DISSERTATION

BLACK BEAR ECOLOGY AND HUMAN-BEAR INTERACTIONS IN AN URBAN SYSTEM

Submitted by

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ABSTRACT

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Human-dominated landscapes offer spatially concentrated and reliable food resources that attract bears and lead to human-bear conflicts. Many conflicts occur in urban areas where traditional management strategies targeting bears can be difficult to implement or unpopular with local constituencies, and consequently, wildlife managers are increasingly considering management tools targeting people. Regardless of whether management is targeting humans or bears, effective implementation depends on understanding human and bear behaviors. In general, rigorous examination of bear ecology in urban environments and efficacy of traditional and non-traditional management tools is lacking. Therefore, the goal of my research was to address these short-comings by focusing on American black bear (*Ursus americanus*; hereafter bears) ecology in and around the city of Aspen, Colorado.

Through a collaborative research effort involving federal and state wildlife agencies, I examined the degree of bear synanthropy using detailed GPS data collected in Aspen (Chapter 1) and implemented three experiments measuring the efficacy of education and enforcement in changing human behavior to better secure attractants from bears (Chapter 2). In addition, I demonstrated how foraging models can be used as a decision support tool to evaluate how mitigation strategies influence bear foraging decisions (Chapter 3). Below I provide a short summary of conclusions and management recommendations for each chapter.

In Chapter 1, I assessed the degree of bear synanthropy, i.e., dependency on anthropogenic resources and subsequent changes to behavior and population dynamics, and its relationship to individual and environmental covariates to test hypotheses about irreversible and fluctuating synanthropy. Synanthropy is likely a continuum that varies among individuals and across time, although in a management context bears are often perceived dichotomously as synanthropic or not, and the degree of synanthropy with its spatial and temporal fluctuations are rarely considered. Understanding such patterns is especially important for managing urban bears and for resolving conflicts with people. I used six years of detailed GPS location and activity data that were collected for bears in Aspen. I modeled space use (home range size, its overlap with human development, and mean human density within home range) and daily activity patterns as a function of individual and environmental covariates, estimated survival using known-fate models and modeled its relationship to covariates, and summarized reproduction in years of good and poor natural food production.

Bears had greater mean human density within their home ranges and increased nocturnal activity patterns in poor natural food years when they foraged more extensively in urban areas; however patterns were reversible in subsequent good food years. Survival in good years was similar to that of Colorado wildland bears, but was lower in poor food years, while reproductive output was similar across all years. Bears demonstrated behavioral plasticity in space use of urban areas and their activity patterns; both were strongly dependent on natural food availability with bears having lower survival when they used urban areas. The data refuted the hypothesis that bears are irreversible synanthropes and suggested that degree of synanthropy fluctuates with the availability of natural foods. I therefore recommended increased tolerance in managing bears that are fluctuating synanthropes to prevent urban areas from becoming population sinks.

In Chapter 2, I experimentally evaluated efficacy of education and enforcement in changing human behavior to better secure bear attractants. Evidence-based decision-making is critical for implementing management actions, especially for human-bear conflicts. Wildlife managers are recognizing that long-term solutions should include altering human behaviors, and public education and enforcement of wildlife-related laws are two management actions frequently implemented, but with little empirical evidence evaluating their success. I conducted three experiments in Aspen to evaluate: 1) on-site education in communal dwellings and construction sites, 2) Bear Aware educational campaign in residential neighborhoods, and 3) elevated law enforcement at two levels in the core business area. I measured human behaviors as the response including: violation of local wildlife ordinances, garbage availability to bears, and change in use of bear-resistance refuse containers. As implemented, I found little support for education, or enforcement in the form of daily patrolling in changing human behavior, but found more support for proactive enforcement, i.e., dispensing warning notices. More broadly I demonstrated the value of gathering evidence before and after implementing conservation actions, and the dangers of measuring responses in the absence of detailed knowledge of the system (e.g., natural food production, bear movements, etc.). I recommended development of more effective educational methods, application of proactive enforcement, and continued evaluation of tools by directly measuring change in human behavior. I provided empirical evidence adding to the conservation managers' toolbox, informing policy makers, and promoting solutions to human-wildlife conflicts.

In Chapter 3, I demonstrated the application of patch-selection models to examine how changes in energetic costs and benefits that result from management targeting bears and people can influence bear foraging decisions. Urban landscapes offer spatially concentrated and reliable

food resources that attract bears and lead to human-bear conflicts. Conflict management is often directed at humans (e.g., education) to reduce attractants or foraging benefits to bears, or at bears (e.g., hazing) to increase foraging costs, but strategies can be expensive and ineffective. A key driver of conflict is pursuit of food by bears, thus I used patch selection models (a dynamic, state-dependent modeling approach based on foraging theory) to assess how benefit reduction and cost increase affect bear foraging decisions. I applied the patch selection models to the urban system of Aspen, in which bears forage in human-dominated patches and conflicts are common. I used survival as a fitness currency and body fat reserves as a state variable. I incrementally reduced availability of anthropogenic foods and increased energetic costs of movement in response to aversive management to search for thresholds resulting in avoidance of human-dominated patches. Benefit reduction ≥60% in both human-dominated patches resulted in bears of almost all states avoiding those patches. Cost increases achieving similar results exceeded 1300% in the urban patch and 400% in the urban-interface patch, and are unrealistic to implement. Given modeling results and that control strategies targeting wildlife are unpopular with constituencies, I suggested allocating management resources to strategies that reduce availability of anthropogenic food.

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To my husband Moshe

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CHAPTER 1

URBAN BLACK BEAR (*URSUS AMERICANUS*) ECOLOGY: IRREVERSIBLE OR FLUCTUATING SYNANTHROPY?

Introduction

A milestone was reached in 2008 when more than half of the world's population resided in urban areas; by 2050, 70% (90% of North America) will consist of urban residents, with more than half expected to live in small urban centers (United Nations Population Division 2008). Urbanization is a major force shaping our world, gaining interest in diverse fields of ecology including ecosystem (McDonnell and Pickett 1990), community (Faeth et al. 2005), landscape (Breuste et al. 2008), disease (Bradley and Altizer 2007), and behavioral and evolutionary ecology (Shochat et al. 2006). Ecological effects of urbanization are considered for many taxa including plants (Williams et al. 2009), arthropods (Raupp et al. 2010), amphibians (Hamer and McDonnell 2008), birds (Marzluff 2001), and mammals (Baker and Harris 2007). Despite the growing interest, few studies have been conducted in urban systems (Collins et al. 2000, Miller and Hobbs 2002), and urban ecology is considered by some as an unexplored frontier (DeStefano and DeGraaf 2003, Gehrt et al. 2010).

Ecological effects of urbanization are long lasting and include land transformations, biotic modifications, and changes to biogeochemical cycles (Vitousek et al. 1997, McKinney 2006, Grimm et al. 2008). Beyond such broad-scale changes, urbanization has negative and positive impacts on the ecology of individuals and populations (Marzluff 2001, Baker and Harris 2003, DeStefano and DeGraaf 2003, Shochat 2004, Gehrt et al. 2010). Negative effects include lower survival and reproductive success resulting from increased human-related stress and mortality and reduced nutritional quality. Positive effects include increased survival and reproduction resulting from reduced predation pressure and increased availability of resources (e.g., food, cover, nesting or denning structures). The latter positive effects can lead to exploitation and dependency on anthropogenic resources, or species synanthropy.

Synanthropization, first discussed by Tomialojć (1970) and also similarly defined as synurbization by Andrzejewski et al. (1978), implies that species benefit from anthropogenic resources and therefore live in human-dominated or urban habitats. Johnston (2001) suggested three levels of synanthropy: full, casual, and tangential that respectively correspond to exploitation and dependency, exploitation but no dependency, and incidental use of human resources. Blair (1996) provided similar classifications of species as suburban adapters (causal synanthropes) and urban exploiters (full synanthropes; McKinney 2006). Urban areas offer novel environments with spatially concentrated, highly productive, and temporally predictable resources (Beckmann and Berger 2003a, Shochat 2004, Rodewald and Shustack 2008). Successful synanthropes often possess behavioral traits that allow use of these novel environments including generalized diets, high learning capacity, and behavioral plasticity (e.g., Shochat et al. 2006, Gehrt et al. 2010, Evans et al. 2011).

As synanthropic species apply these traits to exploit anthropogenic resources, behavioral changes ensue. Synanthropic species presumably need less area to obtain adequate resources compared to their wildland counterparts, and they may exploit resources during times that allow avoidance of high human activity. Evidence across taxa concurs, with synanthropic individuals having smaller territories and home range sizes (e.g., Rolando et al. 2003, Harveson et al. 2007, Rodewald and Shustack 2008) and modifying their normal activity patterns (e.g., Grinder and

Krausman 1999, Kilpatrick and Spohr 2000, Rutz 2006). A number of authors have suggested that successful synanthropy can eventually lead to changes in fitness including increases in survival and reproduction (Marzluff 2001, Shochat 2004, Rodewald and Shustack 2008).

For most animals, the degree to which they are synathropic likely varies over time, thus synanthropy should be considered a continuum rather than a dichotomy (Harveson et al. 2007). However in a management context, individuals and populations are commonly considered dichotomously as synanthropes or not, and the degree of synanthropy with its temporal fluctuations, or lack thereof, are rarely considered. If synanthropy promotes fitness with little additional costs, individuals become dependent on human resources, which leads to lasting behavioral changes described above (hereafter termed irreversible synanthropy hypothesis). This hypothesis has the implicit assumption that urban areas are always more beneficial than wildlands due to the high productivity and predictability of urban resources. However if synanthropy incurs greater fitness costs, then it will be beneficial when other natural resources are scarce (e.g., periods of natural food failures or inclement weather), and behavioral changes will be reversible and fluctuate in response to the cost/benefit ratio of urban and natural resources (hereafter termed fluctuating synanthropy hypothesis). In this framework I assume that some costs (e.g., increased stress, decreased nutritional quality) and benefits (e.g., increased food intake, decreased predation risk) are perceived by the individual, and that behavioral changes lead to costs and benefits in population-level fitness as they relate to changes in survival and reproduction.

Bears are omnivores, have high learning capacity, and exhibit behavioral plasticity (McCullough 1982, Gilbert 1989), traits that make them successful synanthropes. Bears enter a state of intense feeding, or hyperphagia, during late summer and fall to gain energy reserves for winter hibernation (Nelson et al. 1983). During hyperphagia, bears subsist mainly on plant species that produce hard- and soft-mast, and in years of mast failure, they may move extensively in search of food (Mattson et al. 1992, Hellgren et al. 2005, Ryan et al. 2007). When natural mast production is low, bears may also forage on alternative anthropogenic sources near human developments (Mattson et al. 1992, Ryan et al. 2007). While to date, no studies examined the relationship between the degree of bear synanthropy and temporal patterns of natural food availability, evidence suggests that human-bear conflicts and the subsequent human-related bear mortality increase during years of mast failure (Mattson et al. 1992, Oka et al. 2004, Ryan et al. 2007, Baruch-Mordo et al. 2008).

It is generally believed that when bears use human developed areas they become habituated, food-conditioned, and dependent on anthropogenic food sources (McCullough 1982, Herrero et al. 2005, Hristienko and McDonald 2007). Behaviorally, synanthropic bears had smaller home ranges compared to wild bears (Beckmann and Berger 2003b) and exhibited nocturnal activity patterns (Beckmann and Berger 2003a, Lyons 2005). Studies have shown mixed effects of synanthropy on black bear fitness, with positive impacts, e.g. increased litter size (Beckmann and Berger 2003b) and cub survival (Hostetler et al. 2009), and negative impacts, e.g. decreased subadult (Beckmann & Lackey 2008) and adult female survival (Mattson et al. 1992, Hostetler et al. 2009), and overall reduced population growth (Beckmann and Lackey 2008, Hostetler et al. 2009). If the fitness benefits associated with synanthropy outweigh potential costs, then bears should use anthropogenic resources regardless of variations in production of natural food, leading to permanent synanthropy in accordance with the irreversible synanthropy hypothesis. This is often the paradigm for bear management (Hristienko and McDonald 2007). Alternatively, if bears that forage in urban areas incur fitness costs that are offset only by the temporary scarcity of natural foods, then resultant behavioral changes relating to synanthropy will have a strong relationship to seasonal and annual patterns of natural food production, thus resulting in patterns of reversible synanthropy and lending support to the fluctuating synanthropy hypothesis.

Bear synanthropy can lead to an increase in human-bear interactions and conflicts with risks to human safety and increased bear mortality. Therefore, it is important to understand the ecological mechanisms determining synanthropy in bears to better manage conflicts. I present results of a six-year study of American black bears (*Ursus americanus*) in the urban environment of Aspen, Colorado, USA. By collecting detailed GPS location and activity data, I examined the behavioral ecology of urban bears as manifested by space use and daily activity patterns, and its relationships with urbanization, bear characteristics, and environmental covariates related to seasonal and annual changes in natural food availability. In addition, I explored supportive information on bear survival and reproductive output to gain insights on potential impacts of synanthropy to the fitness of the urban bear population. Overall, I asked whether behavioral and population ecology patterns lend support to the irreversible or fluctuating synanthropy hypothesis.

Methods

Study area and animals

I studied bears in Aspen and the surrounding areas of Pitkin County, located in the central mountains of Colorado (hereafter collectively referred to as Aspen). Elevation in the study area ranged from 2,300 to 3,150 m. Aspen is situated at the confluence of Maroon, Castle, and Hunter Creeks and the Roaring Fork River. Areas at lower elevation consisted of riparian vegetation, which changed with increasing elevation into mountain-shrub community on south-facing slopes, including Gambel oak (*Quercus gambelli*), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus virginiana*), and into aspen (*Populus tremuloides*) and lodgepole (*Pinus contorta*) forest communities on north-facing slopes. Land cover at higher elevations had sparse to no human development and was comprised of Douglas fir (*Pseudotsuga menziesii*) and spruce (*Picea* spp.)-subalpine fir (*Abies lasiocarpa*) coniferous forests, talus slopes, and alpine meadows. The city of Aspen had 6,846 residents in 2009 (Colorado State Demography Office 2011) and included in its core a business district and dense residential areas. Less dense residential neighborhoods surrounded the core of Aspen and interspersed within the surrounding mountain-shrub and forest communities.

From 2005-2010 I captured 50 bears in the urban environment of Aspen. I defined urban as a land cover characteristic of and related to human development (Marzluff et al. 2008). I captured bears according to Colorado State University's approved Animal Care and Use protocols #05-128A and #08-078A. I determined the gender of each bear and used Matson's Laboratory (Milltown, MT, USA) for aging of bears > 1 year old from cementum annuli of the vestigial premolar tooth (Willey 1974). I augmented my sample with data from four individuals captured due to nuisance activities; three were translocated but returned to the study area and one was released near its capture location with aversive conditioning measures. To avoid potential bias due to capture or management actions, I excluded data collected in the 48 hours following release from capture, or, if translocated, while bears were outside of the study area.

I fitted bears with Lotek© 3300L and 4400M GPS collars that collected a GPS location every 30 minutes from May to September, and every hour in the weeks before and after expected den entry and emergence. Collars also collected activity sensor data that recorded the number of head movements (range 0 - 255) at 5-min intervals throughout collar deployment. I fitted GPS collars with a mechanism to allow for drop-off in the event of substantial neck growth, and I programmed mortality sensors to trigger if no activity was logged in a period of several hours. Collars emitting a mortality pulse were investigated in a timely manner to determine whether the bear dropped its collar or died, and for the latter, to determine the cause of death. I monitored bears on a daily basis, and aerially searched for missing individuals outside of the study area every 2-4 weeks. I visited bears during their denning period to replace collar battery and determine the reproductive status of females.

Space use

I examined the relationship between home range characteristics and individual and environmental covariates to explore the mechanisms of space-use by bears in the urban environment. I estimated home ranges using GPS locations that, based on positional dilution of precision, met the screening criteria: ≤10 for 3D- and ≤5 for 2D-locations (D'Eon and Delparte 2005, Lewis et al. 2007). This resulted in removal of 11 % of locations on average ($SE = 0.75$), and visual examination of the data suggested no effect on overall space-use patterns. I stratified analyses by season because mast production can result in altered space use and activity patterns of bears (Davis et al. 2006, Munro et al. 2006). I defined two seasons based on the fruiting phenology of important mast species (Gambel oak, serviceberry, and chokecherry) and the local denning behavior of the bears: pre-hyperphagia from the approximate date of den emergence (16 April) to mast fruiting (31 July), and hyperphagia, from fruiting to the approximate start date of reduced activity in preparation for denning (15 October). Only bears with data spanning at least 90% of the duration of a given season were included in the analyses.

I estimated seasonal home ranges using fixed kernel with plug-in bandwidth method (Duong and Hazelton 2003, Gitzen et al. 2006) and implemented analyses using the ks package

(Duong 2010) in program R (R Development Core Team 2009). I used the multivariate plug-in function with the Sum of Asymptotic Mean Squared Error pilot option (Duong and Hazelton 2003). I defined home range as the polygon resulting from the 95% contour of the utilization distribution, and I generated three response variables to model space use: 1) total home range area (km^2; Area), 2) the amount of overlap (km^2) between a given seasonal home range and human development (HDoverlap), where I defined human development as areas within a 50-m buffer of any human structures, and 3) the mean human density within the home range (HDdensity). I used an address layer available for Pitkin County to generate point density of addresses per 1 km^2 (range 0 – 627), and calculated the mean density value within the seasonal home range of each bear.

I modeled the three space-use response variables as a function of bear age (continuous) and gender, season (pre-hyperphagia and hyperphagia), and the quality of natural forage production (FoodYr). The latter was a qualitative index of good (2005, 2006, 2008, and 2010) and poor (2007 and 2009) mast-production years assessed from observed annual yields of the main masting plants in the study area and confirmed by local wildlife managers. I natural-log transformed all responses to stabilize the variance and used linear mixed-effects models in nlme package in R (Pinheiro et al. 2010), where I modeled bears as a random effect. I ran all possible additive models, including an interaction term between season and food year for a total of 20 models, and I ranked models using AICc (Burnham and Anderson 2002). I model averaged the parameter estimates and evaluated fixed effects by examining whether the 95% CI of the model-averaged parameter estimates overlapped zero. I estimated the amount of variability explained by each model as the squared correlation between fitted and observed values. Lastly, to assess model prediction ability I conducted 10-fold cross validation, where I subset the data based on number of bears such that 10 % of the bears were kept as test dataset and the rest as training dataset (Konishi and Kitagawa 2008). I used the fixed effect parameter estimates obtained from the global (most parameterized) model based on the training set to calculate the Root Mean Squared Error (RMSE) of observed and fitted values for each training and test set. I conducted 1000 iterations, each time randomly selecting different test and training sets, and report the mean RMSE of the test and training sets.

