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Hourly movement decisions indicate how a large carnivore inhabits developed landscapes

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Abstract

The ecology of wildlife living in proximity to humans often differs from that in more natural places. Animals may perceive anthropogenic features and people as threats, exhibiting avoidance behavior, or may acclimate to human activities. As development expands globally, changes in the ecology of species in response to human phenomena may determine whether animals persist in these changing environments. We hypothesize that American black bears (*Ursus americanus*) persist within developed areas by effectively avoiding risky landscape features. We test this by quantifying changes in the movements of adult females from a population living within exurban and suburban development. We collected hourly GPS data from 23 individuals from 2012 to 2014 and used step-selection functions to estimate selection for anthropogenic features. Females were more avoidant of roads and highways when with cubs than without and were more responsive to increased traffic volume. As bears occupied greater housing densities, selection for housing increased, while avoidance of roads and responsiveness to traffic increased. Behavioral flexibility allowed bears in highly developed areas to alter selection and avoidance for anthropogenic features seasonally. These findings support the hypothesis that black bears perceive human activity as risky, and effectively avoid these risks while inhabiting developed areas. We document a high amount of individual variation in selection of anthropogenic features within the study population. Our findings suggest that initially, wildlife can successfully inhabit developed landscapes by effectively avoiding human activity. However, variation among individuals provides the capacity for population-level shifts in behavior over time.

Keywords Adaptation · Functional response · Movement behavior · Risk avoidance · Selection · Urban

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This work quantifies habitat selection during movements of a large carnivore through humandevelopment, including neighborhoods with different housing densities. The movementstrategies we identify indicate how wildlife live within and may adapt to human development.

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Introduction

The global proliferation of developed landscapes may significantly impact the ecology and persistence of wildlife populations (DeStefano and DeGraaf 2003; Shochat et al. 2006). While some species avoid humans, certain 'urban adapted' wildlife (McKinney 2006) can exploit novel resources associated with developed areas (Bateman and Fleming 2012; Merkle et al. 2013). However, positive numerical association with development does not necessarily equate to long-term fitness benefits, or increased population viability if mortality is elevated (Van Horne 1983; Remeš 2000). Development often modifies environmental conditions faster than evolutionary processes respond, creating the potential for maladaptive behavior and ecological traps (Robertson et al. 2013). For instance, attractive habitat patches with negative impacts on demographic rates can produce population sinks (Delibes et al. 2001; Naves et al. 2003). The expansion

of human-modified landscapes necessitates that animal behavior be integrated into wildlife conservation and management (Anthony and Blumstein 2000) to understand how wildlife adapts to these new environments.

Animals often change behaviors when living among human development (Tuomainen and Candolin 2011). Two hypotheses potentially explain how wildlife persist amongst human development. The risk–disturbance hypothesis postulates that animals will exhibit behaviors like predator avoidance (Frid and Dill 2002), effectively avoiding anthropogenic features. Alternatively, the risk allocation hypothesis (Lima and Bednekoff 1999) states that animals will decrease avoidance behavior with greater exposure to risk, acclimating to these environments (Rodriguez-Prieto et al. 2009) contingent on risky situations not resulting in mortality. This may occur through human habituation, food conditioning, or naivety to threats (Elfstrom et al. 2012). Animal movement patterns and space use in and around developed areas can reveal perceived tradeoffs between the benefits of anthropogenic resources and risks associated with human activity (Baruch-Mordo et al. 2014; Johnson et al. 2015).

Even urban adapted species may perceive developed areas as risky, avoiding specific anthropogenic landscape features (Riley et al. 2003; Kertson et al. 2011; Gehrt et al. 2011). Functional responses—changes in resources selection as a function of changes in resource availability—can indicate whether animals perceive habitat as risky and provide insight into the cumulative effects of development on wildlife populations (Matthiopoulos et al. 2011). As animals can incur fitness costs when individuals overestimate the risk associated with human disturbances (Koops and Abrahams 1998), discerning patterns of perceived risk and adaptation are of importance to conservation of wildlife in developed contexts (Groffman et al. 2006).

Quantifying patterns in wildlife selection for anthropogenic resources can also help wildlife managers effectively reduce human–wildlife conflicts in developed landscapes. Conflict reduction has become particularly important for some large carnivores. Many populations have recovered following widespread extirpation in North American and Europe prior to the 1900s, and increasingly live within developed areas (Linnell et al. 2001; Chapron and Lopez-Bao 2014). In North America, conflicts related to American black bears (*Ursus americanus*) using developed areas have been increasing (Hristienko and McDonald 2007). Some research suggests that black bears living among development modify their foraging behavior to target anthropogenic food sources (Messmer 2009) and that this behavior is learned from conspecifics (Mazur and Seher 2008; Hopkins 2013). However, use of anthropogenic resources can be temporally dynamic, with selection for developed areas occurring primarily when natural food sources are scarce (Baruch-Mordo et al. 2014; Johnson

et al. 2015), suggesting perceived risks associated with human activity (Nellemann et al. 2007; Ordiz et al. 2011).

In Connecticut, a recolonizing population of black bears includes individuals with houses distributed throughout the entire home range, while others occupy almost exclusively forested home ranges. Previous research demonstrated that black bears density in this area is highest within exurban development (Evans et al. 2017). In addition, there is currently no hunting season in Connecticut, and vehicle collisions are the only notable anthropogenic source of mortality for bears. This context provided an opportunity to determine how black bears perceive human development, measure variability in avoidance behavior, and quantify changes in behavior across a gradient of human development. In this paper, we test hypotheses potentially explaining how large carnivores establish and maintain populations within developed landscapes.

First, we tested the hypothesis that bears perceive human development as risky, indicated by selection or avoidance of anthropogenic features and changes in selection with reproductive status. We assume that females with cubs exhibit more risk-avoidant movement relative to females without cubs, due to the high cost associated with losing a dependent offspring (Dahle and Swenson 2003; Rode et al. 2006). This could involve either avoidance or selection of developed areas, as these places can provide food as well as refuge from conspecific aggression (Steyaert et al. 2016). Second, we distinguish between the competing hypotheses that bears adapt to developed landscapes by acclimating to human activity or occupy these areas through effective avoidance. If bears acclimate to development, we would expect increased selection for anthropogenic features in areas with greater human exposure (i.e., higher housing densities). Alternatively, either consistent selection, or a negative functional response to greater housing densities would indicate effective avoidance.

