THESIS

INFLUENCE OF URBAN ENVIRONMENTS ON BLACK BEAR POPULATIONS AND FORAGING BEHAVIOUR

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ABSTRACT

INFLUENCE OF URBAN ENVIRONMENTS ON BLACK BEAR POPULATIONS AND FORAGING BEHAVIOUR

For most large carnivores, the impact of human development on their population is poorly understood. American black bears (*Ursus americanus*) use urban environments to forage, often resulting in negative human-bear interactions and management removal of conflict bears. There is a general consensus that available human food sources are the underlying cause of human-bear conflict, but the subtle patterns of how bears use urban resources and the impact that using these resources has on the population is poorly understood. My research focused on understanding how available human foods and management actions in urban environments influence black bear foraging behavior and populations.

The National Wildlife Research Center, Colorado Parks and Wildlife and Colorado State University collaborated on a six year urban bear study in Aspen, Colorado. The overall goal of the study and the objectives of my research were to better understand how bears use urban food resources and the influence that these resources have on their population, so that better management practices can be developed. In Chapter 1, I focus on the impacts that natural food failure, available human food, and management removal of conflict bears has on a population. Chapter 2 describes general foraging patterns and models resource use in the urban environment at a fine spatial scale. A brief chapter summary, findings, and management implications are given below.

In Chapter 1, we developed a stochastic projection matrix model parametrized with data from the literature and the 6 years of study (2005-2011) in Aspen, Colorado to evaluate the positive and negative influences of urban environments on bears. We modeled the influence that failure of natural food sources, available human food, and different levels of conflict-bear removals could have on a bear population by comparing a scenario where

bears do not benefit from human food sources or experience conflict-bear removals with two urban scenarios where bears have access to human foods, but conflict bears are removed. Perturbation analyses were used to evaluate consequences that changes to population vital rates could have. We found that the benefit of increased cub production after natural food failure years from available human food sources was quickly negated if conflict-bear management removals reduced adult female survival. Increasing the frequency of natural food production failure years resulted in greater impacts from available urban food and conflict-bear removals. Our findings suggest that managers may need to utilize non-lethal practices in managing conflict bears and municipalities will need to secure human food sources to avoid management removals and population declines.

In Chapter 2, we used GPS radio-telemetry data and information obtained from visiting bear foraging locations in Aspen, Colorado from 2007-2010 to determine the food resource bears were using and what factors influenced anthropogenic foraging events. We used a resource selection study design to evaluate fine-scale foraging behavior during periods of prehyperphagia and hyperphagia. Overwhelmingly garbage was the main resource bears used and modeling efforts determined that selection of foraging sites was not only influenced by the presence of garbage but also by the proximity to riparian habitat and presence of ripe fruit trees. We documented inter- and intra-annual foraging patterns of bears foraging extensively in urban areas when natural food sources were not available and a switch back to natural food sources when they became available. These patterns suggest that bears balance an energy budget and individual safety when making foraging decision. We suggest management action focus on reducing available human foods to make the urban environment less energetically beneficial for foraging than natural habitat. Management efforts should be prioritized and focus on securing garbage and replacing anthropogenic fruit trees with non-fruiting varieties especially near riparian habitat.

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DEDICATION

To the bears

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CHAPTER 1. Population Management of Black Bears in Variable Natural Environments
1.1 Introduction

For most wildlife, natural food sources vary over time and space, thereby directly impacting the behavior, population dynamics, and ecology of animals. In ecosystems where wildlife coexist with people, natural food shortages can lead to increased use of anthropogenic food sources (e.g., livestock and garbage) that can positively impact the demographics (e.g., survival and reproduction) of animals utilizing these resources (Fedriani et al., 2001; Webb et al., 2004). In other cases, lack of tolerance to wildlife conflict by humans and subsequent wildlife removal can lead to negative demographic impacts and population decline (Linnell et al., 2001; Mech, 1995). Thus, knowing how a wildlife population responds to availability of anthropogenic food requires understanding of natural food production variability, the intensity of management of conflict wildlife, and the resulting demographic response. The complexity of this issue is global, and particularly relevant to the management and conservation of large carnivores as more large carnivores are forced to exist in human dominated systems. However, studying the impacts that humans have on large carnivores is challenging, because of the long life spans of many carnivores and the corresponding expense and challenge of monitoring them.

Population models can provide insight about population responses under complex environmental scenarios (Conner et al., 2008; Heppell et al., 2000). In particular, perturbation analyses can be used to predict how changes in population vital rates, e.g., survival and reproduction, influence population growth or abundance (Caswell, 2001). Furthermore, new demographic tools can be used to evaluate scenarios where stochastic environments are modeled, allowing for a more realistic evaluation of how changing management actions impact a population. Our goal was to utilize these new demographic tools to explore how variation in natural food sources, availability of anthropogenic resources, and management of human-wildlife conflicts can impact a carnivore population.

We used black bears ($Ursus\ americanus$) as a model species for this exercise because they are well studied across their range (see Beston (2011) for summary of population studies), will readily take advantage of anthropogenic resources, and wildlife managers are challenged with trends of increasing human-bear conflict rates and maintaining productive bear populations (Hristienko and McDonald, 2007). Bear populations that use urban food sources potentially have vital rates that differ in comparison to populations relying solely on natural food sources that vary seasonally and annually (Beckmann and Lackey, 2008; Elowe and Dodge, 1989; Inman and Pelton, 2002; Rogers et al., 1976). For example, natural food production can fail from environmental factors, e.g., spring freeze, drought, disease, insect infestation (Kasbohm et al., 1995; Neilson and Wullstein, 1980; Pierre, 1989; Sharp and Sprague, 1967; Tomback and Achuff, 2010). During these food failure years adult survival is thought to remain high (Kasbohm et al., 1996; Noyce and Garshelis, 1994; Schrage and Vaughan, 1995), but cub production declines (Beck, 1991; Beckmann and Lackey, 2008; Bridges et al., 2011; Elowe and Dodge, 1989; Rogers et al., 1976). But bears near urban environments can supplement their diets to include available urban food, eliminating seasonal and annual variation in food resources that may artificially boost cub production (Beckmann and Lackey, 2008). While urban food sources can provide the benefit of stable cub production, wildlife managers often remove or destroy bears using the urban environment to prevent property damage and for human safety. For example, Aspen, Colorado (USA), experienced two natural food failure years during a 6-year study from 2005-2011 (Baruch-Mordo, 2012). During these poor natural food years, annual mortalities of adult females increased 2-3 times, with the majority of mortalities being attributed to removal of conflict bears. Unlike non-urban studies that observed declines in reproduction after food failure years (Beck, 1991; Bridges et al., 2011; Elowe and Dodge, 1989; Jonkel and Cowan, 1971; Rogers et al., 1976), the Aspen population exhibited normal cub production.

We developed a population projection matrix model that included survival and reproduction as a function of variations in natural food production, use of urban food resources, and conflict-bear management. We parametrized our models using demographic data from a 6-year study of urban bears (Aspen study), supplemented with vital rates from a meta-analysis of Western black bear populations (Beston, 2011). We developed a baseline scenario where the bear population did not have access to urban food sources or experience management removal of conflict bears and compared this with two management scenarios where bears utilized human foods and managers removed conflict bears. We evaluated the impact that different frequencies of natural food failure years could have by calculating growth rates over a range of different natural food failure year frequencies. We quantify the potential impact that vital rate changes could have on the stochastic growth rate using prospective perturbation analyses to calculate vital rate elasticity values. Additionally we use elasticity values in conjunction with changes to vital rates between scenarios to assess overall cost and benefit of each management scenario and to show the impact each vital rate change had on the population growth rate. We then used additional computer simulations to assess how much each vital rate was contributing to variation in the growth rate over 50-year projections. Our modeling effort is unique because we model changing environment conditions, allowing a more realistic understanding of the influence that changes in vital rates will have when management actions respond to changing environment conditions.

1.2 Methods

1.2.1 Study Area

We used data from a bear study (2005-2011) in and around the cities of Aspen and Snowmass, Colorado, (USA) within Pitkin County (combined human population size of approximately 17,100) to develop the bear population model parameters (Fig. 1.1). Aspen and Snowmass are surrounded by a variety of important natural foods for bears including oak brush (Quercus gambelli), service berry (Amelanchier alnifolia), chokecherry (Prunus virginiana) and other fruiting and masting species. Annual variation in natural food

production can directly affect bear behavior, in particular whether bears come into town to forage for anthropogenic foods (Baruch-Mordo et al., 2013). Bears are a game species in Colorado and are managed by Colorado Parks and Wildlife (CPW). Managers responded to human-bear conflicts with a two-strike policy, where upon first capture (1st strike) bears deemed to pose a low threat to human safety were ear tagged and translocated, and if recaptured (2nd strike) were euthanized (administrative directive W-2, CPW).

