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Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States

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ABSTRACT

As landscapes across the globe experience increasing human development, it is critical to identify the behavioral responses of wildlife to this change given associated shifts in resource availability and risk from human activity. This is particularly important for large carnivores as their interactions with people are often a source of conflict, which can impede conservation efforts and require extensive management. To examine the adaptations of a large carnivore to benefits and risks associated with human development we investigated black bear behavior in three systems in the western United States. Our objectives were to (1) identify temporal patterns of selection for development within a year and across years based on natural food conditions, (2) compare spatial patterns of selection for development across systems, and (3) examine individual characteristics associated with increased selection for development. Using mixed effects resource selection models we found that bear selection for development was highly dynamic, varying as a function of changing environmental and physiological conditions. Bears increased their use of development in years when natural foods were scarce, throughout the summer-fall, as they aged, and as a function of gender, with males exhibiting greater use of development. While patterns were similar across systems, bears at sites with poorer quality habitat selected development more consistently than bears at sites with higher quality habitat. Black bears appear to use development largely for food subsidy, suggesting that conflicts with bears, and potentially other large carnivores, will increase when the physiological demand for resources outweighs risks associated with human activity.

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1. Introduction

As landscapes across the globe rapidly change due to increased human development (Vitousek et al., 1997; Ellis et al., 2010), there is uncertainty about the behavioral responses of wildlife to these changes given associated shifts in resource availability and risk. Urban and exurban development (hereafter development) typically reduce native food resources for animals, but introduce novel anthropogenic foods (garbage, crops, livestock, watered landscaping, etc) and risks associated with foraging in human-dominated landscapes (mortality from vehicle collisions, lethal removal; hereafter risk). The initial response of animals to human development is typically a change in behavior, as animals have been observed to alter patterns of habitat selection (Nellemann et al., 2007), vigilance (Mccleery, 2009), daily activities (Riley et al., 2003 and Beckmann and Berger, 2003a) and foraging (Robinson et al., 2010), often in highly diverse ways (Tuomainen and Candolin, 2011). These behavioral responses reflect perceived trade-offs between the benefits of acquiring key resources and the risks associated with human activity (Frid and Dill, 2002). While these trade-offs should be dynamic in space and time as a function of habitat quality, natural food conditions and the physiological states of individuals, little is known about how animals in human-altered landscapes behaviorally adapt to such variation.

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Elucidating the behavioral responses of wildlife to human development is particularly important for large carnivores as their home ranges frequently overlap with human infrastructure and activities (Mladenoff et al., 1997), and their interactions with people are often a major source of conflict (Treves and Karanth, 2003). In many cases, large carnivores avoid people (Oakleaf et al., 2006 and Nellemann et al., 2007) and exhibit antipredator behavior indicating they associate humans with risk (Ordiz et al., 2011). Some carnivores, however, have been observed to forage within human development on their natural foods (Gehrt et al., 2009 and Dellinger et al., 2013) or on anthropogenic foods (Bateman and Fleming, 2012 and Merkle et al., 2013), exploiting novel resources associated with human infrastructure. Such behavior has been linked to increased reports of human–carnivore conflicts, generating concern over human safety and property, and stymieing conservation efforts for some carnivore species (Treves and Karanth, 2003). If wildlife managers and conservation practitioners are going to be successful at reducing human–carnivore conflicts in an increasingly developed landscape, they need to understand how these animals behaviorally respond to development, and the conditions that modify their behavior.

These concerns are particularly relevant for the American black bear (*Ursus americanus*). Bears can readily exploit the wealth of reliable, high-calorie food resources available around human development (i.e., garbage, fruit trees, livestock), but are also susceptible to increased mortality from vehicle collisions, conflict-related euthanasia, and other human-related factors (Beckmann and Berger, 2003a,b; Hostetler et al., 2009 and Baruch-Mordo et al., 2014). Although studies have demonstrated that bears perceive risk associated with human activity (Beckmann and Berger, 2003a; Nellemann et al., 2007 and Ordiz et al., 2011), human–bear conflicts have generally increased over time (Hristienko and McDonald, 2007), displaying high temporal and spatial variation (Baruch-Mordo et al., 2008 and Treves et al., 2010). As a long-lived species with relatively stable population dynamics (Beston, 2011), high temporal variation in conflict activity within and across years is presumably a consequence of shifting foraging behavior, not shifting demography, as bears reassess the trade-offs of using anthropogenic foods. Factors such as natural food conditions, a bear's physiological state (e.g., reproductive status), or degree of exposure to human activity, likely influence the benefits and risks (perceived or real) of foraging in human-dominated landscapes, driving observed variation in conflict activity. Indeed, Baruch-Mordo et al. (2014) documented a shift in bear space-use to incorporate additional human development in poor natural food years. However, no information is currently available about how bears temporally alter their use of development within a year, whether bears in different locations similarly interpret the costs and benefits of foraging in developed landscapes, or whether certain characteristics of individuals may exacerbate or inhibit their use of human development.

To understand how a large carnivore adapts to the shifting benefits and risks of foraging among human development, we examined patterns of black bear habitat selection using GPS location data from 109 bears around three developed areas in the western US (Aspen [CO], Durango [CO], and Lake Tahoe [NV]). Throughout our investigation, we interpret a bear's selection for development as the behavioral outcome of their perceived forage/risk assessment (Frid and Dill, 2002). Specifically, our objectives were to (1) examine temporal patterns of selection for development within the active bear season and across years based on natural food conditions, (2) compare patterns of selection for development among study systems, and (3) identify individual attributes (maternal status, age, etc.) associated with selection for development. We expected that the benefits of foraging around human development would outweigh the perceived consequences when bears were physiologically stressed and needed additional food resources. Within study systems, we expected bears to increase their use of development in years when natural foods were scarce, during hyperphagia (the period of increased foraging prior to hibernation) and when females were experiencing increased energetic demands with lactation. Across study systems, we expected bears at more xeric sites with fewer natural food resources to exhibit stronger and more consistent selection for development than bears in more mesic sites with a greater abundance of natural foods.

