

4-21-2016

Ecological Effects of Development on American Black Bear

Michael J. Evans

University of Connecticut, michael.evans@uconn.edu

Follow this and additional works at: <https://opencommons.uconn.edu/dissertations>

Recommended Citation

Evans, Michael J., "Ecological Effects of Development on American Black Bear" (2016). *Doctoral Dissertations*. 1115.
<https://opencommons.uconn.edu/dissertations/1115>

Ecological Effects of Development on American Black Bears

Michael John Evans, PhD

University of Connecticut, 2016

ABSTRACT Global patterns of human land use have shifted towards increasingly sprawled development intermixed with natural land cover, creating coupled human and natural systems. To understand how these patterns may affect the persistence of wildlife populations, I studied changes in American black bear (*Ursus americanus*) population density, dispersal, movement behavior, and conflicts with humans across a gradient of development in Connecticut. Forest fragmentation, and intermixture with housing promoted conflicts between bears and people. Median census tract household income was associated with spatial autocorrelation in reported conflict locations, illustrating the importance of accounting for social carrying capacity in managing human-wildlife conflict in intermixed ecosystems. Variation in bear densities were more associated with housing density than forest cover, or a measure of intermixture. Bear densities were elevated in exurban, relative to rural areas, and decreased above 18 houses/km² suggesting urban tolerance, rather than adaptation, among the Connecticut population.

Cohabitation with development can negatively impact wildlife populations, if population dynamics and evolutionary trajectories are detrimentally altered. Therefore, identifying changes in population dynamics and behavior in response to human development are important to wildlife conservation and management in intermixed ecosystems. To identify potentially maladaptive dynamics, I quantified changes in black bear dispersal, spatial genetic structure, and migration between differing levels of development. Increased housing density was associated with longer dispersal movements, and female philopatry was thus disrupted within more

developed areas. Subpopulations occupying developed landscapes were not only sustained by local recruitment, but may serve as a source of female immigrants to surrounding areas.

I estimated selection for anthropogenic landscape features by black bears to discern movement patterns indicative of perceived risk, or habituation. Bears increasingly avoided housing and highways with increased intensity of development, and females with cubs were more avoidant of housing, providing evidence of perceived risk. However, bears decreased avoidance of development during hyperphagia, and exhibited increases in selection for roads and highways from day to night, indicating behavioral plasticity in response to perceived risk. Individual behavior in response to anthropogenic landscape features was highly variable within the population, indicating the potential for changes in the population mean.

Ecological Effects of Development on American Black Bear

Michael John Evans

B.A., Oberlin College, 2008

M.S., University at Buffalo, 2011

A Dissertation

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

at the

University of Connecticut

2016

Copyright by
Michael John Evans

2016

APPROVAL PAGE

Doctor of Philosophy Dissertation

Ecological Effects of Development on American Black Bear

Presented by

Michael John Evans, B.A., M.S.

Major Advisor

Tracy A.G. Rittenhouse

Associate Advisor

Jason C. Vokoun

Associate Advisor

Lori S. Eggert

Associate Advisor

Chadwick D. Rittenhouse

Associate Advisor

Isaac M. Ortega

University of Connecticut
2016

Table of Contents

ACKNOWLEDGEMENTS	1
HUMAN-BLACK BEAR CONFLICT	2
INTRODUCTION.....	2
STUDY AREA.....	4
METHODS.....	4
Data.....	4
Analyses.....	5
RESULTS.....	9
DISCUSSION	11
IMPLICATIONS.....	16
CHANGES IN BEAR DENSITY WITH DEVELOPMENT.....	17
INTRODUCTION.....	17
METHODS.....	19
Study Area and Sample Collection.....	19
Genetic Methods	21
Density Modeling	22
RESULTS.....	25
DISCUSSION	28
IMPLICATIONS.....	32
SPATIAL AND LANDSCAPE GENETICS.....	34
INTRODUCTION.....	34
METHODS.....	37
Sample Collection.....	37
Genetic Methods	38
Population Genetic Structure.....	40
Recent Migration Rates	41
Spatial Genetic Structure	42
Landscape Genetics	43
RESULTS.....	46
Population Structure	47
Recent Migration Rates	48