1.2.2 Population Model

We used a projection matrix to model the female portion of the bear population through time using

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t), \tag{1.1}$$

where $\mathbf{n}(t)$ is a vector of stage densities at time t and \mathbf{A}_t is a 4×4 stochastic projection matrix that varies at each time step giving stage densities in the next year, n(t+1). We assumed the following: a post-birth census in late March, litter sex ratio of 0.5, male densities do not affect breeding success, and equal immigration and emigration rates. We used a projection matrix similar in structure to those used for other bear populations (Freedman et al., 2003; Hunter et al., 2010), where the adult stage classes are distinguished by the developmental state of offspring still under maternal care. We separated females into 4 distinct life stages: cubs (age 0-1), subadults (not mature enough to breed), adults available to breed (i.e., adult females that did not successfully produce a litter at the previous census, produced and lost the entire litter from the previous census soon enough to breed again during the summer, and females that separate from yearlings to breed after

the previous census), and adults with yearlings (see Table 1.1 for parameter descriptions and Fig. 1.2 for a life cycle diagram). The projection matrix had the form

$$\mathbf{A}_{t} = \begin{bmatrix} 0 & 0 & s_{a}\tau_{ar}L & 0 \\ s_{c} & s_{s}(1-\tau_{sa}) & 0 & 0 \\ 0 & s_{s}\tau_{sa} & s_{a}(1-\tau_{ar}) & s_{r} \\ 0 & 0 & s_{a}\tau_{ar} & 0 \end{bmatrix},$$
(1.2)

(see Table 1.1 for definitions). This model structure allowed the following life history traits: ~16 months maternal investment in offspring leading to a 2-year litter production cycle (Lee and Vaughan, 2004), age of primiparity ranging from 3-7 years (Beston, 2011), and litter production in consecutive years is possible when females breed after loss of an entire litter (Barber and Lindzey, 1986).

We developed a sequence of stochastic matrices in two steps. First, we define ρ as the frequency of good natural food years and generate an independent identically distributed (iid) environmental sequences of good and poor natural food years, i.e., previous years do not influence natural food production in future years, using random draws from a binomial distribution with the success rate set to ρ . Second, we used vital rate estimates from Aspen (Baruch-Mordo, 2012) in conjunction with mean and 95% credible intervals for Western bear populations determined by Beston (2011) as a reference for selecting vital rate means and standard deviations for good and poor natural food years in each scenario (scenarios developed in section 1.2.3). We used these vital rate means and standard deviations to calculate parameters for beta and gamma distributions (see Appendix: 1.A for calculations of beta and gamma distribution shape parameters) associated with each management scenarios. We used random draws from beta distributions to generate stochastic survival rates and stage transition probabilities (White, 2000) and random draws from a gamma distribution for the average number of female cubs

per litter. All computations where performed using program R (R version 2.12.2, www.r-project.org, accessed 25 February 2011).

1.2.3 Scenario Development

We evaluated the influence that frequency of poor natural food production years, available human food sources, and conflict-bear management in urban environments could have on a bear population under 3 scenarios. We created a baseline scenario to represent a population free from the influence of urban food sources and conflict-bear management, which provided a starting point for developing both urban scenarios. We used meta-analysis results from Beston (2011) to set good and poor natural food year survival and transition rates of the baseline scenario. For survival rates we set good and poor year means at respectively higher and lower values than the meta-analysis means calculated for Western black bears (Beston, 2011), allowing overall survival rates to be near the values calculated from the meta-analysis. We assumed that poor natural food production more negatively influenced younger stage class survival rates than adult survival (Eiler et al., 1989; Schrage and Vaughan, 1995; Noyce and Garshelis, 1994; Kasbohm et al., 1996) and modeled this as larger good and poor year deviations from the average survival rates of cubs and subadults than for adults. During good natural food years transition from subadult to breeding adult was assumed to occur on average at age 4 such that bears typically would give birth to their first litter at age 5 (Baruch-Mordo, 2012; Beston, 2011). Literature on the influence that low food availability has on subadults transitioning to adults was sparse (Eiler et al., 1989), but we assumed a decrease. We also assumed a decrease in the transition rate of breeding adults to adult with cub(s) during poor natural food years as litter production depends on body condition (Noyce and Garshelis, 1994) and has been observed to decrease when natural foods are not available (Beck, 1991; Bridges et al., 2011; Rogers et al., 1976).

We developed two urban scenarios where vital rates were changed to reflect the influence of urban food resources and conflict-bear removal. For both urban scenarios (Low and High Removal), we assumed that available anthropogenic food sources resulted in

normal cub production during poor natural food years (Baruch-Mordo, 2012; Beckmann and Lackey, 2008). During the Aspen Study all adult females consistently gave birth on a two year cycle and the number of cubs/litter remained steady regardless of good or poor natural food availability, i.e., $\tau_{ar} = 1$ and 2.21 cubs/litter (Baruch-Mordo, 2012). Because fewer than 10 adult females were monitored annually, we conservatively set $\tau_{ar}=0.95$ and L=1.15 female cubs/litter for good and poor natural food years. For the Low Removal Scenario vital rates during good years essentially mimicked the Baseline Scenario except for higher transition probabilities and cub production. During poor natural food years cub and sub-adult survival increased along with the transition probabilities and cub production, but adult survival dropped. For the High Removal scenario good forage years vital rates were the same as the Low Removal scenario. During poor forage years we we reduced cub and subadult survival rates to be less than and equal to survival for the Baseline scenario and based adult survival rates on empirical estimates from the Aspen Study (Baruch-Mordo, 2012) (see Table 1.2 for a comparison of scenario vital rates). We set standard deviation for good and poor natural food year vital rate distributions as follows: cub and subadult survival ($\sigma = 0.05$), adults with and without cubs survival ($\sigma = 0.025$), transition probabilities ($\sigma = 0.02$), and number of female cubs/litter ($\sigma = 0.10$).

1.2.4 Stochastic Long-term Projections

We used the stochastic projection matrix model framework developed by Tuljapurkar (1990) and analysis methods derived in Caswell (2005) to calculate stochastic growth rates and elasticities. The stochastic growth rate is defined as

$$\log(\lambda_s) = \lim_{t \to \infty} \frac{1}{t} \log ||\mathbf{A}_{t-1} \cdot \cdot \cdot \mathbf{A}_0 \mathbf{n}_0||, \tag{1.3}$$

which can be approximated with

$$\log(\lambda_s) \approx \frac{1}{T} \sum_{t=1}^{T} \log(\mathbf{R}_t), \tag{1.4}$$

when T, the number of time steps is large (T = 100,000). The annual population growth between time step t and t + 1 is $\mathbf{R}_t = \frac{\mathbf{A_t n}(t)}{||\mathbf{n}(t)||}$ (Caswell, 2001), $||\cdots||$ is a sum of the vector elements. We calculated elasticity of $\log(\lambda_s)$ for good and poor year vital rates by forward projecting a stage vector $\mathbf{n}(t)$ setting $||\mathbf{n}(0)|| = 1$, and back projecting a reproductive value vector $\mathbf{v}(t)$ setting $||\mathbf{v}(T)|| = 1$ (Caswell, 2005). Elasticities were calculated using

$$\frac{\partial \log(\lambda_s)}{\partial \log \theta_i} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T-1} \frac{J_i \theta_i(t) \mathbf{v}^{\mathsf{T}}(t+1) \frac{\partial \mathbf{A_t}}{\partial \theta_i(t)} \mathbf{n}(t)}{\mathbf{R_t} \mathbf{v}^{\mathsf{T}}(t+1) \mathbf{n}(t+1)},\tag{1.5}$$

where J_i is 0 or 1 depending on which year-type elasticities are being calculated, $\theta_i(t)$ is a vector of vital rates, and $\frac{\partial \mathbf{A}_t}{\partial \theta_i(t)}$ is a differentiation of the projection matrix with respect to the vital rate vector $\theta_i(t)$. We discarded the first 30,000 time steps in the projection sequence and used only the remaining 70,000 time steps for calculating growth rates and elasticity values. For each scenario we determined stochastic growth rates and elasticity of this growth rate to vital rates at six different frequencies of good natural food years $\rho = \{0.45, 0.55, 0.65, 0.75, 0.85, 0.95\}$. We then determined the influence that a set of vital rate changes had on population growth. The increase or decrease in a growth rate due to a different set of vital rates was determined with

$$\triangle log(\lambda_s) = \sum_i e_{\theta_i} \delta_i, \tag{1.6}$$

where e_{θ_i} is the elasticity value of vital rate θ_i and δ_i is a proportional change in the vital rate calculated with

$$\delta_i = \frac{\theta_i' - \theta_i}{\theta_i},\tag{1.7}$$

where θ'_i and θ_i are the new and original vital rate values, respectively (Caswell, 2001). A positive value determined from eq (1.6) can be interpreted as a beneficial set of vital rate changes, i.e., increased growth, while a negative value suggests a decline in growth due to the changes. We calculated the proportional vital rate changes that would be required to

change the Baseline scenario's vital rates to match rates of the Low and High Removal scenarios (see percent change Table 1.2). We evaluated the predicted growth rate determined from the vital rate changes and elasticity values with the growth rate calculated for Low and High Removal scenarios from eq (1.4).

