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# Individual and population fitness consequences associated with large carnivore use of residential development

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**Abstract.** Large carnivores are negotiating increasingly developed landscapes, but little is known about how such behavioral plasticity influences their demographic rates and population trends. Some investigators have suggested that the ability of carnivores to behaviorally adapt to human development will enable their persistence, and yet, others have suggested that such landscapes are likely to serve as population sinks or ecological traps. To understand how plasticity in black bear (*Ursus americanus*) use of residential development influences their population dynamics, we conducted a 6-yr study near Durango, Colorado, USA. Using space-use data on individual bears, we examined the influence of use of residential development on annual measures of bear body fat, cub productivity, cub survival, and adult female survival, after accounting for variation in natural food availability and individual attributes (e.g., age). We then used our field-based vital rate estimates to parameterize a matrix model that simulated asymptotic population growth for bears using residential development to different degrees. We found that bear use of residential development was highly variable within and across years, with bears increasing their foraging within development when natural foods were scarce. Increased bear use of development was associated with increased body fat and cub productivity, but reduced cub and adult survival. When these effects were simultaneously incorporated into a matrix model, we found that the population was projected to decline as bear use of development increased, given that the costs of reduced survival outweighed the benefits of enhanced productivity. Our results provide a mechanistic understanding of how black bear use of residential development exerts opposing effects on different bear fitness traits and a negative effect on population growth, with the magnitude of those effects mediated by variation in environmental conditions. They also highlight the importance of monitoring bear population dynamics, particularly as shifts in bear behavior are likely to drive increases in human–bear conflicts and the perception of growing bear populations. Finally, our work emphasizes the need to consider the demographic viability of large carnivore populations when promoting the coexistence of people and carnivores on shared landscapes.

**Key words:** behavioral plasticity; black bear; ecological trap; human development; human-caused mortality; population growth; population sink; space-use; survival; *Ursus americanus*.

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## INTRODUCTION

Residential human development is rapidly expanding across landscapes worldwide (Seto

et al. 2011), causing native wildlife habitat to be infiltrated with anthropogenic infrastructure, activities, and resources (Radeloff et al. 2010). In response to increasing residential development,

animals often exhibit strong avoidance behavior, evading portions of their range, and altering their movements and habitat use patterns (Polfus and Krausman 2012, Wilmers et al. 2013, Wyckoff et al. 2018). Some animals, however, have learned to regularly navigate developed landscapes (Gese et al. 2012) and even utilize novel anthropogenic resources within residential areas (Sih et al. 2011). While the behavioral adaptations of some animals to residential development have been well studied (Tuomainen and Candolin 2011, Lowry et al. 2013), little is known about the demographic outcomes of their plasticity, and whether there may be individual- or population-level fitness consequences (Wong and Candolin 2015).

The growing footprint of residential development is particularly relevant for large carnivores with expansive home ranges. In many parts of the world, these animals must negotiate an increasingly complex matrix of natural and human-modified habitats to fulfill their life-history requirements. Large carnivores have responded to this change by exhibiting an array of behavioral modifications when in close proximity to development, including becoming more nocturnal, selecting more strongly for cover, avoiding certain types of infrastructure, and shifting their diet (Knopff et al. 2014, Ordiz et al. 2014, Moss et al. 2016, Evans et al. 2019). Species most capable of utilizing developed landscapes are dietary generalists (Bateman and Fleming 2012) that have learned to forage on a host of anthropogenic foods (i.e., garbage, livestock, pets; Oro et al. 2013) and, in some cases, appear to be increasing their use of development over time (Knopff et al. 2014, Johnson et al. 2015, Moss et al. 2016). Researchers have hypothesized that such behavioral adaptations will enable carnivore populations to persist in the future, as their native habitats become increasingly developed (Carter and Linnell 2016).

While studies have documented the increasing use of development by large carnivores, little is known about how this behavioral change is influencing their demographic rates and, ultimately, their population performance (Bateman and Fleming 2012, Magle et al. 2012). Animals have evolved to select habitat that maximizes their fitness (Fretwell and Lucas 1970), but human-modified landscapes can alter the cues

animals use to make selection decisions, rendering them unreliable (Battin 2004, Robertson et al. 2013). As a result, the behavioral plasticity that enables large carnivores to interact with development could potentially be maladaptive, if it reduces their fitness potential. Although the dynamics of carnivore populations within developed landscapes are largely unknown, rates of human-caused mortality are often high (due to causes such as vehicle collisions, management removals, poaching, and other accidents). As a result, investigators have hypothesized and in some cases demonstrated that human settlements can serve as population sinks, or even ecological traps (Hostetler et al. 2009, Balme et al. 2010, van der Meer et al. 2013, Lamb et al. 2017). Such demographic consequences are a significant concern, as the long-term persistence of large carnivores in an increasingly developed world will rely upon the ability of carnivores and people to coexist on shared landscapes (Chapron et al. 2014).

Uncertainties about the demographic influence of human development have posed particular challenges in the management of the American black bear (*Ursus americanus*). Black bear distributions are expanding from historic lows in North America (Scheick and McCown 2014), and bears are increasingly living alongside human development and learning to forage on anthropogenic foods (Merkle et al. 2013, Baruch-Mordo et al. 2014, Evans et al. 2019). These shifts in bear behavior have been associated with increased human-caused mortality (Beckmann and Lackey 2008, Hostetler et al. 2009, Baruch-Mordo et al. 2014, Laufenberg et al. 2018), but also, in some cases, increased reproduction (Beckmann and Lackey 2008). Investigators have suggested that high mortality rates around development may induce black bear population sinks (Beckmann and Lackey 2008, Hostetler et al. 2009, Baruch-Mordo et al. 2014, Lewis et al. 2014), but demographic studies on black bears are rare and inferences have been hampered by small sample sizes. Meanwhile, increasing numbers of interactions between black bears and people within residential areas (Hristienko and McDonald 2007, Baruch-Mordo et al. 2008) have fueled the perception that bear use of human foods within development is bolstering

their populations, often leading to increases in public hunting (Obbard et al. 2014).

Our objectives were to understand how black bear use of residential development influences bear fitness traits and, ultimately, population dynamics. To do so, we deployed global positioning system (GPS) collars on female bears in the vicinity of Durango, Colorado, USA, a city that experiences high use of residential development by bears (Johnson et al. 2015, Johnson et al. 2018b) and high rates of human–black bear conflicts (Baruch-Mordo et al. 2008, Johnson et al. 2018a, Wilbur et al. 2018). Using fine-scale location data on individual behavior, we examined the influence of bear use of human development on annual measures of bear body fat, cub productivity, cub survival, and adult female survival, after accounting for variation in natural food conditions and individual bear attributes (e.g., age). We then used our vital rate estimates to parameterize a matrix projection model (Caswell 2001) that simulated population growth for bears using development to different degrees, projecting the combined effects of development-influenced vital rates on population performance. Whereas past studies have compared vital rates between black bears categorized as either urban or wild (Beckmann and Berger 2003, Hostetler et al. 2009), we capitalized on the observed continuum of bear behavior (ranging from bears that avoid development to those that strongly select development and bears in-between those extremes; Johnson et al. 2015) to quantify annual variation in the use of residential development by individual bears. By explicitly linking bear use of residential development to their demography, we provide a mechanistic understanding of how development uniquely influences different bear fitness traits and its collective effect on bear population trends.

## METHODS

### Study area

The city of Durango is located along the Animas River in southwest Colorado (37.2753° N, 107.8801° W) and consists of ~18,000 residents (U.S. Census Bureau 2015; Fig. 1). Lands surrounding Durango range between 1930 and 3600 m in elevation and are largely owned and managed by city, county, state, and federal

entities. The vicinity of Durango 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 native crab apple (*Pera-phyllum ramosissimum*). Durango has experienced higher population growth rates than the rest of Colorado (from 1970 to 2010 growth in Durango was 67%; statewide it was 57%; U.S. Census Bureau 2015), and residential growth has largely occurred in areas considered to be high-quality black bear habitat.

### Data collection on black bear fitness traits

We captured black bears between May and September 2011 and 2016 using cage traps and Aldrich foot snares (Colorado Parks and Wildlife; CPW; Animal Care and Use Protocol #01-2011). Trapping efforts occurred within ~10 km of Durango to sample bears within the population that all had access to both natural and human developed habitats. Female bears estimated to be  $\geq 3$  yr old were immobilized and fit with Vectronics Globalstar collars (Vectronic Aerospace GmbH, Berlin, Germany) programmed to collect hourly GPS locations. A premolar tooth was removed to determine age by cementum annuli ( $n = 76$ ; Willey 1974), and on occasions where tooth samples were not collected ( $n = 5$ ), age was estimated by assessing tooth wear, bear size, and evidence of previous lactation. We used GPS collars to monitor adult female survival throughout the year, investigating any occasion when a collar was stationary for  $\geq 8$  h and emitting a mortality signal. For females  $\geq 3$  yr old, we estimated baseline year-specific adult female survival rates with Cox proportional hazard models using the survival package (Therneau 2015) in program R (R Core Team 2018). Annual survival was assessed from 1 April in year  $t$  through 30 March in year  $t + 1$ , coinciding with the biological year once bears emerge from their winter dens.