In addition, we evaluated the hypothesis that bears use behavioral plasticity to occupy developed areas by testing for temporal changes in selection for anthropogenic features. Bears overcome winter food shortages by intense late summer feeding, or hyperphagia, followed by hibernation (Powell et al. 1997), and bears might be more risk tolerant during hyperphagia, relative to summer because of the elevated importance of feeding. Finally, we hypothesized that bears that were less avoidant of development would be more prone to conflict with humans. We provide insight into how individual black bears respond to features of development (e.g., houses, roads, and highways), the degree of variation within a recolonizing population, and discuss how these patterns may affect population growth and viability, and conflicts with humans.

Materials and methods

Data collection

Hourly GPS location data were collected from independent (≥ 2 years) female black bears fitted with Lotek GPS 3300 collars beginning in 2012. We define the relocations of an individual bear in a given year as a bear-year and collected a total of 68 bear-years from 23 individuals in 2013, 22 individuals in 2014, and 23 individuals in 2015. Eight individuals were collared in all 3 years and 16 individuals were collared in 2 years. We determined reproductive status during annual den visits during winter hibernation. We eliminated all GPS relocations obtained from fewer than five satellites (Hulbert and French 2001), and applied differential correction using GPS Pathfinder software (Trimble Navigation Ltd.). We characterized the intensity of development inhabited by bears by calculating mean housing density (houses/km^2) within seasonal home ranges, which we refer to as home range housing density (HRHD). Home ranges were estimated using a 95% kernel density estimate at 100 m^2 resolution, using fixed least-squares cross-validated bandwidth, implemented in the Geospatial Modeling Environment (Beyer 2014).

Ethics note

Capture and collaring was performed by Connecticut Department of Energy and Environmental Protection Wildlife Division biologists (J. Hawley and P. Rego), following guidelines for the capture, handling, and care of animals approved by the American Society of Mammalogists' Animal Care and Use Committee (Animal Care and Use Committee 1998). All research was completed under the Institution for Animal Care and Use Committee at the University of Connecticut protocol A12-018.

Modeling approach

We used step-selection functions (SSF) to estimate relative probabilities of selection and avoidance of features associated with human development (hereafter anthropogenic variables) by bears (Coulon et al. 2008). This approach estimates selection by comparing covariates at observed steps (i.e., successive relocations) with simulated steps taken from the same starting point using conditional logistic regression (Fortin et al. 2005). We defined steps as the straight line between successive GPS relocations and only used successive hourly steps, omitting steps that covered missing or removed relocations. We compared landscape characteristics between each observed step and a set of simulated steps at each relocation, comprising a use–availability design (Lele et al. 2013) evaluating third-order selection (Johnson 1980). At each relocation, we generated simulated steps by drawing a sample of random lengths and turn angles from a bear's empirical step length and turn angle distributions using the Geospatial Modeling Environment. Step lengths were not correlated with turn angle within any bear-year at $\alpha = 0.05$, and only 7 bear-years exhibited correlation at $\alpha = 0.10$. The log odds of an observed step were estimated as a function of landscape covariates by conditional logistic regression using the clogit function in the survival package (Therneau 2015) for R (R Core Team 2016). We determined adequate sample size for simulated steps by taking successive subsamples of $n = 1$–50 from an initial sample of 50 random steps at each relocation and plotting coefficients from a full model. The sample size at which parameter estimates and standard errors stabilized was used for all subsequent analyses (Supplemental Fig. 1).

Step-selection models

To estimate both individual variability and population-level selection for features of development, we applied a two-step approach—fitting the same set of candidate models to each individual bear and making population-level inferences by averaging coefficients among individuals (Knopff et al. 2014). We used Akaike's Information Criterion (AIC; Akaike 1974) to evaluate model support and obtain model-averaged parameter estimates. We considered using a global mixed effect model with individuals treated as random effects. However, variation in selection among bears is more easily understood, quantified, and modeled as a function of individual covariates (i.e., reproductive status) with models fit to individual bears.

We developed a set of a priori models designed to quantify the relative importance and effect of specific anthropogenic variables on black bear movement decisions while accounting for natural landscape features. The first was a model consisting of only natural landscape features; elevation, slope, distance to streams, and landcover classification. We refer to this model as the 'Natural' model. We calculated elevation (m) at step endpoints, and length weighted mean slope along step lengths from 30 m National Elevation Data Set digital elevation models (available from the USGS). Distance from streams was measured at 30 m resolution using Connecticut and Massachusetts hydrography line files. We reclassified 30 m National Land Cover Data (Fry et al. 2011) to delineate 4 land cover classes relevant to black bear habitat selection: forest, grassland, shrub, and wetland.

We considered that bears moving within development may respond differently to buildings, where people and human food resources are located than to roads with high traffic volumes that are a primary source of mortality for

bears. We estimated bear selection for these features by adding relevant anthropogenic variables to the Natural model (Roever et al. 2010; Thurfjell et al. 2014). To create the 'House' model, we added a variable measuring housing density at step endpoints (Res), and a variable measuring distance (km) from step endpoints to local and neighborhood roads (RoadDist) to the 'Natural' model. We included neighborhood roads in the 'House' model as a specific feature potentially affecting bear movement in residential areas, since accurate GIS layers of house locations were unavailable. The 'Highway' model included a categorical variable indicating whether a step crossed a highway (HwyXing), and a measure of distance (km) to highways (HwyDist). Distances to roads and highways were calculated at 30 m resolution using TIGER/Line shapefiles (available from the U.S. Census Bureau). We classified Interstate, U.S., and State highways as highways, and all other named roadways as local roads. The 'Full' model contained all variables in the Natural, House, and Highway models. We tested predictor variables for correlation ($|r| > 0.7$) and included all independent covariates in the base model for each bear (Hosmer and Lemeshow 2000).

To identify potential plasticity in step selection, we also created models with interaction terms that represented temporal variation in selection at two scales. First, bears may shift selection of anthropogenic variables in response to daily variation in human activity, which we approximated using hourly traffic counts. Traffic data were collected each day by Connecticut Department of Transportation in the towns of Simsbury, Watertown, and Kent. We created variations of the 'House', 'Highway', and 'Full' models that contained interactions between anthropogenic variables and

traffic volume recorded by the closest station to each bear home range at the time of each step (e.g., 'House × Traffic'). We refer to these interaction parameters as the effect of traffic volume on selection. Second, bears may change selection seasonally. We categorized GPS relocations into summer (01-May–31-Jul), hyperphagia (01-Aug–30-Sep) and pre-denning (01-Oct–30-Nov) periods and created candidate models containing interactions between anthropogenic variables and season (e.g., 'Highway × Season'). We also considered three-way interactions between anthropogenic variables, traffic counts, and season. We fit the final candidate model set (Table 1) to GPS data from each bear-year.