1.2.5 Simulation: 50 Year Projections

Elasticity values do not show how much vital rate variations contribute to variation in growth, so we used simulation to evaluate how variation in vital rates influenced variation in growth for 50-year projections. We used a mark-recapture estimate of 94 individuals from the Aspen study as initial conditions for simulations (P. M. Lukacs, Colorado Parks and Wildlife, personal communication). We started each projection sequence at a stable stage distribution (SSD) with the initial number of individuals separated into the 3 older stage classes. We used the populo package in R (populo version 2.4, http://cran.r-project.org/web/packages/popbio/index.html, accessed 25 February 2011) to calculate the SSD for each scenario determined from the eigen-vector associated with the dominate eigen-value of a projection matrix populated with good year vital rate means. Natural food failures in Aspen are often attributed to late spring freezes, so we used 30 years of minimum daily temperatures during the month of June and assumed temperatures below -2.2° C caused a failure of the main natural food sources (Neilson and Wullstein, 1980; Pierre, 1989). Using this criteria we determined that good years occurred at $\bar{\rho} = 0.75$, so we created a set of 200 iid environmental sequences of good and poor years where the frequency of good years was simulated at $\rho = 0.75$. For each environmental sequence, we ran 100 iterations of a 50-year stochastic projection (Fig. 1.3). We summarized simulated population totals from the 20,000 iterations with the median, 10th percentile, and 90th percentile of population totals at each time step. For each 50-year projection, we determined the standard deviation of annual growth $(\lambda_{\text{sim}} = \frac{N_{t+1}}{N_t})$ over the 50 years and the coefficient of variation of each vital rate. We then used linear regression to determine the relationship between standard deviation of growth $(\sigma_{\lambda_{sim}})$ to vital rate coefficient of variation. The regression took the form

$$\sigma_{\lambda_{sim}} \sim \beta_0 + \beta_1 \text{cv} s_c + \beta_2 \text{cv} s_s + \beta_3 \text{cv} s_a + \beta_4 \text{cv} s_r + \beta_5 \text{cv} \tau_{sa} + \beta_6 \text{cv} \tau_{ar} + \beta_7 \text{cv} L.$$
 (1.8)

1.3 Results

1.3.1 Stochastic Long-term Projections

The stochastic growth rate $\log(\lambda_s)$ in the High Removal scenario was 1.5 times more sensitive to the frequency of good natural food years (ρ) than in the Baseline scenario and 1.9 times more sensitive than in the Low Removal scenario as indicated by the steeper slope for High Removal scenario (Fig. 1.4). For all values of ρ considered, the Low Removal scenario with increased cub production and survival of the 2 younger stage classes had higher growth rates than the Baseline scenario even with 6% declines in survival for both adult stage classes during poor food years. For the Low Removal scenario, reduction in adult survival was fully offset by normal litter sizes during poor natural food years (L_b) . In the High Removal scenario, the negative influence of reduced survival for just breeding adult females during poor years (s_{ab}) was higher than the benefit of poor year cub production (see Table 1.3).

In each scenario for all frequencies of good food years considered, elasticities were always higher for survival of both adult stages (s_a and s_r) even with elasticity being partitioned between these two stage classes (Fig. 1.5). Considering all vital rates from both good and poor years shows that elasticities of subadult survival and litter size during good years are of similar magnitude as adult survival during poor natural food years (Fig. 1.5). When $\rho = 0.75$, elasticity values and proportional vital rate changes predicted an increase of $\log(\lambda_s)$ from -0.0118 in Baseline scenario to 0.0112 in Low Removal scenario and a decrease to -0.0228 in High Removal scenario, near approximations to eq (1.4), where $\log(\lambda_s)$ was 0.0072 and -0.0263 for Low and High Removal scenarios respectively (see

Table 1.3 for proportional vital rate changes, elasticity values, and changes in growth due to changes in each parameter). Positive contributions to the growth rates of the Low and High removal scenarios came mostly from consistent litter size during poor natural food years, while reductions in growth were mainly from reduced survival of available breeding adults.

1.3.2 Simulation: 50 Year Projections

Trends in median population totals declined for both Baseline and High Removal scenarios, and increased for Low Removal scenario (Fig. 1.6). At year 50, positive growth occurred in 12%, 78%, and 3% of the Baseline, Low Removal, and High Removal scenario iterations, respectively. The vital rates with the most influence on variation in population growth differed between scenarios. For the Baseline scenario, variance in growth could mostly be attributed to variance in τ_{ar} and average litter size (L), while for Low and High Removal scenarios variation in these vital rates contributed little to variation in growth as they remained more constant between good and poor natural food years. For the two removal scenarios, s_a was responsible for most of the variation in growth, followed by variation in cub survival. The pattern between the Low and High Removal scenarios was similar, but with greater differences in regression coefficients for the High Removal scenario (Fig. 1.7). We estimated a negative regression coefficient for the coefficient of variation of the transition rate from subadult to breeding adult (τ_{sa}) in the Baseline scenario. The relationship between variation in growth and the coefficient of variation for this vital rate was positive, but covariance between τ_{sa} and τ_{ar} resulted in a negative regression coefficient for τ_{sa} .

1.4 Discussion

Our modeling results demonstrate the importance of considering a variety of factors when determining the impact of anthropogenic resources on large carnivore populations. First, our model supports the idea that a high removal rate of individuals in response to human-carnivore conflict can result in anthropogenic resources being the bait of an

ecological trap, i.e., the benefit of anthropogenic foods is lower than the cost of conflict animals being removed from the population (Schlaepfer et al., 2002). Our model also supports the notion that carnivore populations can benefit from anthropogenic food sources when management response includes a certain level of tolerance to wildlife conflict. However, tolerance of carnivore conflict and failure to limit anthropogenic food resources will likely support population densities that are beyond the natural carrying capacity, e.g., bears in Lake Tahoe (Beckmann and Berger, 2003b) and coyotes in California (Fedriani et al., 2001). Our model helps identify critical variables that should be considered for measurement when management involves similar human-wildlife dynamics.

We demonstrated that urban environments may have greater impacts on bear populations in the future if the frequency of natural food failures increases. We showed that increasing the frequency of natural food shortage years reduced the growth rate in all scenarios, with the impacts being disproportionate between scenarios (i.e., the growth rate decline was 1.5 faster in the High Removal scenario than the Baseline scenario). We determined that the stochastic growth rate $\log(\lambda_s)$ had the highest elasticity for survival of breeding adult females, indicating that wildlife managers should focus on understanding how removal of bears from the population due to conflicts changes this vital rate.

We found that reduced survival of adult females and normal litter sizes during poor food years contributed most to the differences in population growth rates between the baseline and urban scenarios, making these vital rates important for understanding the impact urban areas could have on bear populations. Our simulations indicated that if conflict-bear removal is low, then the overall population can still grow due to increased cub production during poor natural food years. However these benefits are negated and result in a population decrease when adult survival is reduced by greater conflict-bear removals as in the High Removal scenario. Our simulations also showed that litter size and the transition of breeding adults to adults with cubs were responsible for most variation in the Baseline scenario growth rate and that survival of breeding adults was the main

contributor to variation in the growth rate for both Low and High removal scenarios. This indicates that variation in the growth rate would likely come from either annual variation in natural food sources when anthropogenic food sources are managed or management removal of conflict bears in systems where supplemental human foods are available.

Natural food failures and their impacts on population vital rates are mentioned in several bear studies (Beck, 1991; Bridges et al., 2011; Powell et al., 1996; Rogers et al., 1976), but our study explicitly incorporated them into the population model. We found that increasing the frequency of poor natural food years increased the differences between growth rates of the Baseline scenario and both removal scenarios. Many climate models predict warming and increased drought in the Rocky Mountains (Rangwala et al., 2012; Strzepek et al., 2010) that could lead to an increase in the frequency of poor natural food years. Under future scenarios of increased natural food failure and continued availability of urban food sources, our results suggest that management efforts will need to ensure that fewer adult females are killed from urban conflicts or accept smaller bear populations in the vicinity of cities. Population models are a critical tool for understanding potential challenges wildlife populations face and they provide managers with a more informed perspective of how their actions could impact a population, e.g., protection of polar bears due to projected loss of sea ice (Hunter et al., 2010) and modeling impacts of small increases in human development on grizzly bears (Doak, 1995).

We assumed no correlation in the sequence of good and poor years, but acknowledge that correlated poor years may have compounding impacts that were not addressed with our model. For example, weather patterns can occur over several years (e.g., the North Atlantic Oscillation, Hurrell, 1995), and could result in grouped good or poor natural food years. Under such scenarios, which are predicted to increase in some climate models (Seager et al., 2007), even the survival rate of adults in the Baseline scenario may decline after several poor natural food years, resulting in both of our urban scenarios having an overall benefit to the population.

Prospective bear population models typically assume stable stage or age class distributions, i.e., constant vital rates through time (Beston, 2011; Freedman et al., 2003; Hebblewhite et al., 2003). We relaxed this assumption allowing vital rates to change with respect to good and poor natural food years and found that elasticity of $\log(\lambda_s)$ was highest for survival of breeding adults during good natural food years, but poor years elasticity values for survival of this stage class was lower than survival of other good year vital rates, e.g., elasticity of subadult survival during good natural food years. Calculating elasticities for vital rates during good and poor natural food years allows for a more realistic understanding of the influences that year specific management actions could have on the population. Previous bear studies have also identified adult survival as having the highest elasticity (Beston, 2011; Freedman et al., 2003; Hebblewhite et al., 2003). Powell et al. (1996) reported that growth rate elasticities were highest for survival of the 3 youngest age classes at the Pisgah Bear Sanctuary; this differs from most bear studies and other long-lived species (Heppell et al., 2000). Freedman et al. (2003) suggested that this was a result of elasticities being partitioned between several adult survival rates that are typically combined. We agree with Freedman et al. (2003) that these adult age classes should be combined, unless the age classes are managed differently or are thought to have biologically different vital rates. Ranking vital rate elasticity values allows for a quick initial assessment of how a population will respond to potential changes in vital rates (Caswell, 2000). The high elasticity value for adult survival suggests that managers need to focus on understanding how different management responses to conflict affect this rate.