2. Materials and methods

2.1. Study areas

We evaluated black bear habitat selection around three developed areas in the western U.S.: Aspen (CO), Durango (CO), and Lake Tahoe (NV; hereafter Tahoe). All areas have experienced high rates of human-black bear conflicts and have been the focus of long-term studies on this issue (Johnson et al., 2011; Lackey et al., 2013 and Baruch-Mordo et al., 2014). At all three sites, grizzly bears (*Ursus arctos*) were absent.

Among the three study systems, Aspen is the most mesic and Tahoe is the most xeric, with associated differences in precipitation, elevation and vegetation. Over the last 10 years, annual precipitation averaged 62.8 cm in Aspen (http://ccc.atmos.colostate.edu/dataaccess.php), 48.5 cm in Durango (http://ccc.atmos.colostate.edu/dataaccess.php), and 7.5 cm in Tahoe (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?nv4618); elevations of the towns at each site are approximately 2 405 m, 1 985 m, and 1 919 m, respectively. Vegetation around Aspen is dominated by gambel oak (*Quercus gambelli*), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), aspen (*Populus tremuloides*), lodgepole (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and spruce (*Picea* spp.)-subalpine fir (*Abies lasiocarpa*) forests. Around Durango, vegetation is primarily oak, serviceberry, chokecherry, aspen, pinyon–juniper (*Pinus edulis*/*Juniperus* ssp.) woodland, and ponderosa pine (*Pinus ponderosa*) and spruce-fir forests. On the east side of the Lake Tahoe basin, vegetation is dominated by manzanita (*Arctostaphylos* manzanita), serviceberry, aspen, Jeffrey pine (*Pinus jeffreyi*), ponderosa pine, lodgepole, Douglas-fir, and western white pine (*Pinus monticola*) forests. Key late summer and early fall mast species around Aspen and Durango include chokecherries, serviceberries and acorns (gambel oak); in Tahoe they include manzanita berries, pinyon pine nuts and other conifer seeds. Around human development, bears primarily forage on garbage and fruit trees (i.e., apple, crabapple, pear; Lewis, 2013; Nevada Department of Wildlife and Colorado Parks and Wildlife, unpublished data).

Human development at the Aspen site consisted of the towns of Aspen (6658 residents) and Snowmass (2826 residents), with additional development along the Roaring Fork valley. The Durango site consisted of the town of Durango (16,887) with additional development along adjacent valleys and mesas. In the Tahoe system, the major towns were South Lake Tahoe, CA (21,403 residents), Stateline, NV (842 residents), and Incline Village, NV (8777 residents), with additional development along the eastern shoreline of Lake Tahoe. All population sizes are reported for 2010 (United States Census Bureau, 2014). During the time period relevant to our analysis, the number of black bear harvest licenses was similar among years for the Aspen and Durango sites, and there was no hunting around Tahoe.

2.2. Black bear data

Bears were caught using culvert traps, box traps, Aldrich foot snares, and free-range techniques (Jonkel, 1993). Captured bears

were immobilized, had a tooth pulled for age estimation (Willey, 1974), and were fitted with a GPS collar so that their locations could be tracked. In Aspen, collar locations were obtained from 2005 to 2010 on males and females (Lotek collars, 3300L and 4400M). In Tahoe, collar locations were collected from 2005 to 2011 on females only (Northstar, Telonics collars). In Durango, collar locations were collected in 2011 and 2012 on females only (Vectronics Globalstar collars). In Aspen and Durango locations were collected or sub-sampled on an hourly basis and in Tahoe locations were collected every 2–3 h. At all sites, trapping efforts occurred within approximately 10 km of urban development to collar a cohort of bears that experienced similar natural food conditions and had anthropogenic resources readily accessible. Each year, collared female bears were tracked to their winter dens, immobilized, and monitored for newborn cubs.

2.3. Habitat covariates

We investigated bear selection for human development after accounting for topographic, vegetation, and moisture variables. Topographic variables included elevation, slope, aspect, and terrain ruggedness, all derived from 30 m USGS Digital Elevation Models. Aspect was coded as a categorical variable with 9 classes (Flat, N, NE, E, SE, S, SW, W, NW; N was the reference class). We estimated terrain ruggedness using an index developed by Sappington et al. (2007). We used the USDA/USDOI LANDFIRE existing vegetation type coverage (www.landfire.gov/NationalProductDescriptions21.php) to delineate 9 vegetation classes relevant to black bear habitat: conifer mixed forest, aspen mixed forest, alpine mixed forest, meadow/grassland, oak association, pinyon–juniper, riparian, shrub, and agriculture. We then calculated the proportion of each vegetation type within a 9-pixel neighborhood (pixels were 30 m) across each study area, creating nine vegetation variables that were used in analyses. To identify drainages with water and higher soil moisture, we used the National Hydrology Dataset (1:24,000 scale), and calculated distance-to-drainage for each pixel within each study area.

We quantified the density of human structures across each study site to investigate bear selection for human development. For Aspen and Durango, we used point data available from the relevant counties which mapped all human structures. For Tahoe we used a combination of address points and parcel data (creating a point in the center of every parcel known to have a structure) obtained from relevant counties. For each pixel, we quantified human development (HD) as the mean density of points/km^2 within a circular neighborhood with a radius of 1 km. All spatial covariates were depicted as site-specific rasters (30 m). Rasters encompassed all areas used by collared bears throughout the year.

To assess temporal variation in bear selection for development across seasons we included a binary covariate describing natural food conditions (Food Year). Locations collected during moderate or good years were coded as 0, and locations collected during poor years were coded as 1. Based on the abundance of acorns, serviceberries, and chokecherries, poor food years around Aspen were 2007 and 2009 (Baruch-Mordo et al., 2014) and around Durango was 2012. At both sites, information about species-specific mast availability is qualitatively scored each fall by Colorado Parks and Wildlife District Wildlife Managers. In addition, around Durango, 15 transects were surveyed every two weeks between mid-July and mid-September. Transects were 1 km in length, and randomly selected within the study area from existing trails and stream drainages. During each survey, mast species were qualitatively scored based on phenology and mast abundance. In 2011, 25–50% of masting plants on all transects had acorns or berries. In 2012, no berries were observed and <25% of transects with gamble oak had nuts. In Tahoe, there were not enough data across good and poor natural food years to include this covariate in analyses. To assess temporal variation in bear selection for development within a season, we attributed each location a continuous number from 1 to 26 representing the week it was collected (1 May–31 October).