For each bear, we used model AIC weights (ω_i) from the candidate set to calculate full-model-averaged selection parameter estimates (β_ω) and standard errors (SE_ω) for anthropogenic variables (Lukacs et al. 2009). As in Knopff et al. (2014), we used the mean weight of a model among bears ($\bar{\omega}_i$) to evaluate support for that model within the population, and mean model-averaged parameter and standard error estimates ($\bar{\beta}_\omega$, $\overline{SE}_\omega$) to estimate population-level selection for anthropogenic variables. We refer to these measures as population weights and population parameter estimates. We calculated $\bar{\omega}_i$, $\bar{\beta}_\omega$ and $\overline{SE}_\omega$ among all bears, as well as the set of bears with cubs, and without cubs.

Perceived risk

If bears perceive development as risky, we expected avoidance of anthropogenic features that increased when females were with cubs. We tested for avoidance of anthropogenic features using the 95% confidence interval around population parameter estimates ($\bar{\beta}_\omega$). If this range did not

Table 1 Model selection results for step-selection functions among female black bears

Model	All bears		With cubs		No cubs	
	$\bar{\omega}_i$	Rank	$\bar{\omega}_i$	Rank	$\bar{\omega}_i$	Rank
Full × traffic × season	0.375	1	0.451	1	0.319	3
Highway × traffic × season	0.299	2	0.271	2	0.393	1
Full × season	0.295	3	0.190	3	0.366	2
Highway × traffic	0.141	4	0.154	5	0.076	8
House × traffic	0.125	5	0.128	7	0.128	4
Full	0.109	6	0.177	4	0.043	11
House × traffic × season	0.103	7	0.132	6	0.110	5
Full × traffic	0.076	8	0.095	8	0.046	10
Highway × season	0.064	9	0.032	11	0.105	6
Highway	0.056	10	0.050	10	0.078	7
House	0.048	11	0.080	9	0.014	13
Natural	0.031	12	0.013	13	0.060	9
House × season	0.020	13	0.029	12	0.018	12

The mean AIC weights $\bar{\omega}_i$ for each model among all bears, bears with cubs and bears without cubs, as well as relative ranks are shown. Interactions between anthropogenic variables, traffic volume, and season are indicated with an asterisk (*)

include zero, we inferred population-level selection or avoidance. To determine whether bears increased avoidance when with cubs, we identified changes in relative population model weights ($\bar{\omega}_i$) and population parameter estimates that overlapped zero between bears without cubs and bears with cubs. Unless specified, we consider changes in model weights and parameter estimates among bears with cubs, relative to bears without cubs. Such changes indicated differences in the importance of anthropogenic features in determining bear step selection between individuals with and without cubs.

To test for an effect of reproductive status (i.e., with or without cubs) on selection, we also fit pairs of mixed effects models using individual model-averaged parameter estimates (β_ω) from step-selection models fit to each bear-year as the response variable. We applied inverse variance weighting to β_ω observations using SE_ω^2 to account for estimate uncertainty. For each anthropogenic variable, we fit an intercept-only model and a model with a fixed effect on reproductive status (i.e., with or without cubs). All models included a random intercept per bear, accounting for the correlation among repeated measures obtained from the same individual in different years. We report the AICc weight for each model and the effect size of reproductive status on selection for anthropogenic variables using Cohen's d. We inferred support for changes in selection with reproductive status if the weight for the model including reproductive status was $\omega_i > 0.7$ (i.e., ΔAICc > 2), and the 95% confidence interval around the estimated effect of reproductive status did not include zero.

Acclimation vs. effective avoidance

To test whether bears persist among human development by acclimating to, or effectively avoiding anthropogenic features, we quantified the relationship between selection for each anthropogenic variable and HRHD. We fit a set of three linear mixed models to model-averaged parameter estimates (β_ω) obtained from step-selection models fit to each bear-year. This mixed model set included an intercept-only model, a model with a linear response to HRHD, and a logarithmic response to HRHD. Each model included a random intercept per individual bear. We fit this candidate set to β_ω estimates for each anthropogenic variable, again applying inverse weighting using SE_ω^2. We report AICc weights for each relationship, and size of the effect of HRHD on selection. We inferred support for a relationship between an anthropogenic variable and HRHD if the intercept-only model received less than $\omega_i = 0.18$ (i.e., ΔAICc < 2), and the 95% confidence interval around the estimated relationship did not include zero. In addition, if model support for a relationship changed among seasons for a given variable,

we interpret these differences as a change in the functional response.

Behavioral plasticity

We tested whether bears changed selection and avoidance of anthropogenic features among seasons, and in response to traffic volumes. We used relative population model weights ($\bar{\omega}_i$) from the candidate set of step-selection models to assess support for the interaction terms indicating variation in selection by season and traffic. As with reproductive status, we also fit pairs of mixed models to individual model-averaged parameter estimates from each bear-year (β_ω). These mixed models included an intercept-only model and a model with a fixed effect on season. We report the AICc weight for each model and inferred support for seasonal change if the weight for this model was $\omega_i > 0.7$ (i.e., ΔAICc > 2). We estimated changes in selection between seasons using the effect size (Cohen's d) of differences between interaction terms from pairs of seasons (e.g., $d = \beta_{Res*Hyperphagia} - \beta_{Res*Summer}/SE_{pooled}$). All changes were estimated relative to the preceding season. We inferred differences in selection between seasons if the 95% confidence interval surrounding the estimated effect did not included zero.

We followed a similar procedure to test the hypothesis that bears increase avoidance of anthropogenic features during high traffic volumes. First, we used population model weights to indicate whether traffic volume was an important predictor of selection. Second, we inferred population-level relationships between traffic volume and selection for an anthropogenic variable if the 95% confidence interval around population parameter estimates ($\bar{\beta}_\omega$) for interactions between selection coefficients and traffic did not include zero. Finally, interactions between selection for anthropogenic features and traffic volume were included as response variables in the sets of mixed models testing for changes in selection with reproductive status, by season, and with HRHD. As previously described for these analyses, we use AICc weights and 95% confidence intervals around effect sizes to identify changes in the effect of traffic volume on selection.