Manipulating the vital rates with the highest elasticity values may not always provide the best overall solution to broader management goals. For example, the most efficient short-term solution for suppressing a bear population that has become too large due to access to urban food sources would be to reduce survival of adult females by increasing hunting and management removals. Unfortunately, increased harvest rates near urban areas may not be practical, and management removals are not always supported by

the public (Campbell, 2013) and can be expensive (Hristienko and McDonald, 2007). Although litter size during poor natural food years (L_b) has a low elasticity value, it is higher when urban foods are available and made positive contributions to $\triangle \log(\lambda_s)$ that were enough to offset reduced adult survival in the Low Removal scenario. A long-term solution to maintaining a stable bear population and public support would be to develop a management plan that reduces L_b through limiting the availability of urban foods. In Yellowstone and Yosemite National Parks, management action aimed at securing available human food sources were thought to have reduced bear conflicts and subsequently the role that conflict removals and human food sources were having on these populations (Gunther, 1994; Keay and Webb, 1987). Even if securing human food sources does not immediately reduce the number of conflicts, our results suggest that, if managers can reduce cub production during food failure years by securing human foods, this may provide a mechanism to decrease population growth and subsequently the potential number of bears that must be removed in future years.

We based our model structure on observations from the Aspen region where bears switched from using human food sources in poor natural food years to using natural foods when available (Baruch-Mordo, 2012). This flexible foraging behavior differs from the Lake Tahoe, Nevada, region where bears primarily remained in either urban or wildland areas regardless of natural food production (Beckmann and Lackey, 2008); in addition, patterns of mortality from management and other causes were different. Comparing the Lake Tahoe and Aspen studies demonstrates the importance of understanding local dynamics of bear behavior and management actions for paramaterizing and structuring models. Applying our model to Lake Tahoe would thus not work without restructuring and reparameterizing our model, but this could readily be accomplished for Lake Tahoe and other systems.

The Aspen Study lacked information on whether females permanently migrated from more remote areas to forage in Aspen during poor natural food years. Our model does not account for migration between a wildland and urban population. However, the possibility of a distinct wildland population that bears are immigrating to or from was not well supported in the Aspen region. First, female home range sizes in Aspen were 5-10 km² (Baruch-Mordo, 2012) and wildland bears typically utilize larger areas (Beckmann and Berger, 2003a). In the Aspen region, large areas of undeveloped land between adjacent cities is lacking and the habitat of more remote areas primarily consisted of coniferous forests, high alpine tundra, and talus, which do not produce abundant fall food sources for bears in this region. Second, seasonal movement distances observed by Noyce and Garshelis (2011) suggest that even bears located in more remote areas of Colorado may be within a reasonable distance to supplement their diets in the nearest urban environment.

Our modeling effort was unique as it modeled bear population in a stochastic environment and showed the influence that climate and conflict-bear management strategies could have. As a generalist species, black bears inhabit a variety of North American habitats, and climate change scenarios underscore the need for managers to better understand future challenges of maintaining viable populations. Ultimately, management plans will need to rely more on proactive measures of reducing human-bear conflicts (Hopkins III et al., 2010), if bear populations are to be sustained in and near urban areas in the future. This means that in cities like Aspen, where cub production and adult survival rates are more similar to our High Removal scenario, communities will need to better secure human food sources like garbage; a method that has been successfully implemented in many of our national parks (Gunther, 1994; Keay and Webb, 1987; Schirokauer and Boyd Hilary, 1995) and some municipalities (Peine, 2001).

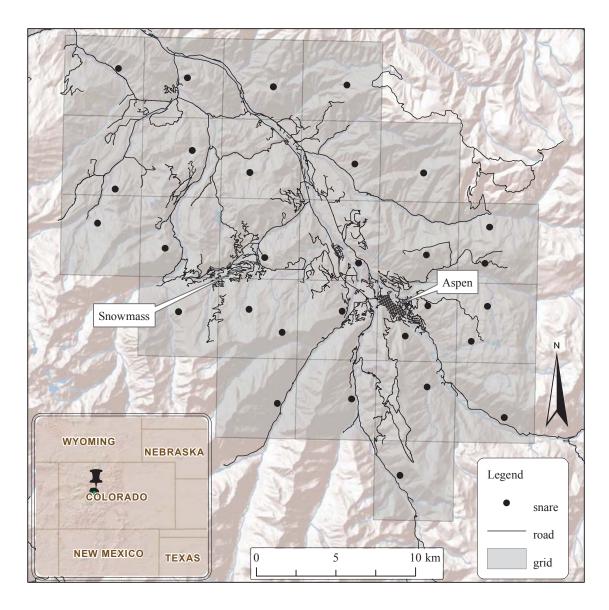


Figure 1.1. Pushpin in lower left map indicates general location of Aspen, Colorado. Locations of hair-snares (circles) surrounding the cities of Aspen and Snowmass, Colorado were used to estimate bear abundance within the grid from DNA mark-recapture data.

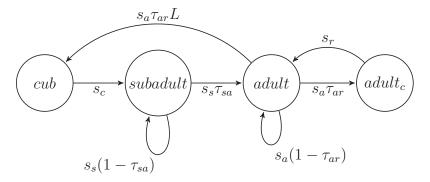


Figure 1.2. Four stage classes in the female black bear life cycle are represented by circles; arrows indicate possible transitioning between stages or staying in the same stage class; s_i are survival probabilities for stage i: s_c (cubs), s_s (subadults), s_a (adults available to breed), and s_r (adults with cubs); τ_i are transition probabilities τ_{sa} (subadults to adults without cubs) and τ_{ar} (adults without cubs to adults with cubs); L is the average number of female cubs per litter.

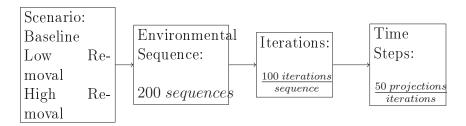


Figure 1.3. Simulation of population projections of a female bear population over 50 years occurred in 4 steps (boxes). For each management scenario we used the same 200 environmental sequences of good and poor years, performing 100 iterations of a 50-time-step projection.

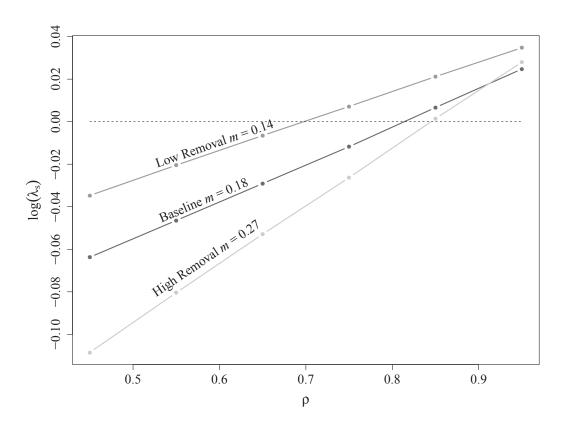


Figure 1.4. Stochastic growth rate for a female black bear population (y-axis) with respect to the the frequency of good natural food years, ρ (x-axis). Horizontal dotted line indicates no increase or decrease in the population and m is the slope of $\log(\lambda_s)$ with respect to ρ . Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals.

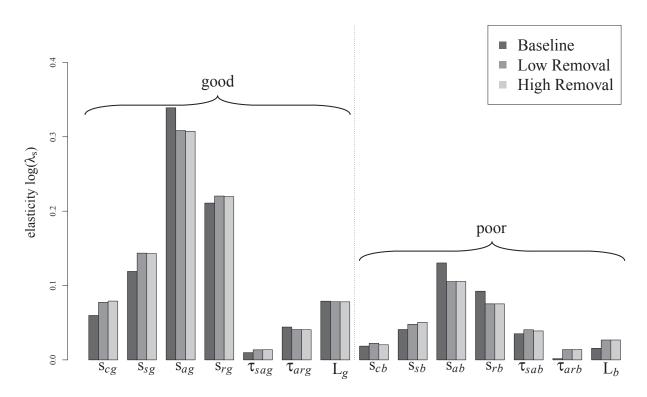


Figure 1.5. Elasticity values of long-term stochastic growth $\log(\lambda_s)$ for 3 black bear management scenarios (y-axis) separated by vital rates of good and poor natural food years (x-axis). Proportion of good years was $\rho = 0.75$ for this set of elasticity values. Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals. See Table 1.1 for variable definitions.