2.4. Examining temporal and spatial patterns of bear selection for human development

To investigate variation in bear selection for human development we used mixed-effects resource selection models (RSFs) to evaluate third order selection (Johnson, 1980), following a use-availability design (Manly et al., 2002). "Used" GPS locations were assessed on an animal-year-specific basis, collected from May to October; approximately 55% of collared bears had data for 1 year and 45% had data for >1 year. Habitat attributes associated with locations from each animal-year were compared to an equal number of randomly selected locations in habitat considered "available" to each individual. To determine available habitat for each bear we calculated animal-specific 95% minimum convex polygons (MCPs) from all May to October locations. Using Geospatial Modeling Environment software (Beyer, 2012) available locations were then randomly drawn from the MCPs and attributed for each animal-year-specific dataset. We randomly assigned a week and food condition value to each available location.

We extended the fixed effects RSF model to include random effects. To construct population-level models we used generalized linear mixed models (GLMMs) with the logit link, taking the form:

$$\text{Logit}(y_{ij} = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} \ldots + \beta_n x_{nij} + \gamma_{0j})$$

where β_0 is the fixed-effect intercept, β_n are estimated fixed-effect selection coefficients, x_n are habitat covariates at location i for bear j, and γ_{0j} is a random intercept for bear j. We included the random intercept to account for autocorrelation within animal datasets and differences in sample sizes among individuals (Gillies et al., 2006). For the random intercept we nested data for each animal-year within animal to account for the hierarchical nature of the data.

We generated separate site-specific models of bear selection for human development, and ran models separately for Aspen females and Aspen males (Aspen was the only site with data on males). We first ran a "Base" model for each study site that included topographic, vegetation and drainage variables. We examined habitat covariates to ensure that no two variables were highly correlated (Pearson's correlation coefficient $r > |0.6|$), and conducted univariate tests to confirm that base variables were significant for bear selection at all sites (Hosmer and Lemeshow, 2000; all tests $P < 0.05$).

To examine bear selection for human development, we then compared a series of models. We first ran the base model for each site with only the addition of HD (no temporal variation in selection). Next, to test whether temporal variation in selection for development occurred across years, we ran base models with an interaction between HD and Food Year (and their main effects). Then, to test whether temporal variation for selection for development occurred within a year, we ran base models with an interaction between HD and Week (and their main effects). We also tested whether selection for development was subject to both across- and within-year temporal variation by running a model that included a 3-way interaction between HD $*$ Food Year $*$ Week (and main effects and 2-way interactions). For each model structure, we tested whether a quadratic term for HD improved fit, allowing for a non-linear selection response by bears to human development (Merkle et al., 2011). We fit models using maximum likelihood estimation and used minimum Akaike Information Criterion (AIC) scores to assess the relative support of models with different fixed effects (Burnham and Anderson, 2002). Modeling was

conducted with the package 'lme4' (Bates et al., 2013) in program R version 3.0.2 (R Core Team, 2012).

We assessed the predictive power of each site- and sex-specific model with cross-validation using hold-out data (Boyce et al., 2002). We had randomly selected 80% of animal-year datasets to develop and select models, and withheld 20% for validation. For each site and sex (in Aspen) we extrapolated the spatial predictions of the top RSF model across the study area, dividing the predicted values into 10 equal area bins. We then used the top models to calculate predicted RSF values from hold-out data, and used Spearman's rank correlation to compare the frequencies of hold-out predictions with the training predictions for each bin.

2.5. Identifying individual attributes associated with bear selection for human development

We estimated individual selection coefficients from GLMMs to investigate factors associated with individual animal differences in bear selection for human development (Hebblewhite and Merrill, 2008 and Wagner et al., 2011). To compare bear selection coefficients across sites we re-ran the "Base + HD" model with data only on females. We restricted this analysis to locations collected during August–September, allowing us to assess bear selection for human development during the time period of peak conflict activity across sites. As in the site-specific analyses, we randomly choose an equal number of available locations from animal-specific 95% MCPs (based on data collected May–October), as we were interested in bear selection for development during late summer/fall relative to their selection throughout the remainder of the year. Models took the form:

$$\text{Logit}(y_{ij} = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} \ldots + \beta_n x_{nij} + \gamma_{HDj} x_{HDj} + \gamma_{0j})$$

which included a random selection coefficient (γ_{HDj}) for HD for bear *j*. We also included the random intercept of animal-year nested within animal.

We extracted animal-year-specific individual selection coefficients for HD from the multisite model, and then used them as the response variable in a linear regression to test whether individual selection for HD was associated with several covariates. Covariates included the bear's age, maternal status (cubs or no cubs based on den visits the previous winter), mean HD within the total known 95% MCP for an individual (HD_{all}), and mean HD within the year-specific August–September 95% MCP ($HD_{hyperphagia}$). These last 2 variables (HD_{all} and $HD_{hyperphagia}$) were included to test for a functional response in selection for human development (Mysterud and Ims, 1998), whether bears selected for development based on its availability within either their overall home-range (HD_{all}) or their year-specific late summer range during hyperphagia ($HD_{hyperphagia}$). We used regression coefficients to assess the effect of each covariate on bear selection for HD (95% confidence intervals non-overlapping zero). Statistical analyses were conducted in R 3.0.2 (R Core Team, 2012).

3. Results

3.1. Temporal and spatial patterns of bear selection for human development

During May–October we collected a total of 331,851 locations from 109 different bears; 87,530 locations for Aspen females (14 different bears), 82,272 for Aspen males (29 bears), 152,365 for Durango females (50 bears), and 9684 for Tahoe females (16 bears). The mean number of animal-year locations was 2823 for Aspen females, 1870 for Aspen males, 2177 for Durango females and 372 for Tahoe females (fewer locations on Tahoe bears were due to reduced fix schedules and high rates of collar failure).