Each winter (2012–2017) bears were recaptured at their dens to collect data on cub productivity, cub survival, and body fat. Captures typically occurred late January through March, although one capture was conducted in December and another in April. We recorded the number of newborn cubs and yearlings with each collared female and

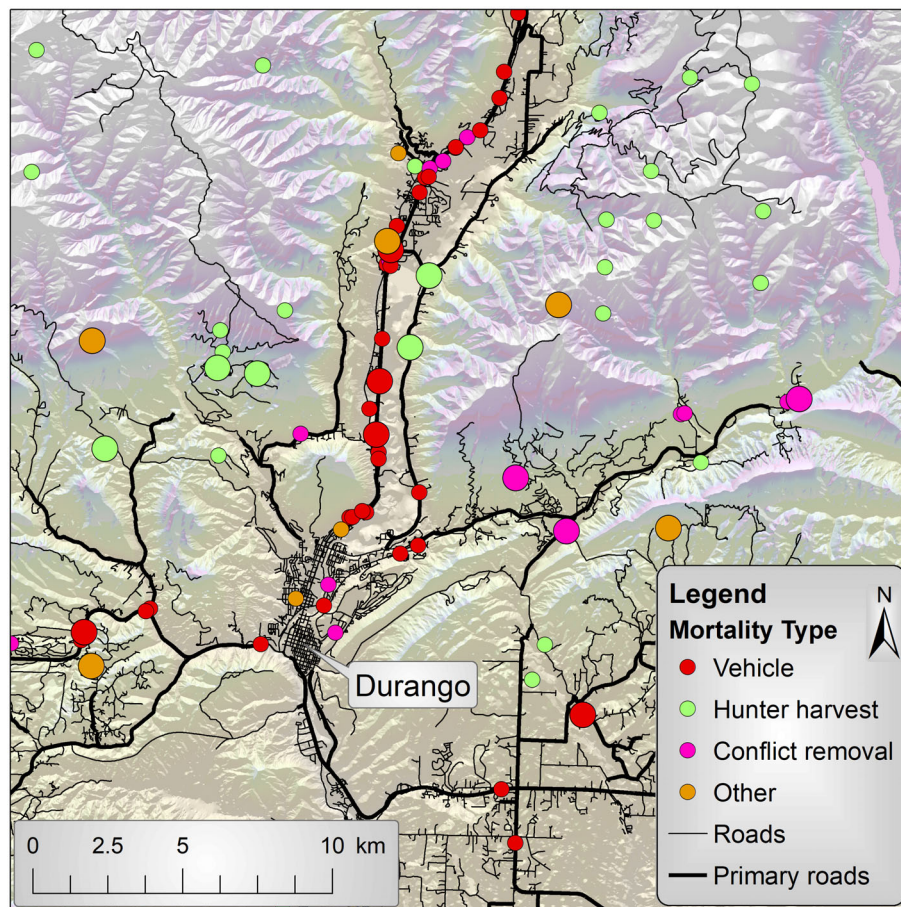


Fig. 1. Locations of female black bear mortalities (all ages) in the vicinity of Durango, Colorado, USA, from 2011 to 2016. Sources of mortalities were categorized as vehicle collision, hunter harvest, conflict removal (by agency or landowner), and other (e.g., electrocution, poison, unknown). Larger circles indicate mortality locations of collared bears, and smaller circles represent mortality locations of uncollared bears.

uniquely marked offspring with passive integrated transponder tags. Because yearlings hibernate with their mothers, we used consecutive annual den checks of collared females to determine the fate of each cub from the newborn to yearling age class. If a yearling was not observed in the den with its mother, it was assumed dead. We used intercept-only logistic regression models to estimate year-specific cub survival.

We weighed all collared female bears and their cubs, and during winter captures from 2013 to 2017, used bioelectrical impedance analysis to estimate the percent body fat of adults (Farley and Robbins 1994, Hilderbrand et al. 1998). Most bears could be removed from their dens to collect mass ( $n = 136$ ) and fat ( $n = 105$ ) measurements.

In instances where adult bears could not be removed but body measurements were obtained from within the den ( $n = 28$ ), we used chest girth to estimate mass (Johnson et al. 2018b). Data were not obtained on either mass or chest girth for 26 adult female winter captures. Because captures during hibernation occurred over  $\sim 9$  weeks when bear body condition notably declines, we back-calculated adult female mass measurements to their predicted values on 20 January (when winter captures typically commenced each year), given estimated daily declines in female bear weight during the capture season (0.28 kg/d; Johnson et al. 2018b).

To account for mass gained by cubs during the capture season due to lactation, we standardized

cub mass to its predicted value on 10 March, the median date of den visits to bears with newborn cubs. We estimated daily gains in cub mass using a linear mixed model (LMM) where cub mass was modeled as a function of the capture date and a nested random effect structure that accounted for cubs from the same litter and sows that were repeatedly sampled. We obtained mass measurements on 162 cubs from 78 litters produced by 46 different adult females. We estimated that cubs gained 0.03 kg/d (standard error [SE] = 0.01,  $t$  value = 3.75; Appendix S1) over the course of the capture season (18 February–19 April).

#### *Quantifying natural food conditions and use of human development*

To quantify annual variation in natural food availability, we assessed the abundance of late summer and fall mast from chokecherry, native crab apple, Gambel oak, and pinyon pine shrubs and trees. Each summer, between 2011 and 2016, we surveyed 15 transects, 1 km in length, every two weeks during August and September. During each survey, on each transect, the abundance of fruit or nuts for each species (if present) was estimated as the percentage of plants with no mast (value = 0), scarce mast (value = 0.25), moderate mast (value = 0.50), abundant mast (value = 0.75), or a bumper crop (value = 1.0). We then multiplied the percentage of plants in each category by their assigned value (i.e., 0, 0.25, 0.5, 0.75, or 1.0) and summed the results to estimate an index of mast abundance for each species on each transect. Each year, for each forage species, we used the median of the highest abundance score across all transects where the species was present as the annual index of mast conditions across the study area.

We then used annual mast abundance indices to calculate the relative amount of food of each forage species that was available to each bear based on their year-specific home range. Annual, bear-specific home ranges were calculated from the 95% kernel utilization distribution of hourly locations collected between 1 June and 30 September. We estimated the utilization distribution based on 80% of the reference bandwidth (Kie et al. 2010) using the R package *adehabitatHR* (Calenge 2006). We then used the USDA/USDOI LANDFIRE existing vegetation type coverage ([www.landfire.gov/NationalProductDesc](http://www.landfire.gov/NationalProductDesc)

[riptions21.php](http://www.landfire.gov/NationalProductDesc)) to calculate the proportion of different landcover types associated with chokecherry, native crab apple, Gambel oak, and pinyon pine within each bear's annual range (corresponding to our mast surveys) and multiplied these proportions by the annual abundance index of each forage species.

While all these forage species are used by bears in Colorado (Beck 1991), we had no information about their relative value for enabling bears to amass weight. To ensure that our index of natural food availability was meaningful to bears around Durango, we tested all possible additive combinations of the different late summer forage species (given their annual mast abundance and proportion of a bear's home range) to determine which were most strongly correlated with bear mass the subsequent winter, after accounting for other factors known to be associated with bear mass (see details in Appendix S2). Using Akaike's information criterion corrected for small sample sizes (Burnham and Anderson 2002), we found that a natural food index including native crab apple, Gambel oak, and pinyon pine was most strongly associated with variation in female bear mass (Appendix S2). We summed the amounts of each of these foods within the annual ranges of each bear (the proportion of the annual home range consisting of that forage type  $\times$  annual mast abundance) and treated this value as our bear-specific annual index of natural food availability.

To quantify annual bear use of human development, we buffered all human structures within La Plata County by 100 m ([ftp://ftp.laplata.co.us/shapefiles](http://ftp://ftp.laplata.co.us/shapefiles)). We then used hourly GPS locations to calculate the percentage of time that each bear spent each year within that development buffer during their active season (1 June–30 September; development). Use of development was not calculated for bears that were only collared outside the active summer season or when GPS locations were not consistently acquired due to collar malfunctions (10 animal-year data sets of 235 in total).

As bears increased their use of development, we assumed they would consume more anthropogenic foods (Lewis et al. 2015). To explicitly test this assumption, we used isotopic analysis to evaluate  $^{13}\text{C}$  enrichment in bear hair samples, as bears that consume anthropogenic foods high in corn and cane sugar have higher levels of  $^{13}\text{C}$  than those with native plant-based diets (Jacoby

et al. 1999, Kirby et al. 2016, 2017). By sampling hair collected during winter den visits, we could make inference about the assimilated diets of bears during the previous active season, when hair growth occurred (Jacoby et al. 1999). We collected a hair sample from the brow of each bear captured during the winter. Samples were cleaned, homogenized, and weighed into tin capsules to quantify  $^{13}\text{C}$  using a Costech 4010 and Carlo Erba 110 Elemental Analyzer (Costech, Valencia, California, USA) attached to a Thermo Finnigan Delta Plus XP Continuous Flow Isotope Ratio Mass Spectrometer (Thermo Fischer Scientific, Waltham, Massachusetts, USA) following Kirby et al. (2017). We then employed a LMM to test for a relationship between bear use of development during summer and  $^{13}\text{C}$  enrichment in hair samples ( $n = 153$ ) the subsequent winter, using a random effect to account for repeated sampling of some bears across years.