Activity patterns

I developed a new approach to analyze activity patterns and model its changes in relation to individual and environmental covariates. I fitted a sine curve to the mean counts of up-and-down head movements (y) and extracted the parameters related to number of peaks (b) and x-axis shift (c) for the i_{th} bear, j_{th} year, and k_{th} season according to the equation:

$$y_{ijk} = a_{ijk} \sin(b_{ijk}\, x - c_{ijk}) + d_{ijk}$$

where $|a|$ is amplitude, x is time from 0 – 24 hours represented in degrees radian, and d is an offset parameter about the y-axis. I focused analyses on the b and c parameters because they allowed respective inference on the number and timing of activity bouts within the 24-hour period (2π). For example, nocturnal activity patterns could be described with $b \sim 1$ and $c \sim -\pi/2$, or one activity bout around midnight (Figure 1.1, dashed grey line). Conversely, crepuscular activity patterns can be described with $b \sim 2$ and $c \sim \pi/2$, or a bimodal curve with activity bouts in early morning and late evening (Figure 1.1, dashed black line). I used the non-linear least squared (nls) function in R, while bounding a and d between 0 and 255, b between 0 and 5, and c between $-\pi/2$ and $\pi/2$. I modeled number of daily peaks and timing of activity bouts as response variables to individual and environmental covariates as described above; I used mixed-effects models with individuals as a random effect, ranked models using AICc, evaluated fixed-effects based on 95% CI of model-averaged parameter estimates, and assessed the amount of variability explained by correlating fitted and observed values. I also assessed model fit using the same cross-validation procedures described above.

Survival and reproduction

I summarized the number of bear mortalities into three categories: harvest, conflict management, and unknown and used known-fate models in program MARK (White and Burnham 1999) to estimate subadult (1-3 years old) and adult (≥4 years old) survival. I created yearly encounter histories with 15 bi-monthly time intervals from April 16 to November 30 and used staggered entry to include bears captured from 2005 – 2010. I assumed survival during the denning period, December 1 – April 15, was 1 (Hebblewhite et al. 2003, Lee and Vaughan 2005). I censured bears that went missing, dropped their collars, or were removed from the resident population due to translocation. If a bear was recaptured, or if it returned to the study area after translocation, I incorporated it into the analysis. Because some translocated bears returned to my population, I did not consider translocations a mortality event (Hebblewhite et al. 2003), although approximately 40% of the translocated bears (*n* = 13) died while away from Aspen. Hence, I acknowledge my survival estimates are likely an overestimate. I modeled effects of gender, age, season (pre-hyperphagia or hyperphagia), food year (good or poor), and season*food year interaction on survival, ranked models using AICc, and model-averaged parameter estimates to calculate unconditional survival estimates (Burnham and Anderson 2002).

To assess reproductive output, I determined upon capture if females were reproductively active by presence of cubs at capture or at the den (no females showed lactation evidence without having cubs present). I assigned cub count as litter size, and I modeled mean litter size with age of sows and food year during conception using generalized linear models (glm in R, Poisson family) and examined their correlations.

Results

Space use

I used 57 seasonal home ranges from 23 bears to model space use. Models explained on average 60 - 66% of the variability in the data, depending on the response variable (ln(Area): $\overline{r^2} = 0.60$, $SE = 0.01$; ln(HDoverlap): $\overline{r^2} = 0.62$, $SE = 0.01$; ln(HDdensity): $\overline{r^2} = 0.66$, $SE = 0.02$; full model output, Appendix 1.1). Cross validation results were similar across the response variables with test sets having larger mean RMSE compared to the training sets (ln(Area): $RMSE_{train} = 0.89$, $RMSE_{test} = 0.96$; ln(HDoverlap): $RMSE_{train} = 0.56$, $RMSE_{test} = 0.63$; ln(HDdensity): $RMSE_{train} = 1.32$, $RMSE_{test} = 1.54$). When modeling ln(Area) as a response, gender appeared in all top models carrying > 99% of the weight, and had a relatively strong effect in each of the models ($\hat{\bar{\beta}}_{males} = 1.26$, $SE = 0.34$; Tables 1.1A.1-2, Appendix 1.1). Male home ranges were larger than females and smallest during hyperphagia season in poor food years (Figure 1.2). Gender and age were always important in explaining variation in the degree of overlap between home range and human development (Tables 1.1A.3-4, Appendix 1.1), where males and younger bears had greater overlap with human development ($\hat{\bar{\beta}}_{males} = 0.55$, $SE = 0.20$; $\hat{\bar{\beta}}_{age} = -0.034$, $SE = 0.016$). Lastly, when modeling the mean human density within bear home ranges, I found strong support for age and food year effects in each of the models (Tables 1.1A.5-6, Appendix 1.1), with bears having greater mean human density in their home ranges in poor ($\bar{x} = 153.6$, $SE = 34.2$) compared to good ($\bar{x} = 19.6$, $SE = 3.6$) natural food production years and with younger bears having greater mean human density in their home ranges ($\hat{\bar{\beta}}_{age} = -0.080$, $SE = 0.038$).

Activity patterns

I fitted 61 seasonal activity curves for 25 bears to extract the number of activity peaks (*b*) and their timing in the 24-hour period (*c*) and model activity. Models explained up to 52% of the variability in the data and on average, explained more variability in *c* ($\overline{r^2}$ = 0.29, *SE* = 0.07) compared to *b* ($\overline{r^2}$ = 0.14, *SE* = 0.03; full model output, Appendix 1.2). Cross validation results showed better fit when modeling *b* as a response ($RMSE_{train}$ = 0.44, $RMSE_{test}$ = 0.48) compared to *c* ($RMSE_{train}$ = 0.80, $RMSE_{test}$ = 0.96). Season was the only important predictor of number of peaks in activity (*b*; Tables 1.2A.1-2, Appendix 1.2), where modality increased during pre-hyperphagia ($\hat{\bar{\beta}}_{pre-hyperphagia}$ = 0.41, *SE* = 0.014). Season, food year, and season*food year interaction were strong predictors of timing of daily activity (*c*; Tables 1.2A.3-4, Appendix 1.2). Unconditional parameter estimates for season and food year were positive ($\hat{\bar{\beta}}_{pre-hyperphagia}$ = 1.92, *SE* = 0.42; $\hat{\bar{\beta}}_{good\_foodyr}$ = 1.66, *SE* = 0.28), indicating that bears were more crepuscular during pre-hyperphagia and in good food production years. Parameter estimate for season*food year was negative ($\hat{\bar{\beta}}_{pre-hyperphagia\_good\_foodyr}$ = -1.60, *SE* = 0.49), with bears becoming more nocturnal during hyperphagia in poor natural food-production years (Figure 1.3).

Survival and reproduction

I recorded 6 mortalities from harvest (*n* = 1), conflict management (*n* = 4), and unknown (*n* = 1) causes. I included 63 encounter histories for 39 bears in the known-fate models, and I censured 27 bears due to dropped collars or translocations. Survival was lower in poor food years for all gender and age combinations, where model-averaged estimates ranged from a low of 0.675 (*SE* = 0.158) for subadult males to a high of 0.718 (*SE* = 0.117) for adult females (Table 1.1). Food year was an important factor explaining variability in survival and appeared in all top models carrying > 98% of the weight (full model output in Table 1.3A.1, Appendix 1.3).

I monitored 19 litters totaling 42 cubs that were produced by 13 females of ages 3 – 20 years. Litter size varied from 1 – 3 cubs ($\bar{x}$ = 2.21, *SE* = 0.18), and all litters with 1 cub were born to females ≤ 5 years old. There was no relationship between mean litter size based on conception in good ($\bar{x}$ = 2.4, *SE* = 0.16) versus poor ($\bar{x}$ = 2.0, *SE* = 0.20) years, nor between litter size and female's age at conception ($\hat{\beta}_{age}$ = 0.02, *SE* = 0.03) or food year ($\hat{\beta}_{poor\_foodyr}$ = -0.14, *SE* = 0.37).

Discussion

In this study I examined the degree of synanthropy of urban black bears and found that bears demonstrated temporal fluctuations in space-use and activity-pattern behaviors that were strongly dependent on the availability of natural food resources. Bears used dense human development areas and were active at night during poor mast production years, but they also demonstrated behavioral plasticity, where in subsequent good food years they reversed their behavior to daytime foraging away from urban areas. Additional supportive evidence showed bears had lower survival in poor food years when they foraged in urban areas, with most mortality being human-caused. Collectively, my data support the fluctuating synanthropy hypothesis.

When bears used urban areas, patterns of space use (smaller home ranges) and activity (nocturnal) were similar to those reported for black bears and other species. However, the patterns of fluctuating synanthropy observed in this study contradicted results from a detailed study of urban black bear ecology in Lake Tahoe, Nevada USA, in which bears appeared to have an irreversible dependency on human foods that rapidly changed their ecology (Beckmann and Berger 2003a). One reason for the difference might be attributed to the landscape context of the two study systems. Lake Tahoe is surrounded by large desert basins that are marginal habitats for bears (Beckmann and Lackey 2004), whereas bear habitats surrounding Aspen are considered one of the most productive in Colorado (Beck 1991). Consequently, Aspen bears have good natural resources to shift back to in good food years, but such resources may not be available to Lake Tahoe bears. Therefore, the landscape matrix in which an urban area is situated is likely to affect the degree of species synanthropy and should be considered when studying its dynamics.

Several authors have suggested that urban areas can serve as sanctuaries for wildlife populations in times of low natural food production, providing a safeguard against mortality, reproduction failure, and overall population decline (Hristienko and McDonald 2007, Waite et al. 2007). For example, in India, urban Hanuman langur (*Seemnopithecus entellus*) populations avoided massive die offs during La Niña drought events by feeding on anthropogenic foods (Waite et al. 2007); in Poland black-billed magpies (*Pica pica*) with access to anthropogenic foods had lower nest failure during inclement weather (Jarzek 2001); and in California, USA, urban kit foxes (*Vulpes macrotis*) were in better physiological condition than their rural counterparts during a 2-year drought event (Gehrt et al. 2010). The fact that black bears in my study increased their degree of synanthropy during poor food years may at first glance lend support for such a city-sanctuary hypothesis. However, urban areas may not serve as sanctuaries for bears if survival is reduced due to increased human-caused mortality.

Adult female survival of black bears is generally high, less variable, is believed to influence population growth more than recruitment (Freedman et al. 2003, Mitchell et al. 2009), and evidence suggests it is similar between good and poor natural food years (Kasbohm et al. 1996, Schrage and Vaughan 1998, but see Hellgren et al. 2005). In my study, survival of adult female urban bears in good food years (0.98) was comparable to those of wildland bears in south-central Colorado (range 0.92 – 1.0; Beck 1991), and in Rocky Mountain National Park in north-central Colorado (1.0, *SE* = 0.0; Baldwin and Bender 2009). Adult female survival was lower for my study bears in poor food years (0.76), but estimates were similar to female bears occupying residential areas in Florida, USA (0.776, *SE* = 0.074, Hostetler et al. 2009) and all management bears (i.e., male and female bears defined as problem bears) in Alberta, Canada (0.66, *SE* = 0.113, Hebblewhite et al. 2003). Although I did not concurrently monitor wildland bear populations, the fact that 1) survival in good years was comparable to published estimates of survival from wildland populations, 2) adult survival is a less variable demographic parameter with some studies showing that it is similar in poor natural food years, and 3) population growth is sensitive to changes in adult female survival suggests that low survival rates of females in urban areas in poor natural food years possibly contributes to reduced fitness of the population. Consequently, Aspen might not serve as a city sanctuary but rather as a population sink (Hostetler et al. 2009).

During poor natural food years, mortality of bears increased and was largely human-caused resulting from conflicts near human development (Mattson et al. 1992, Ryan et al. 2007). Managers commonly believe that removing bears is necessary because urban bears are irreversibly habituated, food-conditioned, and dependent on human resources. My conclusion that urban bears can demonstrate behavioral plasticity and are overall fluctuating synanthropes challenges the concept they are irreversible synanthropes. I demonstrated that the same individuals, who in poor food years foraged in town on anthropogenic resources, foraged on natural foods outside of urban areas in subsequent good food years. Similar patterns were reported for herring gulls (*Larus agrentatus*) that switched from foraging on mussels to foraging on garbage in inclement weather years when prey in intertidal areas was difficult to obtain

(Pierotti and Annett 1991). Because urban areas can attract bears in poor food years, a time when the population growth may already be stressed, removal of fluctuating synanthrope bears could negatively affect the population locally or regionally, depending on the attraction distance of urban areas. There is no doubt that to minimize management risks to people and bears removal of synanthropic bears will be required in some cases; however, increased tolerance might be called for if management goals are to sustain the population and avoid conflict-caused mortalities.

Alternatives to change bear behavior and degree of synanthropy are to increase costs or reduce benefits of foraging in urban areas. Aversive conditioning is a non-lethal method used to increase costs of foraging (e.g., Beckmann et al. 2004, Mazur 2010), but such methods are expensive, lack popularity with urban stakeholders, and are considered short-term solutions (Fall and Jackson 2002). A growing management consensus is that long-term solutions entail reducing the availability of anthropogenic attractants, or reducing benefits of foraging. Most examples of such successes are within natural reserves and agricultural villages. The closure of refuse pits resulted in a distributional shift away from these areas for spotted hyenas (*Crocuta crocuta*) in Masai Mara reserve in Kenya (Kolowski and Holekamp 2007) and for grizzly bears (*Ursus arctos*) in Yellowstone National Park, USA (Craighead 1995), and increased sanitation and proper disposal of poultry carcasses in agricultural villages in Israel resulted in distributional shifts of red fox (*Vulpes vulpes*) to nearby pristine areas (Bino et al. 2010). Additional studies are needed to test the effects of reduction of anthropogenic attractants on the behavior and degree of synanthropy of urban wildlife. However, it is generally agreed that such an approach is warranted to reduce synanthropy in wildlife and aid in reducing urban human-wildlife conflicts (Fall and Jackson 2002, Spencer et al. 2007).

A first step in successfully removing anthropogenic attractants is identifying key attractants. The more challenging second step is devising effective management tools directed at people to minimize attractants. For example, in my study I backtracked bears and found garbage as the main anthropogenic resource for bears (S. Baruch-Mordo and D. Lewis, unpublished data). I then tested the efficacy of education and enforcement management tools in reducing garbage availability, and found current efforts to be ineffective (Baruch-Mordo et al. 2011). Consequently, I joined others in calling for collaboration with social scientists to develop more effective tools directed at people (Gore et al. 2008, Baruch-Mordo et al. 2011). While it may not be possible to completely eliminate anthropogenic attractants, a reduction beyond a threshold for which foraging in urban areas is no longer beneficial should be attempted. Ecological theory on optimal foraging, resource matching, and giving up densities can assist in determining such thresholds (Shochat 2004, Mitchell and Powell 2007, Rodewald and Shustack 2008).

Table 1.1. Unconditional annual survival estimates (*SE*) for urban black bears in Aspen, Colorado from 2005 – 2010. Gender-specific subadult (1-3 years old) and adult (≥ 4 years old) survival was calculated for poor and good natural food production years using known fate models in program MARK.

	Males	Females
	Poor food year	
Subadults	0.675 (0.154)	0.707 (0.141)
Adults	0.684 (0.137)	0.718 (0.117)
	Good food year	
Subadults	0.998 (0.020)	0.998 (0.017)
Adults	0.998 (0.019)	0.998 (0.016)

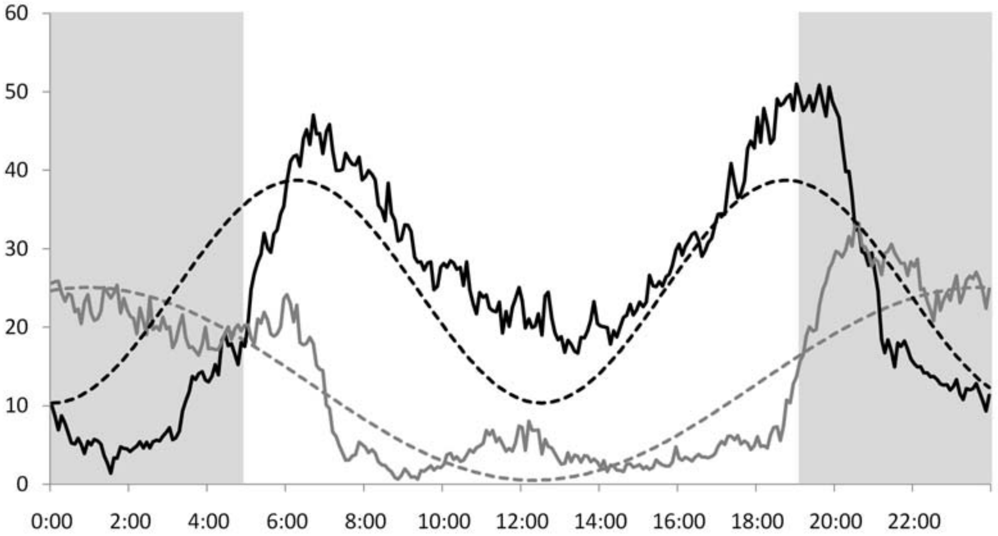

Figure 1.1. Example sine curves fitted to describe daily activity patterns in hyperphagia season in good (black) and poor (grey) natural food production years, where 0 - 24 hours correspond to a scale of 0 - 2π in radian degrees. Solid lines are the head up-down movements recorded at 5-min intervals and averaged across season, and dashed lines are the fitted sine curves with *b* (number of peaks in 24 hours) and *c* (timing of activity peaks within the 24 hours) parameters of 1.92 and 1.57 in a good food year and 1.05 and -1.32 in a poor food year, respectively. Patterns demonstrate crepuscular activity with two peaks (black) and nocturnal activity with a single peak (grey).

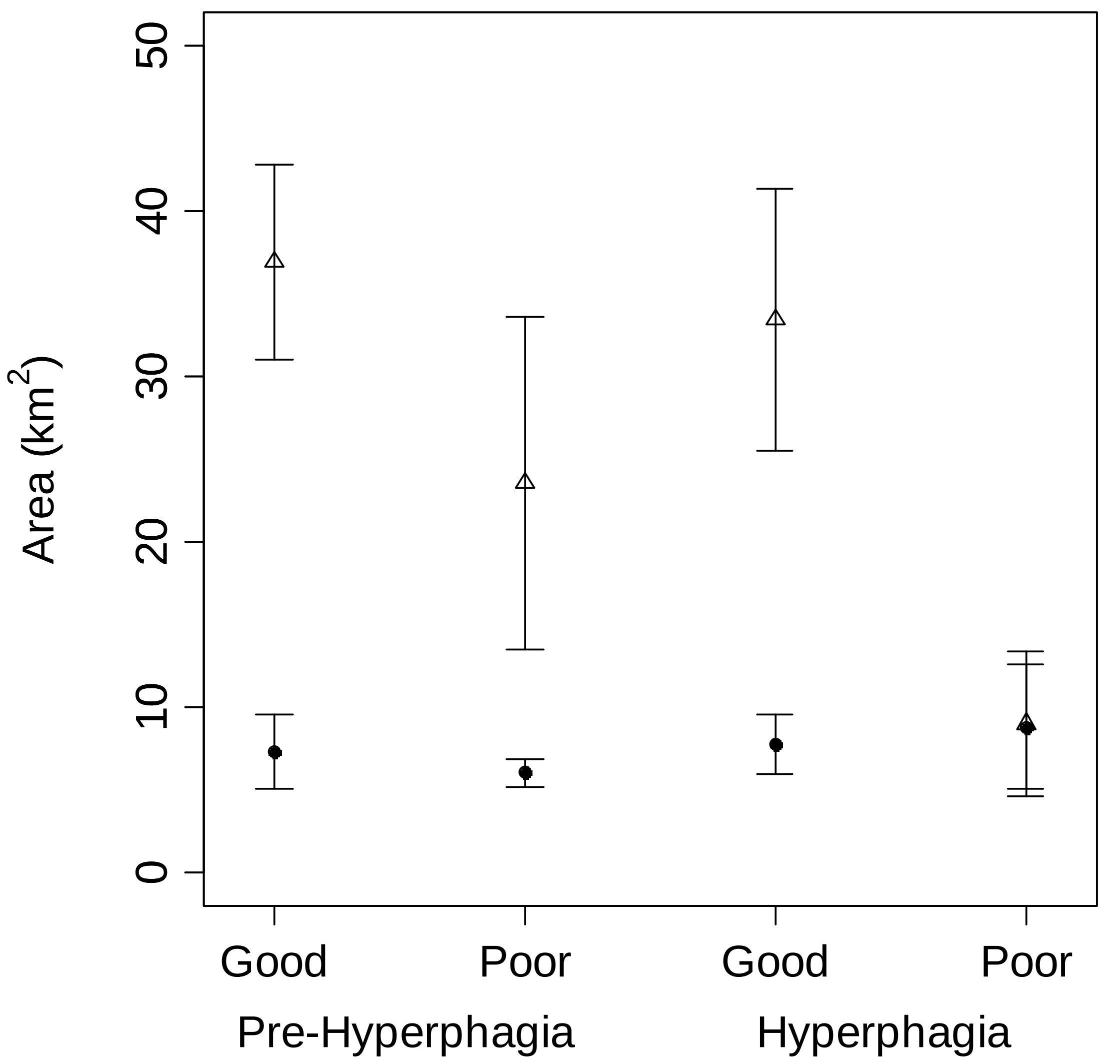

Figure 1.2. Average seasonal home range areas in km^2 (± 1 *SE*) from 2005-2010 for male (open triangle) and female (solid circle) urban black bears in Aspen, Colorado. Home ranges were calculated as the 95% contour of a utilization distribution estimated using fixed kernel density with a plug-in bandwidth.