Coefficients for base model covariates demonstrated that bears at all sites selected for steeper slopes and for areas with greater proportions of aspen, riparian, and conifer mixed forest vegetation (Table 1). Bears at all sites avoided shrublands, and had site-specific responses to alpine, meadow, oak, and pinyon–juniper communities (Table 1). Bears in Aspen avoided agriculture, but bears in Durango and Tahoe selected for agriculture. Bears in Aspen and Durango selected for lower elevations while bears in Tahoe selected for higher elevations. Females at all sites generally selected for more rugged terrain, but males in Aspen avoided rugged terrain. Bears in Aspen generally selected all non-flat aspects, while bears in Durango and Tahoe avoided southern and western aspects (Table 1).

Bears at all sites selected positively for human development. Unequivocally, the best model for males in Aspen and females in Aspen and Durango, included both between- and within-year temporal variation in bear selection for human development (Table 2, second best models had ΔAIC scores >800; Aspen females $r^2 = 0.31$, Aspen males $r^2 = 0.33$, Durango females $r^2 = 0.17$). Bears increased their selection for development in poor natural food years (Figs. 1 and 2). During poor years, selection for development increased throughout the active season (May–October), while in good years, selection for development decreased throughout the active season (Fig. 1). In Tahoe, the best model illustrated that bear selection for development increased toward late summer/fall (second best model had ΔAIC score = 8; Table 2; $r^2 = 0.18$), although the temporal effect was minor (Fig. 1). The best supported model for each site/sex included non-linear selection for HD (Fig. 1, Table 2).

While there were similarities in bear selection for human development across sites, there were also idiosyncratic differences between them. For example, Aspen males, Aspen females, and Tahoe females tended to select for intermediate development densities, while Durango females displayed a bimodal pattern of either selecting for very low or very high HD (although the maximum HD for Durango was 375 structures/km^2, which was an intermediate development density in Aspen and Tahoe, where maximum HD was >540 structures/km^2; Fig. 1). In Aspen, males selected for intermediate HD in good and poor natural food years, while females avoided high HD in good food years and strongly selected for high HD in poor years, particularly during hyperphagia (Figs. 1 and 2).

All top models had high predictive power when tested against validation data. Spearman rank correlations of selection probabilities between training and validation data were $\geqslant 0.95$ for all sites/sexes (all tests $P < 0.001$).

3.2. Individual attributes associated with bear selection for human development

We calculated 107 individual selection coefficients from 72 female bears: 30 for Aspen (14 bears), 62 for Durango (48 bears), and 15 for Tahoe (10 bears). During Aug-Sep individual female bear selection coefficients for HD were highly variable, and at all sites in a given year, some bears selected for HD (positive selection coefficient) while others avoided HD (negative selection coefficient; Fig. 3). The median selection coefficient for Aspen was −0.002, for Durango was 0.002 and for Tahoe was 0.000. There were no significant differences in coefficient values among sites ($F_{2,104} = 0.165$, $P = 0.849$). Selection coefficients are small as they reflect the change in bear selection for HD given a change in one human structure/km^2.

On average, female bears were 7.8 years old (range 2–24; SD = 5.1). Based on annual observations of reproduction, 31 bear- and year-specific selection coefficients were associated with

Table 1
Fixed-effect coefficients from the top model of black bear selection for human development (HD) around Aspen (CO), Durango (CO), and Lake Tahoe (NV), USA.

	Aspen females			Aspen males			Durango females			Tahoe females		
Variable	β	SE	p	β	SE	p	β	SE	p	β	SE	p
Intercept	4.0070	0.1324	<0.0001	3.6117	0.1496	<0.0001	2.9400	0.0946	<0.0001	−2.0580	0.2585	<0.0001
Elevation	−0.1674	0.0041	<0.0001	−0.1562	0.0033	<0.0001	−0.2042	0.0035	<0.0001	0.0609	0.0093	<0.0001
Slope	0.0237	0.0007	<0.0001	0.0011	0.0008	0.1516	0.0361	0.0006	<0.0001	0.0087	0.0025	0.0006
Ruggedness	3.8780	0.8424	<0.0001	−2.2840	0.8475	0.0071	0.5739	0.7105	0.4193	9.1680	2.6450	0.0005
Distance to Drainage	−0.0995	0.0031	<0.0001	−0.0846	0.0038	<0.0001	0.0169	0.0025	<0.0001	−0.0095	0.0075	0.2037
Agriculture	−0.3353	0.0613	<0.0001	−0.6480	0.0972	<0.0001	0.7177	0.0508	<0.0001	3.1210	0.4419	<0.0001
Alpine	−0.1559	0.0427	0.0003	0.9268	0.0411	<0.0001	1.3400	0.0606	<0.0001	−0.8655	0.2891	0.0028
Aspen	0.8787	0.0280	<0.0001	1.5053	0.0357	<0.0001	1.4290	0.0408	<0.0001	2.4000	0.1854	<0.0001
Conifer	0.3791	0.0344	<0.0001	0.7273	0.0422	<0.0001	0.3593	0.0368	<0.0001	0.7281	0.1150	<0.0001
Meadow	−3.4770	0.1018	<0.0001	−1.3043	0.0678	<0.0001	0.2133	0.0397	<0.0001	−0.7606	0.1990	0.0001
Oak	−0.2089	0.0353	<0.0001	0.7903	0.0428	<0.0001	0.9337	0.0478	<0.0001	−0.0345	0.6029	0.9544
Pinyon Juniper	−2.3210	0.0713	<0.0001	−1.0859	0.0616	<0.0001	0.0684	0.0359	0.0569	0.1070	0.2155	0.6193
Riparian	0.4233	0.0500	<0.0001	1.2544	0.0594	<0.0001	1.5250	0.0462	<0.0001	1.3090	0.1597	<0.0001
Shrub	−1.0830	0.0565	<0.0001	−0.3324	0.0576	<0.0001	−1.1200	0.0580	<0.0001	−0.2833	0.1458	0.052
Aspect (Reference = North)												
Flat	−1.6330	1.1650	0.1610	−4.2060	1.0300	<0.0001	−1.7930	0.2070	<0.0001	−1.3470	0.4550	0.0031
Northeast	0.0446	0.0215	0.0382	0.0204	0.0253	0.4200	0.1330	0.0204	<0.0001	0.1583	0.0687	0.0213
East	0.0988	0.0235	<0.0001	0.3569	0.0262	<0.0001	0.0220	0.0198	0.2661	0.1912	0.0713	0.0073
Southeast	−0.2218	0.0309	<0.0001	0.2011	0.0302	<0.0001	0.0078	0.0192	0.6867	0.0082	0.0688	0.9048
South	0.3213	0.0278	<0.0001	0.2514	0.0287	<0.0001	−0.1612	0.0193	<0.0001	−0.1491	0.0658	0.0234
Southwest	0.3439	0.0229	<0.0001	0.2018	0.0255	<0.0001	−0.3066	0.0202	<0.0001	−0.1330	0.0653	0.0416
West	0.5162	0.0219	<0.0001	0.0762	0.0251	0.0023	−0.0406	0.0201	0.0282	−0.1690	0.0623	0.0067
Northwest	0.2127	0.0220	<0.0001	−0.0125	0.0257	0.6267	−0.0198	0.0206	0.3367	−0.0738	0.0584	0.2062
HD	0.0047	0.0003	<0.0001	0.0128	0.0004	<0.0001	−0.0080	0.0004	<0.0001	0.0137	0.0007	<0.0001
HD2	−1.8E−05	5.6E−07	<0.0001	−3E−05	7.2E−07	<0.0001	3.8E−05	8.9E−07	<0.0001	−3.2E−05	1.7E−06	<0.0001
Week	−0.0003	0.0013	0.7859	−0.0403	0.0018	<0.0001	0.0355	0.0013	<0.0001	−0.0102	0.0030	0.0008
FoodYr	−0.2716	0.0303	<0.0001	−0.5613	0.0310	<0.0001	1.8560	0.0273	<0.0001	NA	NA	NA
HD ∗ Week	−8.8E−05	1.8E−05	<0.0001	−6.5E−05	2.3E−05	0.0041	−2.6E−04	1.8E−05	<0.0001	7.7E−05	2.9E−05	0.0072
HD ∗ FoodYr	0.0028	0.0003	<0.0001	0.0028	0.0004	<0.0001	−0.0035	0.0004	<0.0001	NA	NA	NA
Week ∗ FoodYr	−0.0559	0.0020	<0.0001	0.0517	0.0022	<0.0001	−0.0861	0.0016	<0.0001	NA	NA	NA
HD ∗ Week ∗ FoodYr	0.0005	2.3E−05	<0.0001	1.4E−04	3.1E−05	<0.0001	0.0005	2.3E−05	<0.0001	NA	NA	NA