In addition to quantifying the annual use of development for each collared female, we used consecutive GPS collar locations to determine the number of times bears crossed roads each active season (1 June–30 September). Given that vehicle collisions are responsible for numerous bear mortalities near Durango (Laufenberg et al. 2018), we wanted to better understand the specific influence of road crossings on adult and cub survival. Using road data obtained from La Plata County, we determined the number of times that each collared female each active season crossed any road (all roads; paved and gravel) and primary roads with speeds  $\geq 64$  km/h (primary roads; county roads and highways). Because all bears were not monitored throughout the entire active season (due to staggered entry and bear mortalities), we converted the number of crossings into weekly rates (the number of crossings of each road type divided by the number of weeks monitored) to obtain a standardized measure across individuals. Although the road and development indices were generally correlated, portions of our study area had several primary roads with limited housing development (Fig. 1).

#### *Assessing the influence of human development on black bear fitness traits*

Our primary objectives were to understand the influence of black bear use of human development on different bear fitness traits and their

collective effect on bear population growth. To that end, our analytical approach was to test a single global model for each fitness trait (body fat, cub productivity, cub survival, and adult survival) that included bear use of development (the primary covariate of interest), along with relevant covariates known or hypothesized to be important (e.g., age, natural food availability). Prior to running a global model for a fitness trait, we checked for multicollinearity among covariates ( $r < |0.7|$ ). To determine whether development or other covariates had biologically significant influences on fitness traits, we examined whether their 90% confidence intervals excluded zero, as an alpha of 0.1 balanced the ability to detect relationships of conservation relevance while minimizing type I errors. We used R version 3.5.2 for all modeling (R Core Team 2018).

*Body fat.*—We used a LMM to assess the influence of use of development during the summer active season on body fat (an indirect measure of fitness) the subsequent winter, after accounting for bear age,  $\text{age}^2$  (allowing for age to have a non-linear effect), natural food availability during the preceding summer, and the ordinal day that fat was measured (to account for fat being metabolized over the winter capture period; McLellan 2011). Because reproductive status is strongly associated with bear body condition during winter (Elowe and Dodge 1989), we also classified females as barren (reference class), with cubs, or with yearlings. In addition to these fixed effects, we included a random effect to account for the repeated sampling of bears over the course of the study. Model fitting was performed using the R package lme4 (Bates et al. 2015).

*Cub productivity.*—We used a cumulative link model (for ordinal categorical data) to assess the influence of use of development during the active season on subsequent winter cub productivity. Female black bears provide care for their offspring for  $\sim 16$  months, typically reproducing every other year. Due to this 2-yr reproductive cycle, we only analyzed litter sizes of female bears available to reproduce (i.e., those that did not have yearlings in the den), determining whether their use of development influenced the probability they had either 0, 1, 2, or 3 cubs. In addition to testing for an effect of development, we modeled cub productivity as a function of

bear age and natural food availability, as these factors have been associated with black bear litter sizes in other studies (Elowe and Dodge 1989, Bridges et al. 2011). We also included a quadratic effect for age, as we observed that old females in our study area rarely produced offspring and we wanted to allow for a non-linear relationship. We did not include bear mass or fat in the model, despite its known influence on litter size (Samson and Huot 1995), due to the number of missing values for that covariate. Initially, we included a random effect for each bear (as 63% of collared sows were observed more than once), but the model was overfit (indicated by the condition number of the Hessian  $>10^4$  and the variance of the random effect being effectively 0; Christensen 2019). As a result, we fit a global model with only fixed effects. Model fitting was performed with the R package *ordinal* (Christensen 2015).

*Cub survival.*—To examine the influence of use of development on annual cub survival (survival from the newborn to yearling age class), we used a generalized linear model with a logit link. Cubs were not collared to obtain their locations, but because they spend the first year of life with their mother, we assigned each cub its mother's year-specific development value. We also modeled cub survival as a function of newborn mass, the age of the mother (age and age<sup>2</sup>; Elowe and Dodge 1989), and the mother's index of natural food availability (Eiler et al. 1989). We initially used a nested random effects model structure to account for cubs from the same litter and sows that could have multiple litters over the course of the study. However, due to small sample sizes, and that we only observed  $>1$  litter from 33% of the sows, the random effects were estimated to be zero (indicating there was not excess variability beyond that induced by the residual). As a result, we dropped the random effects terms and fit the model with only fixed effects (Pasch et al. 2013). In addition to assessing a global cub survival model with development, we also assessed a second global model where we replaced development with the number of weekly crossings of all roads and primary roads. Time spent within development was highly correlated with crossings of all roads ( $R^2 = 0.84$ ) so we did not include those covariates in the same model. This second model allowed us to quantify the specific influence of different road types on cub survival.

Model fitting was performed with the R package *lme4* (Bates et al. 2015).

*Adult survival.*—We used a Cox proportional hazard model to determine whether use of development influenced annual adult survival, while also accounting for age, reproductive status, and natural food availability. Annual survival was monitored from 1 April in year  $t$  to 31 March in year  $t + 1$ , coinciding with the biological year once bears emerge from their winter dens. We used an annual recurrent study design (Fieberg and DelGiudice 2009) and bears that slipped their collars or experienced a collar malfunction were censored. We coded the reproductive status of bears as being with cubs or alone (reference class), since yearlings disperse in early summer leaving adults independent for most of the active season. Similar to cub survival, we also assessed a second global model where we replaced development with the number of weekly crossings of all roads and primary roads. For both Cox models, we assessed the proportional hazards assumption by inspecting Schoenfeld residuals with respect to time (Schoenfeld 1982). Models were fit using the R package *survival* (Therneau 2015).

#### *Assessing the cumulative effects of human development on black bear population growth*

To examine the cumulative influence of bear use of development on population dynamics, we inserted the modeled effects of development on bear vital rates (cub productivity, cub survival, and adult survival) into a female-based population matrix model. We used the model to estimate changes in the asymptotic bear population growth rate as bear use of development increased from 0% to 100%, in 5% increments. Our model was an age-structured population matrix that operated on an annual time step, projecting age classes from birth to 20+ yr (Appendix S3). We developed the matrix with a post-birth-pulse structure to match the sampling methods of data collection. Because reproductive females (ages 3–20) typically give birth every other year, each adult age class was partitioned into two groups, females available to reproduce and females already caring for offspring (Lewis et al. 2014). For each adult age class and group, we calculated predicted values of survival and cub productivity based on our global vital rate



models. Assuming an equal sex ratio at birth, we divided cub productivity by 2 to account for a female-only model. Because cub survival was influenced by the age of the mother, we split the cub age class into 18 groups reflecting the survival probabilities of cubs with different aged mothers from 3 to 20 yr old. We calculated cub survival rates for mothers of each age class from our logistic regression model. Because vital rate parameters from our models (cub survival, cub productivity, adult survival) were estimated from data collected across all years of our study, they accounted for total variance (temporal and sampling variation). We did not collect field data on the survival of yearlings (Sy) or subadults (Ss), so we parameterized our models using values reported in a meta-analysis of black bears in the western United States (Sy mean = 0.72 and SE = 0.07; Ss mean = 0.77 and SE = 0.04; Beston 2011). See Appendix S3 for a detailed life cycle diagram and population matrix.

For every 5% increase in bear use of development, we calculated the mean asymptotic population growth rate, given the unique influence that development had on cub productivity, cub survival, and adult survival. To account for parameter uncertainty for different levels of development, mean population growth rates were calculated from 50,000 replicate matrices derived from randomly drawn vital rate values from beta distributions of cub productivity, cub survival, and adult survival. Beta distributions for cub and adult survival were derived from model results for each level of development for each age (i.e., female age for adult survival, and age of the mother for cub survival) and reproductive class (adult females were either available to reproduce or had cubs), holding cub mass at its mean value in the cub survival model. To account for the influence of variation in natural food abundance on bear vital rates, population models were run using mean, low (10% quantile) and high (90% quantile) values of the natural food index.

Given that our cumulative link model of cub productivity described the probabilities that females would have litter sizes of 0, 1, 2, or 3 cubs, our estimates of development- and age-specific litter sizes were based on four different probabilities. Random draws of probabilities of each of the four potential litter sizes would not

necessarily equal 1.0, so for each replicate matrix, we first randomly selected the order that litter size probabilities would be drawn (e.g.,  $P[2 \text{ cubs}]$ , then  $P[0 \text{ cubs}]$ , then  $P[1 \text{ cub}]$ , and last  $P[3 \text{ cubs}]$ ). Following that order, we used beta distributions to select the first probability (i.e., in this example,  $P[2 \text{ cubs}]$ ) and then the second probability (i.e.,  $P[0 \text{ cubs}]$ ). If the sum of those probabilities was  $<1$ , we randomly drew the third probability ( $P[1 \text{ cub}]$ ), with the constraint that the sum of all probabilities was  $\leq 1.0$ . Finally, the last probability was calculated as the difference between 1.0 and the sum of the other 3 probabilities. The probability of having each litter size was then multiplied by that number of cubs, and the four values were summed and then divided by two (to account for a female-only model).