Spatial Genetic Structure	49
Landscape Genetics	50
DISCUSSION	51
IMPLICATIONS.....	55
STEP SELECTION MOVEMENT MODELS	57
INTRODUCTION.....	57
METHODS.....	60
Data Collection	60
Individual Step Selection.....	64
Changes in Selection Among Bears	66
RESULTS.....	69
Model Selection	69
Housing.....	70
Highways	71
DISCUSSION	73
IMPLICATIONS.....	78
SUMMARY	79
Predicting Future Black Bear Distributions.....	79
Habitat Selection.....	80
Tolerance of Development	81
Male Biased Sex Ratios	82
Preventing Human-Bear Conflict	83
Future Research Directions	84
REFERENCES	87
TABLES	112
Table 1.1.....	112
Table 1.2.....	113
Table S1.1.....	114
Table S1.2.....	115
Table S1.3.....	116
Table 2.1	117
Table 2.2.....	118

Table S2.1.....	119
Table S2.2.....	120
Table S2.3.....	121
Table 3.1.....	122
Table 3.2.....	123
Table 4.1.....	124
Table 4.2.....	125
Table 4.3.....	126
FIGURES	127
Fig. 1.1.....	127
Fig. 1.2.....	128
Fig. 1.3.....	129
Fig. 2.1.....	130
Fig. 2.2.....	131
Fig. 2.3.....	132
Fig. S2.1	133
Fig. 3.1.....	134
Fig. 3.2.....	135
Fig. 3.3.....	136
Fig. 4.1.....	137
Fig. 4.2.....	138
Fig. 4.3.....	139
Fig. 4.4.....	140
Fig. 4.5.....	141
Fig. 4.6.....	142

ACKNOWLEDGEMENTS

This dissertation is the culmination of a lot of belief and hard work on the parts of many people besides myself. First, the project would not have been possible without the help of biologists at the Connecticut Department of Energy and Environmental Protection. Beyond providing funding, Jason Hawley, Paul Rego, and Rick Jacobson were wonderful to work with. Their expertise and patience while developing study ideas were crucial, and they were totally supportive of the research - from assisting with field efforts to providing data. Dr. Emily Puckett was incredibly patient and generous with her time sharing and teaching me the genetic lab procedures that I used, which she had worked hard to develop, and bailing me out with fresh primers on occasion. Although he had nothing to do with this project, Carl Morrison (wherever you are) gave me the opportunity to jump out of marine ecology to get my first experience in wildlife research, and provided a once-in-a-lifetime experience. Finally, I would like to thank my parents, Gail and John, for their lifelong support and encouragement to pursue my passions and dreams. My Dad may have regretted that support when he volunteered to help out with field work, and found himself alone, crawling in and out of a culvert trap with stale donuts, but I couldn't appreciate his enthusiasm more.

HUMAN-BLACK BEAR CONFLICT

INTRODUCTION

The unique landscapes represented by exurban development bring wildlife into close proximity with humans, increasing the potential for conflict. Land-use pattern in Connecticut is typical of New England, with the state comprised almost entirely of exurban housing (Theobald 2001). Concurrently, black bear (*Ursus americanus*) abundance is increasing throughout the northeast United States, and their range has expanded into Connecticut. The interspersed forest and housing in the state, and bears' ability to exploit human food sources simultaneously facilitate human-black bear conflicts, and present substantial challenges to conflict management.

Exurban development patterns (6–25 homes/km²) are characterized by housing densities between rural and urban embedded within natural cover types, and were the fastest growing form of land use in the United States as of 2000 (Brown et al. 2005). Such development may have strong effects on biodiversity and biological communities, with specific impacts varying among species (Hansen et al. 2005). Human development has historically been thought to displace native wildlife (Vogel 1989, Theobald 1997). However, exurban land-use patterns produce a more multidimensional human-wildlife interface, as interspersed housing and native vegetation benefits some human-adapted guilds (Miller and Hobbs 2002, Glennon and Porter 2005, Hansen et al. 2005).