females with cubs, 75 were associated with females without cubs, and reproductive data was not available on 1 female in 1 year. Based on linear regression we found that individual female bear selection for development was positively associated with age and $HD_{hyperphagia}$ (Age: $\beta = 0.0016$, 95% CI = 2.0E−7 − 0.0031, Fig. 4; $HD_{hyperphagia}$: $\beta = 0.0002$, 95% CI = 0.0001 − 0.0003) and was not associated with maternal status or HD_{all} (Maternal Status: $\beta = -0.0049$, 95% CI = −0.0218 − 0.0120; HD_{all}: $\beta = -0.0002$, 95% CI = −0.0004 − 5.0E−5).

4. Discussion

For three areas in the western US, we found that black bears selected positively for human development, increasing their use of development in years with poor natural food conditions, throughout the summer-fall, and as a function of age and gender. These patterns were generally consistent across study systems and over numerous years of data collection, despite variation in individual bear behavior (Fig. 3). Such patterns suggest that bears are similarly interpreting the shifting benefits and risks associated with foraging in human-dominated landscapes, as factors such as natural food conditions, physiological state (i.e., hyperphagia), and age, simultaneously shape their habitat selection decisions.

At study sites with enough data to examine natural food conditions (Aspen and Durango) bears dramatically increased their selection for human development during poor food years, and reduced selection for development in good years (Figs. 1 and 2). These results imply that bears use anthropogenic foods as a source of subsidy when natural foods are scarce, dynamically modifying their behavior based on physiological needs. Indeed, the fact that bears do not consistently select for development across all food conditions, suggests that they perceive a cost associated with that behavior. Our findings corroborate with Baruch-Mordo et al. (2014) who found bears increased time spent in urban development during years when natural foods were scarce, and with Zach et al. (2003) who documented an increase in human–bear conflicts during drought. Indeed, our work identifies the mechanism responsible for these patterns, demonstrating shifts in bear selection for development, given shifts in environmental conditions. Given that climate change is expected to increase the frequency of droughts and late spring frosts (Karl et al., 2009), conditions associated with reduced mast production for bears, poor natural food years will likely be more common, potentially escalating bear use of development in the future.

In addition to displaying temporal variation across seasons, bears also displayed variation in selection for human development within the active bear season (Fig. 1). During good natural food years (in Aspen and Durango), bears selected most strongly for development early in the season, decreasing this selection throughout the summer and fall, likely in response to the availability of hard and soft mast. In poor natural food years, however, bears displayed the opposite pattern, and increased their use of human development throughout the summer and fall. We suspect that this behavior reflected the onset of hyperphagia, as in poor food years, bears amplified their use of human foods to satisfy pre-hibernation nutritional requirements. The combined effect of natural food availability and physiological state was most pronounced for female bears in Aspen (Fig. 1). In good food years they selected for low development densities, but in poor food years they selected for intermediate development densities at the beginning of the season and high densities at the end of the season. While within-year temporal variation in human–bear conflicts has been documented (Charoo et al., 2011), this is the first evidence of within-year variation in bear selection for human food resources. Most studies that evaluate temporal patterns of resource selection break data into pre-defined seasons, but we treated time as a continuous variable that could interact with other covariates (i.e., HD,

Table 2
Model selection results[a] for generalized linear mixed-models of black bear selection for human development density (HD) given temporal variation within the active bear year (Week; May–October) and between years under good and poor natural food conditions (Food). Models were generated from bear locations collected around Aspen (CO), Durango (CO), and Lake Tahoe (NV), USA.

