2018

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Abstract: Selection of den sites is a crucial aspect of American black bear (*Ursus americanus*) life history. High-quality dens provide thermal insulation, protection from disturbance, suitable environment for parturition and cub development, and proximity to available forage upon emergence. Black bears are increasingly coexisting with people in human-dominated landscapes; however, little is known about whether urban environments influence characteristics of dens and den site selection. Our objective was to determine the effect of housing density (a proxy for human activity and availability of anthropogenic resources) on selection of den sites in years of good and poor natural forage. We additionally compared size, shape, and location of dens of males and females to describe den characteristics and explore whether differences existed between males and females. We revisited 34 den locations detected during a 6-year (2005–2010) urban black bear study in Aspen, Colorado, USA, and measured den entrance and den volume. We fit a conditional logistic regression model using a resource selection function framework to determine the importance of housing density and other landscape variables (elevation, slope, aspect, and vegetation type) associated with den site selection. Slope was the best predictor of den site selection and there was no relationship between den selection and housing density, indicating that black bears were neither avoiding nor seeking urban areas for denning. Dens were smaller for females ($\bar{x} = 3.30$ m^3, SE = 1.94, $n = 22$) than for males ($\bar{x} = 7.56$ m^3, SE = 3.31, $n = 8$), supporting the idea that females have greater constraints in den characteristics, possibly related to cub development and security from predation or because females generally are smaller than males.

Key words: black bear, Colorado, denning, den site selection, human–wildlife interaction, logistic regression, resource selection, *Ursus americanus*

DOI: 10.2192/URSUS-D-17-00004.2 ***Ursus 29(1):25–31 (2018)***

A growing management issue for bear biologists is understanding how human-dominated landscapes and urbanization affect bear (*Ursus* spp.) behavior, ecology, and human–bear conflict (Bateman and Fleming 2012, Chapron et al. 2014, Elfström et al. 2014). For American black bears (*U. americanus;* hereafter, "bears"), recent studies have demonstrated that anthropogenic food associated with urban areas can alter bear morphology, home ranges, diurnal activity of individuals, densities, sex ratios and reproduction (Beckmann and Berger 2003, Baruch-Mordo et al. 2014), and the intensity of human–bear conflict (Merkle et al. 2011). Furthermore, growing evidence suggests that selection of human-developed areas is dynamic and a function of natural food production, with bears selecting urban areas to a greater extent in years of poor natural food production (Baruch-Mordo et al. 2014, Johnson et al. 2015). However, although a fair amount of work has focused on various aspects of urban development on bear ecology and behavior, little is known about the influence of urban development and natural food production patterns on bear denning behavior.

Hibernation is an essential part of bear ecology triggered by a decrease in available forage during winter and resulting in radical changes in bear behavior and

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metabolism (Hellgren 1998). The selection of a den site is an important decision for bear life history because dens provide shelter from harsh climatic factors and security from predators (Davis et al. 2011, Libal et al. 2011). Previous den studies have focused on denning chronology (Beecham et al. 1983, Smith et al. 1992, Beckmann and Berger 2003, Manchi and Swenson 2005), micro-scale habitat qualities (Pelton et al. 1977, McLoughlin et al. 2002, Baldwin and Bender 2008), and landscape-level patterns of den site selection (Gaines 2003, Ciarniello et al. 2005, Reynolds-Hogland et al. 2007, Elfström et al. 2008, Waller et al. 2013, Pigeon et al. 2016). Of the latter studies, distance to roads (most common) and road density were included as explanatory variables related to human disturbance. However, none of these studies focused on understanding the degree of human development near den sites, nor did they explore variations of selection trends with natural food production.