We estimated shape parameters of all beta distributions using confidence intervals of vital rates with the `beta.select` function in the R package `LearnBayes` (Albert 2014). Asymptotic population growth rates ( $\lambda_i$ ) were calculated from the replicate matrices for each level of bear use of development and for different levels of the natural food index, using functions from the R package `popbio` (Stubben and Milligan 2007). It is important to note that our calculation of  $\lambda$  did not include immigration, but based on our GPS collar data (Laufenberg et al. 2018), we suspect its contributions were relatively minor. We estimated the confidence intervals of the growth rates as the range encompassing 95% of the  $\lambda_i$  values for each level of development (Devenish Nelson et al. 2010).

## RESULTS

### *Summary statistics for black bear fitness traits and covariates*

During summers 2011–2016, we captured and collared 81 female black bears ( $\geq 3$  yr old). The median age of collared females during the study was 7 yr (range 3–28). During the first year of the study, we collared 21 bears, and for the remainder of the study, we maintained a sample of  $\geq 41$  bears/yr for a total of 235 bear years (Table 1). Individual adult females were monitored for an average of 3 yr during the study (range 1–6 yr), as bears were continuously tracked until they died ( $n = 21$ ), slipped their collar ( $n = 12$ ), experienced a collar failure ( $n = 14$ ),

Table 1. Annual estimates (mean and standard error [SE]) of black bear adult female body fat (%), adult female productivity (cubs/adult female), probability of cub survival, and probability of adult female survival in the vicinity of Durango, Colorado, USA, 2011–2017.

Year	Body fat		Cubs/adult female		Cub survival		Adult survival	
	<i>n</i>	Mean (SE)	<i>n</i>	Mean (SE)	<i>n</i>	Mean (SE)	<i>n</i>	Mean (SE)
2011	0	No data	0	No data	0	No data	21	0.95 (0.05)
2012	0	No data	22	0.95 (0.24)	10	0.40 (0.15)	45	0.80 (0.07)
2013	13	20.75 (3.13)	28	0.50 (0.16)	11	0.55 (0.15)	41	0.87 (0.06)
2014	22	22.73 (2.09)	34	0.79 (0.18)	23	0.48 (0.10)	41	0.95 (0.03)
2015	26	27.08 (1.27)	39	1.08 (0.18)	31	0.65 (0.09)	45	0.92 (0.04)
2016	24	28.30 (1.86)	33	0.76 (0.19)	21	0.67 (0.10)	42	0.90 (0.05)
2017	20	31.90 (0.95)	34	1.06 (0.20)	0	No data	0	No data
All years	105	26.58 (0.87)	190	0.87 (0.08)	96	0.57 (0.05)	235	0.89 (0.02)

Note: Data on body fat and cub productivity were collected between January and March of year *t*. Cub and adult survival in year *t* were monitored from 1 April in year *t* (once bears emerged from their winter dens) through 31 March in year *t* + 1.

or were translocated out of the study population due to conflict behavior ( $n = 1$ ). Over the course of the study, the average annual survival rate of adult females was 0.89 (range 0.80–0.95; Table 1). Twenty-one collared females died during the study due to vehicle collisions (7), hunter harvest (5), conflict removal (4), unknown causes (3), an accident (1; consumption of rodenticide), and natural death (1 at age 28; Fig 1).

During winter den captures, we obtained 190 observations of the reproductive status of collared females; in 57 instances, bears were barren, 80 had newborn cubs, and 53 had yearlings. The age range for successful litter production was 3–21 yr old, and adult females produced an average of 0.87 cubs/yr (range 0.50–1.08; Table 1). Litter sizes of females available to have cubs (i.e., not caring for yearling offspring) were either 0, 1, 2, or 3 which occurred 42%, 9%, 37%, and 12% of the time, respectively. From 2012 to 2017, 33 adult females produced 46 litters that were monitored over consecutive winters, enabling estimates of cub survival. Of those litters, nine had no offspring survive their first year (20%), while 37 had at least one cub survive (80%). Across the study, average annual cub survival was 0.57, ranging between 0.40 and 0.67 (Table 1). On 20 January, the mean mass of adult females was 92 kg (range 46–156 kg), and on 10 March, the mean mass of cubs was 2.2 kg (range 0.96–3.67 kg). During winter captures, adult female bears had an average of 26.6% body fat (range 0.0–41.1%), with annual average

winter fat estimates ranging from 20.8% to 31.9% (Table 1).

Annual abundance scores of native crab apple, Gambel oak, pinyon pine, and chokecherry were highly variable among years (Appendix S4). On average, oak habitat comprised 40% of bear home ranges (range 2–76%), while the other mast species typically covered 17–19% of home ranges (range 0–84%). When native crab apple, Gambel oak, and pinyon pine values were summed within annual bear-specific home ranges to index natural food availability, we found that the median score was 9.12 (range 0.01–31.39; Table 2). Annual median values of natural food ranged from a low of 2.28 in 2012 to a high of 21.92 in 2011. Natural foods were notably low in 2012 when freezing temperatures in June badly damaged the fruiting bodies of mast and resulted in a subsequent natural food shortage (Appendix S4; Laufenberg et al. 2018).

The median percentage of time bears spent within residential development (1 June–30 September) was 7.8% (range 0.0–90.3%), although annual median values varied widely from a low of 2.4% in 2014 to a high of 17.1% in 2012 (Table 2). Across all years of the study, the median value of  $^{13}\text{C}$  in bear hair samples was  $-21.11$  (range  $-22.95$  to  $-18.25$ ). We found a strong positive relationship between use of development during the active season and  $^{13}\text{C}$  isotope levels sampled the subsequent winter ( $\beta = 0.021$ ,  $\text{SE} = 0.004$ ,  $t$  value = 5.488), confirming that bears that spent more time within residential development consumed more human

Table 2. Annual summary statistics (median and range) for the index of natural food availability within adult female black bear home ranges, the percentage of time adult female black bears spent within residential development, and the number of times adult female black bears crossed all roads or primary roads ( $\geq 64$  km/h) on a weekly basis in the vicinity of Durango, Colorado, 2011–2016.

Year	Natural food index	Time in development (%)	All road crossings/week	Primary road crossings/week
2011	21.92 (10.56–29.11)	3.86 (0.00–65.68)	24.85 (4.75–116.41)	0.49 (0.00–15.75)
2012	2.28 (0.01–12.86)	17.09 (0.04–90.34)	37.03 (4.29–143.88)	3.13 (0.00–20.83)
2013	3.17 (1.29–7.50)	12.77 (0.00–59.57)	27.43 (0.00–116.48)	2.83 (0.00–23.06)
2014	12.95 (7.40–18.24)	2.39 (0.00–46.52)	17.60 (0.18–103.41)	1.11 (0.00–25.29)
2015	8.60 (2.79–31.39)	7.78 (0.00–49.47)	16.06 (0.88–82.21)	1.56 (0.00–19.24)
2016	13.22 (4.56–31.16)	4.54 (0.00–35.16)	26.13 (0.00–72.47)	1.51 (0.00–11.96)
All years	9.12 (0.01–31.39)	7.78 (0.00–90.34)	23.77 (0.00–143.88)	1.75 (0.00–25.29)

Note: Percentage of time spent within development and road crossing values were calculated from 1 June through 30 September.

foods (Fig. 2). The median number of times bears crossed primary roads/week during the active season was 2 (range 0–25), and for all roads, it was 24 (range 0–144; Table 2). The highest annual median number of crossings for primary and all roads occurred in 2012 (i.e., during a notable poor natural food year).

#### *Influence of development and other covariates on black bear fitness traits*

Over the course of the study, we obtained 104 winter measurements of body fat from 48 collared adult female bears that also had valid location data. Bears with greater use of development during the summer had more body fat the subsequent winter (Table 3, Fig. 3a). An increase in use of development by 10% was associated with an average increase in body fat of 1.4%. Similarly, increases in natural food availability during the previous summer were associated with increases in fat (Fig. 3b), with natural food abundance having a greater magnitude of effect than development (Table 3). Body fat exhibited a strong non-linear effect with age, as it was low in younger bears, increased in middle-aged bears (peaking at age 13), and then declined in older bears (Fig. 3c). As expected, bears processed at their dens earlier in the winter had more body fat than those processed late in the season (Table 3, Fig. 3d). On average, over the course of the winter capture season, body fat declined in adult female bears by an average of 0.16% per day. Body fat was greatest for bears with newborn cubs. Compared to barren females, on average,

sows with cubs had 8% more body fat while sows with yearlings had 1% less body fat (Fig. 3e).

We obtained 137 observations of cub productivity from 62 adult female bears that were available to reproduce (i.e., were not caring for yearlings). As bear use of development increased, so did cub productivity (Table 3). At

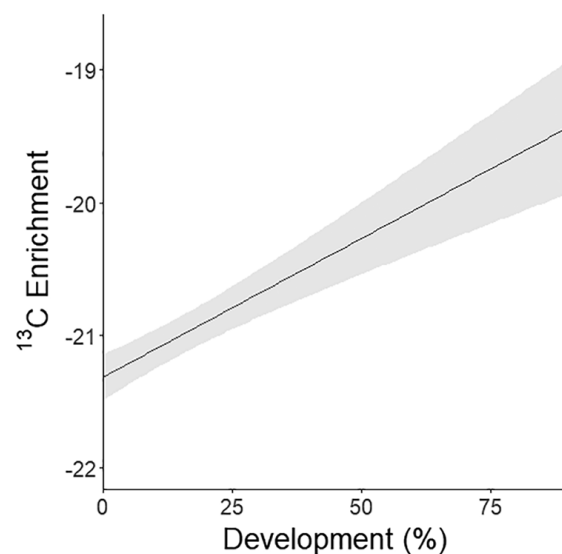


Fig. 2. Isotope  $^{13}\text{C}$  enrichment levels (and 90% confidence interval) of collared female black bear hair samples ( $n = 153$ ; sampled during winter) modeled as a function of the percentage of time spent within 100 m of human development the previous summer near Durango, Colorado, USA, 2011–2016.