As opportunistic omnivores, black bears may readily adapt to, and thrive in, forested exurban and suburban areas. Although black bears may be sensitive to large-scale anthropogenic removal of natural habitat (Mattson 1990, Brodeur et al. 2008), housing interspersed within forest provides additional food sources that bears exploit (Ranglack et al. 2009, Baruch-Mordo et al. 2014). In many developed areas, black bears have significantly modified their foraging and

reproductive behavior because of the regular availability and abundance of anthropogenic foods (Beckmann and Berger 2003, Ellingwood 2003, MacKenzie 2003, Moyer et al. 2007, Beckmann and Lackey 2008). In addition to providing consistently available foods, housing within suitable bear habitat may accelerate the rate and extent of bear habituation to humans (McCullough 1982).

A consistent finding of predictive models of conflict between humans and large mammals is the importance of the proximity of wildlife habitat to human development (Wilson et al. 2006, Baruch-Mordo et al. 2008, Krester et al. 2008, Merkle 2011). However the majority of this research has focused on rural areas where livestock depredation was the primary form of conflict (Bradley and Pletscher 2005, Michalski et al. 2006, Wilson et al. 2006, Baruch-Mordo et al. 2008). Unlike the distinct boundaries between bear habitat and human land use found in such areas, exurban landscapes contain exploitable human food sources within a matrix of relatively natural bear habitat. Therefore, the proximity of habitat and housing may be less important in determining the distribution of conflicts than landscape variables describing their interspersions in exurban contexts.

Our first objective was to use public reports of black bear property damage to identify landscape factors that explain the spatial distribution of human-black bear conflicts in exurban Connecticut. We then used these factors to predict relative risk of conflict across the state to identify potentially high-risk areas. We hypothesized that Connecticut's exurban housing patterns would result in the spatial distribution of human-black bear conflicts being related to variables associated with the level of integration of housing and forest. Our second objective was to address the effect of demographic variability and reporting bias implicit in using citizen reports (Howe et al. 2010) to understand the spatial distribution of human-wildlife conflict.

STUDY AREA

Human-bear conflicts were most frequent in northwestern Connecticut (Fig. 1.1). Connecticut had a population of 3,590,347 people about the time of our study (U.S. Census 2012).

Connecticut's landscape was largely forested (Fig. 1.2a), with 58.8% of land cover in the state forest according to the 2006 National Land Cover Database (NLCD; Fry et al. 2011). Mean housing density in Connecticut was 5.18 houses/ha, with most urban development concentrated along the coast and the U.S. Interstate 91 corridor (Fig. 1.2b). Outside of high density urban areas, housing in Connecticut was dispersed and perforated the forest canopy. 51.7% of the state was categorized as intermixed (i.e., >1 house/16 ha and >50% forest cover) according to the Wildland Urban Interface classification (Radeloff et al. 2005).

We restricted analyses to a 4-km buffer surrounding locations of reported human-bear conflict. A 4-km radius corresponds to a circle of roughly 50 km². The median female home range size for Connecticut black bears is about 30 km² (Connecticut Department of Energy and Environmental Protection, unpublished data); therefore, this buffer restricted the study extent to an area of the state where bears are regularly reported to occur.

METHODS

Data

The Connecticut Department of Energy and Environmental Protection (DEEP) documented all black bear incidents in a formal database. These include citizens' sightings, reports of property damage, and vehicle collisions. Because our objective was to describe the spatial distribution of conflicts between bears and humans, we excluded all reports of bear sightings and considered only reports involving nuisance behavior (e.g., damaging property, eating garbage, etc.) for analysis. We used the address locator function in ArcView 10.1

(Environmental Systems Research Institute, Inc., Redlands, CA) to obtain coordinates from addresses associated with conflict records occurring during 2008–2012. This function generates a match score, which indicates how well input addresses match candidate locations. We manually located reports with <70% match score using aerial photography cross-referenced with Google Earth (Google, Mountain View, CA) imagery. We similarly cross-referenced the location of a random sample of 100 points to compare the spatial accuracy of automated geocoding to the actual location of buildings at incident addresses. We determined the percentage of geocoded incidents that fell within 30 m of buildings, because this distance corresponds to the cell size of rasters associated with predictor variables. Hereafter, these locations are referred to as conflict locations.