Conflict

Finally, we tested the hypothesis that bears exhibiting greater selection for anthropogenic features would more frequently be involved in conflicts with people by estimating the relationship between frequency of conflict and individual β_ω estimates for Res, RoadDist, HwyDist, and HwyXing. We used the number of incidents reported to DEEP between 2012 and 2015 in which individually identifiable (i.e., ear tagged) bears damaged property (e.g., garbage cans, birdfeeders, etc.) as a measure of conflict frequency. We fit

an intercept-only model, and models predicting conflict frequency as a function of strength of selection (β_ω) and HRHD alone and in combination, using a log link to model conflict counts as a Poisson distribution. In this case, we used HRHD to control for the density of housing available to each bear, because we might expect this availability to predict greater conflict regardless of individual wariness/boldness. For each anthropogenic variable selection coefficient, we report the sum of model-averaged AICc weights ($\Sigma\omega_i$) for models in which the variable appeared, and size of the effect on conflict frequency. All mixed models were fit using the "lmer" function in the *lme4* package (Bates et al. 2014) for R, maximizing the full log-likelihood. We examined both model residuals for departures from normality by inspecting Q–Q plots and plots of residuals against predicted values. We inspect Q–Q plots to confirm that random effects followed a normal distribution.

Results

We fit candidate SSF models to GPS data sets from 67 bear-years. There were 28 bear-years from females with cubs, 27 from females without cubs, and 12 from females of unknown reproductive status. Home range housing density ranged from 0.51 to 214.43 houses/km². HRHD did not

differ between bears without cubs ($\bar{x} = 45.65$ houses/km², $\sigma^2 = 55.51$) and bears with cubs ($\bar{x} = 47.83$ houses/km², $\sigma^2 = 50.86$). Model support varied among individual bears. The maximum population model weight ($\bar{\omega}_i$) was 0.375, and all but one model was the most supported for at least one individual (Table 1).

Perceived risk

Model-averaged selection coefficients (β_ω) also varied among bears (Fig. 1). However, bears consistently avoided steps near local roads, indicated by a positive effect of distance from local roads on step selection that was consistent during all seasons (Table 2). Bears with cubs were less variable in selection of anthropogenic features than bears without cubs. The full model with no temporal interactions was the 11th most supported model among bears without cubs, but the 4th among bears with cubs—the largest change in support among all models. Likewise, the Highway × Season model was 6th amongst bears without cubs, and 11th amongst bears with cubs (Table 1).

Population parameter ($\bar{\beta}_\omega$) estimates indicated differences in selection for steps near highways between bears with and without cubs (Table 2). Bears without cubs selected steps near highways ($\bar{\beta}_\omega$ 95% CI − 1.29 to − 4.07) but avoided steps in residential areas ($\bar{\beta}_\omega$ 95% CI − 0.025 to − 0.355)

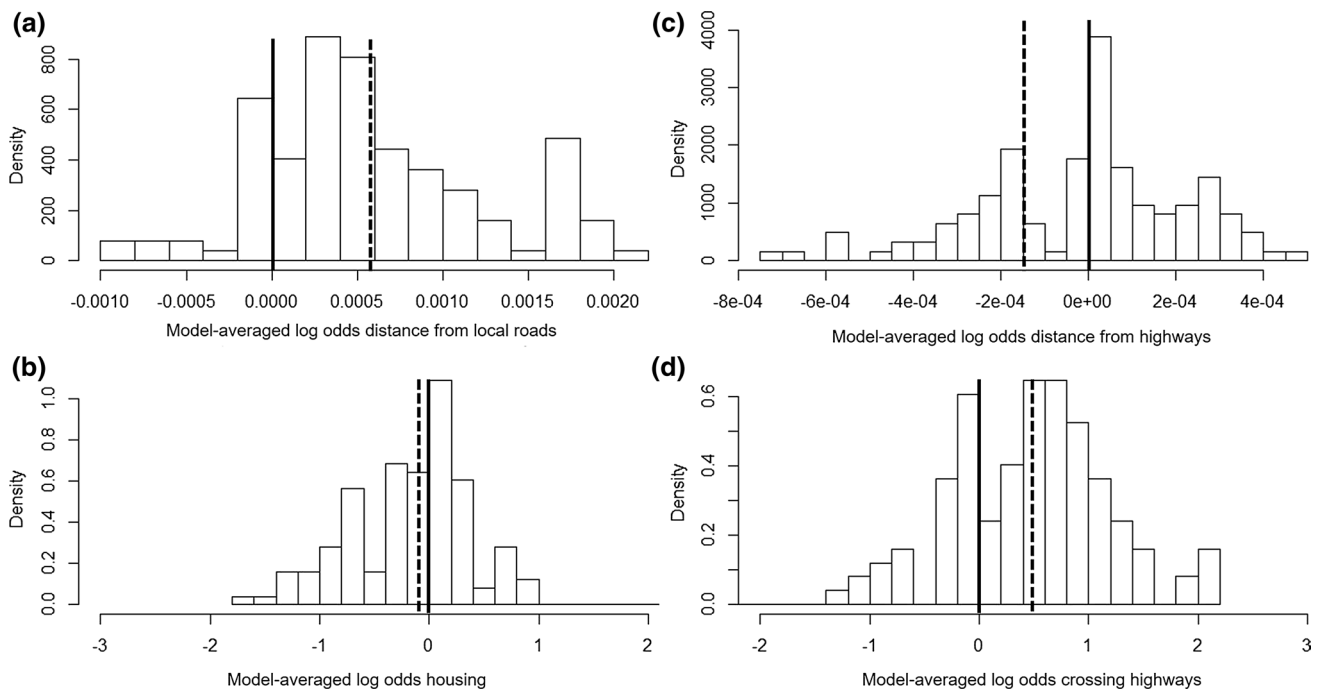**Fig. 1** Distribution of model-averaged selection parameter estimates (β_ω) from step-selection models fit to individual black bear GPS data. Values indicate selection for **a** distance from local roads, **b** housing density, **c** distance from highways and **d** crossing highways. Solid vertical lines at zero delineate regions indicating selection or avoidance. Dashed vertical lines indicate the mean of the observed distribution. Effect sizes (*d*) are displayed

Table 2 Effect sizes of population parameter estimates ($\bar{\beta}_\omega$) for all anthropogenic variables in the full step-selection model, ordered by effect size