Table 3. Standardized and unstandardized coefficients, standard errors (SE), and 90% confidence intervals of covariates used to model variation in black bear adult female percent body fat, annual cub productivity (litters of 0, 1, 2, or 3 cubs), annual cub survival, and hazards to annual adult female survival in the vicinity of Durango, Colorado, USA, 2011–2017.

Fitness trait model	Standardized				Unstandardized			
	$\beta$	SE	L90%	U90%	$\beta$	SE	L90%	U90%
Body Fat								
Intercept	24.908	1.733	22.039	27.788	18.577	3.952	11.705	25.265
Development	2.486	0.738	1.210	3.727	0.144	0.043	0.070	0.216
Natural food	4.070	0.726	2.863	5.274	0.550	0.098	0.387	0.713
Age	1.518	1.029	-0.194	3.304	1.265	0.517	0.399	2.174
Age <sup>2</sup>	-1.679	0.628	-2.785	-0.625	-0.050	0.019	-0.082	-0.018
Ordinal day	-2.973	0.899	-4.497	-1.473	-0.161	0.049	-0.243	-0.080
Reproductive status (reference = barren)								
Cub	8.183	1.878	5.073	11.292	8.183	1.878	5.073	11.292
Yearling	-0.810	2.079	-4.270	2.644	-0.810	2.079	-4.270	2.644
Cub productivity								
0 1	-2.208	0.364	-2.807	-1.609	5.844	1.200	3.870	7.818
1 2	-1.680	0.338	-2.236	-1.125	6.372	1.224	4.358	8.386
2 3	0.796	0.317	0.274	1.318	8.848	1.344	6.638	11.058
Development	0.372	0.220	0.011	0.733	0.020	0.012	0.001	0.040
Natural food	0.530	0.201	0.199	0.862	0.070	0.026	0.026	0.113
Age	0.652	0.268	0.211	1.093	1.260	0.224	0.892	1.628
Age <sup>2</sup>	-2.397	0.429	-3.102	-1.692	-0.056	0.010	-0.073	-0.040
Cub survival								
Intercept	0.989	0.314	0.487	1.524	-4.565	1.879	-7.830	-1.604
Development	-0.314	0.272	-0.775	0.126	-0.025	0.021	-0.061	0.010
Natural food	0.181	0.255	-0.235	0.610	0.026	0.037	-0.034	0.088
Mother's age	0.302	0.275	-0.145	0.764	1.091	0.375	0.494	1.735
Mother's age <sup>2</sup>	-0.696	0.229	-1.091	-0.334	-0.059	0.019	-0.092	-0.028
Cub mass	0.127	0.270	-0.315	0.580	0.232	0.492	-0.575	1.058
Hazards to adult survival								
Development	0.357	0.199	0.031	0.684	0.020	0.011	0.002	0.038
Natural food	-0.268	0.273	-0.718	0.182	-0.037	0.038	-0.099	0.025
Age	-0.225	0.231	-0.605	0.155	-0.040	0.041	-0.108	0.028
Reproductive status (reference = alone)								
Cubs	0.059	0.495	-0.755	0.872	0.059	0.495	-0.755	0.872

Note: We used a linear mixed model for body fat, a cumulative link model for cub productivity (coefficients are log odds), a logistic mixed model for cub survival (coefficients are log odds), and a Cox proportional hazard model for adult female survival (coefficients are log hazard ratios; positive values indicate increased risk of death; and negative values indicate reduced risk of death).

low levels of development, female bears had the highest probability of producing twins, but once use of development was  $\geq 46\%$ , bears were most likely to produce triplets (Fig. 4a). Our index of natural food availability had a similar but stronger influence on cub productivity (Table 3). When natural foods were scarce, female bears were most likely to produce twins, but as the natural food index increased, their probability of producing triplets increased while their probabilities of being barren, or producing 1 or 2 cubs declined (Fig. 4b). Once the natural food index

was  $\geq 20$ , bears were most likely to produce triplets. Of the factors we evaluated, age had the strongest influence on cub productivity, exhibiting distinct non-linear relationships with different litter sizes. Female bears were most likely to be barren  $\leq 5$  and  $\geq 17$  yr old (Fig. 4c). The probability of producing a single cub was low for all ages, but peaked at ages 5 and 17. The probability of producing twins was highest for bears 6–16 yr old, displaying a minor dip between the ages of 10 and 12 when the likelihood of having triplets peaked (Fig. 4c). By age 20, bears

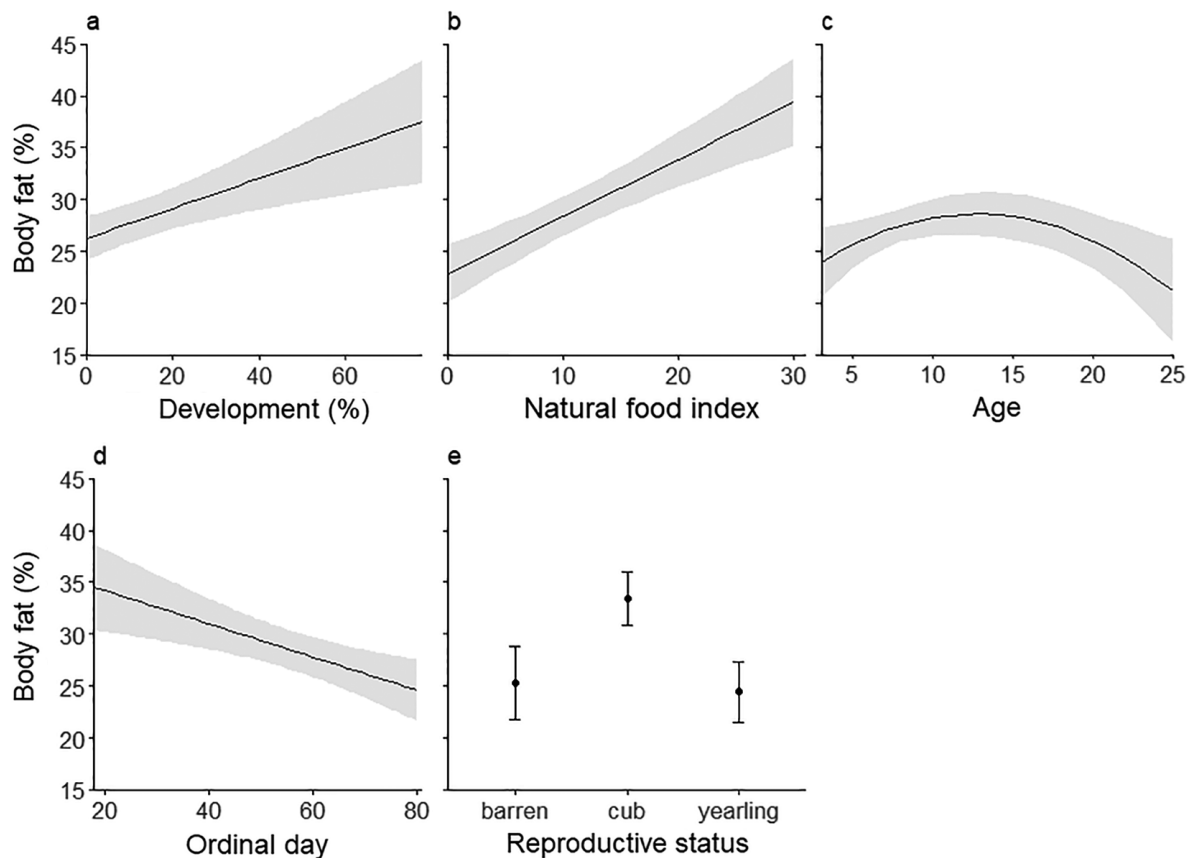


Fig. 3. Percent body fat of adult female black bears during winter modeled as a function of (a) the percentage of time spent within 100 m of human development the previous summer, (b) the abundance of natural foods within their home range the previous summer, (c) their age, (d) the ordinal day that body fat was measured during the winter capture season, and (e) their reproductive state (i.e., barren, with cubs, or with yearlings). Shaded areas depict 90% confidence intervals. Data were collected in the vicinity of Durango, Colorado, USA, 2011–2017.

displayed reproductive senescence as the probability of being barren was 90% (Fig. 4c).

Of the 96 newborn cubs that we marked in winter dens and checked on the following year, 55 survived their first year of life to re-den with their mothers. There was not a clear relationship between cub survival and development (90% confidence interval overlapped zero; Table 3), although cub survival appeared to decline with increased use of development (Fig. 5a). The effects of natural food availability and cub mass were also non-significant (Table 3). The only factor we evaluated that was strongly associated with cub survival was the age of the mother. Cubs with younger and older mothers had

reduced survival compared to those with middle-aged mothers (survival peaked for cubs with 9-yr-old mothers; Fig. 5b). When we replaced development with the road indices, we found that the weekly crossing rate of all roads was negatively associated with cub survival, while there was no additional effect of primary roads (Table 4). Over our observed range of variation in road crossings, on average, an increase in 10 road crossings/week was associated with a 6.9% reduction in the probability of cub survival (Fig. 5c).