Bears may den in urban areas because of the availability of anthropogenic resources, but may also avoid them because of increased human activity. Developed areas can offer numerous denning structures and an increase in concentrated food sources upon den emergence. However, human activity can disturb denning bears, causing den abandonment and cub mortality (Linnell et al. 2000). Accordingly, several studies found that bear den sites occur at greater distances from roads (e.g., Gaines 2003, Ciarniello et al. 2005, Elfström et al. 2008, Waller et al. 2013) and other human structures (Sahlén et al. 2015). Effects of human activity on den site selection might be further altered by shortages in natural food production. It is possible that in years of poor natural food production, when bears use human development to a greater extent during hyperphagia, they will be more likely by chance alone to den near these areas where their most recent foraging activity was concentrated; it is also possible that bears become habituated and may choose dens in or near urban areas in subsequent years.

In this study, we explored whether urban development influenced selection of den sites in years of poor and good natural food production. Our primary objective was to determine whether human development influenced the selection of black bear den sites. We note that we did not aim to differentiate bears as urban or not in a binary manner because utilization of the urban environment is a continuous and dynamic variable. Additionally, a bear that crossed an arbitrary town boundary did not always equate to an urban bear that utilized anthropogenic resources. We therefore modeled den use as a function of housing density, a continuous index of human activity and the availability of anthropogenic attractants to bears that is free of the subjective choices of defining the city center or limits of Aspen, Colorado, USA. We additionally modeled environmental factors (elevation, slope, aspect, and vegetation cover) that have been identified as important predictors of den site selection (Beecham et al. 1983, McLoughlin et al. 2002, Reynolds-Hogland et al. 2007, Baldwin and Bender 2008). We used conditional logistic regression that precluded exploration of bear- and year-specific indicator variables; therefore, we summarized mean human housing density by gender and food production year (good or poor) to additionally explore differences in den site selection among these variables.

Finally, we explored differences in 2 den characteristics—entrance area and den volume—between males and females. Differences in the size of dens used by each gender is expected because of discrepancies in size (i.e., females tend to be smaller than males) and vulnerability to predators (i.e., females with young have more motivation to den in smaller, less conspicuous dens; Pelton et al. 1977, Beecham et al. 1983). For these reasons, we expect females in general to use smaller dens on average than are used by males.

Methods

Study area

Our study occurred in and around Aspen, Colorado, from 2005 to 2010, during which time the human population was approximately 6,500–7,000 (Colorado State Demography Office 2014). Across the study area, elevation ranges from 2,000 to 4,250 m. Maroon, Castle, and Hunter creeks join the Roaring Fork River near Aspen, creating extensive riparian areas in these lower elevations. At mid-elevations there is a change in vegetation cover due to aspect. On north-facing slopes, the vegetation is predominantly aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) forest communities. South-facing slopes are covered in mountain-shrub communities consisting of Gambel oak (*Quercus gambelii*), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus virginiana*). Higher elevation vegetation-community types include spruce–fir forests (*Picea engelmannii–Abies lasiocarpa*), alpine meadows, and talus slopes.

Den site selection

We used conditional logistic regression to model den site selection by comparing used den sites with potentially available den sites in a resource selection function approach (Manly et al. 2002). Available den sites were drawn at random from a 99.5% minimum convex polygon

Table 1. Candidate model coefficient estimates (±1 SE) and fit statistics (AIC_c [small sample-size correction of Akaike's Information Criterion], ΔAIC_c [difference relative to the top model], w_i [model wt], and K [no. of parameters estimated]) for modeling American black bear den-site selection (2005–2010) in the urban environment of Aspen (Colorado, USA) using conditional logistic regression. Forest refers to the categorical variable with 2 levels: forested and non-forested. North and East are the 2 continuous variables that measure aspect (see Methods).

Model variables (coeff., ±1 SE)	AIC_c	ΔAIC_c	w_i	K
Slope (0.0615, ±0.0149)	537.9	0.0	0.72	1
Slope (0.0618, ±0.0150) + √Housing Density (0.0119, ±0.0499)	539.9	1.9	0.27	2
Forest (1.238, ±0.550)	548.1	10.2	<0.01	1
Forest (1.322, ±0.575) + √Housing Density (0.0258, ±0.0491)	549.8	11.9	<0.01	2
√Housing Density (−0.0172, ±0.0472)	554.5	16.6	<0.01	1
Elevation (−0.000204, ±0.000659)	554.5	16.6	<0.01	1
Elevation (−0.000469, ±0.000783) + √Housing Density (−0.0347, ±0.0562)	556.1	18.2	<0.01	2
North (0.0394, ±0.276) + East (0.101, ±0.262)	556.4	18.5	<0.01	2
North (0.0447, ±0.276) + East (0.0998, ±0.261) + √Housing Density (−0.0173, ±0.0471)	558.3	20.4	<0.01	3