Variables	Effect size (d)		
	All	No cubs	With cubs
RoadDist × sum[a]	**1.522**	**1.427**	**1.604**
RoadDist × PreDen[c]	**1.506**	**1.501**	**1.567**
RoadDist	**1.413**	**1.133**	**1.626**
RoadDist × hyper[b]	**1.344**	**1.526**	**1.100**
RoadDist × traffic	**1.169**	**0.683**	**1.507**
HwyDist × PreDen	− 1.049	**− 1.924**	− 0.124
Res × sum	− 0.965	− 0.980	− 0.744
HwyDist × traffic × hyper	0.836	0.417	**1.101**
RoadDist × traffic × PreDen	0.834	0.536	**1.030**
HwyXing × traffic × sum	0.782	**1.877**	− 0.067
HwyDist × traffic × sum	− 0.768	− 0.383	**1.343**
HwyDist × traffic × PreDen	0.763	0.797	**1.148**
RoadDist × traffic × hyper	0.696	0.335	0.966
RoadDist × traffic × sum	− 0.409	− 0.446	0.000
HwyDist × traffic	0.365	0.061	0.282
HwyDist × sum	− 0.224	− 0.676	0.369
HwyDist	− 0.212	0.135	− 0.396
HwyXing × traffic × hyper	0.210	0.105	0.209
House × PreDen	− 0.207	**− 1.148**	− 0.071
House × hyper	− 0.122	− 0.794	− 0.078
House × traffic	− 0.098	0.545	− 0.383
HwyXing × hyper	0.063	**2.415**	− 0.002
HwyXing × sum	0.052	**2.499**	− 0.024
HwyXing × PreDen	− 0.047	**− 1.154**	− 0.032
HwyXing	− 0.032	0.947	− 0.045
House × traffic × PreDen	− 0.024	− 0.003	− 0.028
HwyXing × traffic × PreDen	− 0.020	− 0.023	− 0.018
HwyXing × traffic	− 0.017	− 0.085	− 0.017
House	− 0.016	0.321	− 0.003
House × traffic × hyper	− 0.015	− 0.010	− 0.018
House × traffic × sum	0.007	0.717	− 0.664
HwyDist × hyper	0.006	− 0.202	0.470

Bold numbers indicate estimates with 95% confidence intervals that did not overlap zero. Interactions between anthropogenic variables, traffic volumes, and seasons are indicated by an asterisk (*)

[a]Summer

[b]Hyperphagia

[c]Pre-denning

Table 3 Results from mixed effect models estimating differences in black bear selection for anthropogenic variables between bears with and without cubs

Response variables (β_ω)	ω_i	d	95% CI β	
			Lower	Upper
RoadDist	0.997	**2.244**	**0.106**	**1.564**
RoadDist × PreDen[c]	1.000	1.792	− 0.043	0.956
RoadDist × hyper[b]	1.000	**2.629**	**0.137**	**0.943**
RoadDist × sum[a]	1.000	**2.819**	**0.152**	**0.845**
RoadDist × traffic	0.976	1.333	− 0.203	1.067
RoadDist × traffic × PreDen	0.942	**1.990**	**0.002**	**0.258**
RoadDist × traffic × hyper	0.985	− 0.393	− 0.113	0.076
RoadDist × traffic × sum	0.950	1.265	− 0.136	0.631
HwyDist	0.993	0.165	− 0.356	0.422
HwyDist × PreDen	1.000	**3.658**	**0.776**	**2.568**
HwyDist × hyper	1.000	0.881	− 0.335	0.882
HwyDist × sum	0.997	− 0.802	− 0.550	0.231
HwyDist × traffic	0.937	− 0.314	− 0.678	0.491
HwyDist × traffic × PreDen	1.000	**− 2.861**	**− 1.115**	**− 0.208**
HwyDist × traffic × hyper	0.973	0.614	− 0.629	1.203
HwyDist × traffic × sum	0.999	− 1.612	− 1.669	0.162
HwyXing	0.998	− 0.610	− 1.148	0.603
HwyXing × PreDen	1.000	0.490	− 1.263	2.104
HwyXing × hyper	1.000	− 0.988	− 2.701	0.890
HwyXing × sum	1.000	**− 2.572**	**− 5.221**	**− 0.705**
HwyXing × traffic	0.997	− 0.551	− 0.492	0.276
HwyXing × traffic × PreDen	0.984	1.850	− 0.033	1.133
HwyXing × traffic × hyper	0.959	0.462	− 0.660	1.067
HwyXing × traffic × sum	0.999	**− 2.323**	**− 2.491**	**− 0.211**

Coefficients from interactions between anthropogenic variables, traffic volume, and seasons are indicated by an asterisk (*). AICc weights (ω_i) indicate support relative to an intercept-only model. Effect sizes (d) and 95% confidence intervals around the estimated effect of reproductive status on selection are shown. Bold numbers indicate effects with 95% confidence intervals that did not include zero. Variables related to selection for housing are not shown, because all 95% confidence intervals overlapped zero

[a]Summer

[b]Hyperphagia

[c]Pre-denning

during pre-denning, while bears with cubs showed no selection. Bears without cubs also selected steps crossing highways during summer ($\bar{\beta}_\omega$ 95% CI 0.207–0.483) and hyperphagia ($\bar{\beta}_\omega$ 95% CI 0.285–0.687), but avoided such steps during pre-denning ($\bar{\beta}_\omega$ 95% CI − 0.487 to − 0.029), while bears with cubs showed no selection. Bears with cubs exhibited stronger avoidance of step near highways in response to

greater traffic volumes in all three seasons, while selection among bears without cubs generally did not change with traffic volume (Table 2).

Mixed effect models also indicated that bears with cubs showed stronger avoidance of local roads than bears without cubs, primarily during summer and hyperphagia (Table 3). During summer, bears with cubs exhibited stronger avoidance of steps crossing highways relative to bears without cubs, but increased this avoidance as a function of traffic volume to a greater degree (Table 3). Similarly, bears with cubs also exhibited stronger avoidance of steps near

highways during pre-denning relative to bears without cubs, and increased this avoidance as a function of traffic volumes to a greater degree (Table 3).

Behavioral plasticity

The three most supported models—as indicated by population weights ($\bar{\omega}_i$)—among all bears, bears with cubs, and bears without cubs included an interaction between anthropogenic variables and season, indicating that selection for anthropogenic variables changed among seasons (Table 1). Seasonal changes in selection were primarily related to roads and highways (Fig. 2). For all anthropogenic variables, mixed models with a fixed effect on season were more supported than null models ($\omega_i > 0.90$). The strength of change between seasons was most pronounced in selection for steps near highways, steps crossing highways, and steps near local roads (Fig. 2). Bears increased avoidance of highway crossings between hyperphagia and pre-denning ($\bar{\beta}_\omega$ 95% CI -0.019 to -0.193).

