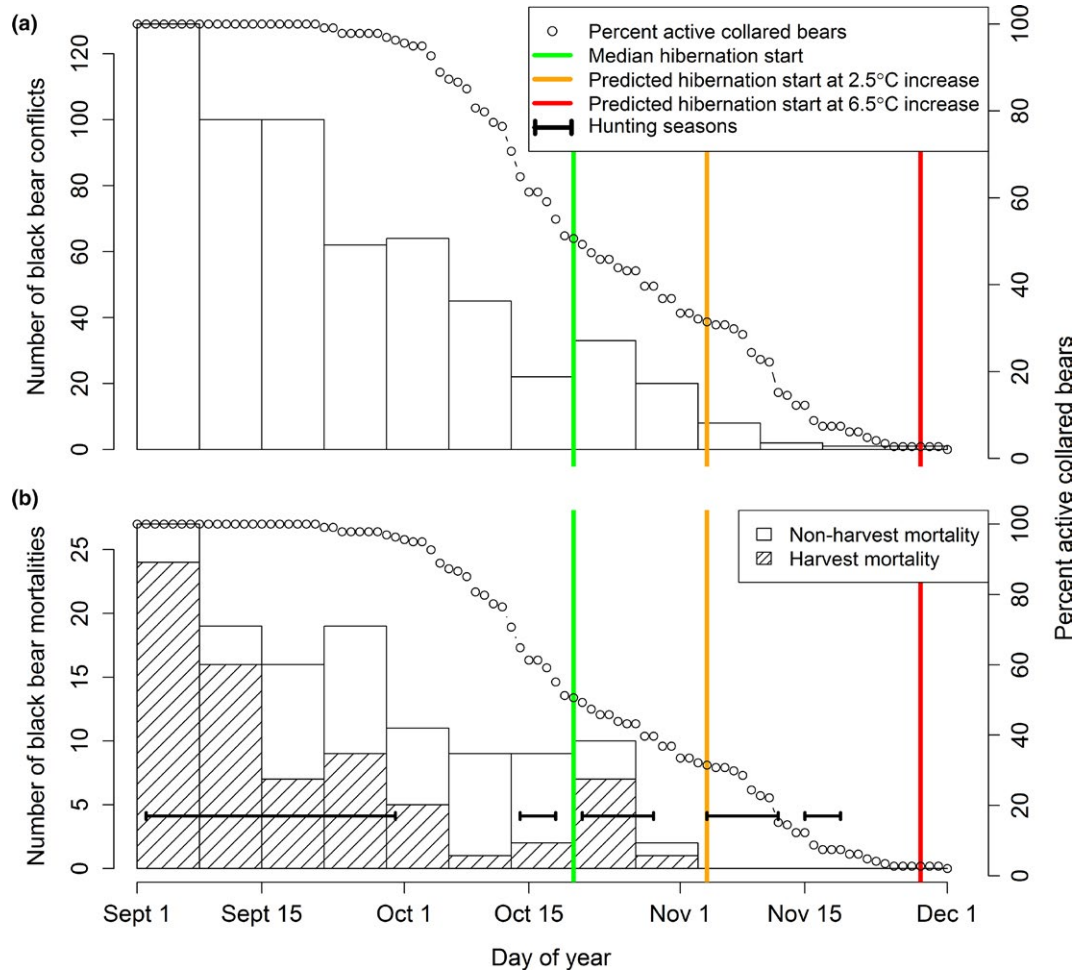


FIGURE 5 Number of human–black bear conflicts (a) and mortalities (b) reported to Colorado Parks and Wildlife near Durango, CO, USA from September to December, 2011–2016, compared to the proportion of GPS collared bears that were active (i.e. not hibernating; circles). Coloured lines show the current median start of hibernation (green) and the projected start of hibernation given a 2.5°C (orange) and 6.5°C (red) increase in winter minimum temperatures. Thick black lines depict black bear hunting seasons in Colorado