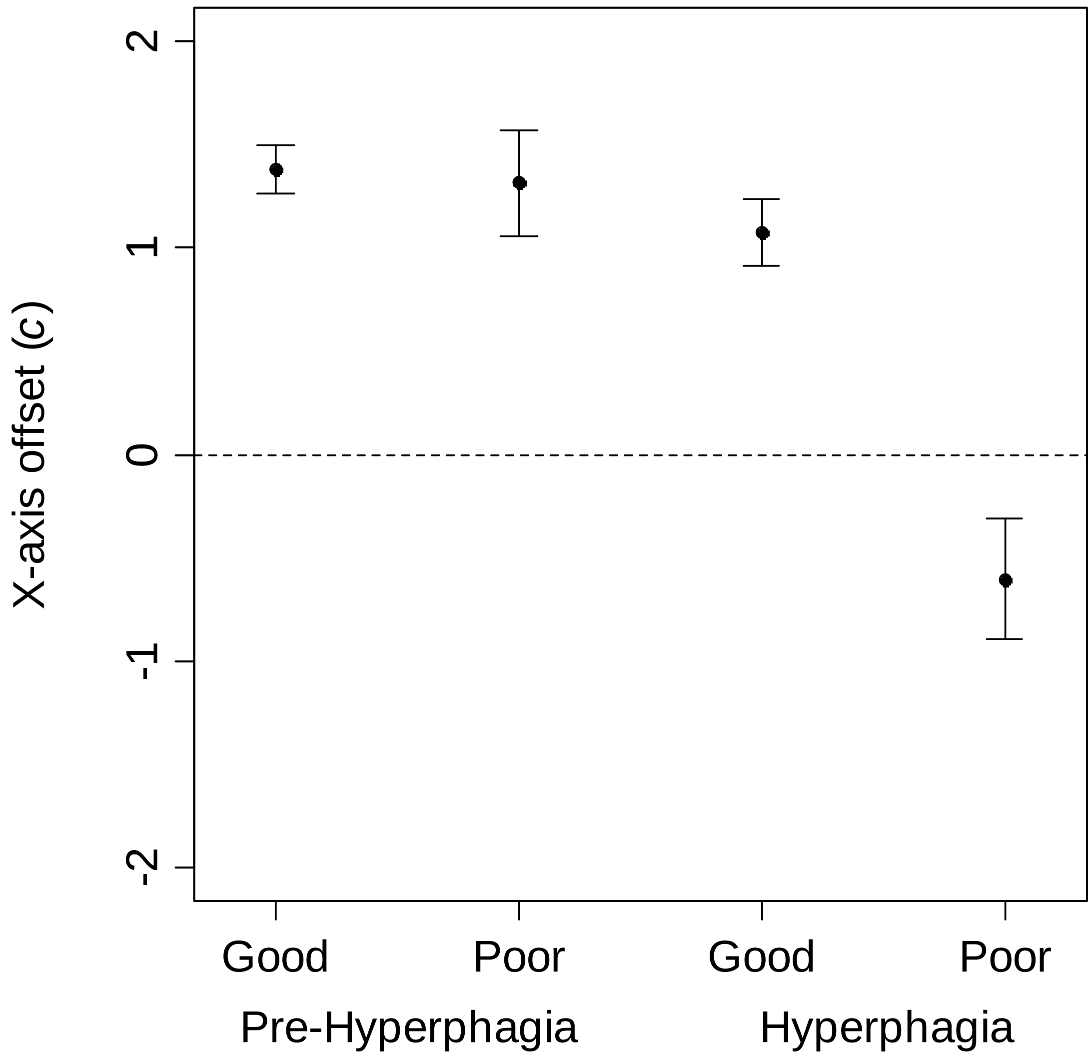

Figure 1.3. Mean (± 1 *SE*) of the x-axis offset shape parameter (*c*) for a sine curve fitted to seasonal (Pre-Hyperphagia, Hyperphagia) activity data of urban black bears from Aspen, Colorado, USA, in good and poor natural food years from 2005-2010. Negative values indicate nocturnal activity and positive values indicate diurnal activity.

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APPENDIX 1.1. FULL MODEL SET AND MODEL AVERAGED PARAMETER RESULTS FOR SPACE USE MODELING

Tables 1.1A.1 – 6. Full model set results (Tables 1.1A.1, 1.1A.3, and 1.1A.5) and model averaged parameter estimates (Tables 1.1A.2, 1.1A.4, and 1.1A.6) for modeling of space use of urban black bears in Aspen, Colorado, USA. Response variables include natural-log transformed seasonal home range area (km^2; ln(Area); Tables 1.1A.1-2), amount of overlap of home range with human development (km^2; ln(HD overlap); Tables 1.1A.3-4), and mean human density within the home range (number of addresses/km^2; ln(HD density); Tables 1.1A.5-6). Home ranges were calculated as the 95% contour of a utilization distribution estimated using kernel density with a plug-in bandwidth approach. Seasons were defined as pre-hyperphagia (April 15 – July 31) and hyperphagia (August 1 – October 15), and natural food production years (FoodYr) were defined as poor or good based on qualitative assessment of yield of important mast producing plants in the study area.

Table 1.1A.1. Model set results, response = ln(Area).

Model	r^{2*}	$k^{\dagger}$	AICc	ΔAICc	*w*
Gender + FoodYr	0.57	5	158.86	0.00	0.23
Gender + Season + FoodYr + Season*FoodYr	0.64	7	159.32	0.46	0.18
Gender	0.54	4	159.89	1.03	0.13
Gender + Season + FoodYr	0.60	6	160.47	1.61	0.10
Gender + Age + FoodYr	0.57	6	160.85	1.98	0.08
Gender + Season	0.58	5	161.17	2.31	0.07
Gender + Age + Season + FoodYr + Season*FoodYr	0.64	8	161.29	2.43	0.07
Gender + Age	0.54	5	161.59	2.72	0.06

Gender + Age + Season + FoodYr	0.60	7	162.36	3.50	0.04
Gender + Age + Season	0.58	6	162.73	3.87	0.03
Intercept only	0.59	3	168.74	9.88	0.00
FoodYr	0.61	4	169.33	10.47	0.00
Season	0.62	4	170.38	11.52	0.00
Age	0.58	4	170.43	11.56	0.00
Season + FoodYr + Season*FoodYr	0.66	6	170.45	11.59	0.00
Season + FoodYr	0.63	5	171.18	12.32	0.00
Age + FoodYr	0.60	5	171.22	12.36	0.00
Age + Season	0.61	5	172.02	13.16	0.00
Age + Season + FoodYr + Season*FoodYr	0.66	7	172.35	13.49	0.00
Age + Season + FoodYr	0.63	6	173.05	14.18	0.00

* Amount of variability explained by each model (r^2) was calculated as the squared correlation between fitted and observed values.

† Number of parameters (*k*) was calculated as the number of fixed-effects parameters plus three for the intercept, random effects, and overall variance.

Table 1.1A.2. Model averaged parameter estimates (*SE*), response = ln(Area).

Parameter	Estimate (*SE*)
Intercept	1.470 (0.364)*
Gender (Males)	1.260 (0.343)*
Age	-0.006 (0.009)
Season (Pre-Hyperphagia)	0.270 (0.229)
Food Year (Good)	0.369 (0.221)
Season * Food Year	-0.224 (0.205)

* Indicates 95% CI did not overlap zero.

Table 1.1A.3. Model set results, response = ln(HD overlap).

Model	r^2	*k*	AICc	ΔAICc	*w*
Gender + Age + FoodYr	0.63	6	101.13	0.00	0.39
Gender + Age + Season + FoodYr	0.65	7	102.82	1.69	0.17
Gender + Age	0.60	5	103.56	2.42	0.11
Gender + FoodYr	0.58	5	104.14	3.01	0.09
Gender + Age + Season + FoodYr + Season*FoodYr	0.65	8	105.53	4.39	0.04
Gender	0.54	4	105.56	4.43	0.04
Gender + Age + Season	0.60	6	105.59	4.45	0.04
Age + FoodYr	0.64	5	105.98	4.85	0.03
Gender + Season + FoodYr	0.60	6	106.30	5.16	0.03
Gender + Season	0.55	5	107.82	6.69	0.01
Age + Season + FoodYr	0.65	6	107.99	6.86	0.01
Gender + Season + FoodYr + Season*FoodYr	0.60	7	108.90	7.76	0.01
FoodYr	0.63	4	108.92	7.79	0.01
Age	0.62	4	109.41	8.27	0.01
Age + Season + FoodYr + Season*FoodYr	0.66	7	110.57	9.43	0.00
Season + FoodYr	0.64	5	111.18	10.05	0.00
Intercept only	0.60	3	111.45	10.32	0.00
Age + Season	0.62	5	111.66	10.53	0.00
Season + FoodYr + Season*FoodYr	0.64	6	113.64	12.51	0.00
Season	0.60	4	113.76	12.62	0.00

* Amount of variability explained by each model (r^2) was calculated as the squared correlation between fitted and observed values.

† Number of parameters (*k*) was calculated as the number of fixed-effects parameters plus three for the intercept, random effects, and overall variance.

Table 1.1A.4. Model averaged parameter estimates (*SE*), response = ln(HD overlap).

Parameter	Estimate (*SE*)
Intercept	1.068 (0.287)
Gender (Males)	0.553 (0.205)*
Age	-0.034 (0.016)*
Season (Pre-Hyperphagia)	0.035 (0.056)
Food Year (Good)	-0.242 (0.124)
Season * Food Year	0.002 (0.016)

* Indicates 95% CI did not overlap zero.

Table 1.1A.5. Model set results, response = ln(HD density).

Model	r^2	*k*	AICc	ΔAICc	*w*
Age + FoodYr	0.75	5	189.50	0.00	0.37
Age + Season + FoodYr	0.76	6	191.02	1.52	0.17
Gender + Age + FoodYr	0.75	6	191.84	2.34	0.11
Age + Season + FoodYr + Season*FoodYr	0.77	7	192.49	3.00	0.08
FoodYr	0.69	4	192.56	3.07	0.08
Gender + Age + Season + FoodYr	0.76	7	193.53	4.03	0.05
Season + FoodYr	0.72	5	193.59	4.09	0.05
Gender + FoodYr	0.69	5	194.73	5.23	0.03
Gender + Age + Season + FoodYr + Season*FoodYr	0.77	8	195.12	5.63	0.02

Season + FoodYr + Season*FoodYr	0.74	6	195.12	5.63	0.02
Gender + Season + FoodYr	0.72	6	195.96	6.46	0.01
Gender + Season + FoodYr + Season*FoodYr	0.74	7	197.61	8.11	0.01
Intercept only	0.51	3	216.29	26.79	0.00
Age	0.56	4	216.68	27.19	0.00
Season	0.54	4	216.93	27.43	0.00
Gender	0.49	4	217.59	28.09	0.00
Age + Season	0.58	5	217.62	28.13	0.00
Gender + Age	0.55	5	218.21	28.72	0.00
Gender + Season	0.53	5	218.63	29.13	0.00
Gender + Age + Season	0.57	6	219.50	30.00	0.00

* Amount of variability explained by each model (r^2) was calculated as the squared correlation between fitted and observed values.

† Number of parameters (*k*) was calculated as the number of fixed-effects parameters plus three for the intercept, random effects, and overall variance.

Table 1.1A.6. Model averaged parameter estimates (*SE*), response = ln(HD density).

Parameter	Estimate (*SE*)
Intercept	4.89 (0.581)*
Gender (Males)	0.042 (0.125)
Age	-0.080 (0.038)*
Season (Pre-Hyperphagia)	-0.175 (0.182)
Food Year (Good)	-1.82 (0.312)*
Season * Food Year	0.082 (0.107)

* Indicates 95% CI did not overlap zero.

APPENDIX 1.2. FULL MODEL SET AND MODEL AVERAGED PARAMETER RESULTS FOR ACTIVITY PATTERNS MODELING

Tables 1.2A.1 – 4. Full model set results (Tables 1.2A.1, and 1.2A.3) and model averaged parameter estimates (Tables 1.2A.2, and 1.2A.4) for modeling of activity patterns of urban black bears in Aspen, Colorado, USA. Response variables include number of peaks (*b*; Tables 1.2A.1-2) and timing (*c*; Tables 1.2A.3-4) of daily activity patterns, and were extracted by fitting a sine curve to mean count of up-down head movements for each season, year, and bear. Seasons were defined as pre-hyperphagia (April 15 – July 31) and hyperphagia (August 1 – October 15), and natural food production years (FoodYr) were defined as poor or good based on qualitative assessment of yield of important mast producing plants in the study area.

Table 1.2A.1. Model set results, response = *b* number of activity peaks within a 24-hour period.

Model	r^{2*}	$k^{\dagger}$	AICc	ΔAICc	*w*
Season + FoodYr	0.20	5	84.26	0.00	0.27
Season	0.16	4	84.60	0.35	0.22
Season + FoodYr + Season*FoodYr	0.21	6	86.30	2.04	0.10
Gender + Season + FoodYr	0.20	6	86.70	2.44	0.08
Age + Season + FoodYr	0.20	6	86.71	2.45	0.08
Gender + Season	0.16	5	86.96	2.71	0.07
Age + Season	0.16	5	86.97	2.71	0.07
Age + Season + FoodYr + Season*FoodYr	0.21	7	88.83	4.57	0.03
Gender + Season + FoodYr + Season*FoodYr	0.21	7	88.83	4.58	0.03
Gender + Age + Season + FoodYr	0.20	7	89.25	5.00	0.02
Gender + Age + Season	0.16	6	89.41	5.16	0.02
Gender + Age + Season + FoodYr + Season*FoodYr	0.21	8	91.47	7.21	0.01

FoodYr	0.06	4	91.74	7.48	0.01
Intercept only	0.18	3	93.21	8.95	0.00
Age + FoodYr	0.06	5	93.87	9.61	0.00
Gender + FoodYr	0.06	5	94.07	9.81	0.00
Gender	0.00	4	95.19	10.94	0.00
Age	0.00	4	95.20	10.94	0.00
Gender + Age + FoodYr	0.06	6	96.32	12.06	0.00
Gender + Age	0.01	5	97.38	13.12	0.00

* Amount of variability explained by each model (r^2) was calculated as the squared correlation between fitted and observed values.

† Number of parameters (*k*) was calculated as the number of fixed-effects parameters plus three for the intercept, random effects, and overall variance.

Table 1.2A.2. Model averaged parameter estimates (*SE*), response = *b* number of activity peaks within a 24-hour period.

Parameter	Estimate (*SE*)
Intercept	1.335 (0.121)*
Gender (Males)	0.001 (0.030)
Age	0.000 (0.003)
Season (Pre-Hyperphagia)	0.414 (0.141)*
Food Year (Good)	0.129 (0.093)
Season * Food Year	-0.026 (0.047)

* Indicates 95% CI did not overlap zero.

Table 1.2A.3. Model set results, response = *c* timing of activity within a 24-hour period.

Model	r^2	*k*	AICc	ΔAICc	*w*
Season + FoodYr + Season*FoodYr	0.50	6	162.85	0.00	0.47
Age + Season + FoodYr + Season*FoodYr	0.51	7	164.31	1.47	0.23
Gender + Season + FoodYr + Season*FoodYr	0.51	7	164.75	1.91	0.18
Gender + Age + Season + FoodYr + Season*FoodYr	0.52	8	165.85	3.00	0.10
Season + FoodYr	0.41	5	170.85	8.00	0.01
Gender + Season + FoodYr	0.41	6	172.69	9.84	0.00
Age + Season + FoodYr	0.41	6	172.82	9.97	0.00
Gender + Age + Season + FoodYr	0.42	7	174.45	11.60	0.00
FoodYr	0.29	4	179.19	16.34	0.00
Gender + FoodYr	0.31	5	180.38	17.53	0.00
Age + FoodYr	0.29	5	181.56	18.72	0.00
Gender + Age + FoodYr	0.31	6	182.77	19.93	0.00
Season	0.17	4	189.12	26.28	0.00
Gender + Season	0.19	5	189.70	26.86	0.00
Age + Season	0.17	5	191.18	28.34	0.00
Gender + Age + Season	0.20	6	191.40	28.56	0.00
Gender	0.04	4	197.48	34.64	0.00
Intercept only	0.23	3	197.96	35.11	0.00
Gender + Age	0.05	5	199.80	36.95	0.00
Age	0.00	4	200.23	37.39	0.00

* Amount of variability explained by each model (r^2) was calculated as the squared correlation between fitted and observed values.

† Number of parameters (*k*) was calculated as the number of fixed-effects parameters plus three

for the intercept, random effects, and overall variance.

Table 1.2A.4. Model averaged parameter estimates (*SE*), response = *c* timing of activity within a 24-hour period

Parameter	Estimate (*SE*)
Intercept	-0.511 (0.255)*
Gender (Males)	-0.060 (0.082)
Age	-0.008 (0.009)
Season (Pre-Hyperphagia)	1.916 (0.421)*
Food Year (Good)	1.663 (0.278)*
Season * Food Year	-1.595 (0.487)*

* Indicates 95% CI did not overlap zero.

APPENDIX 1.3. FULL MODEL SET AND RESULTS FROM KNOWN-FATE SURVIVAL MODELING.

Table 1.3A.1. Full model output from program MARK for known-fate models estimating survival of urban black bears in Aspen, Colorado, USA. Seasons were defined as pre-hyperphagia (April 15 – July 31) and hyperphagia (August 1 – October 15), and natural food production years (FoodYr) were defined as poor or good based on qualitative assessment of yield of important mast producing plants in the study area.