Analyses

We used multiple regression to evaluate relationships between landscape characteristics and conflict locations in a resource utilization framework, using a kernel estimate of the intensity of conflicts as the response variable (Millspaugh et al. 2006). We created conflict intensity surfaces using kernel density estimation in Geospatial Modeling Environment (GME version 0.7.2.1, www.spataleecology.com/gme, accessed 10 Oct 2014). We calculated kernel surfaces using least squares cross-validation (LSCV) selected bandwidth, as well as fixed bandwidths of 1 km and 5 km. We chose the appropriate bandwidth using correlations between the resulting intensity surface and univariate predictor variables, selecting the surface with the highest correlation coefficients (R). Kernel intensity surfaces and all predictor variables were represented in 30×30 -m pixel rasters.

We performed a 2-stage analysis to identify significant natural landcover predictors of conflict intensity, and then to assess the additional explanatory value of anthropogenic variables.

We first constructed a set of a priori candidate models composed of variables related to the abundance and configuration of natural bear habitat. These included distance (km) to forest, percent forest cover, forest edge density (as an indicator of forest fragmentation) (Powell et al. 1997, Brodeur 2008, Baldwin and Bender 2012), distance (km) to all streams and main stem streams, and distance (km) to wetlands (riparian vegetation; Young and Beecham 1986, Feske et al. 2002).

To calculate distances to forest and wetlands, we reclassified the 2006 NLCD raster into two binary raster layers. The first combined deciduous, coniferous, and mixed forest classes into a single forest class, from which we created a raster layer depicting distance to the nearest forest. The second binary raster combined forested and emergent wetland into a single wetland class, which we used to create a distance to wetland raster. We estimated forest edge density as the percentage of forest cover within 100 m of non-forest cover types within 0.0625-km², 0.25-km², and 1-km² windows. We calculated percent cover of forested land at a given location within identical windows. We calculated distance from main stem and all streams using the Connecticut DEEP 2005 hydrography shapefile.

We used univariate linear regression models to select the most useful representation of streams (all streams, or main stem) and the window size for quantifying forest cover and forest edge density. We selected the best models representing the effect of streams, forest cover, and edge density on conflict intensity using Akaike's Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002). Distance to main stem streams, and a 1-km² window characterization of forest cover and forest edge density had the lowest AIC scores (see Table S1.1, available online at www.onlinelibrary.wiley.com). We then used these variable representations in multivariate models.

We used scatterplots to identify potentially non-linear univariate relationships between predictor variables and conflict intensity. Percent forest cover, edge density, distance to streams, and distance to wetlands appeared to have quadratic relationships with conflict intensity, and we subsequently compared models with quadratic representations of each of these variables to untransformed models using AIC scores. We selected quadratic representations of percent forest cover and wetland distance for inclusion in multivariate models, because quadratic models had the lowest AIC values and univariate linear models were not competing (i.e., within 2 AIC units; see Table S1.2, available online at www.onlinelibrary.wiley.com). We assessed all predictors for collinearity ($r > |0.5|$) using a Pearson's correlation matrix, eliminating 1 variable from any collinear pair.

We tested candidate models that included natural habitat variables to explore hypotheses that riparian vegetation (wetland, stream), forest configuration (% forest, % edge), and both forest and riparian habitat (% forest, % edge, wetland, stream) explained the spatial intensity of conflicts. We constructed models containing each of the above sets of variables and distance to forest to assess the relative importance of forest structure versus forest proximity based on AIC score. We hypothesized this to be an important distinction in exurban contexts for identifying conflict areas. We refer to these models as natural habitat models.