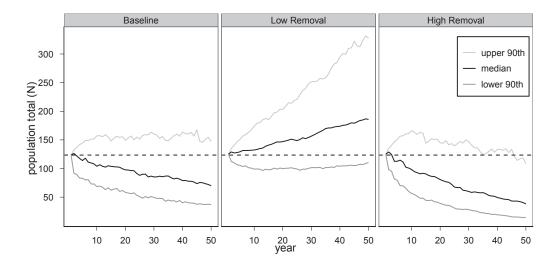


Figure 1.6. Female black bear population totals (y-axis) summarized over 50 years (x-axis) where the frequency of good food years was $\rho \approx 0.75$. At each time step the median, lower 90th, and upper 90th percentile population totals summarize 20000 iterations. Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals.

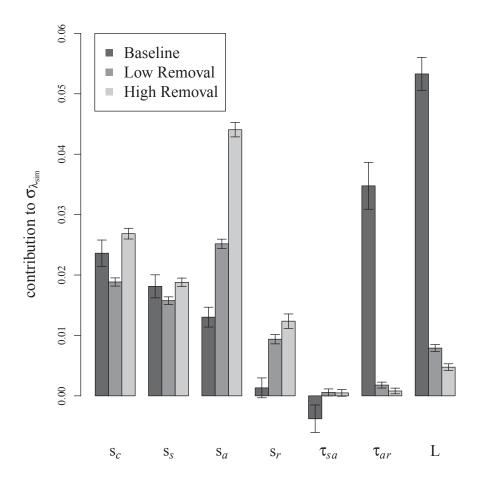


Figure 1.7. Modeled contributions to the standard deviation of the growth rate of a female black bear population (y-axis) with respect to each vital rate. Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals. See Table 1.1 for variable definitions.

Table 1.1. Vital rates used to model the female portion of black bear populations. Additional subscripts g and b are used to indicate if the vital rate is associated with good or poor natural food years.

Symbol	Description
s_c	Survival of cubs to 1 year of age.
S_{S}	Survival of subadults not yet mature enough for breeding.
s_{a}	Survival of adults available to breed in the previous year.
s_r	Survival of adults that raised cubs the previous year.
$ au_{sa}$	Transition rate of subadult to breeding adult.
$ au_{ar}$	Transition rate of breeding adult to adult with newborn cubs. ¹
L	Average number of female cubs per litter.
1.00	

¹Transition probability τ_{ar} is estimated as the proportion of adult females which rear cubs through the next full census period or at least long enough to hinder production of cubs in consecutive years.

Table 1.2. Female bear population vital rates for Baseline, Low Removal, and High Removal scenarios. Baseline scenario represents a population with no access to urban food sources and no conflict-bear removals. Low and High Removal scenarios represent populations that use urban environments to forage during poor natural food years benefiting from urban food, but experiencing reduced survival from conflict-bear removals. Percent changes in population vital rates from the Baseline scenario to Low and High Removal scenarios are shown as \bullet for no difference, + for an increase, and - for a decrease.

	Base	eline	Low Removal						High Removal						
	good	poor		good	l		poor	:		good	l		poor		
vital rate	value	value	value	%	change	value	%	change	value	%	change	value	9	6change	
s_c	0.60	0.40	0.60	•	0.0%	0.45	+	12.5%	0.60	•	0.0%	0.35	_	12.5%	
S_S	0.75	0.60	0.75	•	0.0%	0.65	+	8%	0.75	•	0.0%	0.60	•	0.0%	
s_a	0.90	0.85	0.90	•	0.0%	0.80	_	6%	0.90	•	0.0%	0.70	_	18%	
\mathbf{s}_r	0.90	0.85	0.90	•	0.0%	0.80	_	6%	0.90	•	0.0%	0.70	_	18%	
τ_{sa}	0.33	0.25	0.33	•	0.0%	0.33	+	32%	0.33	•	0.0%	0.33	+	32%	
$ au_{ar}$	0.90	0.60	0.95	+	5.5%	0.95	+	58%	0.95	+	5.5%	0.95	+	58%	
L	1.10	0.60	1.15	+	4.5%	1.15	+	130%	1.15	+	4.5%	1.15	+	130%	

Table 1.3. Contributions that proportionally changed female black bear vital rates had on stochastic growth $(\triangle log(\lambda))$ when vital rates of the baseline scenario (θ_{BL}) were changed to match vital rates of the Low and High removal scenarios. In the baseline scenario the bear population did not benefit from urban foods and had no conflict-bear removals and in the Low and High removal scenarios human food sources were available and removal of conflict bears occurred. Changes in the growth rate were determined from proportional changes in vital rates (δ) and elasticity values from the baseline scenario (e_{BL}) calculated when the frequency of good natural food years was $\rho = 0.75$.

			Basel	line to L	ow Removal		Basel	ine to H	igh Removal
	$ heta_{BL}$	e_{BL}	θ_{LR}	δ	$\triangle log(\lambda)$	_	θ_{HR}	δ	$\triangle log(\lambda)$
τ_{arg}	0.90	0.044	0.95	0.056	0.002		0.95	0.056	0.002
\mathcal{L}_g	1.10	0.079	1.15	0.045	0.004		1.15	0.045	0.004
s_{cb}	0.40	0.019	0.45	0.125	0.002		0.35	-0.125	-0.002
s_{sb}	0.60	0.041	0.65	0.083	0.003		0.60	0.000	0.000
s_{ab}	0.85	0.130	0.80	-0.059	-0.008		0.70	-0.176	-0.023
s_{rb}	0.85	0.092	0.80	-0.059	-0.005		0.70	-0.176	-0.016
$ au_{sab}$	0.25	0.010	0.33	0.333	0.003		0.33	0.333	0.003
$ au_{arb}$	0.60	0.002	0.95	0.583	0.001		0.95	0.583	0.001
L_b	0.50	0.016	1.15	1.300	0.020		1.15	1.300	0.020
			$\sum \triangle$	$log(\lambda)$:	0.023				-0.011

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CHAPTER 2. Foraging by black bears in urban areas: can bear-proofing garbage reduce conflicts

2.1 Introduction

Mitigation of human-wildlife conflict is becoming an important component of wildlife management particularly in urban areas with growing human and wildlife populations (Conover, 1997; Messmer, 2000). Urbanization is increasing across the globe (United Nations Population Division, 2008) impacting the ecology of many wildlife species (Baker and Harris, 2007; DeStefano and DeGraaf, 2003; Gehrt et al., 2010; Marzluff, 2001; Shochat, 2004). These impacts can positively affect some species that can adapt to the altered environment by offering abundant food, exclusion of some predators, and nesting or denning sites (Crooks, 2002; Prange et al., 2004; Withey and Marzluff, 2009). Many species benefiting from urban areas are accepted or even encouraged to reside in urban areas, however other animals like large carnivores can cause property damage, economic losses, or human injury. Understanding how a species is benefiting from urban areas will help better explain the mechanisms of wildlife conflicts and offer insight into methods for reducing conflict in the future.

Resource selection, defined as the disproportionate use of a resource in comparison to its availability, is hierarchical in nature where selection can vary by spatial and temporal scales (Boyce, 2006; Johnson, 1980; Thomas and Taylor, 1990). Three designs are traditionally employed in resource selection studies: design I measures use and availability of resources at the population level, design II measures use at the individual level and availability at the population level, and design III measures both use and availability at the individual level (Manly et al., 2002; Thomas and Taylor, 2006). With the advent of GPS technology for wildlife tracking, collection of fine-scale spatiotemporal data has been possible, enabling a fourth design where use and availability are measured multiple times at the individual level (Erickson et al., 2001; Thomas and Taylor, 2006). However, collection of fine-scale data remains a challenge, especially in the urban environment where resources

frequently vary due to human activity and where resources may not be adequately summarized solely with Geographic Information System (GIS) data (Newsome et al., 2013; Wilmers et al., 2013). Instead, backtracking, i.e., returning to use locations of wildlife in a timely manner, can be employed to capture variables associated with ephemeral resources. Understanding selection at these finer scales can provide insight into potential management solutions, e.g., black bears selection of mini-vans in Yosemite National Park (Breck et al., 2009).

In many places human-bear conflict (e.g., property damage and occasionally human injury) is increasing, a result of growing human populations and increasing bear populations particularly in urban areas (Baruch-Mordo et al., 2008; Hristienko and McDonald, 2007). Mitigation of conflict poses unique challenges with much debate centered on whether to focus effort on managing individual bears through lethal and non-lethal means or to manage people and the availability of anthropogenic food (Baruch-Mordo et al., 2011; Beckmann et al., 2004; Mazur, 2010). Traditionally management response to bear conflicts in urban areas has been removal (i.e., translocation or euthanasia) or hazing of individuals. Euthanasia can be unpopular among urban residents (Manfredo, 2008; Messmer, 2009; Treves and Naughton-Treves, 2005) and preventing future conflicts using translocation and hazing is thought to be ineffective (Beckmann et al., 2004; Landriault et al., 2009) as well as expensive and time consuming for management agencies (Hristienko and McDonald, 2007; Fontúrbel and Simonetti, 2011). Central to finding alternative solutions to minimize urban-bear conflict is an understanding of bear ecology, resources bears use in urban areas, and why these resources are available.