Four of the five most supported models among all bears contained interactions between anthropogenic variables and traffic volume, as did three of the top five models among bears with cubs and bears without cubs (Table 1). Bear avoidance of local roads increased with greater traffic volume, as indicated by a positive interaction between distance to local roads and traffic volume ($\bar{\beta}_\omega$ 95% CI 9.3×10^6–1.20×10^4). The effect of traffic volume on selection for steps near local roads ($\bar{\beta}_\omega$ 95% CI 0.001–0.003) and highways ($\bar{\beta}_\omega$ 95% CI 0.001–0.005) increased from summer to hyperphagia, meaning bear avoidance of roads and highways increased with traffic volume more during hyperphagia than summer (Fig. 2).

Bears with cubs were more responsive to traffic volume than bears without cubs (Table 2). Bears with cubs increased avoidance of highways as a function of traffic volume during all three seasons, indicated by positive interactions between selection for steps near highways and traffic volume in each season (Table 2). While effect sizes for population parameters ($\bar{\beta}_\omega$) estimating selection for housing were small among bears with cubs, mixed effect models indicated an important difference in response to traffic (Table 3). The effect of traffic volume on selection for housing was stronger among bears with cubs than among bears without cubs (β 95% CI -0.917 to -0.075). These results indicate similar selection for houses between these two groups, but increased sensitivity to traffic when with cubs.

Acclimation vs. effective avoidance

Functional responses of selection for anthropogenic features—changes in selection with increased availability—explained some of the variability in selection among individual bears (Table 4). Bears occupying areas of greater housing density (i.e., higher HRHD) exhibited stronger selection for residential areas that was consistent among seasons (Table 4). On average, bears with home ranges that included > 66 houses × km^{-2} selected steps in residential areas, while those with home ranges that contained lower housing densities avoided residential areas (Fig. 3).

The functional response of selection for steps near local roads differed among seasons (Table 4). On average, bears avoided steps near local roads at all housing densities, but
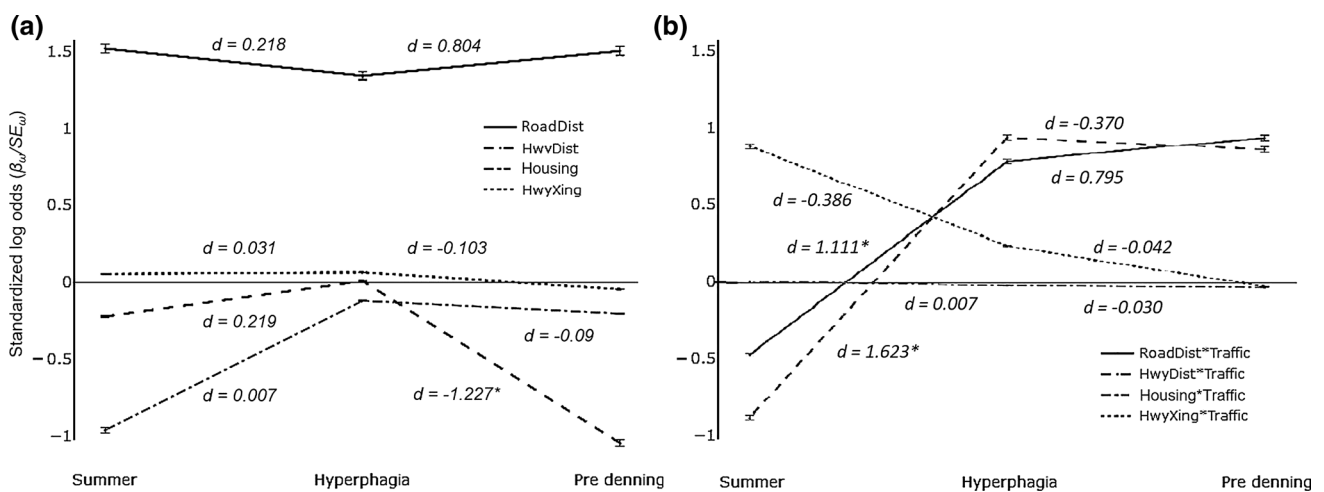

Fig. 2 Changes in mean standardized model-averaged selection parameter estimates ($\beta_\omega/\mathrm{SE}_\omega$) between seasons for **a** effect of anthropogenic variables and **b** interaction effect of anthropogenic variables and traffic volume on log odds of steps. Effect sizes (d) for changes between pairs of seasons estimated from mixed effects models with random effects per individual are displayed adjacent to connecting lines. Asterisks indicates an effect with a 95% confidence interval that did not include zero

Table 4 Results from mixed effect models estimating changes in black bear selection for anthropogenic variables as a function of housing density within home ranges (HRHD)

Response variables (β_ω)	Model support (ω_i)			d	95% CI β	
	HRHD	Log (HRHD)	Null		Lower	Upper
House	**0.902**	0.097	0.005	4.919	0.006	0.013
House × sum[a]	**0.561**	0.339	0.100	2.143	0.003	0.020
House × hyper[b]	**0.778**	0.149	0.073	2.885	0.004	0.019
House × PreDen[c]	**0.613**	0.234	0.153	2.723	0.005	0.031
House × traffic	0.340	0.327	**0.333**	–	–	–
House × traffic × PreDen	**0.540**	0.290	0.170	3.585	− 0.001	− 0.012
House × traffic × hyper	0.222	0.210	**0.568**	–	–	–
House × traffic × sum	**0.940**	0.046	0.015	− 2.174	0.006	0.021
RoadDist	0.273	0.254	**0.473**	–	–	–
RoadDist × sum	**0.797**	0.115	0.089	2.933	0.002	0.008
RoadDist × hyper	**0.648**	0.134	0.218	2.279	0.001	0.007
RoadDist × PreDen	0.502	0.226	0.273	1.979	0.000	0.010
RoadDist × traffic	**0.480**	0.344	0.176	2.150	6E−04	0.0121
RoadDist × traffic × sum	0.211	0.214	**0.574**	–	–	–
RoadDist × traffic × hyper	0.255	0.210	**0.535**	–	–	–
RoadDist × traffic × PreDen	0.380	0.192	**0.428**	–	–	–

Coefficients from interactions between anthropogenic variables and traffic volume or season are indicated by an asterisk (*). AICc weights (ω_i) indicate support for alternative relationships between selection for anthropogenic variables and HRHD. Effect sizes (d) and 95% confidence intervals around the estimated slope (β) are provided from the model with the most support, indicated in bold, unless this was the null model. Variables related to selection for highways are not show, as the null model was most supported in all cases

[a]Summer

[b]Hyperphagia

[c]Pre-denning

the strength of this avoidance increased with HRHD during summer and hyperphagia, while there was no relationship during pre-denning (Fig. 3). The effect of traffic volume on bear avoidance of local roads consistently increased as a function of HRHD (Table 4). Bears across housing densities increased avoidance of local roads during greater traffic volumes, but this response increased with HRHD (Fig. 3). Bear selection for steps near and crossing highways was consistent across housing densities. Null models were supported for relationships between HRHD and all highway variables (Table 4).