Model	*k**	AICc	ΔAICc	*w*	Model Likelihood
Season + FoodYr	4	62.44	0.00	0.24	1.00
FoodYr	3	62.99	0.55	0.18	0.76
Gender + Season + FoodYr	5	64.15	1.72	0.10	0.42
Age + Season + FoodYr	5	64.41	1.97	0.09	0.37
Season + FoodYr + Season*FoodYr	5	64.47	2.03	0.09	0.36
Gender + FoodYr	4	64.80	2.37	0.07	0.31
Age + FoodYr	4	65.00	2.57	0.07	0.28
Gender + Age + Season + FoodYr	6	66.16	3.72	0.04	0.16
Gender + Season + FoodYr + Season*FoodYr	6	66.20	3.76	0.04	0.15
Age + Season + FoodYr + Season*FoodYr	6	66.45	4.02	0.03	0.13
Gender + Age + FoodYr	5	66.84	4.40	0.03	0.11
Gender + Age + Season + FoodYr + Season*FoodYr	7	68.21	5.77	0.01	0.06
Season	3	71.08	8.65	0.00	0.01
Intercept only	2	71.24	8.80	0.00	0.01

Gender + Season	4	72.65	10.21	0.00	0.01
Gender + Age + Season	4	72.65	10.21	0.00	0.01
Gender	3	72.89	10.45	0.00	0.01
Age + Season	4	73.10	10.66	0.00	0.00
Age	3	73.26	10.82	0.00	0.00
Gender + Age	4	74.91	12.48	0.00	0.00

* Number of parameters (*k*) was calculated as the number of parameters plus two for the intercept and overall variance.

CHAPTER 2

THE CARROT OR THE STICK? EVALUATION OF EDUCATION AND ENFORCEMENT AS MANAGEMENT TOOLS FOR HUMAN-WILDLIFE CONFLICTS

Introduction

In recent years, several authors called upon the conservation community to apply evidence-based conservation in order to maximize the use of limited resources, direct policy, and advance the field of conservation biology (Sutherland et al. 2004, Ferraro and Pattanayak 2006, Pullin and Knight 2009). This call for evidence-based decision-making continues to resonate and was reiterated recently in the May 2010 issue of *Frontiers in Ecology and the Environment* (Cook et al. 2010). This is especially true for the growing discipline of human-wildlife conflict (Conover 2001, Fall and Jackson 2002, Treves and Karanth 2003, Woodroffe et al. 2005), where, despite the potentially grave implications to public safety and wildlife populations, management is sometimes administered based on personal experience and expert opinion rather than evaluation. If substantial resources are expended with little impact, then conservation practitioners risk a decrease in agency credibility, an increase in public frustration, and ultimately hindrance to long-term solutions to human-wildlife conflicts (Messmer 2009). Conservation tools to resolve human-wildlife conflicts are traditionally targeted at wildlife (e.g., removal, translocation, and aversive conditioning), but often have limited, short-term success (Linnell et al. 1997, Fischer and Lindenmayer 2000, Beckmann et al. 2004, Shivik 2006) and lack social tolerance with stakeholders (Fall and Jackson 2002, Manfredo et al. 2003, Manfredo 2008, Messmer 2009). Therefore, there is a growing recognition among conservation biologists and wildlife managers that long-term solutions should include altering human behaviors (Spencer et al. 2007, Baruch-Mordo et al. 2009). Fall and Jackson (2002, p.89) captured this sentiment stating that "Most 'new' animal problems . . . are ones that human create and could solve by modifying their own behavior…" Public education and enforcement of wildlife-related laws are two primary methods for changing human behaviors, and despite common implementation, little research has been conducted to evaluate whether these strategies are achieving their intended goal of altering behaviors (Gore et al. 2008, Keane et al. 2008).

Education is considered the panacea for conflict resolution and is frequently recommended as a management tool (e.g., Treves and Karanth 2003, Spencer et al. 2007, Tchamba 1996). Research evaluating education has focused primarily on changing attitudes, behavioral intents, and knowledge towards wildlife and conflicts (e.g., Dunn et al. 2008, Gore et al. 2008). Unfortunately, there is not always a direct link between attitudes, intents, and knowledge and actual change in behavior (McCleery 2009). Furthermore, studies evaluating the efficacy of education often rely on self-reported data collected via surveys (Baruch-Mordo et al. 2009). As such, these studies can include a self-reporting bias (White et al. 2005) and lack a direct measure of human behavioral change (Baruch-Mordo et al. 2009). Wildlife ordinances and laws are commonly passed to alter human behavior and reduce human-wildlife conflict, and are generally viewed as an important tool in wildlife management and conflict resolution (Peine 2001, Keane et al. 2008). Studies evaluating the efficacy of enforcement have focused to date on enforcement of overfishing in Europe and North America, or of illegal poaching of wildlife in Africa (Keane et al. 2008, Jachmann and Billiouw 1997, Jachmann 2008). In these studies researchers compared enforcement effort to rates of illegal take, but rarely utilized an experimental approach.

In this study I experimentally evaluated public education and law enforcement in a system where humans and black bears (*Ursus americanus*) coexist but commonly come into conflict, and where wildlife agencies and municipalities employ both strategies to directly alter human behavior and reduce human-bear conflicts. Human-bear conflicts are increasing worldwide for many ursids (Knarrum et al. 2006, Hristienko and McDonald 2007, Sangay and Vernes 2008), and considering that wildlife agencies prefer to target management at humans rather than bears (Spencer et al. 2007), the gap in knowledge about the effectiveness of education and enforcement is especially glaring for management of human-bear conflicts. I thus collaborated with the local wildlife agency, municipalities, businesses, and residents, to experimentally test the efficacy of on-site education, a neighborhood-wide Bear Aware education campaign, and two levels of elevated law enforcement in changing human behavior.

Methods

Study Site

I conducted experiments in the city of Aspen and surrounding residential areas of Pitkin County, located in the central Rocky Mountains of Colorado, USA (hereafter collectively referred to as Aspen; Figure 2.1). Aspen is situated at the confluence of four major riparian areas, Maroon, Castle, and Hunter Creeks and the Roaring Fork River, at an elevation ranging from 2,300 – 3,150 m. Vegetation communities include aspen (*Populus tremuloides*), lodgepole (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and spruce (*Picea* spp.)-subalpine fir (*Abies lasiocarpa*) forests with pure and mixed patches of Gambel oak (*Quercus gambelli*), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus virginiana*) shrub communities. The Aspen town core consists of a business district and dense residential areas that gradually change into dispersed residential neighborhoods (Figure 2.1), and the 2007 resident population was 6,403 (Colorado State Demography Office 2009). One third of the 4,354 total housing units in Aspen were either vacant or used for seasonal, recreational, or other uses (U.S. Census Bureau 2000a), and monthly occupancy of residences was highest in July and August based on a 21-year average (Aspen Chamber Resort Association 2009). Fifty-one percent of the population worked in service, sales, and construction industries, and 61% commuted to work via car or public transportation (U.S. Census Bureau 2000b). The city had extensive year-round tourism with >8,800 visitors in 2008 who stayed an average of 5.8 nights (U.S. Census Bureau 2000b). In summary, the human population residing and working in Aspen was temporally dynamic and included first- and second-homeowners, seasonal workers, tourists, and service and construction industry workers that traveled daily to and from town.

Most conflicts between humans and bears in Aspen result from bears feeding on human refuse (S. Baruch-Mordo, unpublished data). Therefore, the city of Aspen and Pitkin County passed ordinances in 1999 and 2001, respectively, mandating the proper storage of any wildlife attractants including trash (City of Aspen Title 12 Solid Waste - Chapter 12.08 Wildlife Protection; Pitkin County Title 6 Health and Safety - Chapter 6.44 Wildlife Protection). Violations of the ordinances were punishable by a fine of up to US $1,000 and/or imprisonment of up to a year. With the exception of residential curbside pickup, the city ordinance required waste to be properly disposed and secured at all times in wildlife-resistant refuse collectors. The city forbade overnight placement of residential trash, and allowed curbside placement only between 0600 and 1800 hours on the day of garbage collection. The county ordinance required waste to be properly disposed and secured in wildlife-proof refuse collectors at all times, and starting in 2007, this included residential, curbside trash. Wildlife-proof containers were always required by the county for human food waste considered edible by wildlife at construction sites, but the city also allowed storage in other containers if emptied at the end of each workday.

Refuse collectors

I define *dumpsters* as large, stationary refuse collectors constructed from metal materials that were either free standing or placed in semi-open or closed enclosures. I define *containers* as smaller capacity, movable refuse collectors mostly constructed from rigid plastic material that were used for curbside pickup.

For dumpsters, different storage designs resulted in differential risk of break-in by bears, and I qualitatively assessed a dumpster's break-in risk using low, medium, and high criteria (Figure 2.2). Low-risk designs were considered most bear-proof and included garbage compactors or enclosures with features such as non-chewable metal doors, airtight construction, and round doorknobs. Medium-risk designs included bolted, encasing metal lids over a freestanding dumpster, or enclosures with wooden doors and closing mechanisms other than a round handle (e.g., locking bars or latches). High-risk designs included freestanding dumpsters or semi-open enclosures allowing bears maximum ability for manipulation and break-in; this also included dumpsters with non user-friendly securing methods (e.g., heavy lids) that led people to frequently leave them unsecured.

On-site education experiment

I conducted the on-site education experiment at communal housing complexes and construction sites. I sampled 68 communal housing complexes, with half (34) randomly selected as treatment, and 42 construction sites with 22 randomly selected as the treatment and 20 as the control (for a detailed description of sample size determination see Appendix 2.1). I applied educational signs in English and Spanish on all approachable sides of treatment dumpsters. Signs had two Colorado Division of Wildlife (CDOW) messages “Garbage kills bears – Stash your trash!", and "Help keep wildlife wild by securing the trash receptacle properly", where I adjusted the former message for construction dumpsters as "Garbage kills bears – No food items!" Signs included colored photos of bears climbing in and out of dumpsters to illustrate their capacity to pursue trash, and a photo of a sow and cub for emotional appeal. I added a website link, that was designed for the experiment and contained information about wildlife ordinances in English and Spanish, what to do regarding violations, and Bear Aware information. I detected only one visit and only to the English version site throughout the experiment.

I sampled dumpsters July-September 2007 for three weeks each in pre- and post-treatment periods. I randomly selected four sampling days during each week for a total of 24 sampling occasions. On each visit I recorded whether the dumpster was in violation (1) or compliance (0) with the ordinances, and whether it was empty or not. A violation at a construction site entailed observing any human food trash in the open construction dumpsters. A violation at a communal housing site consisted of presence of trash items just outside, on top, or near the dumpster, or observing a dumpster that was open, or otherwise improperly secured. Because of the many refuse collector designs (see Refuse Collectors section), I additionally categorized the degree of violation at communal housing dumpsters as low, medium, and high, with low indicating little chance for a bear break-in, medium indicating with some work a bear could break-in, and high indicating a bear could easily obtain the garbage. I implemented a conservative approach where a communal housing dumpster was considered compliant if it was rated as low violation or if it was empty due to assumed recent trash collection; otherwise, dumpsters were considered in violation.

I collected covariate data on: 1) the presence of other signs about proper garbage storage, 2) the number of bear visits to a dumpster based on fresh evidence, and 3) the number of visits by Aspen Police Department (APD) or Pitkin county authorities due to bear incidents. I predicted a reduced treatment effect at sites with a previous educational sign and an enhanced treatment effect at sites with a bear incident and subsequent response by authorities. For communal housing, covariates also included the qualitative dumpster break-in risk and the number of units in the complex. I predicted greater probability of violation at higher-risk dumpsters and at complexes with more units. For construction sites, I included whether or not the site had a separate bear-resistant or bear-proof container for human food waste, and I predicted a greater treatment effect at construction sites without such a container. Finally, as part of a separate study, a survey about attitudes of residents towards bears and preference for management actions was conducted during my experiment at some apartment complexes (Don Carlos et al. 2009). Hence I also incorporated the number of units visited during the survey as a covariate to account for potential negative bias in violations due to increased awareness of human-bear conflicts.

I modeled the probability of violation in communal housing complex and construction site dumpsters as a function of fixed treatment and covariate effects, and a random site effect (PROC GLIMMIX; SAS Institute 2002). I examined correlation of covariates using Variance Inflation Factors (VIF), and used VIF >10 to eliminate correlated covariates (Ott and Longnecker 2001). I estimated model fit with an r^2 equivalent method (Cameron and Windmeijer 1997), as one minus the ratio of sum of squares between the global and intercept-only models. I determined support for an effect by examining whether the 95% confidence interval of each parameter estimate overlapped zero, and I report fixed effect F-test statistics.

Bear Aware education

I conducted the Bear Aware experiment in four residential areas: Cemetery Lane (BA1), lower Red Mountain (BA2), lower Smuggler Mountain (BA3), and Mountain Valley (BA4; Figure 2.1). I randomly assigned addresses in the BA1 and BA2 neighborhoods to receive the treatment of a Bear Aware campaign, a strategy commonly employed in the USA in which volunteers visit residents to distribute educational material and talk about ways to reduce attractants and conflict. Educational material was developed by the CDOW, including door hangers, magnets, "living with bears" brochures, and a checklist about how to prevent conflicts. All material instructed residents about properly securing trash in bear-proof containers. Volunteers were trained by the local district wildlife manager using CDOW protocols, and were asked to avoid disclosing the experiment and to record the date of visit and whether education material was left or the residents contacted.

Pre- and post-sampling occurred July-September 2008 for a total of 11 sampling weeks, and I monitored >650 residences (Appendix 2.1). As a result of the continuous treatment application, i.e., volunteers took two weeks to canvass the treatment neighborhoods, pre- and post-treatment periods varied for each residence, lasting 3-5 and 6-8 weeks, respectively. For residences in control neighborhoods, I randomly assigned a date within the two-week treatment application period to define the pre- and post-treatment periods. Because city ordinance did not require residents to place trash for curbside pickup in bear-resistant containers, I focused measurement of the response variables on whether a container was bear-resistant and whether it was secured such that trash was available to bears (1) or not (0). If a residence had a combination of bear-resistant and non bear-resistant containers, I considered it as having a bear-resistant container with trash available to bears, unless the non bear-resistant container clearly contained only yard or recycling waste.

Monitoring residential trash containers introduced several challenges. First, because of large daily variability in container placement for curbside pickup, I determined the day(s) in the week that most garbage collection occurred in each neighborhood. For the duration of the experiment, I then sampled on these days and attempted to increase container detection by sampling early before the trash collection truck arrived. Second, sometimes ambiguity existed about the ownership of a container at an address. When this occurred, I eliminated the residence from the sample. Finally, I tried to minimize being detected and the potential to bias behavior if residents learned about my study. Consequently, I used unmarked vehicles while sampling, avoided small, narrow streets where I could easily be detected, and did not sample if people were close enough to the trash container to potentially engage in a conversation.

I analyzed data at neighborhood and residence scales. For the neighborhood analysis (n = 4) I summarized the probability of trash being available to bears and the proportion of bear-resistant containers for each sampling occasion. I weighted both responses by the proportion of containers detected in each sampling occasion, and assessed treatment effects by the degree of overlap between group means and 95% CI. For the residence-level analysis, I conducted two analyses, one for each measured response: 1) whether a container changed from a non bear-resistant to bear-resistant (binary variable), and 2) whether probability of garbage availability decreased (continuous variable). I used logistic regression (PROC LOGISTIC; SAS Institute 2002) to test whether non bear-resistant containers were replaced, or not, by a bear-resistant container (sample sizes: 25, 7, 18, and 8 for BA1, BA2, BA3, and BA4, respectively; Appendix 2.1). For the second response variable measured, I used mixed effects modeling (PROC GLIMMIX) to assess treatment effect on the probability of trash being available to bears, where residence (site) was modeled as a random effect (sample sizes: 54, 44, 48, and 46 for BA1, BA2, BA3, and BA4, respectively; Appendix 2.1). I used volunteer action (i.e., volunteers made personal contact with residents or left educational material) as a covariate in both analyses and predicted a greater treatment effect for sites in which volunteers had personal contact with the residents. I assessed model performance as described above.

Elevated enforcement

I focused my enforcement experiment in four alleyways in the business area of Aspen (E in Figure 2.1), which consisted of restaurants, shops, offices, and communal housing complexes that were not included in previous experiments. I randomly allocated the treatment to two alleyways (37 dumpsters) with the other two used as control (30 dumpsters). Because it was not feasible to stop all enforcement in the control areas, I considered as a control the status-quo enforcement, and as a treatment the elevated enforcement of daily patrolling by the APD with the application of further measures upon detection of violation. However, after an initial treatment period in which almost no written notices were dispensed, the APD agreed to a second treatment period in which notices were dispensed at least once a week to dumpsters in violation. Hence, there were two treatment levels – additional daily patrolling (hereafter patrolling treatment), and patrolling with notice application (hereafter notices treatment). The notice of violation was taped to the violating dumpster and required a violator's response to "discuss measures that will bring you into compliance."

I censused dumpsters in the core area for eight weeks from 1 July – 25 August, 2008, where pre-, patrolling-, and notices-treatment periods respectively lasted for three, three, and two weeks. The likelihood of dumpsters being improperly secured increased during the day due to frequent use by downtown businesses; therefore I sampled dumpsters between 0500 and 0600 hours when no, or minimal, activity occurred. Similar to the on-site education experiment, I recorded whether dumpsters were in violation or compliance with city ordinance, and whether they were empty or not. I used the guidelines described to assess the qualitative degree of violation based on dumpster type and securing methods, where a dumpster was considered in violation if it had high or medium violation and was not empty. I grouped dumpsters assigned to treatment alleyways as treatment, and used mixed effects models to test for a treatment effect (PROC GLIMMIX; dumpster as a random effect). I also conducted a *post-hoc* analysis comparing compliance of dumpsters that received written notices ($n = 18$) and those that did not ($n = 49$) regardless of alleyway location. Finally, I qualitatively assessed dumpster risk categories (Refuse Collectors section) and summarized the number of notices given to each.

Results

On-site education

For the communal housing analyses I used all covariates (i.e., no correlations were detected), except number of APD visits, which was eliminated due to sparseness of data ($n = 4$). Overall, the model explained 44% of the variability in the data. The probability of a violation showed little support for a treatment effect ($F_{1,66} = 2.6$, $p = 0.11$) but showed stronger support for a temporal effect with a decrease in probability of violation for the post-treatment period ($F_{1,66} = 55.2$, $p = <0.0001$; Figure 2.3). A previously posted educational sign ($n_{control} = 12$, $n_{treatment} = 17$, ~60% of complexes) had a slight effect on probability of violation, while bear visits to dumpsters (23 detected at 20 dumpsters) had no effect ($F_{1,66} = 2.8$, $p = 0.10$ and $F_{1,66} = 0.3$, $p = 0.58$, respectively). Ninety-five percent of dumpsters sampled were categorized as high ($n_{control} = 19$, $n_{treatment} = 20$) or medium ($n_{control} = 12$, $n_{treatment} = 10$) risk and high-risk dumpsters had more violations ($F_{1,66} = 17.1$, $p = <0.0001$; Figure 2.3). The number of units in a complex ($\overline{x}_{control} = 30$, *SE* = 9.3; $\bar{x}_{treatment}$ = 25, *SE* = 6.0) and the number of units visited by survey researchers ($\bar{x}_{control}$ = 3, *SE* = 0.60; $\bar{x}_{treatment}$ = 3, *SE* = 0.67) had no effect ($F_{1,66} = 1.9$, $p = 0.17$, and $F_{1,66} = 1.0$, $p = 0.33$, respectively).