Black bears (*Ursus americanus*) are opportunistic omnivores that have adapted to long periods of winter food shortage by foraging intensively, i.e., hyperphagia, during the months prior to winter and then entering a state of lethargy with no foraging during winter (Nelson et al., 1983). During hyperphagia masting plant species provide bears with a food source high in caloric energy, e.g., acorns and berries, critical for survival and reproduction

(Inman and Pelton, 2002; McDonald and Fuller, 2005; Mosnier et al., 2008; Rogers et al., 1976). Periodically these masting crops fail to produce during years of unfavorable conditions, e.g., late-spring freezes and droughts (Neilson and Wullstein, 1980; Sharp and Sprague, 1967), resulting in bears seeking alternative food sources. The result can be increased use of urban areas that offer supplemental anthropogenic food, such as garbage, bird feeders, livestock, and cultivated crops (Baruch-Mordo, 2012; Jones and Pelton, 2003; Rogers, 1987).

In this study, we examined resource selection by bears utilizing urban resources in Aspen, Colorado, USA (Fig. 2.1). Aspen experienced numerous human-bear conflicts in recent years, and these required large expenditures of resources by Colorado Parks and Wildlife (the state fish and wildlife agency) to trap, translocate, and euthanize bears (Baruch-Mordo et al., 2009, 2011). Prompted by the increase in conflicts, our study goal was to aid managers in better predicting the attributes of urban foraging locations in order to inform mitigation measures. We fitted bears with downloadable GPS collars and backtracked to in-town use locations to categorize bear activity and quantify use of anthropogenic resources during prehyperphagia (1 May-31 July) and hyperphagia (1 August-30 September) seasons of good and poor natural food production years. We collected fine spatiotemporal attributes associated with each foraging event and its associated availability locations, and we modeled bear resource selection to identify factors that best explained anthropogenic feeding events. Finally, given that we identified garbage as the main attractant, we summarized garbage container designs and their effectiveness related to preventing bear feeding events.

2.2 Methods

2.2.1 Study Area

Aspen's resident population increased from 8,593 in 2000 to 9,467 in 2010 (United States 2000 and 2010 Census, Aspen County Division). The city has a central business area that is surrounded by high density residential areas comprised of apartment buildings and

private homes with little or no native vegetation between residences (Fig. 2.1). Surrounding the city's core area are lower density neighborhoods and ranch style estates often with native vegetation among homes. Elevation ranged from 2,260-3,024 m, with most human development located in the valley bottom and lower density residential areas located on lower portions of surrounding mountain slopes.

Four mountain valleys converge into the Roaring Fork river that bisects Aspen (Fig. 2.1). Main landcover types (percentages determined from maps digitized from high resolution aerial photos) included: mountain shrub communities (23%) comprised of service berry (Amelanchier alnifolia), choke cherry (Prunus virginiana), gambel oak (Quercus gambelli); deciduous trees (20%) including aspen (Populus tremuloides), cottonwood (Populus angustifolia), mountain maple (Acer glabrum), and various non-native urban trees; grassland (20%) in the form of mountain meadows and agricultural lands; evergreen trees (12%) comprised of juniper (Juniperus osteosperma), pinyon pine (Pinus edulis), douglas fir (Pseudotsuga menziesii), spruce (Picea spp.), subalpine fir (Abies spp.); developed areas (16%) in the form of buildings, asphalt, and lawn; sagebrush (5%, Artemisia spp.); and riparian communities (3%) accounted for remaining areas.

The city of Aspen and Pitkin County passed ordinances in 1999 and 2001 that required proper storage of wildlife attractants (for details see (Baruch-Mordo et al., 2011)). In 2007, Pitkin County began requiring that garbage be secured in wildlife resistant refuse containers (Ordinance 020-2007, Pitkin County), and in 2010, the City of Aspen instituted a similar ordinances (Ordinance Sec. 12.08.020, City of Aspen). There were numerous approved refuse container designs that included metal or plastic construction and various securing methods such as side doors secured with a carabiner, bar secured over dumpster lid with a carabiner, hand latch on a top lid, and many more (see detailed list and descriptions in section 2.2.5).

2.2.2 Location Use and Availability

We captured bears in Aspen from May-August 2005-2010 (Colorado State University Animal Care and Use Committee protocols 05-128A-03 and 08-078A-01). We fitted bears with Lotek 4400M GPS remote-downloadable radio collars that were programmed to record locations every 30 minutes May-September and collect activity sensor data every 5 minutes. Following Baruch-Mordo (2012) we used only locational fixes of high PDOP quality and summed activity counts 15 minutes before and after each scheduled location acquisition, which allowed us to gain additional information on animal activity levels and to evaluate potential fix bias.

From 2007-2010 we backtracked bears during their active season (May-September) using the following methodologies: 1) we used a randomized list of collared bears to determine backtracking order, 2) we remotely downloaded collar data and backtracked to the most recent 24 hours of location data, 3) we did not backtrack to the last location to avoid disturbing a bear that might still be in the area, 4) we backtracked only locations within 50 m of building structures (pilot study showed infrequent evidence of anthropogenic foraging beyond this distance), and 5) if backtracking to private property, we first obtained permission. When two locations were within 20 m, one location was used to represent both locations and for larger location clusters that spanned > 20m, two or more locations, as needed, were sampled to represent the cluster. At each location we searched a 20-m radius looking for natural and anthropogenic foraging evidence. Natural foraging evidence included broken vegetation (e.g., woody berry shrubs), disturbed logs, rolled rocks, disturbed soil, animal carcasses, visual observations by persons present during natural foraging, or other miscellaneous indicators of natural foraging. Anthropogenic foraging evidence included scattered garbage, toppled garbage containers, paw prints on attractants, broken limbs of anthropogenic fruit trees (e.g., crabapple), visual observation by persons present during anthropogenic foraging, or other evidence such as broken windows and doors. When foraging evidence was found, we visited 5 randomly selected

locations from a circular area centered on each use location with radius equivalent to the average distance the bear had moved between each of the days 48 locations. These random locations provided a sample of available foraging sites, allowing spatial and temporal matching between the foraging location and the sample of available locations.

2.2.3 Attribute Data Collection

We collected attribute data (potential explanatory variables) within 20 m of each use and random location to capture the availability of anthropogenic and natural resources (attributes and predicted influence on selection are summarized in Table 2.1). Attributes included the number of anthropogenic attractants, e.g., barbeque grills, bird feeders, and pet food, presence or absence of secure and unsecure garbage containers, and presence or absence of ripe natural mast (e.g., serviceberry, chokecherry, gambel oak, or riparian fruit) and ripe anthropogenic fruit (e.g., crabapple). In addition to field sampling, we determined GIS attributes in ESRI® ArcMapTM 10.0 using geographic data provided by Pitkin County GIS department. Because foraging on anthropogenic resources could be opportunistic, we expected bears to select foraging locations that were surrounded by higher percentages of natural food producing habitat and in close proximity to travel corridors. We used high resolution aerial photos to digitize vegetation cover and summarized percent landcover types associated with mast producing shrubs within 50 m, and we calculated distance to the nearest water or riparian areas including bodies of water and streams. We also included attributes that might increase the probability of a bear detecting or encountering anthropogenic food. For the former, we recorded, within 50 m of the location, the presence or absence of restaurant(s), which typically produce large amounts of food waste and vent food-scented air. For the latter, to quantify human density, we summed the number of addresses that were within 50 m of a location at a 5-m grid cell. We then used this data to determine the mean address density within 20 m of each location. We thought bears would select foraging sites at some intermediate human density with more plentiful food resources and reduced potential for human interaction.

We rescaled human density, %vegetation, and distance to riparian areas by dividing each value by the largest value within each respective attribute.

2.2.4 Anthropogenic Foraging Model

We used a discrete choice model where the probability of the foraging location being chosen from the set of 6 locations (1 foraging location and 5 random locations) can be written as,

$$p_j(A) = \frac{e^{\beta \mathbf{x}_{Aj}}}{\sum_{i=1}^6 e^{\beta \mathbf{x}_{ij}}},\tag{2.1}$$

where A is the foraging location, j indexes a single foraging event, i indexes the set of 6 locations associated with a foraging event (1 foraging location and 5 random locations), and x is a vector of location attributes. The β 's were obtained by maximizing the likelihood

$$L = \prod_{k=1}^{m} \prod_{j=1}^{n} p_{jk}; \tag{2.2}$$

where k indexes m collared bears and j indexes the n foraging events of a single bear. We estimated β 's using conditional logistic regression with the clogit function from package survival (survival version 2.36, http://CRAN.R-project.org/package=survival, accessed 15 March 2012) in R (R version 2.14.2, www.r-project.org, accessed 15 March 2012), which uses a stratified Cox proportional hazards routine to obtain maximum likelihood coefficient estimates (Manly et al., 2002:208). We stratified by foraging event so that each foraging location and its associated 5 random locations were considered a unique stratum and we accounted for repeated sampling of individual bears using the cluster option in the regression to calculate robust standard errors for coefficient estimates. We assessed model fit using the pseudo-R² value of the global model (see list of model parameters in Table 2.2) and ran all 255 possible models to obtain model averaged coefficient estimates, 95% confidence intervals, and relative importance values (Burnham and Anderson, 2002). We used a bootstrap approach for model validation running 10,000 iterations of the dataset

being partitioned, with 80% of the foraging events being used to estimate the regression coefficients and the remaining 20% of the foraging events being used to evaluate model performance. To evaluate performance, we ran the data from the 20% of foraging events through the model developed with the 80% of foraging events and computed the number of times (as a percent of the 10,000 iterations) that each foraging location was ranked first, i.e., most probable, and compared this result to a random ranking of the locations (i.e., foraging location and the 5 associated random locations).