We simultaneously collected data on survival and hourly space-use from 81 adult female bears for a total of 225 bear years. We found that

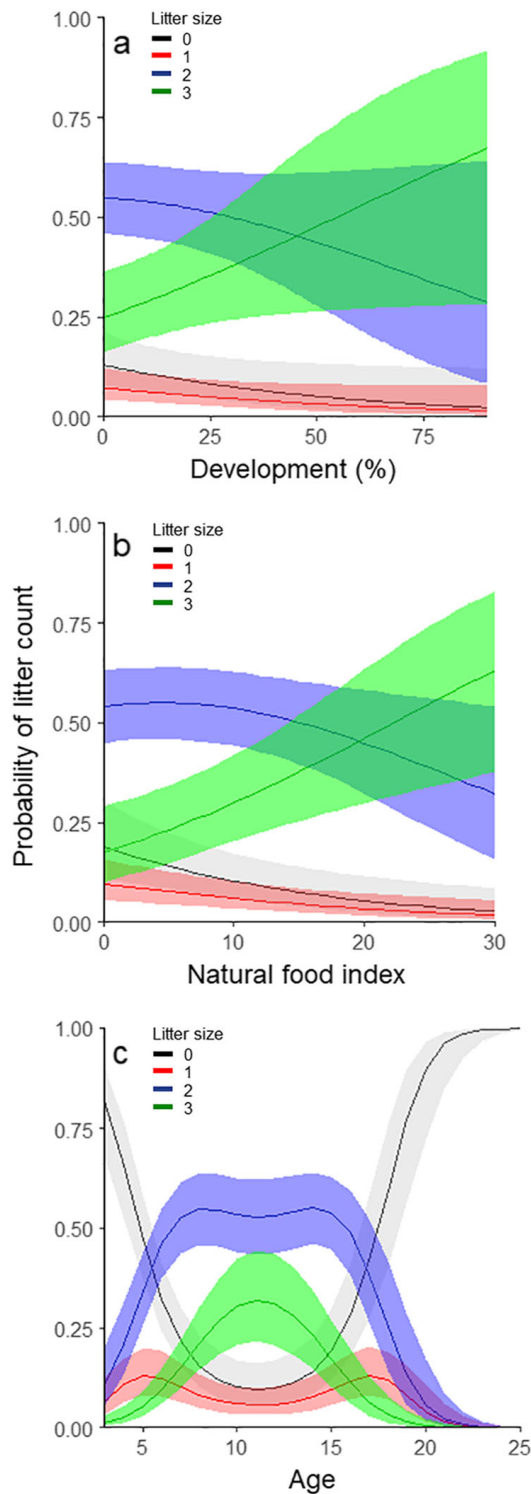


Fig. 4. Probabilities of adult female black bears giving birth to zero, one, two, or three cubs modeled as a function of (a) the percentage of time spent within

increasing use of development resulted in decreased annual survival for adult female bears (Fig. 6a); this was the only covariate that had an effect (Table 3). Over the observed range of variation, an increase in the proportion of time spent within development of 10% was associated with an average decline in the annual survival rate of 3.2% (Fig. 6a). When we ran a second adult survival model where we replaced development with the road indices, the covariate for weekly primary road crossings failed the proportional hazards assumption ( $P = 0.03$ ). Mortality from primary roads increased later in the summer, causing the violation. To account for this, we re-fit the model evaluating the influence of primary roads separately for two distinct time periods (Therneau et al. 2019): early summer (1 May–31 July) and hyperphagia (1 August–30 September). We found that increased crossings of primary roads significantly reduced adult female survival during the hyperphagia period, but not during early summer (Table 4). There was no relationship with any other covariate that we tested (Table 4). During the hyperphagia period, for every five additional crossings of primary roads/week, annual adult female survival declined by an average of 8.3% (Fig. 6b).

#### Cumulative effects of human development on black bear population growth

Increased use of development by black bears resulted in declines in  $\lambda$  (Fig. 7). When bear use of development increased, higher rates of cub productivity (Fig. 4a) did not compensate for reduced cub and adult survival (Figs. 5a, 6a), and the population was projected to experience a net decline (Fig. 7). Under average natural food conditions, when bears did not use any development, median  $\lambda$  was projected to be 1.001. Lambda declined below 1.0 when bears used

(Fig. 4. Continued)

100 m of human development the previous summer, (b) the abundance of natural foods within their home range the previous summer, and (c) their age. Shaded areas depict 90% confidence intervals. Data were collected in the vicinity of Durango, Colorado, USA, 2011–2017.

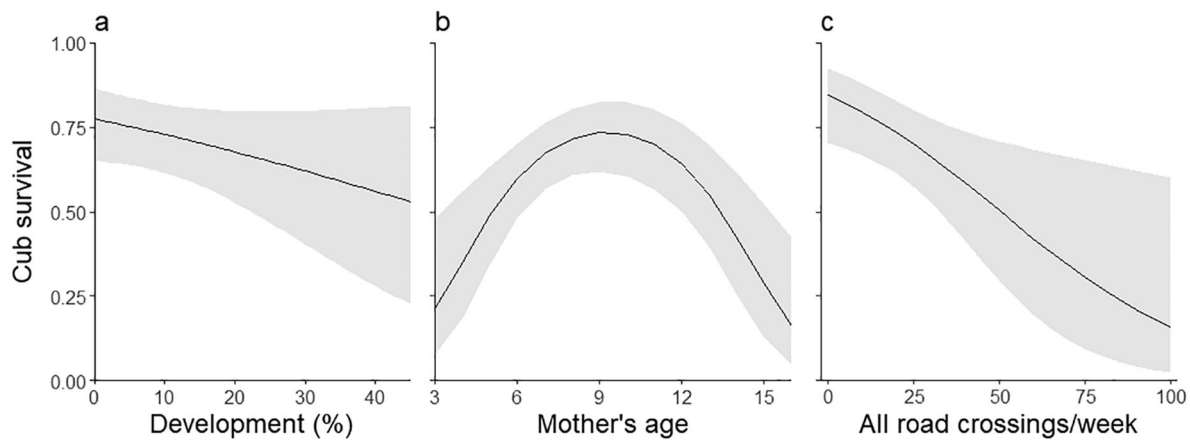


Fig. 5. Probability of annual black bear cub survival modeled as a function of (a) the percentage of time their mother spent within 100 m of human development, (b) the age of their mother, and (c) the weekly crossing rate of all roads. Shaded areas depict 90% confidence intervals. Data were collected in the vicinity of Durango, Colorado, USA, 2011–2017.

Table 4. Standardized and unstandardized coefficients, standard errors (SE), and 90% confidence intervals of covariates used to model annual black bear cub survival and hazards to adult female survival in the vicinity of Durango, Colorado, USA, 2011–2017.

Survival model	Standardized				Unstandardized			
	$\beta$	SE	L90%	U90%	$\beta$	SE	L90%	U90%
<b>Cub survival</b>								
Intercept	0.963	0.332	0.430	1.531	-4.489	2.054	-8.084	-1.261
Primary roads	0.204	0.344	-0.349	0.791	0.108	0.182	-0.185	0.420
All roads	-0.777	0.370	-1.428	-0.203	-0.033	0.016	-0.061	-0.009
Natural food	0.317	0.288	-0.140	0.818	0.046	0.042	-0.020	0.118
Mother's age	0.194	0.284	-0.269	0.671	1.008	0.402	0.367	1.698
Mother's age <sup>2</sup>	-0.660	0.245	-1.083	-0.271	-0.056	0.021	-0.092	-0.023
Cub mass	0.249	0.273	-0.196	0.711	0.455	0.499	-0.357	1.298
<b>Hazards to adult survival</b>								
Primary roads, early summer	-0.827	0.899	-2.306	0.652	-0.164	0.178	-0.456	0.129
Primary roads, hyperphagia	0.577	0.189	0.266	0.888	0.114	0.037	0.053	0.176
All roads	0.140	0.211	-0.207	0.487	0.005	0.008	-0.008	0.018
Natural food	-0.280	0.272	-0.727	0.168	-0.038	0.037	-0.099	0.023
Age	-0.132	0.250	-0.543	0.279	-0.023	0.044	-0.096	0.049
Reproductive status (reference = alone)								
Cubs	0.224	0.522	-0.635	1.082	0.224	0.522	-0.635	1.082

Note: Covariates include the average weekly crossing rate of primary roads ( $\geq 64$  km/h) and all roads, natural food availability, bear age, cub mass, and reproductive status (alone or with cubs). We used a logistic mixed model for cub survival (coefficients are log odds) and a Cox proportional hazard model for adult female survival (coefficients are log hazard ratios; positive values indicate increased risk of death; and negative values indicate reduced risk of death).

development  $\geq 1\%$  of the time, and the upper 95% confidence interval was  $<1.0$  when use of development was  $>16\%$ . When the natural food index was low, estimates of  $\lambda$  were depressed. Even when bears did not use any development,