For construction sites, projects at seven sites terminated before the end of the sampling periods and three control sites had missing covariate information, resulting in 21 treatment and 11 control sites. Additionally, no actions by the APD were recorded in the sampled construction sites, and when a bear visit was detected, I had difficulty determining the date; thus both covariates were eliminated. Overall, the model explained 28% of the variability. The probability of a violation was not influenced by the treatment ($F_{1,30} = 0.33$, $p = 0.57$) but declined (88 to 82% for control and 85 to 75% for treatment) between the pre- and post-treatment periods ($F_{1,30} = 12.15$, $p = 0.0015$). Sixteen percent of the dumpsters had a previously posted sign ($n_{control} = 2$, $n_{treatment} = 3$) with no effect on probability of violation ($F_{1,30} = 0.00$, $p = 0.94$). Eighteen percent ($n_{control} = 2$, $n_{treatment} = 4$) of dumpsters had a container for human food waste, with little effect on probability of violation ($F_{1,30} = 2.75$, $p = 0.11$).

Bear Aware education

Volunteers spent two weeks in treatment neighborhoods visiting 235 (91% of residences) and 122 (87% of residences) addresses in the BA1 and BA2 subdivisions, respectively, while directly contacting 36% and 25% of the residences. I detected no difference in the probability of availability of trash to bears or the proportion of bear-resistant containers between control and treatment groups (Figure 2.4). The percent (19) of non bear-resistant containers that changed to bear-resistant ones was the same as the percent of bear-resistant containers that changed to non bear-resistant ones. For the residence analyses, the Bear Aware treatment had no effect on residents changing non bear-resistant containers to bear-resistant ones ($\chi^2 = 0.100$, $p = 0.95$), however the model explained <1% of the variability in the data. In addition, the treatment did not reduce the probability of trash being available to bears ($F_{2,289} = 1.66$, $p = 0.19$) with the model explaining 10% of the variability in the data.

Elevated enforcement

The APD gave 22 written and 2 verbal warnings in the treatment area, of which 4 and 20 were given during the patrolling- and notices-treatment periods, respectively. In addition, one dumpster in the control area inadvertently received three written warnings. Most dumpsters (78%) receiving tickets were high risk, and a written warning resulted in approximately 40% reduction in the probability of violation for the ticketed dumpsters between pre- and notices-treatment periods (Figure 2.5). I found no evidence for a treatment effect when grouping and modeling all dumpsters in the treatment alleyways as the treatment group ($F_{2,130} = 0.05$, $p = 0.95$), but did detect a period effect ($F_{2,130} = 35.23$, $p = <0.0001$) with the model explaining 30% of the variability. I found greater support for a treatment effect when grouping and modeling dumpsters receiving a written notice as the treatment ($F_{2,130} = 2.43$, $p = 0.092$) with the model explaining 31% of the variability (Figure 2.5).

Discussion

Evidence-based conservation is critical to assess effectiveness of management, guide policy, and help resolve conflicts. In this study, I experimentally evaluated education and law enforcement management tools commonly used to change human behavior to reduce human-wildlife conflicts. I found that as currently implemented in my system, education had little impact in changing human behavior, while proactive enforcement was more effective in altering human behavior. I also found that it is paramount to include a rigorous monitoring protocol in order to adequately evaluate management actions.

Whether applied at specific sites, or in broad campaigns, education is often the preferred management tool to reduce conflicts between humans and wildlife (e.g., Tchamba 1996, Spencer et al. 2007), and although costs can be substantial, there has been little evidence to its effectiveness. My findings are similar to results reported from New York, where a Bear Aware education campaign had no effect in changing human behavior in better securing bear attractants (Gore et al. 2008). Other studies focused on education showed mixed results (e.g., George and Crooks 2006, Dunn et al. 2008), but no studies focused on human-wildlife conflicts related to human development or explicitly measured change in human behavior. One potential explanation for my result is that the message and delivery were not adequate. For example, the low use of my education website during the on-site experiment was perhaps due to the need to write down the website address at the dumpster location. However, the education message in my signs was less likely the cause, because it included basic elements of information delivery including factual, emotional, moral, and nonverbal elements (Jacobson et al. 2006). Additionally, in delivering my educational information in Spanish, I ensured that my message could reach the diverse Aspen population (Jacobson and McDuff 2009). Regardless, the methods of education that I applied are commonly used by conservation managers, suggesting that current management methods are not effective.

Conservation biologists and wildlife managers should therefore develop new education approaches to better deliver the information. Both new and existing methods need to be continually evaluated for delivery and content, ideally by incorporating social science studies to evaluate material reception and retention (Baruch-Mordo et al. 2009). Education could also be coupled with enforcement to increase its effectiveness in changing human behavior. Studies in game theory review the strategies of reward and punishment in achieving collaboration between unrelated individuals (Sigmund 2007, Hilbe and Sigmund 2010, Szolnoki and Perc 2010), and can guide the development of programs aimed to improve public cooperation. Examples for the implementation of joint education and enforcement programs include campaigns aimed at reducing underage smoking (Feighery et al. 1991), increasing seatbelt wearing (Vasudevan et al. 2009), and decreasing the use of alcohol while driving (Shults et al. 2009).

In past years, citizen-based groups and wildlife agencies have promoted the passage of wildlife ordinances as a means of reducing human-bear conflicts. An implicit assumption with respect to the passage of natural resources laws, ordinances, and regulations is that they will bring about compliance without active enforcement (Rowcliffe et al. 2004, Keane et al. 2008). My study and others suggest the contrary. For example, legal protection alone had no effect on whether hunters poached protected wildlife in Africa (Jachmann and Billiouw 1997), and passage of wildlife ordinances alone failed to reduce the availability of attractants, and therefore human-bear conflicts, in several North American communities (Peine 2001). Theory related to enforcement examined strategies related to increasing detection of violations (e.g., increasing patrolling efforts) and increasing penalties (e.g., increasing fine amounts) in successfully promoting compliance (Keane et al. 2008, Hilbe and Sigmund 2010). Researchers found that increasing detection of violations, followed with proper enforcement actions, will best improve compliance with wildlife protection laws (Rowcliffe et al. 2004, Keane et al. 2008). Additionally, an inverse relationship was noted between the amount of enforcement resources expended to detect violations (e.g., budget spent and patrolling time) and wildlife poaching in Africa (Jachmann and Billiouw 1997, Jachmann 2008). I evaluated two enforcement levels, one consisting only of elevated patrolling, and one in which written notices provided an indication of the detection of a violation by enforcement authorities. The latter brought about better compliance, suggesting that proactive enforcement in the form of notice application is necessary.

Increased patrolling, detection, and application of warnings can be costly to implement (Keane et al. 2008). However, the alternative costs of continuously managing human-wildlife conflicts are also substantial, e.g., personnel costs, damage costs, indirect costs to human health and safety, and potential costs to the wildlife resource. The CDOW spent >5,000 hours and US $200,000 responding to human-bear conflicts in the Aspen region in 2009 alone, and the International Association of Fish and Wildlife Agencies (International Association of Fish and Wildlife Agencies 2005) reported that wildlife agencies increased expenditure to manage human-bear conflicts by 45%, including a 22% increase in personnel time. Urban residents also incur substantial costs with damages from wildlife conflicts amounting in the USA to approximately 4 billion USD in 1993 (Conover 1997). In a review of management strategies implemented to reduce human-bear conflicts in several municipalities, Peine (2001) summarized that the impetus for conflict management policy formulation and enforcement often followed a specific injury event or economic and public health concerns. Therefore, addressing violations via proactive enforcement could reduce long-term management costs and prevent additional risks to human health and safety.

I stress two important considerations for future studies when evaluating management tools: direct measures of human behavior as a response, and application of rigorous experimental design. Because conflicts arise due to a combination of factors, it can be erroneous to equate a reduction in conflicts with success of management actions without a direct measure of change in human behavior (Gore et al. 2006, Baruch-Mordo et al. 2009). For example, in my system a 2007 outbreak of human-bear conflicts resulted in an education campaign and the passage of emergency ordinances. Then in 2008, few conflicts were reported, leading some to argue that the reactive measures were successful in changing human behavior. However, despite the measures applied in 2007, ordinance violation rates in 2008 were high with relatively low use of bear-proof containers (Figures 2.4 and 2.5). Additionally, movements of GPS-collared bears showed usage shifted to areas outside of town and likely contributed to the decline in conflicts. Such confounding stresses the need for direct measurement of change in human behavior to evaluate conservation management tools (Baruch-Mordo et al. 2009). But even when change in human behavior is directly observed, without proper experimental design causation cannot be inferred. For example, in my on-site education experiment I observed a strong reduction in probability of violation for both treatment and control groups, indicating that factors other than my treatment contributed to the decline. Without a control group, I could have erroneously concluded that the treatment was effective. In fact, the observed declines in 2007 likely resulted from increased probability of personal experience with bears, e.g., sighting or property damage, which could have resulted in increased awareness of bears and the change in human behaviors to better secure attractants. I therefore additionally stress the importance of applying an experimental approach when testing the efficacy of conservation tools.

This study provides evidence that current agency and municipality efforts are not necessarily effective in changing human behavior. I suggest that the conservation community can increase efficacy of management tools by coupling education and enforcement into new management programs based on insights from game theory research (Sigmund 2007, Hilbe and Sigmund 2010, Szolnoki and Perc 2010) and existing examples of society's efforts to change human behavior (Feighery et al. 1991, Shults et al. 2009, Vasudevan et al. 2009). To effectively reduce human-wildlife conflicts or solve other pressing wildlife management issues, I also argue for increased evidence-based conservation efforts that evaluate and refine management tools to promote the coexistence between humans and wildlife.

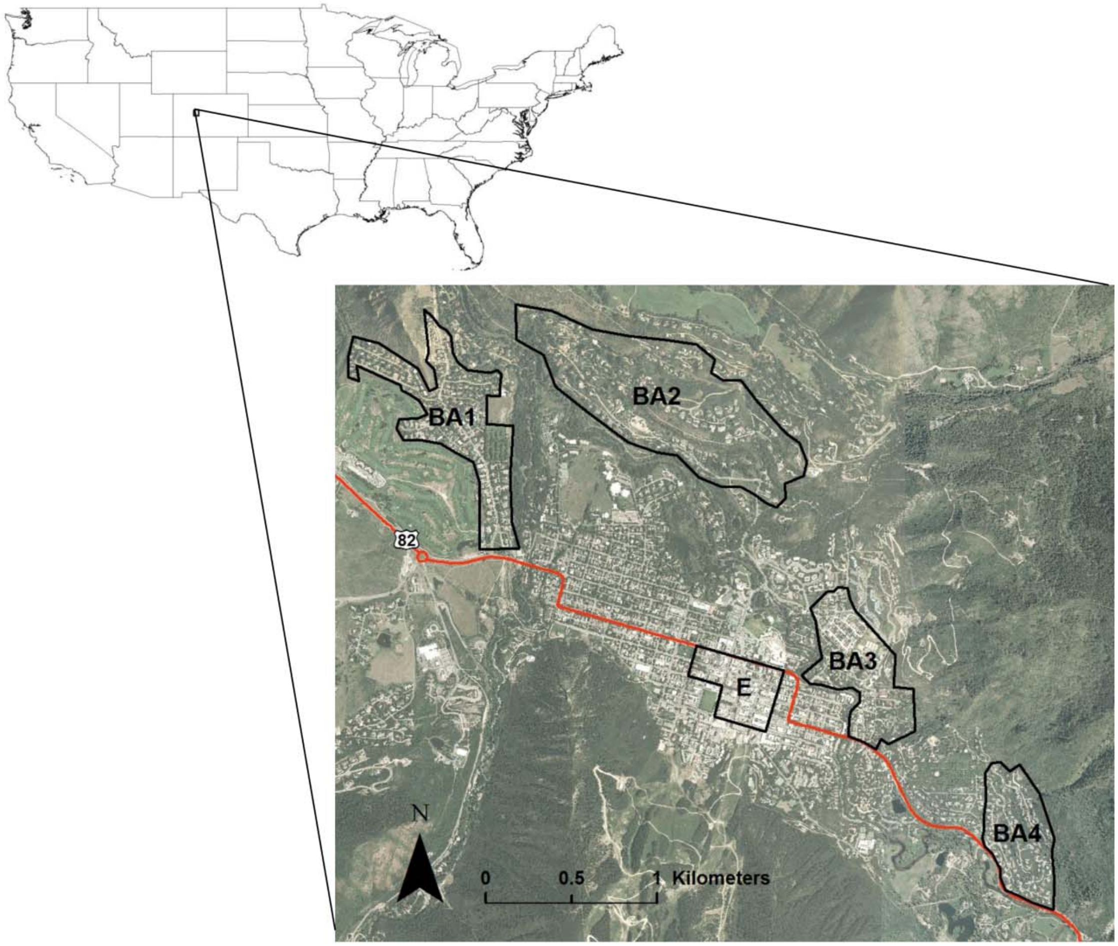

Figure 2.1. Aerial image (National Agriculture Imagery Program 2005) of the city of Aspen, Colorado, USA and its surrounding residential areas where experiments were conducted in 2007 and 2008 to evaluate efficacy of education and law enforcement in reducing availability of garbage to bears. Polygons represent sampling areas for the Bear Aware (BA) and Enforcement (E) experiments, where BA1-4 respectively correspond to Cemetery Lane, lower Red Mountain, lower Smuggler, and Mountain Valley neighborhoods, and E is the core business area.

Figure 2.2. Examples of refuse collector designs that are considered bear-proof in the city of Aspen and the surrounding residential area of Pitkin County including: A) A low-risk dumpster room with metal doors, round handle, and little door clearance, B) a medium-risk dumpster with bolted, metal lid over a free-standing dumpster, and C) a high-risk free-standing dumpster with top-bar securing method that was toppled and broken into by a bear.

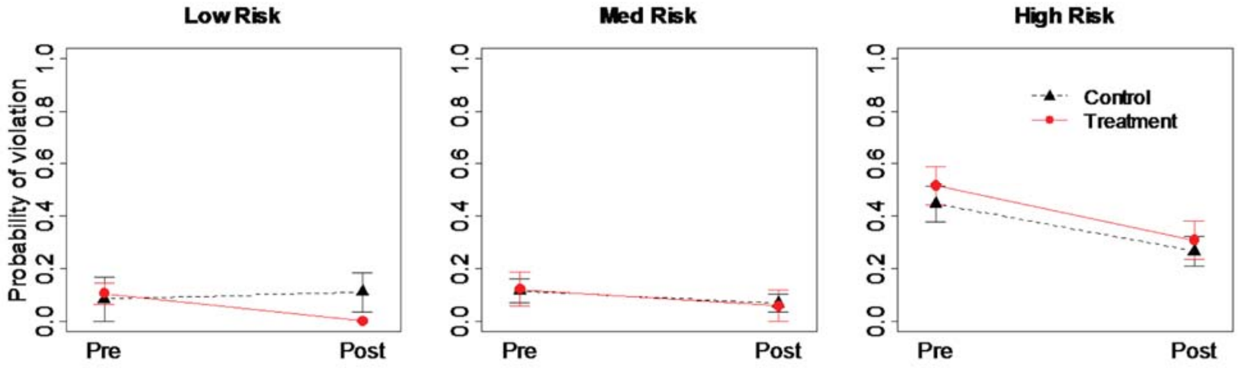

Figure 2.3. Results of on-site education experiment for communal housing complexes. Differences in mean (± 1 *SE*) probability of violation between pre- (Pre), and post-treatment (Post) periods for dumpsters of low, medium, and high risk to break-in by bears for a 2007 experiment testing the efficacy of an on-site education sign as a management tool in reducing availability of garbage to bears in Aspen, Colorado, USA. Note: probability of violation was zero for all treatment low risk dumpsters in the post-treatment period; hence no error bars.

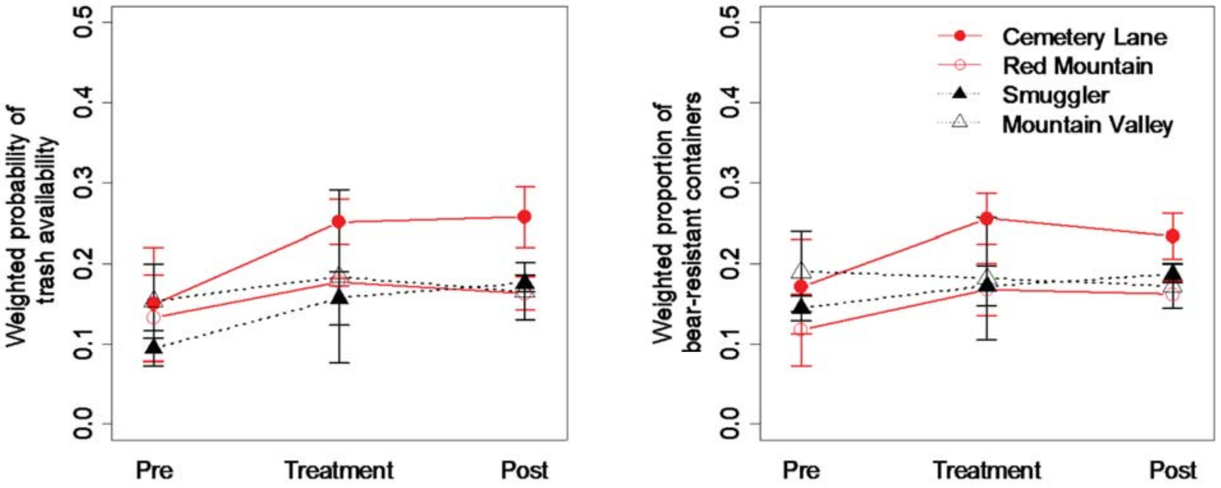

Figure 2.4. Results of Bear Aware education experiment. Differences in mean (± 1 *SE*) weighted probability of availability of trash to bears and mean weighted proportion of bear resistant containers in treatment (red) and control (black) neighborhoods for a 2008 experiment testing the efficacy of a Bear Aware education campaign as a management tool in reducing availability of garbage to bears in four residential neighborhoods in Aspen, Colorado, USA. Responses are weighted by the proportion of containers detected in each sampling occasion. Sampling periods are pre-treatment (Pre), treatment-application (Treatment), and post-treatment (Post). Neighborhoods are Cemetery Lane (BA1), Red Mountain (BA2), Lower Smuggler (BA3), and Mountain Valley (BA4).