We constructed a second set of candidate models including all variables from the top-ranked natural habitat model and additional anthropogenic variables. Anthropogenic variables included housing density (Krester et al. 2008, Merkle et al. 2011) and median household income. We obtained data for both variables from the 2007–2011 United States Census (U.S. Census Bureau 2011). The density of houses represented the opportunity for conflict and may explain spatial conflict intensity beyond the presence of natural bear habitat. The socioeconomic level of

neighborhoods might affect conflict intensity through the presence of unique bear attractants or as a representation of differences in attitudes toward wildlife.

We initially fit generalized linear models with Gaussian error structures and an identity link function using the GLM command in the R language and environment for statistical analyses (R Version 2.15.2, www.r-project.org, accessed 14 Sep 2013). We tested model residuals at conflict locations for global spatial autocorrelation using Moran's I, and local spatial autocorrelation using local Moran statistics in the program GeoDa (GeoDa Version 1.6.0, <http://geodacenter.asu.edu>, accessed 15 Sep 2013). We subsequently evaluated the ability of spatial lag and spatial error regression to improve multivariate model fit using Lagrange Multiplier (LM) statistics in GeoDa. In all cases, spatially lagged and spatial error regression improved fit over ordinary regression, as indicated by LM tests with $P \leq 0.001$ for all candidate models (see Table S1.3, available online at www.onlinelibrary.wiley.com). We additionally performed the same 2-stage analysis on our candidate model sets using spatial error multivariate regression. This approach accounts for spatial autocorrelation in the error term as a nuisance parameter, allowing for better estimation of the beta parameters of interest. We identified models with the greatest support as those receiving the lowest AIC score among the candidate set. We report and discuss the results of those spatial error regression analyses, hereafter referred to as spatial models.

Spatially explicit models and local autocorrelation analyses in GeoDa require specification of a neighborhood distance. We defined neighborhoods as the distance within which conflict locations exhibited spatial clustering. We estimated the nearest neighbor distance distribution function using the Gest command in the spatstat package (Baddeley and Turner 2005) for program R, and compared the observed distribution of nearest neighbor distances

between conflict locations to the distributions generated by simulated random point patterns. The distance at which the observed distribution for conflict locations fell within the 99% confidence envelope of simulated distributions was 1,500 m, indicating locations closer than 1,500 m were more clustered than at random. We therefore used an equal weight matrix defining all conflict locations within 1,500 m as neighbors in spatial models and for local autocorrelation analysis.

We evaluated predictive ability of best fitting models on the original data using *K*-folds cross validation (Boyce et al. 2002). We first divided the data into 10 20% testing and 80% training sets. We partitioned predicted conflict intensity for testing data into 10 equal bins, ranked from high to low, and compared these to the number of actual conflict locations within each bin using Spearman's rank correlation (Boyce et al. 2002). We used variables and coefficients from the top ranked spatial model, which estimated the relationship between variables and conflict intensity after accounting for autocorrelation in locations, to produce a statewide map of predicted conflict intensity, illustrating high and low risk areas.

RESULTS

We spatially referenced 1,589 reports of black bear damage occurring during 2008–2012 (Fig. 1.1). Of the random sample of 100 spatially referenced points, 88% were within 30 m of actual structures at the specified address, indicating sufficient location accuracy. Income, distance to wetland, distance to main stem streams, housing density, distance to forest, forest edge density, and percent forest cover were significant univariate predictors (i.e., $P < 0.05$) based on Wald's chi-square test. Correlations among these variables ranged from $r = -0.38$ to $r = 0.35$. Forest edge density and percent forest cover were correlated within 0.0625-km² ($r = 0.63$, $P = 0.03$, and 0.25-km² ($r = 0.58$, $P = 0.08$) windows. However, they were not collinear as calculated at the 1-

km² window scale ($r = 0.26$, $P \leq 0.001$), which we previously identified as the best characterization for these variables based on AIC score. We selected a bandwidth of 5 km for kernel density estimation because it produced an intensity surface with the strongest correlations to potential predictor variables of those tested.