2.2.5 Garbage Container Design

To determine what makes a more effective bear-proof container, we focused on two aspects in their design: 1) the containers ability to resist bears obtaining food, and 2) the human users properly securing the container. We classified the container designs into seven categories: 1) top door carabiner (typical garbage container for single family home secured by carabiners located around the container rim), 2) top bar (dumpster with a bar placed across the access doors preventing the doors from fully opening), 3) hand latch (mechanism automatically secures container door when closed), 4) enclosure (fully enclosed room built around garbage containers), 5) rubber sling (flexible material used to secure garbage lid), 6) side door carabiner (dumpster with a sliding side door secured by carabiner), and 7) garbage compactor. We used data collected from the 5 random location surrounding all foraging locations to evaluate the frequency that a container of a given type was properly secured. We evaluated the ability of a container to resist bears obtaining garbage by comparing the percentage of foraging events where evidence suggested that bears obtained garbage from a secured container to the percentage that each container type was found in a secure state at random locations.

2.3 Results

2.3.1 General Use Patterns

From 2007-2010, we monitored 40 collared bears and collected >42,500 bear locations within 50 m of structures. GPS collars obtained high quality locations on 89% of

attempts, where low quality and failed GPS fixes were associated with periods of low activity counts. Eliminating attempts that were associated with activity counts of < 20 (conservative given mean bedding site activity counts were 133) increased fix success rate to 97%. This suggested little bias from GPS collar location data while bears where actively moving and foraging.

We backtracked to 2,700 bear locations of n=21 bears (9 females and 12 males), classifying locations as bedding (n=151), foraging (n=539), and unknown (n=2,010). Typically only one foraging event was identified per backtracking occasion, with the maximum being nine. Total number of foraging events per bear ranged from 1-99, where bears with few foraging events typically lost their collars prematurely, were dispersing males, were only collared during good natural food production years when bears typically remained outside of town, or were removed from the population due to conflict.

Natural food production was poor in 2007 and 2009 and during hyperphagia of these years most collared bears used the urban environment to forage, resulting in major differences in the yearly percentages of locations within 50 m of structures 23%, 5%, 24%, and 6% for 2007-2010, respectively. Intensity of location use and the food sources that bears used in the urban environment also varied as a function of natural food production (Fig. 2.1). There were a greater number of foraging events on anthropogenic food sources in 2007 (184) and 2009 (126), years of poor natural food production, compared to 2008 (79) and 2010 (51), years of good natural food production. Natural food sources were utilized within the urban environment in both poor and good natural food production years. The spatial distribution of foraging events differed in poor and good years, where areas of higher human density were used to a larger extent during poor food years.

Garbage was the most frequently used food source in good and poor natural food production years for both prehyperphagia and hyperphagia seasons (Fig. 2.2), but we recorded 5 times fewer garbage foraging events during hyperphagia of good natural food production years. Although garbage foraging events far surpassed all other food sources,

fruit trees and in-home foods (i.e., bear entered structure to obtain food) were commonly found. Barbecue grills were common at both bear locations and random locations, but were typically not disturbed by bears. Pet food and bird feeders were not a common food source, but were also rarely found at available random locations. Even with high calorie human food sources being available, natural food sources were utilized in both year types and seasons within the urban environment.

2.3.2 Anthropogenic Foraging Model

We identified 321 anthropogenic foraging events and sampled 1605 available locations. Based on the average distance a bear moved in 30 minutes, the 5 available foraging locations were located on average within 237 m (range = 21-615 m, n = 449) of foraging locations. The global model had a psuedo $R^2 = 0.28$, with a maximum possible value of $R^2 = 0.45$. Selection of anthropogenic foraging locations were best explained by presence of secured garbage, unsecured garbage, ripe anthropogenic fruit, and distance from riparian areas (Table 2.2). Locations with unsecured garbage containers were more strongly selected for than locations with only secured garbage, but both location types were selected for relative to locations with no garbage containers. Minimum distance to riparian areas had a negative coefficient, indicating that urban locations closer to riparian areas were selected. Relative importance values indicate that secure and unsecure garbage container(s), ripe fruit, distance to riparian areas, and presence of restaurant(s) are important foraging model parameters. From the set of foraging events (1 foraging location and 5 random locations) used to test the model, we found that on average 68% (range = 50-87.5%, n=10,000) of foraging locations were ranked by the model as the most probable foraging location compared to a random ranking that ranked on average 17% (range = 1.5-34.3\%, n = 10,000) of foraging location with the highest probability.

2.3.3 Garbage Container Design

At random locations, 76% of garbage containers were bear-resistant, but only 57% of bear-resistant containers had been properly secured. This resulted in 55% of the garbage

containers at random locations being either unsecured bear-resistant containers or non-bear-resistant containers. Residential containers with a top lid secured by carabiners were the most common container type, comprising 42% of all bear-resistant containers; these containers also had one of the lowest securing rates with only 48% being found secured. Relative to the percentage of overall occurrence, dumpsters with a top-bar securing design provided bears with food more often than other properly secured containers, Table 2.3.

2.4 Discussion

Our results demonstrated that bears primarily used garbage when foraging in Aspen, and that selection of foraging locations was influenced not only by the presence of garbage but also by the proximity to riparian areas and presence of ripe fruit trees. But, perhaps the most striking pattern that we observed was the flexible use of urban environments, i.e., inter- and intra-annual switching of foraging locations between urban and wildland areas, that depended on the availability of natural foods. The greatest shift in foraging behavior occurred during hyperphagia season, when we observed bears switching from foraging in urban areas during poor natural food years to feeding on abundant natural foods during good food years. We also documented intra-annual shifts in foraging behavior with some bears utilizing urban areas during pre-hyperphagia then switching to areas with natural food during the hyperphagia season if natural foods were abundant.

Spatial shifts in habitat use and foraging behavior of Asiatic black bears (*Ursus thibetanus*) due to natural mast production has also been documented (Koike et al., 2012; Kozakai et al., 2011). For American black bears the flexible foraging behavior observed in the Aspen was similar to Minnesota, where bears supplemented their diets during poor natural food production years by feeding in garbage dumps (Rogers, 1987), but differed from the Lake Tahoe region where urban bears continued to forage on anthropogenic resources regardless of natural food availability (Beckmann and Berger, 2003). Unlike Aspen, Lake Tahoe is surrounded by desert basins that provide marginal bear habitat

(Beckmann and Lackey, 2004), hence we speculate that the difference between Aspen and Lake Tahoe is a result of greater difference in the energetic tradeoffs between urban and wildland areas, such that switching in Lake Tahoe may not be beneficial. Understanding the energetic differences in resource availability between urban and wildland areas could be important in predicting switching behavior by bears and determining the appropriate response to urban bear-human conflicts.

The switching behavior indicates conflicts could be mitigated by altering the costs and benefits that bear experience in urban areas. Increasing the perceived cost (risk) through common hazing tactics have been found to be ineffective as a long-term solution (Beckmann et al., 2004), potentially because the energetic cost from hazing is small relative to the benefits of food rewards obtained (Baruch-Mordo et al., 2013). New hazing tactics could possibly be developed that are more effective, but in areas with large bear populations even effective hazing methods will likely be too labor intensive for managers. We argue instead that effort focus more on managing the energetic gains aspect of the foraging decision. The challenge for this solution is whether human communities are willing to to expend the effort and costs required to secure human foods, but examples of successes for this approach include many national parks (Gunther, 1994; Keay and Webb, 1987; Schirokauer and Boyd Hilary, 1995) and some municipalities (e.g., Juneau, Alaska; West Yellowstone, Montana; Gatlinburg, Tennessee [Peine, 2001]; Snowmass, Colorado [L. Smith and T. White, Animal Services Officers, Snowmass Village, personal communication 8 April 2013). For example, from 1960-1967 Yellowstone National Park removed conflict bears but did not secure garbage and human-bear conflicts continued to rise; only when human-food sources were secured (1968-1993) did conflict levels decline (Gunther, 1994). Similar patterns of conflict reduction occurred in other national parks like Denali and Yosemite National Park when management resources were allocated to securing garbage and other human foods (Keay and Webb, 1987; Schirokauer and Boyd Hilary, 1995).

There is a well-established notion among managers that garbage is a major attractant driving human-bear conflict (Spencer et al., 2007), which is supported by our findings. Over half of the garbage containers in Aspen provided no resistance to bears obtaining garbage, either because they were non bear-resistant or, more commonly, because they were bear-resistant containers that were improperly secured. Aspen had much of the infrastructure required to secure garbage, i.e., 76% of garbage containers were bear-resistant, but garbage was still utilized by bears when containers were not properly secured. Our study suggests that solely deploying bear-resistant containers will be inadequate without additional resources for education and proactive enforcement to change human behavior such that containers are secured. Ultimately, this is similar to other campaigns (e.g., to reduce drunk driving) that utilize education and enforcement to change human behaviors.