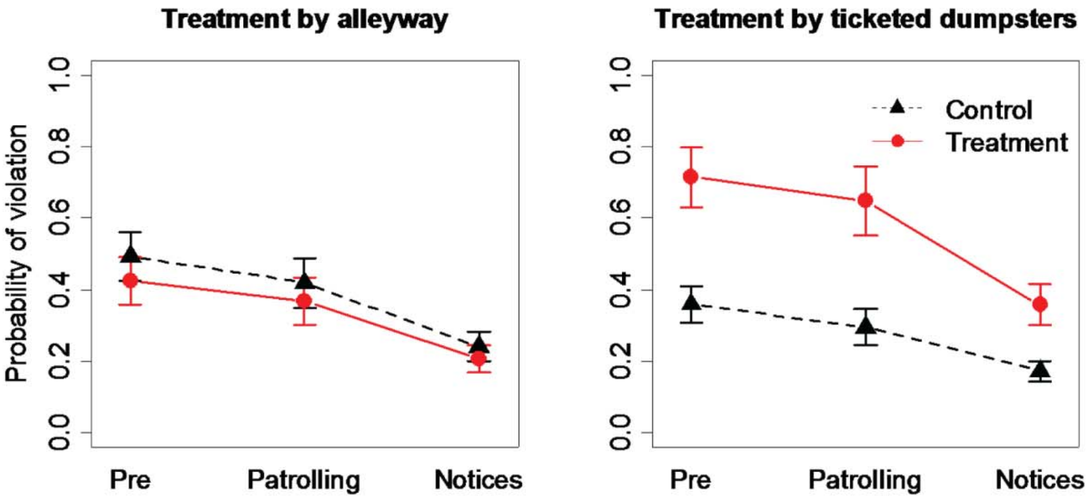

Figure 2.5. Results of elevated enforcement experiment. Differences in mean (± 1 SE) probability of violation in core area dumpsters by treatment group for the pre-treatment (Pre), daily patrolling treatment (Patrolling), and written notices treatment (Notices) periods for a 2008 experiment testing the efficacy of enforcement as a management tool in reducing availability of garbage to bears in the core business area of Aspen, Colorado, USA. Treatment by alleyway included all dumpsters in the daily patrolled alleyways as treatment, whereas treatment by ticketed dumpsters included only dumpsters receiving written notices as treatment.

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APPENDIX 2.1. A DETAILED DESCRIPTION OF SAMPLE SIZE DETERMINATION.

On-site education experiment

I focused the on-site education experiment on communal housing and construction sites based on GPS data showing high bear use of dumpsters in those sites (S. Baruch-Mordo, unpublished data). For communal housing, the sampling frame consisted of 437 complexes based on a GIS layer composed by the city of Aspen and Pitkin County. I applied the following inclusion criteria, complex: 1) was not a hotel nor contained any businesses, 2) had ≥ 5 units, 3) had a centralized dumpster not easily accessible to the general public, and 4) management granted permission for the experiment. This reduced my sample to 68 complexes, with half (34) randomly selected as treatment. Based on power analyses, this sample size allowed detection of 16.5% difference in means with 90% power ($\alpha = 0.05$, hypothesized pre-treatment mean of 55% compliance based on K. Wright, Aspen District Wildlife Manager, personal comm.).

For construction sites, I obtained permission to sample all sites within the city limits. I censused all sites in Aspen, and then applied the following inclusion criteria, the construction: 1) project lasted the duration of the study, 2) site included a commercial type dumpster approximately 2-m high x 2.5-m wide x 10-m long and 3) dumpster was not easily accessible to the general public. This reduced my sample to 38 construction sites in the city limits. I augmented the sample with sites within the county from the 2004-2007 building permit database ($n = 99$), selecting sites based on my criteria ($n = 30$), and obtaining permission from landowners ($n = 4$). This resulted in a total of 42 sites, with 22 randomly selected as the treatment and 20 as the control, and allowed for detection of up to 17.5% difference in means (power = 0.9, $\alpha = 0.05$, starting compliance = 20% K. Wright, personal comm.). After sampling initiation, seven construction sites terminated before the end of the sampling periods. In addition three control sites had missing covariate information. Therefore I excluded these seven sites from the analysis, resulting in 21 treatment and 11 control sites, and a 90% power to detect approximately 20% difference in means.

Bear Aware education

I conducted the Bear Aware experiment in four residential areas: Cemetery Lane (BA1), lower Red Mountain (BA2), lower Smuggler Mountain (BA3), and Mountain Valley (BA4; Figure 1). I delineated the neighborhoods such that they were isolated from other residential areas in their vicinity, and excluded any non-residences, a trailer park, and communal housing complexes included in the on-site education experiment conducted in the previous year. The sampling frame consisted of addresses in the city of Aspen and Pitkin county GIS layer that intersected with each neighborhood polygon for a total of 258, 140, 169, and 121 residences in BA1, BA2, BA3, and BA4, respectively.

For the residence-level analysis in which I tested whether treatment affected the change of a non bear-resistant container to a bear resistant one, I used data from residences for which I detected a non bear-resistant container in the pre-treatment period, and for which I detected a container in both pre- and post- treatment periods. Resultant samples sizes consisted of 25, 7, 18, and 8 residences for BA1, BA2, BA3, and BA4, respectively, and were sufficient to detect approximately 5-15% difference in proportion of bear-resistant containers with 80% power (α = 0.1, starting mean based on pilot data for each neighborhood ranging from 17.4 – 46.9% non bear-resistant containers). For the residence-level analysis in which I assessed treatment affect on the probability of trash being available to bears, I used data from residences with a container detected in both the pre- and post- treatment periods (sample sizes were 54, 44, 48, and 46 residences for BA1, BA2, BA3, and BA4, respectively).

Elevated enforcement

Trash in the core business area of Aspen was deposited in dumpsters located in four alleyways between the main streets. The sampling frame consisted of 67 bear-resistant refuse collectors. I randomly assigned the treatment to 37 dumpsters in two out of the four alleyways, leaving 30 dumpsters as control and allowing detection of <5% difference in probability of violation with 90% power ($\alpha = 0.05$, starting mean based on pilot data = 43% violation). I conducted two analyses one grouping the 37 dumpsters assigned to treatment alleyways as treatment, and a *post-hoc* analysis comparing compliance of dumpsters that received written notices ($n = 18$) and those that did not ($n = 49$) regardless of alleyway location.

CHAPTER 3

USE OF PATCH SELECTION MODELS AS A DECISION SUPPORT TOOL TO EVALUATE MITIGATION STRATEGIES OF HUMAN-WILDLIFE CONFLICT

Introduction

Human-wildlife interactions, and subsequently conflicts, are increasing worldwide (Conover 2001, Woodroffe et al. 2005). Human-dominated landscapes offer spatially concentrated, predicable, and reliable food sources, e.g., livestock, crops, or refuse, which can serve as major attractants to wildlife and lead to human-wildlife conflict (Shochat 2004, Baker et al. 2008). Whether the resultant conflict occurs due to depredation of livestock in South America (e.g., Michalski et al. 2006), raiding of agricultural corps in Europe (e.g., Geisser and Reyer 2004), or use of refuse in urban centers in North America (e.g., Beckman and Berger 2003), a key driver of conflict is the pursuit of food resources by wildlife. Thus, understanding how to best mitigate human-wildlife conflict requires an understanding of how management affects wildlife foraging decisions.

Two major management strategies aimed at humans and wildlife are commonly employed to resolve conflicts. Human-dimensions tools are implemented in conflict communities to change human behavior to reduce the availability of attractants, or foraging benefits, to wildlife. For example, improving husbandry through education reduced livestock depredation by snow leopards (*Panthera uncia*) in India (Jackson and Wangchuk 2004), and proactively enforcing refuse disposal laws reduced availability of garbage to American black bears (*Ursus americanus*) in Colorado, USA (Baruch-Mordo et al. 2011). Wildlife management tools are also implemented to either eliminate (lethal control) or deter (non-lethal control) wildlife from attractant sites (Fall and Jackson 2002, Treves and Karanth 2003). Lethal control is largely unpopular with wildlife managers and constituencies (e.g., Fall and Jackson 2002, Baker et al. 2003, Spencer et al. 2007), and wildlife agencies are increasingly using non-lethal aversive conditioning methods that include hazing, and chemical and physical deterrents. Aversive conditioning offers a source of discomfort or pain to wildlife that often invokes a flight response (Shivik et al. 2003, Mazur 2010) and consequently increases the energetic costs of foraging in human-dominated areas. Examples include hazing of African elephants (*Loxodonta africana*) with fire and noise to reduce crop raiding in Kenya (Sitati et al. 2005), and using chemical repellents to deter badgers (*Meles meles*) from crops in Europe (Baker et al. 2005). Put in the context of foraging decision making by wildlife, conflict management strategies targeting humans and wildlife aim to either decrease wildlife foraging benefits, or conversely, increase wildlife foraging costs that are associated with human-dominated areas.

Conflict management can be expensive and ineffective, and it is generally believed that management cannot successfully eliminate all attractants or deter all individuals (Linnell et al. 1997, Treves and Karanth 2003, Mazur 2010, Baruch-Mordo et al. 2011). Consequently, there is a need to determine which management strategy, or which combinations, are most effective in altering wildlife foraging decisions. Patch selection models (Mangel and Clark 1986) provide a framework to test how benefit reduction and cost increase influence foraging decisions. Under this approach, patches can be considered as human-dominated or not, and patch selection for foraging by wildlife can be optimized based on patch-specific benefits and costs given the energy reserves of the animal (Mangel and Clark 1986). One can evaluate the effects of conflict management on wildlife foraging decisions by using sensitivity analysis where benefits and costs in human-dominated patches are systematically varied and the impacts on foraging success is determined. One can also search for thresholds of benefit reduction and cost increase beyond which wildlife no longer select human-dominated patches, thus providing guidelines for conflict mitigation.

In this paper I demonstrated the application of patch selection models in conservation management. I examined how changes in foraging costs and benefits incurred from the management of human-bear conflicts can influence the foraging decisions of black bears in human-dominated areas. Bears are an ideal organism to use as an example, because their ecology is highly food dependent due to the energetic costs of hibernation, which often leads to conflict with humans over food resources. Bears enter a state of hyperphagia, or intense feeding, in late summer and fall to gain sufficient fat reserves for hibernation (Nelson et al. 1983). If inclement weather or disease events cause natural food production failures during hyperphagia, bears will use alternative anthropogenic food sources and forage near human development (Mattson et al. 1992). Consequently, human-bear conflicts flare in poor natural food production years (Zack et al. 2003, Ryan et al. 2007, Baruch-Mordo et al. 2008) and wildlife managers mitigate conflicts by applying strategies such as education aimed at humans (Baruch-Mordo et al. 2011) or aversive conditioning aimed at bears (Spencer et al. 2007). I evaluated the effects of such strategies on bear foraging decisions using a patch selection model parameterized from literature and field data. I used the model to search for thresholds of benefit reduction and cost increase beyond which bears would not forage in the human-dominated patches to inform the allocation of resources for the management of human-bear conflicts.

Methods

Study system

I used Aspen, Colorado, USA, located in the central mountains of Colorado, as my model system. The human-dominated area of Aspen consists of a downtown business district and high human density residential areas (urban patch) that are surrounded by lower density residential neighborhoods (urban-interface patch). Residential neighborhoods are dispersed within mountain-shrub and forest communities that are adjacent to large national forest and wilderness areas (wildland patch). Hyperphagia season in Aspen lasts from approximately 1 August to 15 October (total of 75 days), a period when fruit ripens providing important local natural food sources for bears including Gambel oak (*Quercus gambelli*), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus virginiana*). From 2005-2010 I deployed GPS collars on bears to better understand their movement patterns and resource use in the urban environment (Chapter 1). Bears used urban and urban-interface areas extensively during hyperphagia season in years of poor natural food production, a time when conflicts with humans flared. I backtracked to GPS locations in Aspen and identified garbage as the main anthropogenic attractant.

Management strategies applied in Aspen to reduce availability of garbage to bears included targeting humans with education and enforcement of local refuse disposal laws. I experimentally evaluated education and enforcement and found proactive enforcement to be most effective in changing human behavior to better secure garbage (Baruch-Mordo et al. 2011). However, despite observing a reduction in garbage availability following treatment, I did not observe a complete elimination of garbage resources, and in fact, found garbage to be readily available to bears throughout Aspen at all times. Alternative management strategies applied in

Aspen to prevent bear use of garbage and therefore reduce human-bear conflicts included non-lethal methods of aversive conditioning. While I did not measure bear response to aversive conditioning as applied in Aspen, the most common response by bears is running away from the source of discomfort (Mazur 2010), a behavior I commonly observed when aversive conditioning was applied.

Patch selection model

Mangel and Clark (1986, 1988) developed a general patch selection model based on optimal foraging theory using a state-dependent modeling approach that is solved by dynamic programming. The patch selection model optimizes a fitness function $F(x,t)$, or the maximum fitness from time step $t = 1$ to terminal time step T given that the organism was alive at time t and had a state variable value of $X(t) = x$. At each time step fitness is updated as detailed in eqn. 1 below, and the selected patch that maximizes fitness is recorded in a patch decision matrix. I applied the patch selection model to my system using two human-dominated patches (urban and urban-interface) and one non human-dominated patch (wildland). I used survival as the fitness currency and body fat reserves (kg fat) as the state variable (detailed parameterization below). I maximized fitness over the hyperphagia season using day as a discrete time unit ($t = 1,2,\ldots,75$). I focused on poor natural food production years in which bears are most likely to forage in the urban environment and conflict management strategies are likely to be applied.

The dynamic state variable $X(t)$ in patch selection models can be constrained between a critical value of x_c and cap value of C, and the terminal fitness at time T is known and represented by a function $\phi(x)$ such that $F(x,T) = \phi(x)$. I used critical and cap values for kg fat reserves that were converted from min and max values reported for body mass (M) of Aspen bears, and I quantified survival as a function of body mass at time T based on an allometric relationship. Once fitness is known at terminal step T, the model can be solved for maximum fitness by backwards iteration using a Markovian decision process (Mangel and Clark 1986). At each time step fitness is calculated as the probability of survival in period t times the probability of survival from period t to $t + 1$, where the latter is composed of survival when food is found plus survival when food is not found. Fitness is maximized across i patches (human-dominated or not) given patch-specific survival (s_i; $1 - \beta_i$ in Mangel and Clark 1986, 1988) and the probability of finding food (λ_i) according to the equation:

$$F(x,t) = \max_i \left[s_i \{ \lambda_i F(x_i', t+1) + (1-\lambda_i) F(x_i'', t+1) \} \right] \quad \text{(Eqn. 1)}$$

where $x_i' = x - \alpha_i + Y_i$ and $x_i'' = x - \alpha_i$ are functions updating the state variable based on patch-specific foraging costs (α_i) and yields (Y_i) if food is found (x_i'), or costs only if food is not found (x_i''). I quantified foraging costs as the loss of kg fat from energetic expenditure on patch-specific movement and foraging yields as the gain of kg fat from food found in each patch. If the resultant values of x_i' or x_i'' are lower than a critical value x_c or exceed a cap value C, then they are set to the critical or cap value, respectively.

I used an adaptation of the patch selection model in eqn. 1 to consider foraging on j different food types in each i_{th} patch. In this approach, the probability of finding food becomes patch- and food type-specific (λ_{ij}), and the probability of not finding food in a patch is inclusive of all food types. Fitness can be maximized using:

$$F(x,t) = \max_i \left[s_i \{ \sum_j \lambda_{ij} F(x_{ij}', t+1) + \left(1 - \sum_j \lambda_{ij} \right) F(x_{ij}'', t+1) \} \right] \qquad \text{(Eqn. 2)}$$

with the functions specified in eqn. 3 updating the state variable according to whether the animal found food or not. Additional expansion of the simple patch selection model is the inclusion of state-dependent costs, $\alpha_i(x)$. If cost is defined as energy lost due to basal metabolic rate, which is a function of body mass *M*, then $\alpha_i(x) = 57.2M^{0.716}$ for mammalian species (Robbins 1993). Redefining yield to be food type-specific and incorporating state-dependency to patch-specific costs, the organism's state can be updated using equations:

$$x'_{ij} = x - \alpha_i(x) + Y_j \qquad \text{(Eqn. 3)}$$

$$x''_{ij} = x - \alpha_i(x)$$

while limiting x'_{ij} and x''_{ij} between critical value x_c and cap value *C*.

I used the adaptations developed in eqn. 2 and 3 to model bear foraging in Aspen. I defined three patches, urban (*u*), urban-interface (*ui*), and wildland (*w*), and two food types, anthropogenic and natural, with an implicit assumption that bears always find and consume both food types according to their availability in each patch (i.e., no food preferences). I focused the model on adult females because their survival and reproductive output is important to bear population growth (Freedman et al. 2003, Mitchell et al. 2009). A detailed description and justification for each parameter is provided below and summarized in Table 3.1.

Model parameterization

I used fat reserves as the state variable because fat is crucial for bear winter survival and reproductive success (Belant et al. 2006, Robbins et al. 2007). Bears can lose up to 50% of their body weight during hibernation (Beecham and Rohlman 1994) with loss consisting primarily of fat (Farley and Robbins 1995, Harlow et al. 2002) and they reproduce via delayed implantation, where females without adequate fat reserves will not implant the blastocyst and consequently forgo reproduction (Eiler et al. 1989). Range of female body mass for Aspen bears, 55 – 110 kg, was within the range reported for black bears in Colorado (Beck 1991). Because body mass of free-ranging black bears consists of approximately 30% fat at the end of hyperphagia season (Belant et al. 2006), I calculated the range of state variable *X*(*t*) as the specified range in body mass divided by three, and used critical and cap values of 20 and 35 kg fat, respectively. I used methods of linear interpolation with n = 100 as suggested by Clark and Mangel (2000), thus I incremented the state variable kg fat by 0.15 when evaluating the model.

I parameterized the terminal fitness function $\phi(x)$ using a log-linear allometric relationship between survival and body mass as: $\exp(-aM^{b}t)$, where t is time interval and a and b are taxa-specific scaling parameters (McCarthy et al. 2008). Terminal fitness therefore had an inverse relationship with both scaling parameters. I calculated $\phi(x)$ over a time interval of 1 day and converted the state variable value of kg fat (x) back into total body mass (M) by multiplying by three. I used the mean predicted values for a and b reported for mammals as 0.61 and -0.25, respectively, but also tested sensitivity of results to different values. To guide parameterization of patch-specific survival, I used adult female survival in Aspen in poor natural food production years ($\hat{s}$ = 0.718, SE = 0.117; Chapter 1). I used exploratory analyses explained in detail in Appendix 3.1 to identify a parameter space for patch-specific survival while restricting results to realistic model behavior. Given those results, I assigned default patch-specific survival as 0.75 in urban, 0.87 in urban-interface, and 0.92 in wildland and patches. Uncertainty in survival was addressed using sensitivity analysis described below.

I calculated the probability of finding food as a function of the composition ($comp_{ij}$) and availability ($avail_{ij}$) of food type j in patch i, such that $\lambda_{ij} = comp_{ij} * avail_{ij}$. I assumed wildland patches were composed only of natural foods and urban patches were composed only of anthropogenic foods. I used aerial photos to visually estimate the composition of natural and anthropogenic food sources at 50% each in the urban-interface patches. I assigned zero availability to anthropogenic food sources (i.e., garbage) in wildland patches and to natural food sources in urban patches. Because I was testing management scenarios occurring in poor natural food production years, I assumed natural food availability in urban-interface and wildland patches to be 10 % (but see sensitivity analysis below). I parameterized availability of garbage in urban and urban-interface patches using pre-treatment data collected in education and enforcement experiments conducted in 2008 (Baruch-Mordo et al. 2011), where mean garbage availability was 0.45 in downtown areas (urban patches) and 0.26 in residential neighborhoods (urban-interface patches). The resultant default probabilities of λ_{ij}, calculated based on the above availability and composition values, appear in Table 3.1.