Fixed effects model structure	K[a]	LL[a]	AIC[a]	ΔAIC
Aspen females				
Base + HD + HD^2 + Week + Food + (HD ∗ Week) + (HD ∗ Food) + (Week ∗ Food) + (HD ∗ Week ∗ Food)	30	−87,599	175,263	0
Base + HD + Week + Food + (HD ∗ Week) + (HD ∗ Food) + (Week ∗ Food) + (HD ∗ Week ∗ Food)	29	−88,113	176,288	1025
Base + HD + HD^2 + Food + (HD ∗ Food)	26	−88,403	176,862	1599
Base + HD + Food + (HD ∗ Food)	25	−88,862	177,778	2515
Base + HD + HD^2 + Week + (HD ∗ Week)	26	−91,327	182,710	7447
Base + HD + Week + (HD ∗ Week)	25	−91,484	183,021	7758
Base + HD + HD^2	24	−91,744	183,540	8277
Base + HD	23	−91,880	183,809	8546
Base	22	−92,755	185,557	10,294
Aspen males				
Base + HD + HD^2 + Week + Food+(HD ∗ Week) + (HD ∗ Food) + (Week ∗ Food) + (HD ∗ Week ∗ Food)	30	−70,019	140,103	0
Base + HD + HD^2 + Food + (HD ∗ Food)	26	−70,430	140,916	813
Base + HD + Week + Food + (HD ∗ Week) + (HD ∗ Food) + (Week ∗ Food) + (HD ∗ Week ∗ Food)	29	−70,596	141,254	1151
Base + HD + HD^2 + Week + (HD ∗ Week)	26	−70,890	141,836	1733
Base + HD + HD^2	24	−70,947	141,945	1842
Base + HD + Food + (HD ∗ Food)	25	−70,974	142,001	1898
Base + HD + Week + (HD ∗ Week)	25	−71,434	142,922	2819
Base + HD	23	−71,486	143,022	2919
Base	22	−72,778	145,603	5500
Durango females				
Base + HD + HD^2 + Week + Food+(HD ∗ Week) + (HD ∗ Food) + (Week ∗ Food) + (HD ∗ Week ∗ Food)	30	−153,805	307,674	0
Base + HD + Week + Food + (HD ∗ Week) + (HD ∗ Food) + (Week ∗ Food) + (HD ∗ Week ∗ Food)	29	−154,762	309,585	1911
Base + HD + HD^2 + Food + (HD ∗ Food)	26	−155,395	310,846	3172
Base + HD + Food + (HD ∗ Food)	25	−156,403	312,860	5186
Base + HD + HD^2 + Week + (HD ∗ Week)	26	−158,320	316,696	9022
Base + HD + HD^2	24	−158,470	316,992	9318
Base + HD + Week + (HD ∗ Week)	25	−159,150	318,354	10,680
Base + HD	23	−159,286	318,623	10,949
Base	22	−159,534	319,116	11,442
Tahoe females				
Base + HD + HD^2 + Week + (HD ∗ Week)	26	−11,095	22,246	0
Base + HD + HD^2	24	−11,101	22,255	8
Base + HD + Week + (HD ∗ Week)	25	−11,310	22,674	428
Base + HD	23	−11,316	22,681	435
Base	22	−11,453	22,954	707

[a] *K*, number of fixed effect model parameters; *LL*, log likelihood; AIC, Akaike's information criterion.

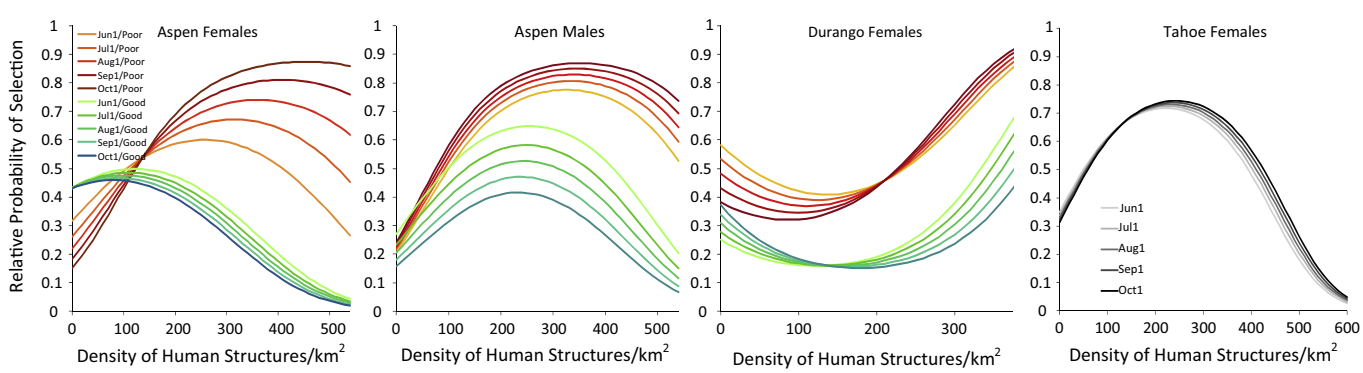

Fig. 1. Black bear relative probabilities of selection for density of human development from May to October in Aspen (CO), Durango (CO), and Lake Tahoe (NV), USA. Warm colors depict selection during poor natural food years and cool colors depict selection in good natural food years. Data for bears in Tahoe were not available for years with different natural food conditions. Note: Durango experienced a maximum of 375 human structures/km^2, while Aspen and Tahoe had maximum densities of 540 and 660 structures/km^2, respectively.

Food Year). Our approach allowed us to uniquely capture dynamic patterns of selection as they occurred across the active season (Johnson et al., 2013).