(MCP) home range that we calculated using package adehabitatHR (Calenge and Fortmann-Roe 2014) in Program R version 3.0.1 (R Development Core Team 2009). We calculated home ranges based on an individual bear's location data for the year leading up to the denning season; for example, to sample availability of sites for a den used by an individual during the 2009–2010 denning season, we created a 99.5% MCP home range from Global Positioning System (GPS) locations collected between den emergence in spring and den entry in autumn of 2009. Of the 39 dens observed in the Aspen study, 30 dens for 22 unique bears had sufficient GPS location data for generating MCP home ranges needed for an availability sample.

We sampled 10,000 random points from each MCP to represent the available den locations based on recommendations in Northrup et al. (2013). For each used (den site) and available (random) point we extracted values for 5 covariates: elevation, slope, aspect, vegetation class, and housing density. We used U.S. Geological Survey (USGS) Digital Elevation Models to derive elevation (m), slope (in degrees), and aspect (in degrees) values. We could not use aspect on the original scale because small values (1°) and large values (360°) both correspond to north. We thus treated aspect as a circular variable and used cosine and sine transformations (Jammalamadaka and Sengupta 2001) where north and south directions were represented by a cosine of 1 and −1, respectively, and similarly, east and west were represented by the sine. Our sample size of den locations was small, so we limited vegetation classes to forested versus non-forested and categorized vegetation classes obtained from USGS LANDFIRE database into these categories (LANDFIRE 2014). The forested class included both coniferous- and aspen-dominated vegetation types and the non-forested class contained all other vegetation classes. We calculated housing density as the mean density of points per km^2 within a circular radius of 1 km for each 30-m pixel as detailed in Johnson et al. (2015). We used a square-root transformation of housing density for our models because the original variable was positively skewed.

We had a small sample size, so our analysis strategy was to include only 1 or 2 covariates in our models. We began by evaluating each of the 4 environmental factors separately, then tested the impact of human development by adding housing density to each of the 4 environmental models. We also included a model with just housing density. We ran our 9 candidate models (Table 1) and compared them using Akaike's Information Criterion (AIC) corrected for small sample size (AIC_c) and model weights (w_i; Burnham and Anderson 2003). We checked for correlation between the continuous environmental variables and housing density and none of the correlations were >0.58. We performed all modeling using conditional logistic regression (function clogit) in the survival package in Program R (Therneau and Lumley 2014), where we conditioned on den identification number to compare the used and available locations for the specific bear and year.

During years of poor natural forage, bears showed much greater use of the city of Aspen, especially during the hyperphagia season (Baruch-Mordo et al. 2014); thus, their use of town during years of poor natural forage possibly influenced where they selected dens. Selection of den sites also possibly varied between males and females. However, the use of conditional logistic regression does not allow incorporation of indicator variables such as gender and food year. The likelihood is maximized conditional on the den identification number, which only has one value for gender and forage year, making it impossible to estimate a gender or forage-year covariate effect. On account of small sample sizes, we conducted basic exploratory comparisons of the values of housing density for males and females in poor and good forage years. Details of how we defined good and poor forage years can be found in Baruch-Mordo et al. (2014).