I calculated the state-dependent foraging costs $\alpha_i(x)$ based on the amount of energy needed to travel in each patch converted into kg of fat loss. Watts et al. (1991) reported that polar bears (*U. maritimus*) used 12 times the energy of their basal metabolic rate (*BMR*) to run at a speed of 2.2 m/sec. Using the mammalian formula (see patch selection model section) I calculated *BMR* as $57.2M^{0.716}$ (kcal/day), where I multiplied the state variable of kg fat by three to obtain total body mass *M*. I converted the speed of 2.2 m/sec to km/day and divided 12*BMR* by the result to provide a state-dependent estimate of the amount of kcal needed to move one km (kcal/km). To obtain the daily energy expenditure on movement (kcal/day), I multiplied the energy expended per km by the mean daily distance moved (km/day) in each patch as estimated from GPS data collected from Aspen bears (3.82, 3.67, and 6.16 km on average in urban, urban-interface, and wildland patches, respectively; Appendix 3.2). Lastly to estimate kg of fat lost per day, I divided the daily energy expenditure by a conversion factor of 9110 kcal, which is the expected energy in 1 kg of bear fat (Rode and Robbins 2000).

Foraging benefits were based on the amount of kg fat gained from natural and anthropogenic foods. In British Columbia, wild black bears gained between 0.42 – 0.86 kg/day from natural food sources during summer (McLellan 2011), which was within range of similar estimates reported for captive grizzly bears (*U. arctos*) fed on natural diets (Robbins et al. 2007). I found no published data of weight gain for bears feeding on anthropogenic resources; however unpublished data from Minnesota suggested free-ranging black bears that fed on anthropogenic food sources gained up to 2.3 kg/day in late summer and fall (K. Noyce, Minnesota Dept. of Natural Resources, personal communication), and in the Aspen study, one bear gained 1.5 kg/day in summer when feeding almost exclusively on garbage resources. Using the mid-point of the above reported ranges, I assumed a gain in body mass of 0.64 kg/day from natural food sources and of 1.9 kg/day from anthropogenic foods. Given that in captive trials grizzly bears gained 0.79 g fat for each 1 g of body mass on low protein diets (Felicetti et al. 2003), I converted yields from kg/day to kg fat/day using a factor of 0.79. Yield was therefore 0.5 kg fat/day from natural and 1.5 kg fat/day from anthropogenic foods, and I tested uncertainty in yield from anthropogenic food sources as detailed below.

Model implementation and sensitivity analyses

The goal of this study was to find thresholds of benefit reduction and cost increase beyond which bears did not select urban and urban-interface patches. I tested effects of management strategies by incrementally reducing benefits or increasing costs in human-dominated patches. For benefit reduction I reduced availability of anthropogenic foods ($avail_{anthro}$) in urban and urban-interface patches. For cost increase I assumed as mentioned above that the key response to aversive conditioning of bears is flight behavior, thus I increased the km moved per day in each patch which subsequently increased the state-dependent energetic cost $\alpha(x)$. I note that under this approach the default cost parameter values (i.e., status quo with no management actions) reflected movement for foraging activity, and interactions with conspecifics and humans. I acknowledge that additional fitness costs due to lethal control are implicit in the lower survival in human-dominated patches, but I focused my evaluation here on the energetic costs of aversive conditioning.

I ran benefit reduction and cost increase scenarios and consecutively incremented parameter values by 5% of the previous value up to 100% reduction or increase of default value. For example, a 10% reduction in anthropogenic food availability (default values of 0.45 in urban and 0.26 in urban-interface patches) resulted in availability of 0.405 and 0.234 in human-dominated patches and reduced λ_{i_anthro}. A 10% increase in cost resulted in movements of 4.20, 4.04, and 6.78 km/day in urban, urban-interface, and wildland patches (default values of 3.82, 3.67, and 6.16) and increased $\alpha_i(x)$. For each benefit reduction and cost increase iteration, I solved eqn. 2 across all time steps and kept records of patch selection. I defined threshold of benefit reduction and cost increase as the minimum percent reduction or increase that resulted in no selection of human-dominated patches, and I searched for state-dependent thresholds under each scenario. I implemented all analyses in program R (R Development Core Team 2011).

I conducted sensitivity analyses to assess impacts of uncertainty in the following default parameters: 1) scaling parameters a and b for the terminal fitness function $\phi(x)$, 2) availability of natural food sources in a poor natural food production year ($avail_{natural}$), 3) yield from anthropogenic foods (Y_{anthro}), and 4) patch-specific survival (s_u, s_{ui}, and s_w). I used Latin hypercube sampling (LHS) to sample random sets of parameter combinations following methodologies of Blower and Dowlatabadi (1994). I sampled from a normal distribution for the scaling parameters a and b, where I estimated mean and SD for each using the reported posterior distribution for mammals in McCarthy et al. (2008). I used uniform distributions for all other parameters where I set the lower and upper distribution limits as: 0.05 and 0.25 for natural $avail_{natural}$, 1.2 and 1.8 for Y_{anthro}, and 0.5 and 1.0 for s_u. Limits for $avail_{natural}$ were chosen to mimic a poor natural food year with only 5 - 25% of natural food availability based on personal observations. Limits for Y_{anthro} and s_u were based on the data obtained from literature and field data, i.e., Y_{anthro} bound between 0.79 times the lowest and highest reported weight gain from anthropogenic foods and s_u bound within the range of adult female survival in poor years (see also Model Parameterization section and Appendix 3.1). Because only certain combinations of patch-specific survival values resulted in realistic model behavior (Appendix 3.1), I randomly drew a value between 0.03 and 0.21 for the difference $s_{ui} - s_u$ to calculate s_{ui}, and conditional on that I randomly drew a value between 0.01 and 0.09 for the difference $s_w - s_{ui}$ to calculate s_w. I tested whether drawing first the difference between $s_{ui} - s_u$ or between $s_w - s_{ui}$ changed sensitivity results and found results to be robust, hence I show only results for drawing difference of $s_{ui} - s_u$ first. I generated a total of 150 LHS sets, but I ran only 115 sets after limiting s_{ui} and s_w to ≤ 1.0.

I assessed the influence of each parameter on model output by comparing the partial-rank correlation coefficients (PRCC) for the seven parameters (a, b, $avail_{natural}$, Y_{anthro}, s_u, s_{ui}, and s_w). PRCC allow evaluation of the relationships between the input parameters and response variable while accounting for any correlations between the input parameters (Hamby 1995). In my model a positive or negative PRCC value, respectively, indicated an increase or decrease in threshold value with an increase in the parameter values. I evaluated PRCC for thresholds in urban and urban-interface patches under both benefit reduction and cost increase scenarios and for each state.

Results

At default parameter values (i.e., no benefit reduction or cost increase), my model suggested that bears with high fat reserves foraged exclusively in wildland patches, and bears with low fat reserves foraged exclusively in urban patches (Figure 3.1A). The optimization strategy for all other bears was to stay in the safer patches, i.e., patches with higher survival, until later in the hyperphagia season, when selection shifted to riskier patches, i.e., patches with lower survival, that provide higher yield (e.g., from wildland to urban-interface patch, or from urban-interface to urban patch).

When default availability of anthropogenic food sources was reduced by at least 55 % in urban patches and 60 % in urban-interface patches, all bears with fat reserves of ≥ 21.65 foraged exclusively in the wildland patch and thus avoided human-dominated patches (Figure 3.1B and Figure 3.2 top panels). Results varied by state, where fatter bears had lower thresholds compared with bears of low fat reserves, and where bears with fat reserves > 33.95, which never foraged in human-dominated patches to begin with, had zero threshold values. While reductions in anthropogenic food availability in urban and urban-interface patches did not eliminate selection of those patches by bears with fat reserves < 21.65, use decreased and its dynamics changed to selection of human-dominated patches earlier in the season (Figure 3.1B). Completely eliminating anthropogenic food availability in urban and urban-interface patches resulted in selection of only urban-interface patches by bears of lower fat reserves.

I ran the cost increase scenarios for up to a 100 % increase in costs due to movement in human-dominated patches and identified only one threshold (25% in urban patch) for bears with a state of 33.95 kg fat reserves. At cost increases of 100 % in both urban and urban-interface patches, selection of human-dominated patches consisted only of urban patches (Figure 3.1C). I continued to increase movement by 100 % intervals and found that when cost increased by >1300 % of default value in the urban patch and >400 % in the urban-interface patch, cost increase thresholds had similar exclusion properties as the benefit reduction thresholds, i.e., bears of ≥21.65 kg fat reserves did not select human-dominated patches (Figure 3.2 bottom panels).

Similar to patterns observed with the benefit reduction scenarios, dynamics changed to selection of human-dominated patches earlier in the hyperphagia season at those thresholds (Figure 3.1D). Exclusion of all bears, including those with lowest fat reserves, occurred only when costs increased by 4750 % in the urban patch and 1250 % in the urban-interface patch.

Sensitivity of thresholds to parameter uncertainty varied by state, with bears of very low (e.g., <21.65) or very high (e.g., >33.95) fat reserves being less sensitive because they mostly had no or zero threshold values as with default parameter values. I therefore focused result interpretation on bears with states ≥ 21.65 and ≤ 33.95 (Figure 3.3). Benefit reduction thresholds were more sensitive to changes in the scaling parameter a rather than b of the terminal fitness function. In general, threshold values increased with an increase in a and Y_{anthro} and decreased with an increase in $avail_{natural}$. Threshold values in urban and urban-interface patches were more sensitive to their own patch-specific survival with a positive correlation, and thresholds in both patches were inversely correlated to survival in wildland patch. Sensitivity results for cost increase thresholds had similar trends as the benefit reduction thresholds (Figure 3.4).

Discussion

Structured decision making is called for when evaluating the efficacy of mitigation strategies for human-wildlife conflict (Barlow et al. 2010). A crucial component is the understanding of ecological mechanisms that lead wildlife to conflict with humans. Acquiring such knowledge through field studies can be expensive, and results are often not available in a timely manner to guide the mitigation of pressing conflicts, especially when managing species of conservation concern (e.g., tiger [*Panthera tigris*]). In this study I used patch-selection models to understand wildlife response to management aimed at reducing benefits and increasing costs of foraging in human-dominated areas. Implementing the model for black bear foraging in an urban system, I identified potential thresholds beyond which most bears should avoid human-dominated patches and gained insights on shifts in selection dynamics that can result from management. I therefore demonstrated how patch selection models can be a valuable decision making tool to study the effects of management on wildlife behavior and provide guidelines for conflict mitigation. Predictions from such models can also serve as hypotheses to be tested in an adaptive management framework (Grantham et al. 2010).

In my model system I found that benefit reduction thresholds of at least 60 % excluded all bears from human-dominated patches except those with the lowest 10 % body fat reserves. Even when anthropogenic foods were completely eliminated, bears with low fat reserves continued to select human-dominated patches, specifically the urban-interface patch that provided a mix of natural and anthropogenic food sources. There are two direct management implications from my results. First, the thresholds identified can provide guidelines for adaptive management in developing objectives to reduce anthropogenic attractants to bears in the study system. Second, even when anthropogenic attractants are successfully eliminated, bears may still select human-dominated patches to forage there naturally. I observed such bear behavior in the field, where I commonly identified natural foraging events at bear GPS locations near human development (S. Baruch-Mordo, unpublished data). This highlights the fact that despite the best mitigation plans some levels of human-wildlife interaction, and possibly also conflict, may persist in a landscape of mixed natural and human-dominated areas.

Cost increase thresholds were at times an order of magnitude higher than default values, requiring an increase of bear movement in the urban and urban-interface patch by approximately 12 and 45 km/day to achieve similar exclusion results as the benefit reduction thresholds. While a detailed economic cost-benefit analysis for each management strategy is warranted (Hughey et al. 2003), it is likely not feasible to implement such high level costs using aversive conditioning. Therefore, in this study system I would predict that implementing benefit reduction management strategy would be more effective than cost increase strategies. I note that I did not test the effects of various combinations of these strategies (e.g., 50% cost increase and 50% benefit reduction), which may prove more efficient than only implementing benefit increase strategies and that future studies should explore. Also, it is possible that the cost increase parameters used in my models, i.e., the energetic costs of movement resulting from flight behavior, failed to incorporate other energetic costs associated with aversive conditioning such as stress and increased vigilance behavior (Frid and Dill 2002). However, those responses are difficult to quantify energetically, especially in a wild setting, and I am not aware of any data that allows incorporation of such parameters, and field evaluations that likely included all behavioral responses by bears suggested that aversive conditioning methods can be ineffective in deterring bears from human-dominated areas (Beckmann et al. 2004, Mazur 2010).

Some authors advocate that preventative management, i.e., the reduction in benefits from anthropogenic attractants, should be the primary goal of conflict mitigation over reactive management, i.e., the lethal or non-lethal control of wildlife (Dorrance 1983, Fall and Jackson 2002). A key argument is that reactive management without an effective elimination of attractants can perpetuate the problem (Hristienko and McDonald 2007). Others suggest that regardless of the food type consumed, wildlife that forage in human-dominated patches are habituated, pose danger to human safety, and therefore should be removed (Hristienko and McDonald 2007). While resolving this philosophical difference in management views is beyond the scope of this paper, I demonstrated the advantages of patch selection models as a planning tool to assess impacts of each strategy in that they: 1) allow flexibility in model adaptations to address system-specific properties, e.g., the inclusion of multiple food types, 2) provide outputs that can serve as management objectives and research hypotheses, 3) allow measures of uncertainly using sensitivity analyses therefore compare the uncertainty resulting from each strategy, and 4) provide ecological insights on the mechanisms and dynamics of wildlife foraging decisions in response to human-wildlife conflict mitigation. Coupled with a socio-economic cost-benefit analysis, patch selection models can be a useful tool in the conservation managers' toolbox.

Table 3.1. Default parameter values used in patch selection models to test effects of human-bear conflict management on female bear foraging decisions in the human-dominated environment of Aspen, Colorado, USA. Patches included were urban (*u*), urban-interface (*ui*), and wildland (*w*).

Symbol	Meaning	Description and default values	Source
X	State variable of value x at time t	Kg of body fat scaled from female body mass assuming 30% of body fat. Critical (x_c) and cap (C) values of 20 and 35 kg fat based on data from Aspen study bears.	Baruch-Mordo, S,. unpublished data, Belant et al. 2006
s_i	Probability of daily survival period t given patch choice i	Calculated based on range of adult female survival in poor natural food production year in Aspen as $s_u = 0.75$, $s_{ui} = 0.87$, and $s_w = 0.92$, and later converted to daily survival by raising to power of 1/228.	Chapter 1, Sensitivity analyses
$\phi(x)$	Terminal fitness function at time T	Calculated based on allometric equation: $\exp(-0.61M^{-0.25})$ where M is body mass or kg fat times 3.	McCarthy et al. 2008
λ_{ij}	Probability of finding food of	A product of patch-specific food availability (a_{ij}) and composition (c_{ij}). Anthropogenic food availability from	Baruch-Mordo et al. 2011

<table>
<tr><td></td><td>type j in patch i</td><td>experiments conducted in Aspen, natural food availability in poor natural food year from local observations. Composition of anthropogenic and natural foods was 0 in w and u patches, respectively, and 0.5 each in ui patches.
<table><tr><th></th><th>Natural</th><th>Anthropogenic</th></tr><tr><td>Urban</td><td>0</td><td>0.45</td></tr><tr><td>Urban-interface</td><td>0.05</td><td>0.13</td></tr><tr><td>Wildland</td><td>0.1</td><td>0</td></tr></table></td><td></td></tr>
<tr><td>$\alpha_i(x)$</td><td>State-dependent cost of movement in patch i</td><td>Body fat lost (kg/day) based on state-dependent basal metabolic rate, daily distance moved in each patch (Appendix 3.1), and kcal energy needed to lose 1 kg of fat.</td><td>Baruch-Mordo, S., unpublished data, Robbins 1993, Rode and Robbins 2000, Watts et al. 1991</td></tr>
<tr><td>Y_{ij}</td><td>Yield from food type j in patch i</td><td>Body fat gained (kg/day) from natural (0.5) and anthropogenic (1.5) food sources.</td><td>Baruch-Mordo, S., unpublished data McLellan 2011, Noyce, K., unpublished data</td></tr>
</table>

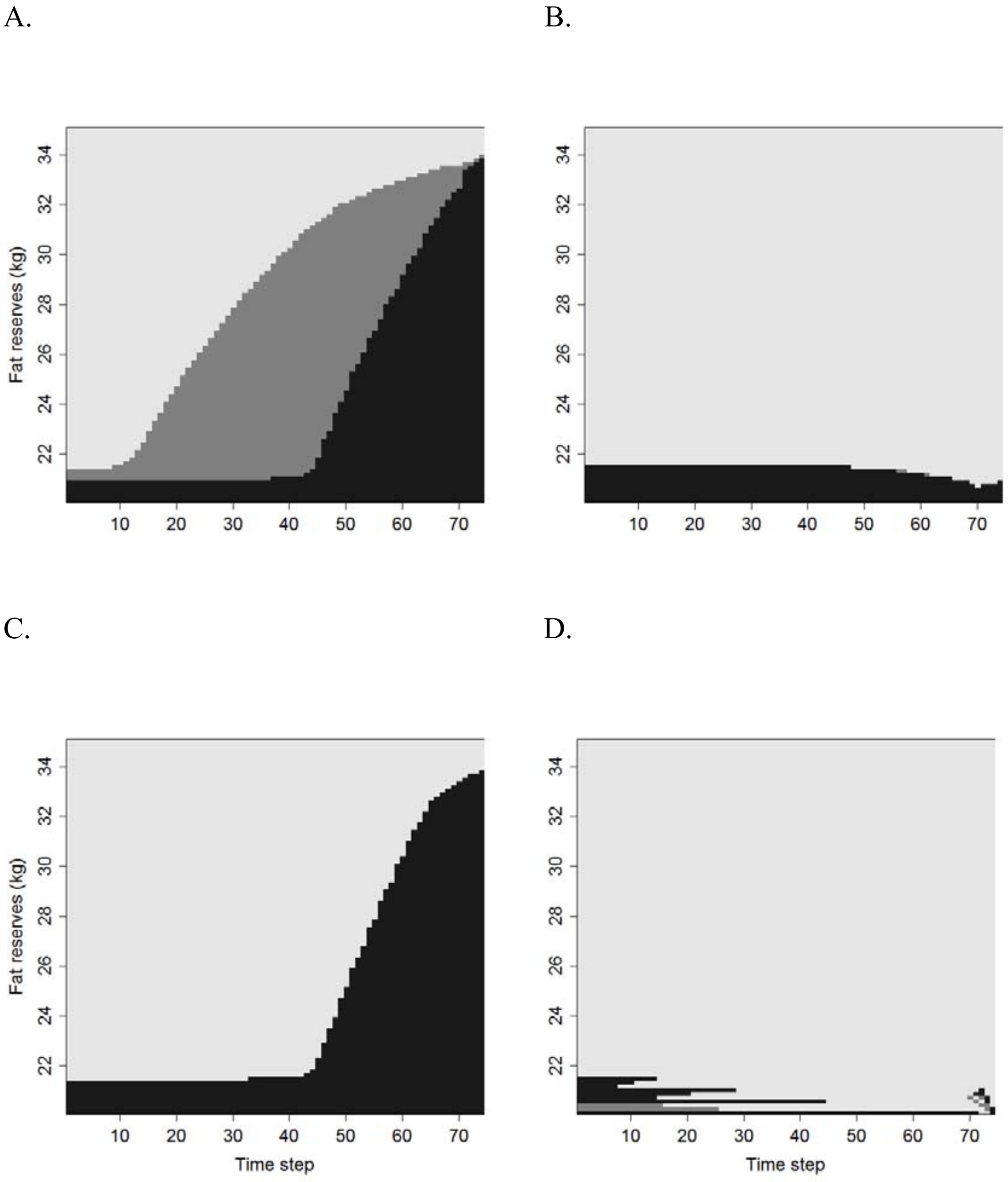

Figure 3.1. Selection of urban (black), urban-interface (dark grey), and wildland (light grey) patches by female black bears with fat reserves ranging from 20-35 kg over days 1 – 75 of the hyperphagia season. Patch-selection model scenarios include: (A) default parameter values, (B) benefit reduction values of 55 % in urban patches and 60 % in urban-interface patches (C) cost increase values of 100 % in urban and urban-interface patches, and (D) cost increase values of 420 % in urban and 1330 % in urban-interface patches.