Although temporal patterns of selection for development were similar across study sites, there were some key spatial differences in selection between sites. For example, bears in Durango showed a bimodal pattern in their selection for development, either selecting for high development or no development, while bears in Aspen and Tahoe generally selected for intermediate development densities (Fig. 1). This result likely reflects different development densities among sites, as Durango had a maximum of 375 structures/km^2, while Aspen and Tahoe had maximum densities of 540 and 660 structures/km^2, respectively. Although bears around Durango displayed a small spike in selection for areas with no development, bears at all sites selected for intermediate housing densities (~200–400 structures/km^2) when considering the range of

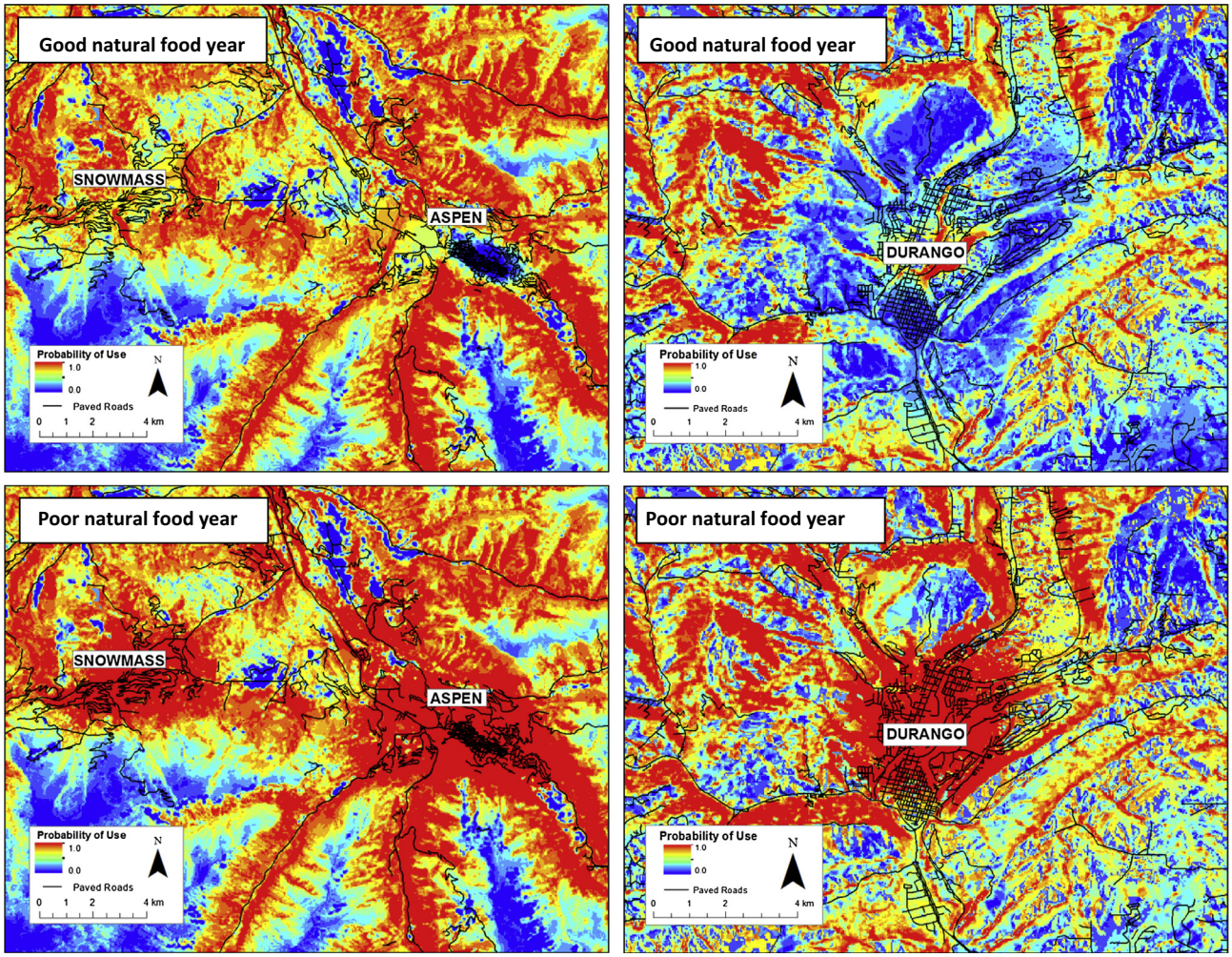

Fig. 2. Spatial predictions of resource selection from female black bears in Aspen and Durango, Colorado, for a good and poor natural food year during fall (October 1st).

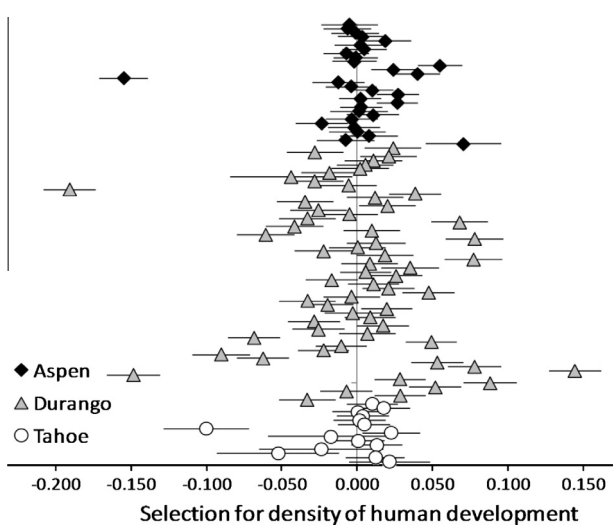

Fig. 3. Individual selection coefficients (±SE) for female bears for density of human development around Aspen (CO), Durango (CO), and Lake Tahoe (NV).

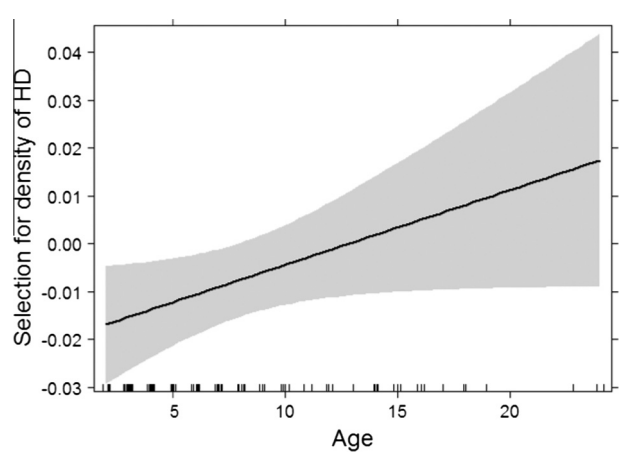

Fig. 4. Effect of age on individual female bear selection for density of human development (HD) based on a linear regression model from data from Aspen (CO), Durango (CO), and Lake Tahoe (NV).

available density values. This similarity across our diverse study systems was striking. We suspect that intermediate development densities provide bears with ample opportunities to obtain anthropogenic foods while minimizing encounters with people (Merkle et al., 2011), potentially providing a range of housing densities important to target for management.