The key results of our study, that increases in temperature and use of anthropogenic foods additively reduce the duration of hibernation, have important implications for both human–black bear conflicts and bear mortality. Future changes in climate and land use are both likely to extend the active bear season and result in more opportunities for people and bears to interact. We expect that this change could have consequences for people and bears, particularly during fall. Fall corresponds to the period of hyperphagia, when bears increase their time spent foraging on both natural and human foods (Johnson et al., 2015; Noyce & Garshelis, 2011), with subsequent increases in human–bear conflicts (Merkle, Robinson, Krausman, & Alaback, 2013). In our study area, conflicts generally subsided as bears initiated hibernation, but delays in hibernation could prolong periods of high conflicts (Figure 5a). Delayed hibernation could also negatively affect black bear survival. Nearly all black bear mortality occurs when bears are active (i.e. non-hibernating; Hebblewhite, Percy, & Serrouya, 2003), with the greatest risk occurring during fall when bears increase their movements to find food, and are more susceptible to harvest, vehicle collisions and lethal conflict management.

Bears that hibernate for shorter periods of time will be subject to additional mortality risk and could experience reduced survival. For example, in Colorado, the primary bear hunting season occurs during September, prior to the onset of hibernation, but CPW has additional hunting seasons in late-October and November after the median hibernation start date (20 October). Currently, fewer bears are available for harvest during these late-season hunts, but a 1- or 2-week delay in denning, due to warmer weather and/or increased bear use of development, could alter the harvest risk for a significant portion of the bear population (Figure 5b).

Our results have important implications for wildlife management agencies, as shifts in black bear hibernation behaviour are likely to exacerbate human–bear conflicts and bear mortalities, irrespective of bear population sizes. Management agencies often assume that increases in conflicts reflect increases in the bear population (Obbard et al., 2014), but this assumption is problematic given that bears modify their behaviour in response to variable environmental conditions (Johnson et al., 2015). While behavioural plasticity is essential for animals to adapt to modified landscapes, it can be

maladaptive if associated with reduced individual and population fitness. Investigators have found that black bears living alongside human development have reduced survival and population growth rates (Beckmann & Berger, 2003; Hostetler et al., 2009) as they are more susceptible to vehicle collisions, lethal conflict management and accidents. In such cases, bear populations can operate as “sinks,” a scenario which may become more common as the human footprint on the landscape expands. If warmer weather and increased use of human development both reduce hibernation in bears, we should expect associated rises in conflicts and mortalities, even in stable or declining populations. Indeed, this was observed in the polar bear population of Manitoba, where human–polar bear conflicts increased as sea-ice declined and bears were forced to spend more time on-land (Townes, Derocher, Stirling, Lunn, & Hedman, 2009). In this population, conflicts increased as a function of changing bear behaviour, even as the number of polar bears declined. Given expected trajectories of climate and land use change, and likely associated shifts in black bear behaviour, it will be increasingly important for wildlife agencies to use reliable demographic methods to monitor bear populations, rather than trends in conflicts or mortalities.

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AUTHORS’ CONTRIBUTIONS

H.E.J., L.K.W. and S.W.B. conceived research ideas and designed methodology; H.E.J., D.L.L., T.L.V., C.F.W., R.M.M., L.K.W. and S.W.B. collected data; H.E.J., D.L.L., T.L.V., C.F.W., R.M.M. and L.K.W. analysed data; H.E.J., D.L.L., T.L.V., R.M.M. and S.W.B. wrote the manuscript. All authors approve publication.

DATA ACCESSIBILITY

Data are available from Colorado Parks and Wildlife: <http://cpw.state.co.us/learn/Pages/ResearchMammalsPubs.aspx>, file “Black Bear Hibernation raw data.” (Johnson et al., 2017). Contact dnr_cpw.info@state.co.us with any difficulties in accessing the data.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Table S1. Raw and standardized coefficient estimates from Bayesian linear mixed models of factors associated with the start (ordinal date), end (ordinal date), or duration (number of days) of black bear hibernation around Durango, Colorado, USA, 2011-2016.