Other management solutions include improving bear-proofing and human-proofing design features of garbage containers. Some container designs are problematic because they allow bears to obtain garbage even when they are technically secure (in this study they included top door carabiner and top bar designs), and therefore should not be deployed. Municipalities and management agencies should not only focus on how bear-resistant a container is, but also consider human engineering factors to increase the ease of securing a container and subsequently the probability of compliance with local ordinances.

Baruch-Mordo et al. (2011) identified designs with a lower probability of bear break-in such as garbage compactors or enclosures with features such as non-chewable metal doors, airtight construction, and round doorknobs.

While garbage was the primary anthropogenic attractant utilized by bears, foraging locations also occurred near ripe fruit trees, which were the main feeding attractant for bears in Missoula, MT (Merkle et al., 2008). It can sometimes be difficult to determine which resources are the greatest attractants to bears, but clearly management efforts will benefit from reducing the availability of fruit trees. For example, in Aspen, a major

attractant was ornamental crabapple trees, and these can either be replaced by a non-fruiting variety (e.g., Malus x; Gilman and Watson, 1994) or sprayed to prevent fruiting. We found that bears selected to forage nearer to riparian areas in the urban environment. Similarly in Missoula, Montana bear conflicts occurred at a disproportionately high rate near riparian areas (Merkle et al., 2011) and in many non-urban studies, bears often select for riparian habitat at a landscape scale (Clark et al., 1993; Elowe, 1984; Fecske et al., 2002; Lyons et al., 2003; Obbard et al., 2010). Our results suggest riparian areas continues to be important for bears even at fine spatial scales within the urban environment, as Aspen bears used riparian habitats to forage on natural food sources and as bedding areas. Management efforts could therefore be maximized by allocating more effort toward securing human foods in areas nearer to riparian habitat.

Human-bear conflicts in urban environments present unique challenges to wildlife managers given the dynamic nature of bear use of anthropogenic resources. Solutions will require long-term commitments from wildlife agencies, municipalities, and urban residents, and can be best achieved by engaging all stakeholders, forming clear management goals, and willingness to share costs (Redpath et al., 2012). Our findings help managers identify primary anthropogenic attractants to bears (garbage and fruit trees) and can help managers prioritize management efforts, e.g., human-proofing garbage containers, removing of fruit trees, deploying management efforts first to areas closer to riparian habitat. Spatially centralizing garbage collection would provide fewer collection points and thus may also be effective in reducing the overall availability of garbage to bears. Additionally, synchronizing garbage collection to only a few collection days for a given neighborhood could limit garbage availability over time. Further work is needed to evaluate the ease of use, longevity, and ability of different bear-resistant containers to resist bears obtaining garbage when these containers are being used by actual residents, garbage collectors, and urban bears. It will also be important to determine the appropriate intensity and timing of education and enforcement that results in an acceptable level of compliance with respect to

ordinances requiring containers to be secured. The cost and effectiveness of various management strategies can then be compared and resources of wildlife agencies, municipalities, and residents optimized.

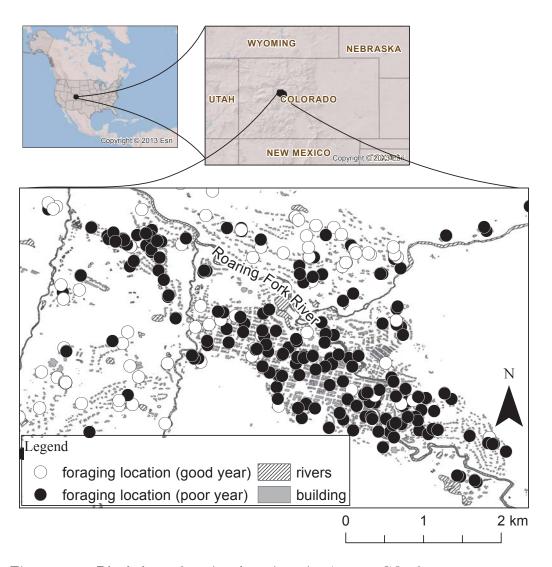


Figure 2.1. Black bear foraging locations in Aspen, CO, from 2007-2010; categorized by good or poor natural food production years.

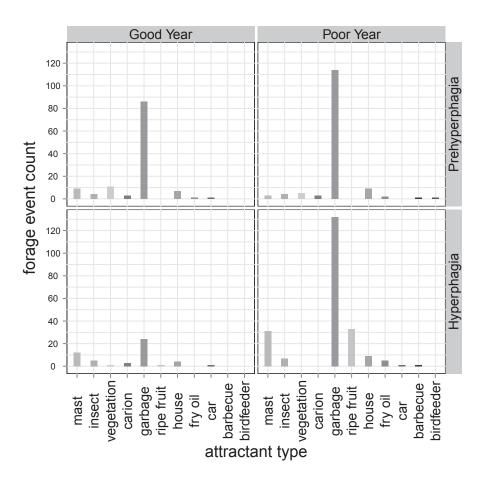


Figure 2.2. Number of black bear foraging events (y-axis) with respect to attractant type (x-axis) observed in Aspen, Colorado from 2007-2010; separated by good natural food years (left panels) and poor natural food years (right panels) and by prehyperphagia, 1 May-31 July (top panels) and hyperphagia 1 August-30 September (bottom panels).

Table 2.1. Location attributes used to model black bear selection of anthropogenic foraging locations. Predicted column indicate the hypothesized influence increasing location attribute values would have on probability of anthropogenic foraging at a location (0 = no influence, - = decrease (avoidance), + = increase (preference), \sim = intermediate selection).

location attribute	predicted	description
secure garbage	0	Only secured garbage container(s) within 20 m of GPS coordinate.
unsecured garbage	+	Unsecured garbage container(s) within 20 m of GPS coordinate.
ripe fruit	+	Presence/absence of anthropogenic fruit (e.g., crab-apple).
ripe natural mast	+	Presence/absence of ripe natural mast (service berry, choke cherry, riparian fruit, acorn).
human density [†]	$\overline{}$	Number of addresses within 50 m of location (average within 20-m of location).
$\%$ vegetation †	+	Percent mountain shrub and deciduous vegetation landcover within 50-m of location.
dist.riparian [†]	=	Distance to nearest water or riparian landcover.
${ m restaurant}^{\dagger}$	+	Presence/absence of restaurant establishment within 50 m of location.

[†]Determined from geographic information system.

Table 2.2. Anthropogenic foraging model for black bears in Aspen, CO, USA from 2007-2010. Predicted and observed influence of attractants and locations attributes on selection, model-averaged parameter estimates, 95%CI, and relative importance values (w_+) . Predicted and observed symbols are preference for (+), avoidance (-), indifference (0), and intermediate preference (\frown) . Parameters were estimated from 321 foraging events of 21 bears.

parameter	predicted	observed	coefficient	95%CI	$\overline{w_+}$
secure garbage	0	+	3.05	(1.50, 4.61)	1.00
unsecure garbage	+	+	4.04	(2.40, 5.68)	1.00
ripe fruit	+	+	5.14	(3.41, 6.87)	1.00
natural mast	+	0	0.08	(-0.40, 0.57)	0.29
human density	\sim	$\overline{}$	2.27	(-0.51, 5.06)	0.42
$(\text{human density})^2$	\sim	$\overline{}$	-5.15	(-11.13, 0.83)	0.42
%vegetation	+	0	0.00	(-0.40, 0.40)	0.26
dist.riparian	-	-	-4.23	(-6.08, -2.39)	0.92
restaurant	+	+	1.18	(-0.16, 2.53)	0.96

Table 2.3. Bear-resistant garbage containers used in Aspen, CO, from 2007-2010. Garbage containers sampled at random locations show percent occurrence of each container type (% occurrence), the percent of time it was found secured (%type), and percentage of all secure containers (% overall). Garbage containers sampled at foraging location show percentages of successful feeding from secured garbage containers by container type.

	rand	om locations	foraging locations	
securing method	%	% type	% overall	% obtained garbage
	occurrence			
top door carabiner	42	48	36	35
top bar	25	62	28	34
hand latch	8	92	14	14
enclosure	8	61	8	10
rubber sling	6	11	1	0
side door carabiner	6	59	6	0
other	4	73	5	2
compactor	1	100	2	4

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Appendix 1.A Beta and Gamma Shape Parameter Calculation

Mean of vital rate (μ) and standard deviation (σ) were used to calculate shape parameters of beta and gamma distributions (White, 2000):

Beta Distribution-

$$\alpha = \frac{(\mu^2 - \mu^3 - \sigma^2)}{\sigma^2} \tag{1.A.1}$$

$$\beta = \frac{\mu - 2\mu^2 + \mu^3 - \sigma^2 + \mu\sigma^2}{\sigma^2}$$
 (1.A.2)

 $Gamma\ Distribution-$

$$shape = \frac{\mu^2}{\sigma^2} \tag{1.A.3}$$

$$rate = 1 (1.A.4)$$

$$scale = \frac{\sigma^2}{\mu} \tag{1.A.5}$$

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