The effect of traffic volume on bear selection for residential areas changed as a function of HRHD, but the nature of this response differed among seasons. The response to HRHD was linear negative during summer (β 95% CI − 0.001 to − 0.012), linear positive during pre-denning (β 95% CI − 0.006 to 0.021) and did not differ from zero during hyperphagia, as indicated by model support (Table 4). Bears occupying home ranges with > 44.7 houses × km^{-2} decreased their selection of residential areas with greater traffic volume during summer, but increased selection as traffic volumes increased during pre-denning (Fig. 3).

Conflict

All 35 collared females included in this study were reported in at least one conflict incident to DEEP from 2012 to 2015. Bears that selected steps crossing highways were involved in more conflicts ($\Sigma\omega_i = 0.911$, $d = 2.51$). The strength of bear selection for proximity to local roads ($\Sigma\omega_i = 0.451$, $d = 1.22$) and selection for residential areas ($\Sigma\omega_i = 0.452$, $d = 1.17$) were also associated with greater conflict frequency, although had a lower effect relative to the availability of houses indicated by HRHD ($\Sigma\omega_i = 0.591$, $d = 7.19$). The effect of bear selection for steps near highways was relatively unimportant ($\Sigma\omega_i = 0.280$, $d = 0.344$) in predicting frequency of conflict, relative to HRHD ($\Sigma\omega_i = 0.921$, $d = 6.11$).

Discussion

As wildlife increasingly live near and within developed areas, effective conservation and management requires an understanding of how animals persist in these landscapes, and the benefits and consequences to individuals
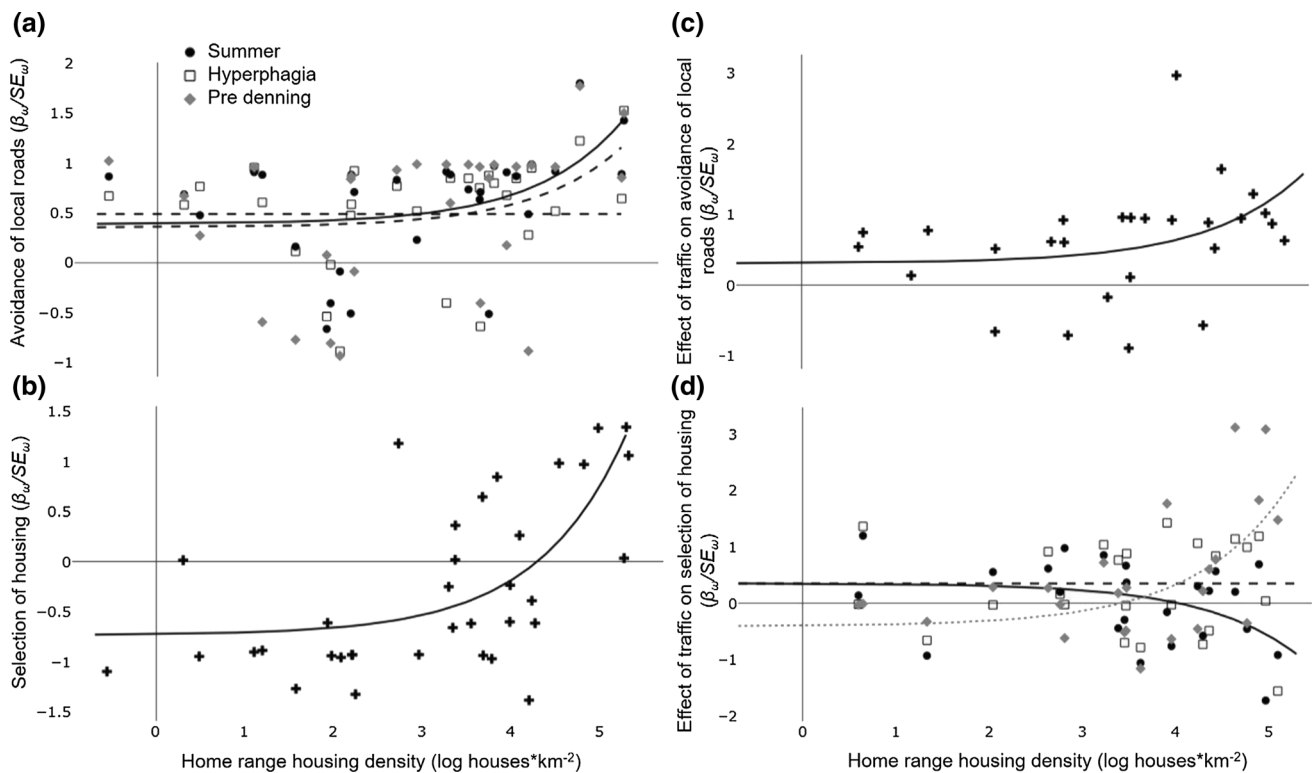
Fig. 3 Linear relationships between log home range housing density, and standardized model-averaged selection parameter estimates (β_ω) of **a** avoidance of local roads and **b** selection for housing, **c** effect of traffic volume on local road avoidance, and **d** effect of traffic volume on selection for housing by black bears. Plots display relationships during summer (solid lines; solid dots), hyperphagia (dashed lines; triangles), and pre-denning (dotted lines; squares) separately, unless the form (linear vs. logarithmic) and direction of these relationships were consistent among seasons

and populations. In this study, we found support for the hypotheses that black bears perceive development as risky, yet persist within developed areas through effective avoidance and behavioral plasticity. Increased avoidance of local roads and highways when bears were with cubs confirmed the perception of these features as risky, and bears across the study area consistently avoided highways. However, stronger selection for residential areas combined with stronger avoidance of local roads within more densely developed areas (Fig. 3) suggests bears are adept at avoiding risky features while exploiting anthropogenic resources. Behavioral plasticity identified by changes in selection among seasons support a growing body of literature indicating that urban expansion homogenizes wildlife communities toward ecologically flexible species (McKinney 2006; Bateman and Fleming 2012). As risk management strategies affect fitness (Anthony and Blumstein 2000), patterns of selection for anthropogenic features in developed landscapes may be an important determinant of population growth (Lewis et al. 2014). Thus, intra-population variation in behavior (Fig. 1) provides capacity for future changes in population-level response to development in these contexts.