Covariate	Start				End				Duration			
	Raw		Standardized		Raw		Standardized		Raw		Standardized	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	254.992	16.141	296.533	2.513	81.291	10.154	101.714	2.381	127.040	18.360	170.765	3.648
Offspring (reference=barren)												
Cubs	-7.242	3.145	-7.113	3.142	2.843	2.876	2.956	2.881	9.668	4.631	9.857	4.652
Yearlings	13.017	3.355	12.747	3.359	-5.672	3.431	-5.590	3.437	-9.870	5.376	-10.073	5.394
Natural Food	0.631	0.198	3.968	1.261	0.032	0.217	0.191	1.466	-0.494	0.334	-3.655	2.311
Elevation	0.006	0.005	1.007	1.596	NA	NA	NA	NA	NA	NA	NA	NA
Snow	NA	NA	NA	NA	-0.007	0.007	-1.871	1.631	0.005	0.014	0.952	2.669
Development	0.138	0.107	1.813	1.477	-0.038	0.107	-0.548	1.525	-0.257	0.163	-3.736	2.403
Minimum temperature	2.286	0.843	3.000	1.122	-3.480	0.838	-5.825	1.423	-6.002	1.536	-7.852	2.165
Age	-0.972	0.284	-5.757	1.698	1.114	0.263	7.136	1.660	2.097	0.409	13.204	2.580
Mass	0.224	0.076	4.404	1.653	-0.073	0.073	-1.607	1.526	-0.083	0.114	-2.191	2.433

Appendix S1. Back-calculating female black bear body mass.

We collected data on female black bear mass during winter captures at dens between January and March, 2012 – 2015. To account for the fact that black bears lose mass during hibernation, and consequently, throughout the capture season, we back-calculated mass to standardize estimates to 20 January each year. This was the approximate start date of the capture season. To estimate daily mass losses we used Bayesian linear regression where mass was the response variable. Capture date was included as an explanatory variable, and we also tested models that included the covariates offspring status (barren, newborn cubs, or yearlings; barren was the reference class) and age. Because we assumed that bear condition deteriorated in very old individuals, we also tested for a quadratic effect of age. Model coefficients were estimated using posterior distributions from Markov chain Monte Carlo simulations, and we used the deviance information criterion (DIC) to compare models. Analyses were conducted using OpenBUGS 3.2.3 (Spiegelhalter et al. 2007) called from R 3.2.3 (R Core Team 2015) using the R2OpenBUGS package (Sturtz et al. 2005). We generated three chains for each model, running 50,000 iterations/chain, discarding the first 10,000 as ‘burn-in’ and sampling one of every 10 iterations thereafter. All models converged well based on trace plots and Gelman-Rubin statistics ($R_{\text{hat}} < 1.1$).

We found that the best model for mass included the capture date, offspring status, age and a quadratic effect of age, and performed significantly better than all other models (Table 1). The mass of female black bears declined over the hibernation period, was higher for bears with cubs, lower for bears with yearlings, and increased with bear age until bears were ~20 years old (Table 2). We used coefficients from the top model to back-calculate mass for each den observation to its projected value on 20 January each year, accounting for individual bear capture

date. Corrected mass values were used to assess associations between mass and the start, duration and end of hibernation.

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Table 1. Deviance information criteria (DIC) and number of parameters (k) for Bayesian linear regression models assessing changes in female black bear body mass during hibernation (January – March). Capture date is included in all models to quantify changes in body condition during the capture season, while testing for the effects of offspring status (barren, newborn cubs, yearlings), age, and a quadratic effect of age.

Model	k	DIC	Δ DIC
Body mass			
date+offspring+age+age ²	6	1177	0
date+age+age ²	4	1185	8
date+age	3	1188	11
date+offspring	4	1189	12
date	2	1191	14
null	1	1189	12

Table 2. Bayesian model coefficients and credible intervals for estimating changes in daily female black bear body mass during hibernation (January – March), after accounting for offspring status (barren, newborn cubs, yearlings), age, and a quadratic effect of age.

Top Model	β	SD	L95%CI	U95%CI
intercept	75.50	8.56	58.65	92.18
date	-0.28	0.12	-0.52	-0.05
offspring (reference=barren)				
cubs	10.15	4.69	0.99	19.36
yearlings	-8.87	5.16	-18.93	1.26
age	3.23	1.11	1.04	5.39
age ²	-0.08	0.04	-0.16	0.00