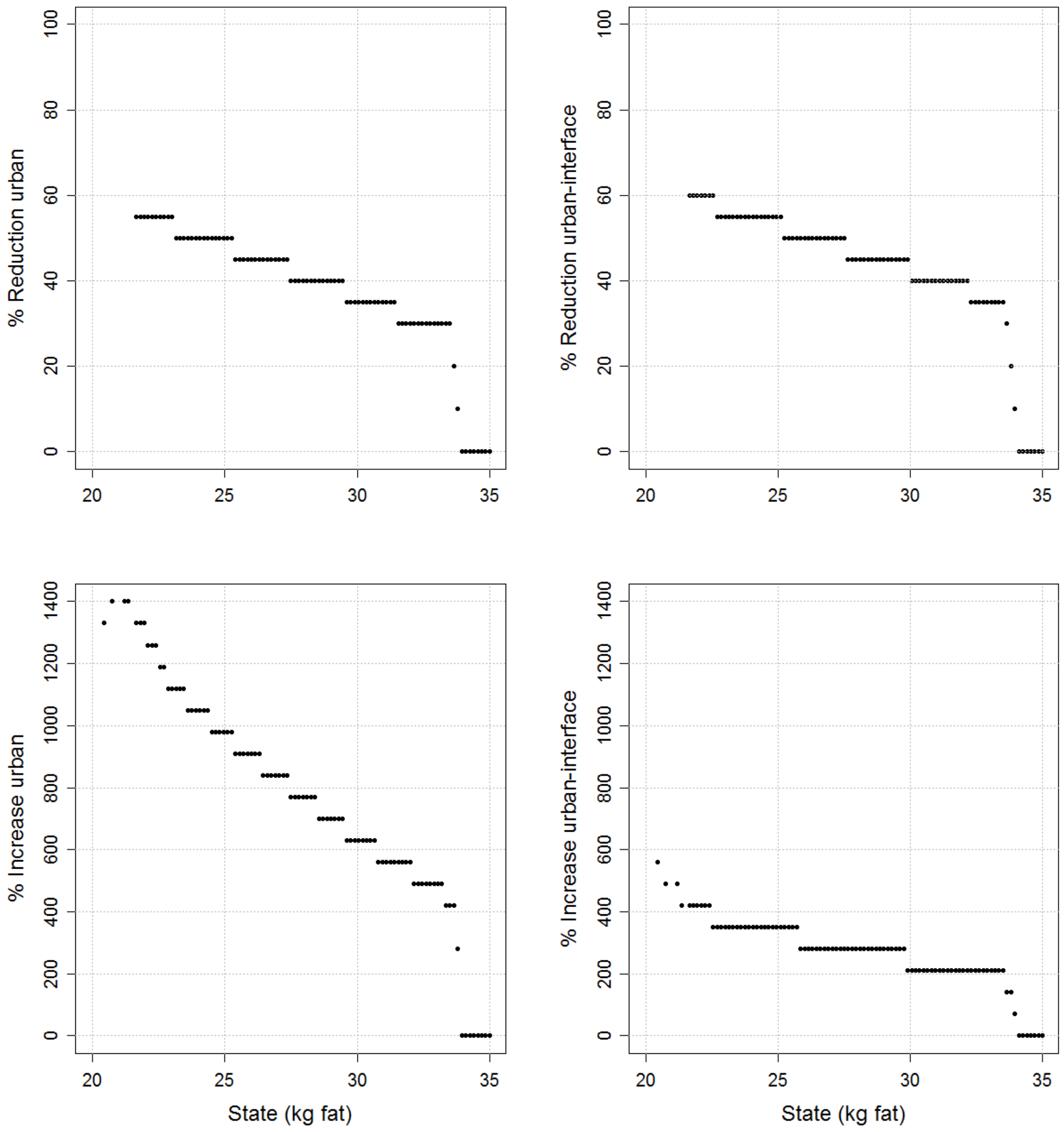

Figure 3.2. Thresholds of percent reduction in benefits (top panels) or percent increase in costs (bottom panels) in urban (left) and urban-interface (right) patches as a function of bear state. Threshold values represent % reduction or increase beyond which bears did not select human-dominated patches.

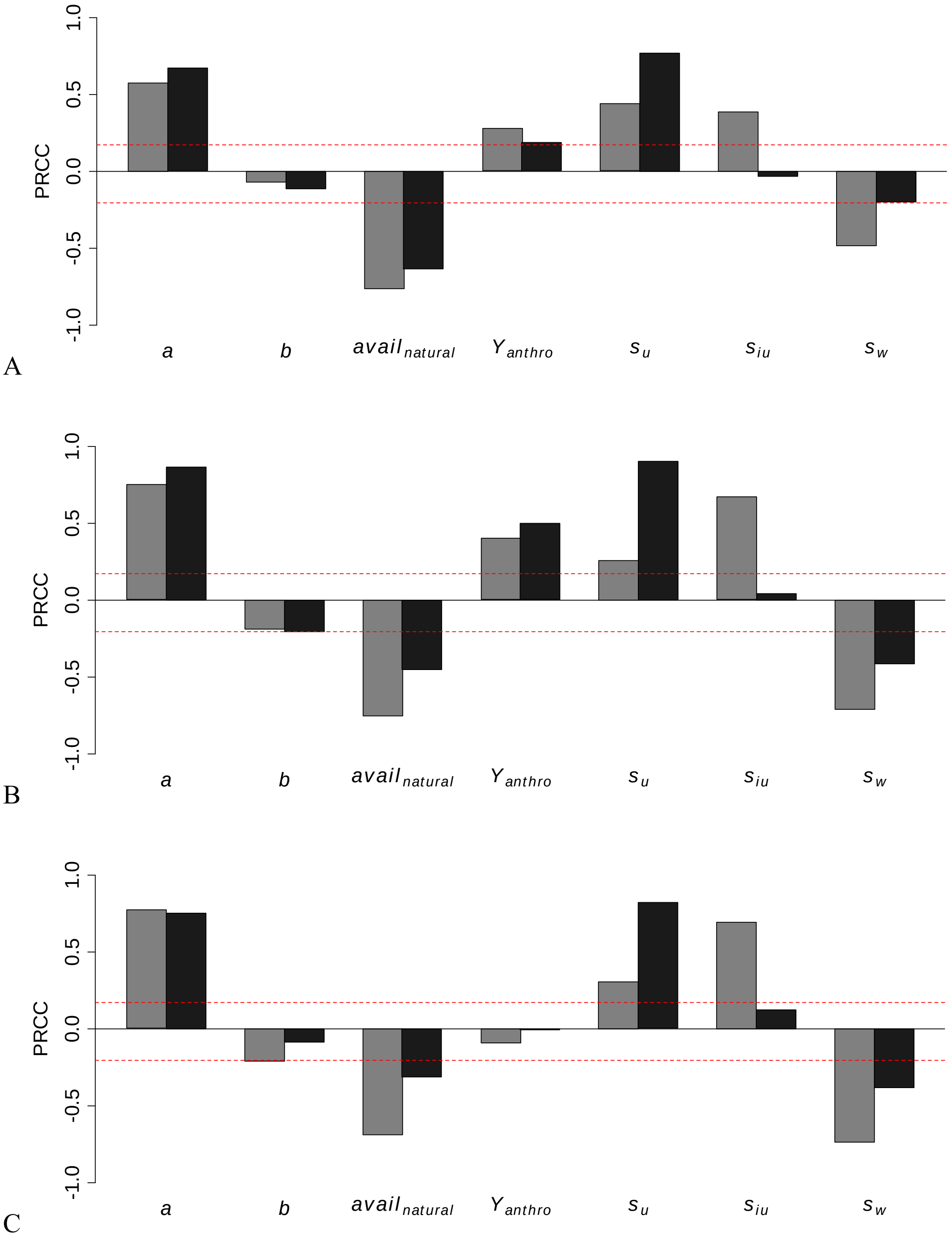

Figure 3.3. Sensitivity results for benefit reduction thresholds in urban (black) and urban-interface (dark grey) patches for bears of low (21.65), medium (27.8), and high (33.95) kg fat reserve states. Dashed lines represent significance at a level of $\alpha = 0.05$.

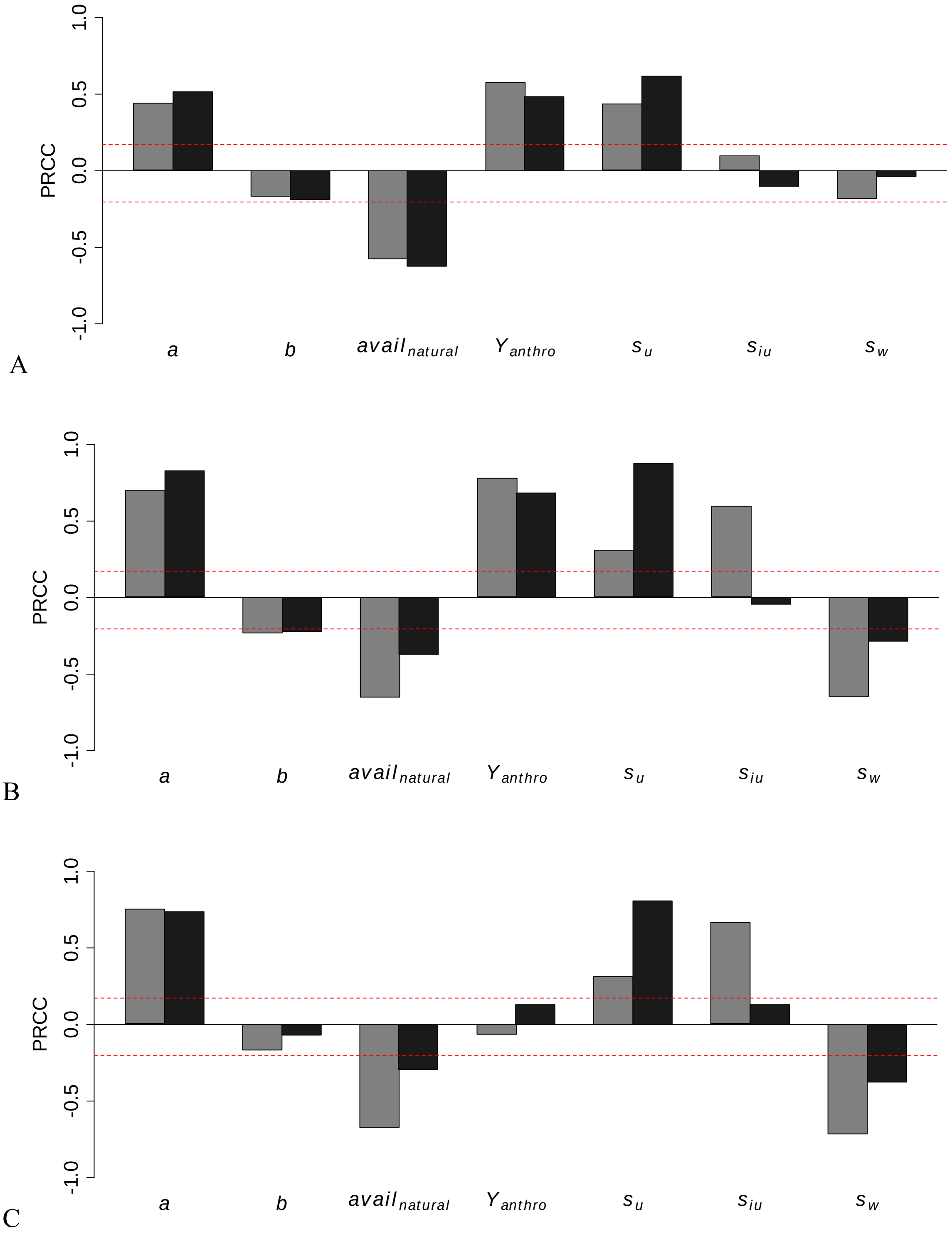

Figure 3.4. Sensitivity results for cost increase thresholds in urban (black) and urban-interface (dark grey) patches for bears of low (21.65), medium (27.8), and high (33.95) kg fat reserve states. Dashed lines represent significance at a level of $\alpha = 0.05$.

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APPENDIX 3.1. PROCEDURES TO OBTAIN DEFAULT PATCH-SPECIFIC SURVIVAL VALUES

Estimated adult female survival ($\hat{s}$) in Aspen in poor natural food production years was 0.718 (*SE* = 0.117; Chapter 1). I converted this active season estimate (April 16 – November 30; total of 228 days) into daily survival by raising $\hat{s}$ to the power of 1/228 and used the range $\hat{s} \pm 1.96 * SE$ as a parameter space in which to search for appropriate combination of patch-specific survival. I ran the patch selection model assigning different urban, urban-interface, and wildland survival values from 0.5 - 1.0 incrementing each by 0.01 (132,651 combinations). I further restricted results based on observed system behavior in Aspen such that the patch decision matrix included all three patches (6,995 combinations), and that the percent selection of each patch across all states and time steps was <90% and >10% (i.e., all bears did not exclusively use or avoid any given patch at all times; 2,248 combinations). I found that to obtain realistic model behavior, survival in urban-interface patch (s_{ui}) was always greater than in urban patch (s_u; range of difference: 0.03 – 0.21, mid-point 0.12) and survival in wildland patch (s_w) was always greater than in urban-interface patch (range of difference: 0.01 – 0.09, mid-point 0.05; Figure 3.1A.1). These results were in accordance with patterns observed in Aspen where urban patches had the least amount of cover, highest availability of garbage, and therefore higher probability of conflict, followed by urban-interface patches in which cover increased and availability of garbage and probability of conflicts decreased. Therefore, for default values I assigned $s_u = 0.75$ (midpoint of 0.5 – 1.0 range) and used the midpoint of the range in differences to run the model with $s_{ui} = 0.87$ (i.e., 0.75 + 0.12) and $s_w = 0.92$ (i.e., 0.87 + 0.05).

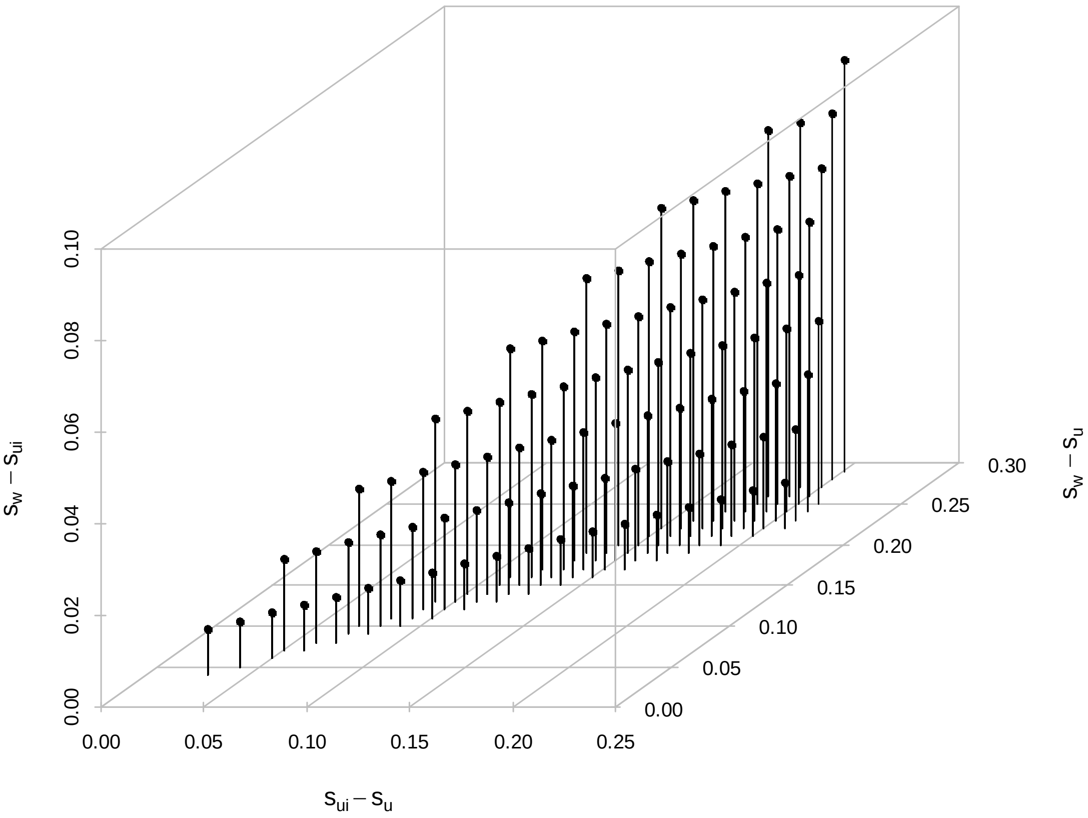

Figure 3.1A.1. Summary of all possible differences in black bear survival between urban-interface and urban patches ($s_{ui} - s_u$), wildland and urban-interface patches ($s_w - s_{ui}$), and wildland and urban patches ($s_w - s_u$). Differences were generated while exploring combinations of patch-specific survival over a parameter space of 0.5 – 1.0. Parameter space was based on survival estimates for bears in a poor natural food production year in Aspen, Colorado, USA. Only parameter value combinations that produced realistic behavior observed in the Aspen system were included in this summary.

APPENDIX 3.2. PROCEDURES TO CALCULATE DAILY DISTANCE MOVED IN EACH PATCH

I estimated daily distance moved in each patch using GPS locations collected from Aspen bears. I first defined urban, urban-interface, and wildland patches in ArcGIS 9.3 (ESRI 2008). I used an address layer to generate a point density raster of addresses per 1-km^2 circular neighborhood. I then reclassified density values ranging from 0 – 865 into three categories using the Jenks optimization method to find natural breaks in their distribution (ESRI 2008), and converted the result into a polygon layer of urban (326 – 865 addresses/km^2), urban-interface (62 – 325 addresses/km^2), and wildland (0 – 61 addresses/km^2) patches. Visual examination of polygons with aerial photos confirmed an accurate overlap between urban, urban-interface, and wildland patches and respectively, the core area of downtown Aspen, its surrounding residential neighborhoods, and the adjacent landscape matrix of mountain-shrub and forest communities.

Once patches were defined, I used the overlay function in sp package (Bivand et al. 2005) in R v. 2.13.2 (R Development Core Team) to clip the GPS locations collected at 30-min interval by the patch polygon layer. I restricted analyses to data from hyperphagia season, poor natural production years, and female bears. Once GPS locations were clipped by patch, I calculated per Julian day the average distance moved (m) between consecutive successful GPS locations. I ensured that the time interval between locations did not exceed 35 min, thus allowing for some GPS clock error but avoiding inflated distances due to missed fixes. I divided distances by 1000 to convert to km, and multiplied the result by 48 to convert to 1 day. I then averaged the daily movements across all bears (n = 11) within patch as 3.82, 3.67, and 6.16 km/day.