$\lambda$  was estimated to be below 1.0 ( $\lambda = 0.955$ ; 95% CI 0.920–0.987) and use of development accelerated projected declines (Fig. 7). Conversely, when the natural food index was high, and bears did not use any development,  $\lambda$  was estimated to

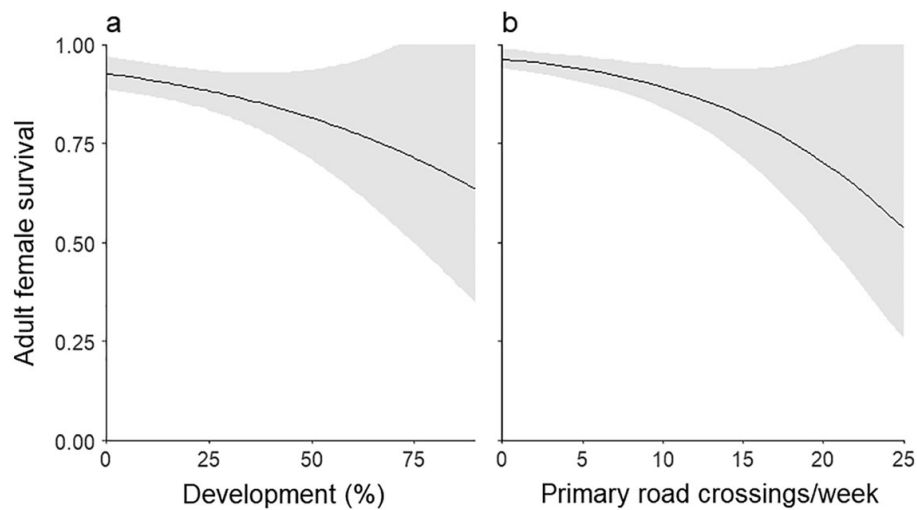


Fig. 6. Probability of annual black bear adult female survival modeled as a function of (a) the percentage of time spent within 100 m of human development and (b) the weekly crossing rate of primary roads ( $\geq 64$  km/h) during the hyperphagia period (1 August–30 September). Shaded areas depict 90% confidence intervals. Data were collected in the vicinity of Durango, Colorado, USA, 2011–2016.

be 1.038 (95% CI 1.005–1.068). Lambda was projected to decline below 1.0 when use of development was  $\geq 21\%$ , with the upper 95% confidence interval declining below 1.0 when use of development was  $\geq 36\%$ . While the annual observed value of development for an individual bear within our study area ranged between 0% and 90%, the median value was 7.8%, which was associated with a  $\lambda$  of 0.989 under average natural food conditions (95% CI 0.960–1.016).

## DISCUSSION

Our results provide a mechanistic understanding of how black bear use of residential development exerts opposing effects on different bear fitness traits, but an overall negative effect on population growth. Increases in human–black bear conflicts and observations of large litter sizes around residential development have fueled the perception that anthropogenic subsidies are bolstering black bear populations (Howe et al. 2010). Meanwhile, high rates of human-caused black bear mortality around development have led investigators to suggest that anthropogenic subsidies can induce bear population sinks (Beckmann and Lackey 2008,

Baruch-Mordo et al. 2014). Given the limited abilities of management agencies to monitor black bear population dynamics (Garshelis and Hristienko 2006), these contradictory patterns have generated uncertainty about the influence of development on bear population trajectories and triggered highly contentious management strategies (e.g., Willett and Vigil 2016). By simultaneously monitoring black bear space-use and demographic rates, we found that these contrasting observations are both correct; bear use of residential development does augment their body condition and reproductive success, but also exposes them to higher rates of mortality. Importantly, when these disparate effects were collectively incorporated into a population matrix model, we found that increased bear use of residential development induced population declines, having a net negative effect (Fig. 7). Enhanced cub productivity could not compensate for reduced adult and cub survival, especially given that adult survival has the greatest potential (elasticity) to influence black bear populations (Freedman et al. 2003, Mitchell et al., 2009, Beston 2011). Surprisingly, the negative effects of development were manifested even at low levels of bear use (Fig. 7), well within our



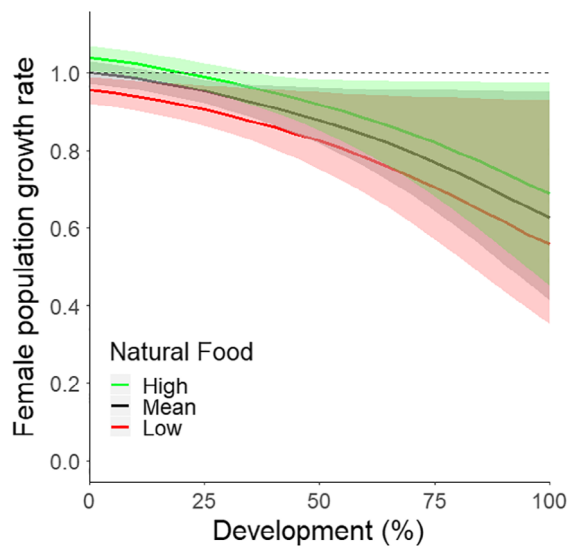


Fig. 7. Simulation results showing the relationship between black bear use of human development (% time spent within 100 m of development during the summer active season) and the female black bear projected population growth rate given the combined influence of development on cub productivity, cub survival, and adult survival. Population growth rates were calculated based on mean, low (10% quantile), and high (90% quantile) values of the natural food index. Mean population growth rates (and 95% confidence intervals) were based on 50,000 simulated matrices (the dashed line signifies stationary population growth at  $\lambda = 1$ ).

observed range of variation. Our results corroborate those from Florida and Nevada that also used field-based vital rate estimates to project population performance for bears using developed landscapes. Both studies found that, due to high human-caused adult mortality, population growth rates were projected to be  $<1$  (Beckmann and Lackey 2008, Hostetler et al. 2009). Similar patterns have been observed for other large carnivore populations across the globe, with high human-induced adult mortality implicated in creating population sinks and ecological traps (Balme et al. 2010, van der Meer et al. 2013, Steyaert et al. 2016, Lamb et al. 2017).

It is often assumed that bears located within developed landscapes are accessing human foods and that such subsidies are providing forage benefits (Baruch-Mordo et al. 2014, Johnson

et al. 2015, Johnson et al. 2018a). We confirmed these assumptions, as black bears that spent more time within residential development consumed greater amounts of anthropogenic foods (Fig. 2) and amassed more body fat (Fig. 3a). Similarly, Ditmer et al. (2016) found that the proportion of black bear GPS locations within agricultural fields reflected their consumption of crops, with greater crop use resulting in heavier, fatter bears. In natural systems, devoid of human influence, foraging strategies of black bears that result in enhanced body condition are translated into fitness benefits, notably greater reproductive success (Noyce and Garshelis 1994, Samson and Huot 1995). It may not be surprising then, that black bears appear to be increasing their use of human foods as they become more widely accessible. For example, Kirby et al. (2016) found that black bear consumption of anthropogenic foods in Colorado broadly tracked housing densities, with human foods comprising  $>30\%$  of bear diets along the highly developed Front Range. Similar to other studies, we found that body fat was higher for females with newborn cubs and increased with greater natural food availability (Harlow et al. 2002, Belant et al. 2006). Indeed, natural food availability had a stronger effect on bear body fat than use of development (Fig. 3a, b), demonstrating the importance of natural foods to bears, even those living along the development-wildland interface. Interestingly, we also found that bear body fat exhibited a curvilinear relationship with age, peaking in prime-age females. Investigators have reported that adult black bears have greater proportions of fat than subadults (Schwartz et al. 2014), but to our knowledge, this is the first time that body fat has been observed to decline in older aged black bears.

Forage benefits from residential food subsidies not only resulted in improved body condition of adult female bears, but also in greater reproductive success (Fig. 4a). Studies conducted in other developed systems both support (Beckmann and Berger 2003, Beckmann and Lackey 2008) and refute (Hostetler et al. 2009, Baruch-Mordo et al. 2014) this finding. In part, we expect that discrepancies may stem from small sample sizes in some studies and from categorizing bears into two discrete groups (i.e., urban vs. wild) rather than modeling reproductive success as a

continuous function of use of development. Compared to development, natural food abundance had a similar, but stronger influence on cub productivity (Table 3, Fig. 4b), corroborating other studies that have found positive relationships between mast availability and black bear reproductive success (Elowe and Dodge 1989, Bridges et al. 2011). Interestingly, Costello et al. (2003) concluded that only a minimum threshold of food was needed for black bears to successfully reproduce, as they found that bears were largely resilient to poor natural food conditions. Our work supports this finding, as bears were most likely to produce twins even when the abundance of natural foods was low (Fig. 4b), with triplet litters being produced only in response to highly abundant natural foods or high use of anthropogenic foods. While other studies have found that reproductive success increases in older bears (Kolenosky 1990, Bridges et al. 2011), our results displayed a more nuanced pattern, with cub productivity highest for prime-age females, and lower in younger and older females (Fig. 4c). To our knowledge, this is the first time that reproductive senescence has been observed in black bears, although it has been detected in brown bears (Schwartz et al. 2003). Litters of  $\geq 3$  cubs are commonly observed in eastern black bear populations (McDonald and Fuller 2001), but triplets in our study system were relatively infrequent and most likely to occur for bears 10–12 yr old. Western black bear populations are known to have lower fecundity rates than eastern populations (Beston 2011), and cub productivity rates in our study system were comparable to values reported in other western systems (Beck 1991, Costello et al. 2003, Beston 2011).