Effective avoidance of human activities may facilitate use of developed landscapes by black bears, as documented among other human-adapted carnivores (Gehrt et al. 2011; Kertson et al. 2011). In this study, the hypothesis that bears perceive human development as risky was supported by avoidance of anthropogenic features (Fig. 1), and greater avoidance of local roads and highways by bears with cubs (Table 3). Female bears with cubs often exhibit more risk-avoidant movement behaviors (Dahle and Swenson 2003; Beckmann and Berger 2003a; Rode et al. 2006), due to the fitness benefits of minimizing mortality risk to offspring. Stronger avoidance of local roads combined with stronger selection for residential areas as bears occupied areas of greater housing density (Fig. 3) suggests that bears persist in developed areas by effectively avoiding risky features.

Behavioral plasticity also likely helps bears occupy developed landscapes, as indicated by changes in selection among seasons and with traffic volumes. Overall, bears were less avoidant of roads and highways during hyperphagia and pre-denning than summer, but also responded more strongly to traffic during these times (Fig. 2). These patterns support the prediction that more risky behavior would be tolerated during times when feeding is of elevated importance. Animals

often choose between foraging and risk avoidance when these behaviors cannot occur simultaneously (Fortin et al. 2004), generally overestimating, rather than underestimating risk. Historically, risk-avoidant strategies often produce net benefits to fitness, because overestimation results in a lost foraging opportunity, while underestimation can result in death (Frid and Dill 2002). However, developed landscapes may represent altered selective regimes to which previously advantageous behaviors could be maladaptive (Schlaepfer et al. 2002; Sih et al. 2004). The more pronounced decreases in avoidance during hyperphagia among bears occupying higher HRHD (Fig. 3) and suggests that bears in developed landscapes can effectively shift risk avoidance in accordance with increased caloric requirements.

Bear response to traffic volume further indicated the importance of behavioral plasticity in effectively avoiding risk associated with human activity. Changes in daily movement patterns that minimize risk exposure can be a sign of behavioral adaptation to human disturbance (Ditchkoff et al. 2006; Kohl et al. 2018). Bears in areas of higher housing density exhibited stronger responses to traffic in avoidance of local roads (Fig. 3). Similarly, females with cubs increased avoidance of highways in response to traffic volumes (Table 2). The increased propensity to move near and/or cross highways when traffic levels were lowest may be the result of greater avoidance during high traffic times, a general shift to nocturnal movements in developed areas (Beckmann and Berger 2003b), or both. Together, our results suggest that bears in developed areas may alter avoidance of highways and roads according to traffic patterns—evidence that flexible behavior may be one mechanism by which bears effectively avoid human disturbance while persisting in developed areas. This behavioral alteration may be adaptive, indicating local selection, or simply represent phenotypic plasticity (Lowry et al. 2013).

Black bears may perceive traffic and human activity as risky, rather than anthropogenic features, as indicated by stronger effects of roads and highways on bear movement, relative to housing. Greater support for highway models than housing models (Table 1) and greater population-level effect sizes for road-related variables than housing (Table 2) indicate a stronger response to roads. One possible explanation for this distinction is that sound is an important source of disturbance and perceived risk. Chronic noise exposure associated with development can be a severe threat to a range of taxa that affect foraging, predator avoidance, and other behaviors (Francis and Barber 2013). Acute auditory disturbances (Darrow and Shivik 2009) that impede communication, or mask sounds (Barber et al. 2010) may all induce behavior modification. Alternatively, bears may respond to roads, because these features are potential mortality sources (Baker et al. 2007; Bateman and Fleming 2012), eliciting stronger risk avoidance response (i.e., overestimating vs. underestimating) than forgoing foraging opportunities around houses.

The recent recolonization of our study area by black bears allows for the possibility that the spatial distribution of bear behaviors is not yet at equilibrium with development. Variation in behavior among individuals including differences in sets of correlated behavioral traits can create 'personalities' (Slater 1981; Dall 2004). Thus, more risk-tolerant individuals may non-randomly populate more developed areas (Martin and Réale 2008). The variability in response to development measured in this study demonstrates a range of movement behaviors among individuals within the study population (Fig. 1), some of which was explained by functional responses (Fig. 3). This broad portfolio of behaviors creates the potential for this recently established population to undergo selection, resulting in future shifts in mean behaviors. As use of anthropogenic food sources can lead to drastic increases in fitness (Garshelis et al. 2012), it is not unreasonable to expect less avoidant behavior proliferating within bear populations in relatively short ecological time. Similarly, maladaptive risk avoidance could rapidly decrease in frequency within bear populations inhabiting developed landscapes.

Observed changes in black bear movement between season and reproductive status may have important effects on population viability. While females with cubs were more avoidant of local roads than females without cubs, they also increased selection of steps crossing highways during hyperphagia (Fig. 3). Considering the importance of caloric intake during hyperphagia for overwinter survival (Rogers and Allen 1987) and reproduction (Eiler et al. 1989), a failure to increase foraging during this time could decrease both female survival and reproductive success. Likewise, increased highway crossings may expose reproductive females to additional mortality. Female survivorship and fecundity are the most important life history transitions determining population growth in bears (Powell et al. 1996; Clark and Eastridge 2006), and even small changes to either of these demographic rates may have cascading effects on population growth and viability (Lewis et al. 2014). Thus, these strategies could represent instances of maladaptive risk avoidance.

The conservation of wildlife increasingly requires an understanding of how human activity changes animal ecology, and the ability to prevent conflicts between wildlife and people. Our results suggest that human-adapted species and populations are not necessarily acclimated to humans. Rather, habituation to development is an individually variable characteristic that may change in frequency within a population over time. These shifts may have occurred in places experiencing more persistent and ubiquitous use of development by bears, like New Jersey and Florida, where populations have existed among

development for longer than in our study (Spencer et al. 2007). Development integrating high housing densities within natural land cover may facilitate this process by providing enough cover for individuals to avoid anthropogenic landscape features while existing near humans. The positive relationship between selection for anthropogenic variables and conflict frequency, suggests a relationship between individual temperament and proclivity to conflict. Therefore, preventative measures reducing the proliferation of bold individuals may be effective in places with recently established bear populations. For example, community programs reducing access to anthropogenic food sources, and/or lethal management actions targeting bold individuals may reduce the proliferation of these behavioral phenotypes, preventing shifts in mean population behavior.

Author contribution statement MJE conceived the study; JEH and PWR designed data collection and conducted fieldwork; and MJE designed and conducted analyses and led the writing of the manuscript, with contributions and supervision from TAGR.

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