Den characteristics

We attempted to measure den characteristics of all the recorded dens between the years 2010 and 2011, but because of accessibility limitations (e.g., one den under a house was boarded up) we were unable to obtain measurements on all dens. We measured physical dimensions of the entrance and interior to estimate entrance area and den volume. For all but 2 dens, we used an ellipse shape to estimate the size of the den entrance (m^2) and den volume (m^3). We chose an ellipse shape over a rectangle because an elliptic shape conservatively estimated the area and volume as a result of the natural, rounded shape of the den. For the 2 remaining dens, an ellipse was inappropriate; we used a semicircle for a den under a footbridge and a triangle for a den formed from slabs of rocks. For dens with ≥2 possible entrances, we considered only the main entrance identified as providing the most obvious and easiest access. The data for den entrance and volume were not normally distributed; therefore, we used a Wilcoxon rank-sum test for our hypotheses that entrance area and den volume were smaller for females than males. We also provide a similar comparison between females with and without offspring (i.e., cubs of the year or yearlings) at time of denning.

Results

Den site selection

The top model indicated slope was the primary environmental covariate predicting the probability of den site selection (Table 1). We found a positive relationship between the probability of use and the estimated slope parameter (0.0615 ± 0.0149 SE; Table 1, Model 1), with the estimated odds of a site being used increasing by 6.15% for each 1° increase in slope. The second-ranked model with slope and housing density showed some support and was the only model within 2 ΔAIC_c of the top model. The slope parameter estimate was positive and similar to the top model, and the housing density parameter estimate was also positive (0.0119), but the 95% confidence interval overlapped zero (−0.086, 0.110). All models that included housing density had 95% confidence intervals that overlapped zero, providing little evidence that housing density influenced den site selection (Table 1). The summary statistics and boxplot suggest that male bears in good forage years had den sites characterized by higher density of housing, as well as more variability in housing density (Table 2).

Table 2. The mean housing density for sites selected as dens by American black bears (male and female) during years of good and poor natural-food production (2005–2010) in Aspen, Colorado, USA.

			Housing density m^2	
Forage year	Gender	*N*	Mean	SD
Good	Female	12	11.0	14.5
Poor	Female	9	16.9	24.8
Good	Male	4	114.6	140.3
Poor	Male	5	10.0	12.2

Den characteristics

We obtained den entrance measurements for 31 dens (23 from females and 8 from males) and den volume for 30 dens (22 from females and 8 from males). Den entrances for females were smaller ($\bar{x} = 0.39$ m^2, SE = 0.059, $n = 23$) than for males ($\bar{x} = 0.46$ m^2, SE = 0.064, $n = 8$; Wilcoxon rank sum test: $W = 131$, $P = 0.04$). The overall mean den volume was 4.43 m^3 (SE = 1.68, $n = 30$) with the smallest den measuring 0.06 m^3 and the largest measuring 43.76 m^3. The den volume for females ($\bar{x} = 3.30$ m^3, SE = 1.94, $n = 22$) was smaller than for males ($\bar{x} = 7.56$ m^3, SE = 3.31, $n = 8$; Wilcoxon rank sum test: $W = 126$, $P = 0.04$).

Discussion

We found no evidence for American black bears avoiding or seeking areas with higher housing density, indicating that either bears did not base denning decisions on the amount of human development or that housing density as measured was an inadequate variable for capturing how black bears respond to urban development. Other studies examining the effects of human land use on den site selection have shown mixed results. Goodrich and Berger (1994) suggested denning black bears in Nevada, USA, avoided areas affected by winter recreation; and similarly, several authors suggested that black and brown bears avoided denning near roads (e.g., Gaines 2003, Ciarniello et al. 2005, Elfström et al. 2008, Waller et al. 2013). However, black bear den-site selection appeared unaltered by human development of oil sands in Alberta, Canada (Tietje and Ruff 1983); and, after summarizing the denning literature, Linnell et al. (2000) hypothesized that bears readily den closer to areas with predictable levels of human use. An important factor in our study that was difficult to quantify was the unpredictable nature of human activity in our study area. Many residences in Aspen were used as vacation properties, which were commonly unoccupied for long periods of time. Thus, instead of the density of houses or other indices of proximity to human development (e.g., distance to roads), bears in Aspen may pay attention to human presence or absence and levels of activity, which we were unable to assess. Future research should attempt to quantify variables of the urban environment that influence bear use, positively or negatively. Ideally, multiple variables would be measured and analyzed for their individual and combined effects, and the effect may change year to year depending on the availability of natural and anthropogenic food resources (Baruch-Mordo et al. 2014).