Of our three study areas, Aspen was the only site with data on both male and female bears. Males consistently used intermediate development densities, magnifying their use of development

during poor natural food years (Fig. 1). Conversely, females in Aspen selected for low development densities in good natural food years and high development densities in poor food years. This behavioral difference may stem from distinct nutritional requirements for each sex, as larger-bodied males generally have higher caloric needs that may motivate their use of development in all years. Our observations corroborate with other studies that have found that male bears tend to use human development more than females (Beckmann and Berger, 2003b and Merkle et al., 2013), and thus are more likely to be involved with human–bear conflicts.

One of the unique contributions of our work was that we were able to compare patterns of bear selection for human development across study systems. We expected selection for development at different study sites to be inversely related to the inherent productivity of those sites, as the Carson range of the Tahoe basin is considered relatively poor quality bear habitat (Beckmann and Lackey, 2004) compared to high quality habitat around Aspen (Beck, 1991). Despite our expectations, individual bears at all sites exhibited a wide range of selection coefficients for human development (Fig. 3), exhibiting both selection and avoidance for HD, and there were no significant differences among sites. That said, our population-level analyses showed that bears in Tahoe selected for intermediate development densities most consistently throughout the active season, while bears in Aspen dramatically altered their selection for development throughout the season, and bears in Durango displayed an intermediate response (Fig. 1). We suspect that bears in areas of poorer habitat quality may exhibit more consistent selection for development, while bears in areas of higher habitat quality may be more variable in their selection responses based on natural food conditions, a pattern that warrants further investigation. Other differences among sites may have also contributed to this pattern, such as variation in bear density or bear conflict management, but we were not able to assess these factors within the scope of our work.

Individual female bear selection coefficients demonstrated that affinity for human development increased with age (Fig. 4), but had no relationship to maternal status. We suspect that age itself is not the mechanism driving this relationship, but that age is correlated with a factor like bear experience with anthropogenic foods, and that selection for development may increase as bears learn to forage on these resources. Our speculation is supported by other wildlife studies that have demonstrated that habitat selection can be influenced by memories from previous foraging experiences (Wolf et al., 2009 and Merkle et al., 2014), and that older animals may display greater efficiency at foraging (Vaillant et al., 2013). This result, that selection for development increases with age, merits additional investigation, particularly as it contradicts studies that have suggested that juvenile brown, black and polar bears are most likely to use development and cause conflicts with people (Towns et al., 2009 and Elkström et al., 2014). We speculate that older bears may have learned to use human foods without incident, resulting in a younger cohort of bears that are more easily captured and associated with conflicts. We were surprised that maternal status was not associated with bear use of development, given the energetic costs of lactation. Perhaps females rearing offspring perceive a greater risk associated with developed habitats, as female brown bears with cubs have avoided high quality natural feeding sites when prioritizing the safety of their offspring (Ben-David et al., 2004).

We suspected that resource selection by individual bears may demonstrate a functional response for development (Mysterud and Ims, 1998), whereby individuals with more human structures within their home range (HD_{all}) would display greater selection for development. On the contrary, we found no relationship between these variables, but there was evidence that selection was related to the amount of development within a bear's year-specific late summer range ($HD_{hyperphagia}$). This suggests that bears do not use development simply in response to its availability, but dynamically alter their use of this resource on an annual basis. Indeed, the amount of development within a bear's year-specific late-summer range was not strongly correlated to the development found within their total home-range (correlation coefficient = 0.53), and bears appear to modify their late-summer movements to incorporate additional development in some years when needed.

Results from this study have key implications for bear management. Wildlife agencies commonly assume that bears exposed to anthropogenic food will consistently exhibit nuisance behavior, but results from three bear populations in the western US suggests that behavior is highly variable within and across years, and that bears use anthropogenic resources as a source of subsidy rather than relying on those resources outright. As a result, many bears may be considered "conflict" individuals in a poor natural food year that otherwise exhibit natural foraging behavior. Reducing the availability of anthropogenic foods to bears, particularly in poor natural food years, may reduce bear-use of developed habitats by diminishing the perceived benefit (Baruch-Mordo et al., 2013). Because bear populations are notoriously difficult to monitor, wildlife agencies also often assume that increases in human–bear conflicts reflect increases in bear populations. Our work, however, suggests that bear selection for development may be increasing as individuals get older and gain experience with anthropogenic foods. This behavior may then be the source of additional conflicts without an associated increase in population size, a pattern that was observed in the polar bear population of Manitoba (Towns et al., 2009). Beckmann and Berger (2003b) similarly suggested that increased use of urban areas could lead to a shift in the bear distribution on the landscape, causing a perceived increase in bear numbers. As human development continues to permeate bear habitat, and as changes in climate reduce natural foods for bears in some areas, we expect that bear exposure to anthropogenic foods will increase as will their selection for those resources.

As human development expands, it is critical to understand how large carnivores are adapting to this change, particularly given concerns about carnivore conservation and human safety and property. Across three urban areas, our work demonstrates that black bears select for human development, but vary their selection based on environmental and physiological conditions. Such variability suggests that bears perceive risks associated with human activity, but that they also perceive the shifting benefits of obtaining anthropogenic foods. How these risks and benefits translate to individual and population fitness is largely unknown, but studies have indicated that bear selection for development may be maladaptive (Beckmann and Berger, 2003b; Hostetler et al., 2009 and Baruch-Mordo et al., 2014). While it is important to document changes in wildlife behavior in response to increasing development, future research should elucidate the demographic impacts of these changes on long-term population viability.

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