The influence of bear use of residential development on cub survival was inconclusive (confidence interval overlapped with zero; Table 3), although cub survival appeared to decline as they spent more time within residential development (Fig. 5a). When we replaced development with road crossings, however, we found that cub survival significantly declined as their number of all road crossings increased (Fig. 5c), crossings which primarily traversed city and neighborhood streets. Given their small body size, we suspect that cubs are particularly susceptible to being killed by motorists, even on slower city

streets, as they are difficult to see and more likely to succumb to their injuries. Our results corroborate other studies finding that vehicle collisions were responsible for high proportions of black bear cub mortalities (Beckmann and Berger 2003, Garrison et al. 2007) and carnivore mortalities in general (Bateman and Fleming 2012). Of the other covariates of cub survival we examined, only the age of the mother was strongly influential, with prime-age adult females (ages 8–11) being the most successful at rearing offspring (Fig. 5b). We expected that cubs with young, inexperienced mothers may have reduced survival, but did not expect survival to decline so sharply in older mothers as well. Noyce and Garshelis (1994) found that cub size and growth were correlated to the size of the mother, but to our knowledge, this is the first time that cub survival has been linked to the age of the mother. We suspect that the superior body condition of prime-aged females not only confers benefits to cub size, but that those females are also able to better defend their cubs from predators or conspecifics and secure adequate food resources. Past black bear studies have yielded mixed results as to the influence of natural food conditions on cub survival, with some investigators finding positive associations (Costello et al. 2003) and others finding no detectable relationship (McDonald and Fuller 2005). In our study area, we did not find a significant relationship.

Annual adult female bear survival declined as use of residential development increased (Fig. 6a), in accordance with previous studies. For example, in Florida, Hostetler et al. (2009) estimated that the average survival rate of bears within residential development was 0.78 compared to 0.97 in nearby forested habitat. Similarly, Baruch-Mordo et al. (2014) found that adult female bear survival strongly declined during poor natural food years (from 0.99 to 0.72) when bears increased their use of urban development. In Durango, under average natural food conditions, we estimated adult female survival to be 0.93 for bears using only natural habitat and 0.82 for bears that spent 50% of their time within residential development. Indeed, we observed our lowest annual survival rate in 2012 (0.80), which coincided with a severe natural food shortage and the highest levels of bear use of development (Table 2). When we replaced development with

road crossings in our survival model, we found that survival declined as a function of the number of times bears crossed fast primary roads during the hyperphagia season, when bears increase their movements in search of food. We suspect that most drivers can easily see adult bears on slower city streets, rendering them more susceptible to collisions on faster thoroughways. Interestingly, Dittmer et al. (2018) recently found that black bears exhibited elevated heart rates when crossing roads, particularly those with increased traffic volumes. These findings suggest that bears perceive increased risk when crossing roads, but in our study system, they do not appear to be able to effectively mediate the risk. While the average adult female survival rate in our study area (0.89) was similar to other western black bear populations (Beston 2011), it was highly variable among years, ranging between 0.80 and 0.95. As with most long-lived, large mammals, adult survival in black bears is typically high with relatively little variation (Beston 2011, Laufenberg et al. 2016), but investigators have reported greater variability in study systems highly influenced by development due to human-caused mortality (Beckmann and Lackey 2008, Hostetler et al. 2009, Baruch-Mordo et al. 2014). In the Durango system, at least 59% of mortalities of collared females occurred by non-harvest human causes (e.g., vehicle collisions, conflict removal; with some unknown causes that may also have been non-harvest human related), while 23% were legally harvested. Factors that induce high variability in a key vital rate like adult survival can reduce long-term population growth rates (Mills 2007) and have been associated with declines in other large mammals (Johnson et al. 2010).

While a growing body of literature is linking human-induced mortality with population declines in large carnivores (Ripple et al. 2014, Rosenblatt et al. 2014, Lamb et al. 2017), our work highlights how the magnitude of such declines can vary in response to changes in environmental conditions and subsequent animal behavior. For example, when natural food availability was moderate to abundant, bear use of development around Durango was relatively low (i.e., median value in 2011 was 3.9%) enabling stable population dynamics (Fig. 7), whereas when natural food availability was low, use of development

increased (i.e., median value in 2012 was 17.1%) resulting in Durango being a population sink (based on our matrix-based estimates of  $\lambda$ ; Pulliam 1988, Runge et al. 2006). Importantly, poor natural food years and increased use of development additively reduced bear population growth rates (Fig. 7). Interestingly, bears appeared to perceive some risk associated with their use of residential development, as they generally reduced this behavior when natural foods were abundant even though human subsidies were consistently available (Johnson et al. 2015). As such, the attractiveness of residential development was dependent on environmental conditions, thereby mediating the fitness consequences. Our findings support Laufenberg et al. (2018), which used a genetic mark-recapture study to estimate changes in female black bear abundance around Durango between 2011 and 2014. They found that abundance was relatively stable from 2011 to 2012 and from 2013 to 2014 but declined dramatically after the natural food shortage of 2012 (2012–2013), in association with high rates of human-caused bear mortality.

While our study elucidates the influence of human development on black bear demographic rates and population trends, there were still limitations that are important to acknowledge. For example, our estimates of  $\lambda$  did not incorporate immigration. While results from Laufenberg et al. (2018) suggest that immigration is likely to be relatively small, we did not have data to measure this parameter. As a result, if immigration is significant, the abundance of bears around Durango could be higher than expected from our trajectories (Pulliam 1988). Additionally, we projected population growth rates based on different values of bear use of development, but this approach assumed that use of development was constant across all bears in the population for each level of the projection. Certainly, this is an oversimplification given our findings that bear use of development is highly variable (Table 2). While our model structure enabled a heuristic understanding of how changes in bear space-use would be expected to influence population growth, the projections do not adequately incorporate the complex nature of bear behavior. In addition, we did not collect data on yearling or subadult survival rates, so we used values for western black bears from the literature (Beston

2011). Because these vital rates did not account for any detrimental effects of development, our population growth rates are likely overestimated. Similarly, other study systems have reported increased bear harvest in years with low natural food abundance (Noyce and Garselis 1997, Obbard et al. 2014), a pattern that was not evident in our known-fate mortality data for bears around Durango (although sample sizes were limited). If poor natural food years are associated with greater harvest mortality, our survival and population growth rates are overestimated. Finally, we had to exclude the random effects terms in our cub productivity and cub survival models (as the models were overfit). Because our models did not account for repeated sampling of some collared females, our coefficient SEs may have been underestimated.

Management agencies often try to reduce human–black bear conflicts around residential development by increasing harvest, under the assumption that trends in conflicts reflect trends in black bear populations (Obbard et al. 2014). Our work suggests that conflicts are related to variation in natural food conditions, and the propensity of bears to seek out subsidies around human development, not population size. Indeed, changing climate conditions are expected to reduce the duration bears hibernate (Johnson et al. 2018b) and increase the potential for natural food shortages (Laufenberg et al. 2018), factors which are both likely to increase bear use of human development and thus human–bear conflicts. Management agencies that respond by increasing harvest near residential development could exacerbate bear population declines while having limited success in reducing conflicts. Instead, wildlife agencies may be more effective at reducing conflicts by implementing strategies that discourage bears from foraging around residential development, effectively reducing the attractiveness of developed habitat (Robertson et al. 2013). In that vein, Johnson et al. (2018a) deployed bear-resistant trash containers in different parts of Durango. Compared to control areas, they found that conflicts were lower in areas that had been given bear-resistant containers, presumably because bear use of these areas had decreased along with the forage benefits (Baruch-Mordo et al. 2013). Regardless of the specific management strategies employed, our results

highlight the importance of monitoring black bear demographic rates to correctly ascribe population trends, particularly as shifts in bear behavior are likely to drive increases in conflicts and the perception of growing bear populations.

The influence of residential development on black bear demography has significant implications for the coexistence of people and bears. As residential development expands, black bears appear to be increasing their reliance on anthropogenic foods (Kirby et al. 2016), unable to perceive the net consequences of this behavior. Indeed, human food subsidies provide bears with significant fitness benefits (increased body fat and reproductive success) *if* they survive. We suspect that the mixed effects of residential development on black bear fitness traits curtail the ability for bears to successfully adapt to this novel environment, particularly when they are more likely to gain annual reproductive benefits than experience death (Lamb et al. 2017). Given that wilderness areas are declining worldwide, researchers have encouraged human–carnivore coexistence on shared landscapes (Chapron et al. 2014), often focusing on the social factors that may be limiting (i.e., human tolerance, governance; Carter and Linnell 2016, López-Bao et al. 2017). Our results, however, add to a growing body of evidence that suggests that areas where carnivores are tolerated may still serve as population sinks due to human-caused mortality (e.g., vehicle collisions, conflict removals). As such, we encourage investigators to carefully consider coexistence in terms of carnivore demographic viability, encouraging coexistence where carnivore populations are intrinsically sustainable (i.e., without immigration) and identifying strategies to bolster population viability where they are not.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3098/full>