Consistent with other studies (McLoughlin et al. 2002, Ciarniello et al. 2005, Reynolds-Hogland et al. 2007, Baldwin and Bender 2008), slope steepness was important in predicting where bears den in Aspen, with most dens occurring on slopes between 20° and 30°. Advantages of denning with steep slope relate to thermoregulation and safety from disturbance. For example, dens on steep slopes may be drier with better drained soils that lessen individual heat loss compared with wetter dens (Pelton et al. 1977). Furthermore, Alt (1984) showed that flooding can cause cub mortality, which can be avoided by denning in steep areas. Many studies also reported that black bears den primarily in forested habitat types (Hamilton and Marchinton 1980, Beecham et al. 1983, Hayes and Pelton 1994, Baldwin and Bender 2008), perhaps because of the increased shading and drifting of snow in forests (Baldwin and Bender 2008). In our study, forested landscapes did not explain site use as well as slope, and our vegetation cover classes—forested and non-forested—were possibly too broad to detect preference for a certain forest type.

Several authors demonstrated that during years of poor natural forage production black bears showed much greater use of the urban environment, but also that this behavior was reversible in that black bears would forage away from towns during years of good natural forage (Baruch-Mordo et al. 2014, Johnson et al. 2015, Lewis et al. 2015). The authors concluded that black bear use of the urban environments was dynamic and dependent on the availability of natural and anthropogenic food sources, and further modeling suggested that bears would likely avoid urban areas if reasonable efforts to reduce anthropogenic food were employed (Baruch-Mordo et al. 2013). Our denning results support this conclusion in that even when bears had spent significant time in Aspen foraging during years of poor natural forage, most bears left town and selected den sites based on environmental variables not associated with the urban environment.

Regarding den characteristics, our results supported previous findings that female black bears are able to use smaller dens than those used by males (Pelton et al. 1977, Beecham et al. 1983, Smith et al. 1992). The smaller size of females make them more vulnerable to predation from male bears and other predators; for example, a female with cubs will avoid adult males to reduce the risk of infanticide (Libal et al. 2011). Smaller den entrances are potentially less conspicuous and thus could be advantageous to females in avoiding interactions with males, and they also might be easier to defend. Alternatively, Pelton et al. (1977) claimed that the larger size of males does not allow them to use smaller dens, and similarly smaller dens may simply be a result of the female's smaller size (Beck 1991).

Our study had several limitations. The models we used assumed random chance of site selection and independent movement in the environment. Independent movement suggests past locations do not influence future locations, but black bear movement does not necessarily meet this assumption. Furthermore, availability as defined by the minimum convex polygon may not reflect the prior spatial knowledge the bear has obtained over its lifetime. A more flexible model incorporating yearly dependencies may provide better insights of trend in the den site selection. Although we had repeated measures on 6 bears, our sample size was too small to statistically examine whether selection at year t was dependent on selection variables in year $(t - 1)$. We encourage future studies with larger sample sizes to explore such selection dependency.

With these caveats in mind, our denning results support the conclusion in that even when bears had spent time in Aspen foraging during years of poor natural forage, most left town and selected den sites based on environmental variables not associated with human development. For a manager, our study underscores the need for continued long-term monitoring of individual bears to better understand the complex relationships between human development and bear ecology, so we can better predict and manage black bear behavior near urban areas.

Acknowledgments

This study was funded by U.S. Department of Agriculture-National Wildlife Research Center and Colorado Parks and Wildlife. We thank L. McNally, who assisted with measuring den characteristics; J. Northrup and M. Hooten, who assisted with data analysis; H. Johnson for providing the housing density for Aspen; and the following entities who assisted with the larger study: Pitkin County, Aspen Ranger district of the U.S. Forest Service, Aspen Field Biology Lab, and Aspen Center for Environmental Studies. We also thank the reviewers and Associate Editor for helpful comments on the manuscript.

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Received: March 25, 2017
Accepted: May 9, 2018
Associate Editor: Waller