The natural habitat model including variables describing both forest and riparian area effects had the lowest AIC score and no other models were competing (i.e., $\Delta AIC > 2$ units). This top-ranked model indicated that increased forest edge density, intermediate percent forest cover, intermediate distance to wetlands, and proximity to streams were predictors of conflict locations in Connecticut (Table 1.1). Distance to forest edge was not included in the top-ranked model, and all models containing percent forest cover and edge density were more supported without distance to edge (Table 1.1). Percent forest cover was quadratically related to conflict intensity, such that an intermediate amount of forested land (42%) was associated with the highest intensity of conflict. At low forest cover, our top-ranked model predicted an increase of 0.03 km² of forest to increase conflict intensity by 1 conflicts/km². Similarly, an increase in forest edge of 13.2% corresponded to an additional 1 conflicts/km².

A model containing housing density in addition to variables in the top-ranked natural habitat model received the greatest AIC support (Table 1.1), and we found a positive relationship between the density of houses and conflict intensity (Table 1.2). An additional 3874 houses/km² was predicted to increase conflict intensity by 1 conflicts/km². Although not the top model, an anthropogenic model with housing density and household income was moderately supported (Akaike weight, $\omega AIC = 0.17$) and received a lower AIC score than the top-ranked natural habitat model (Table 1.1). Additionally, the top-ranked non-spatial regression model included the same set of predictor variables as the top-ranked spatial model but also indicated a positive

relationship with median household income, in which high income census tracts were associated with conflict locations ($\beta = 8.15 \times 10^{-7}$, $P \leq 0.001$).

Residuals produced by the best spatial model had low global autocorrelation among all conflict locations ($I = 0.099$, $P < 0.001$). Additionally, only 4% of locations showed significant local autocorrelation within 1,500 m neighborhoods. Cross validation indicated that the top-ranked spatial model provided good prediction for the spatial distribution of conflicts in Connecticut ($r_s = 1$, $P \leq 0.001$). Using coefficients from the most supported spatial model, the distribution of predicted human-black bear conflict intensities across Connecticut, given statewide occupancy by black bears, indicate low risk of conflict in urbanized areas (i.e., central and coastal Connecticut), and relatively high risk in forested population centers (i.e., western Connecticut) (Fig. 1.3).

DISCUSSION

Human development interspersed within forested habitat facilitated contact between bears and humans in Connecticut, with conflict locations best explained by amount of forest cover and edge density. We attribute this pattern to the high level of housing dispersed within Connecticut's continuously forested landscape. Proximity of forest patches was not important in predicting conflict locations in Connecticut. We also found evidence that the rate of bear damage reporting may differ among neighborhoods according to socioeconomic status, based on the inclusion of census tract median household income in a moderately supported spatial model and the top-ranked ordinary regression model. We conclude that land use patterns strongly affect the spatial distribution of human-black bear conflicts in exurban contexts such as Connecticut.

Intermediate percent forest cover was associated with the highest probability of conflict occurrence, with low probability of conflicts in places with little forest cover (e.g., downtown Torrington) or in places with large tracts of forest (Fig. 1.3). Intuitively, as the amount of forest surrounding a given location increases from 0, the probability of human-bear conflicts is expected to rise as a function of greater overlap between bear habitat and human housing. We found conflict probabilities declined at high forest coverage after an intermediate maximum (42% forest cover). The inclusion of percent forest edge, which is an indicator of forest fragmentation, in the top-ranked model suggested that a description of forest configuration is needed in addition to total amount to explain variation in conflict probabilities across locations (Table 1.1).

Increased forest edge density increased the likelihood of conflict. In rural and undeveloped landscape contexts, fragmented forests can promote bear presence by providing multiple food sources associated with habitat mosaics and edges (Baldwin and Bender 2012), and bears may simply be more likely to frequent these areas in Connecticut. However, exurban forest edges are created in large part by human development. In Connecticut, 68% of all non-forested land is developed, with high edge density indicative of a development footprint on forested lands. This arrangement provides bears greater opportunity and access to anthropogenic foods and attractants relative to the same amount of forest cover consisting of less edge.

The relationships between forest cover, edge density, and conflict intensity are important to consider in the context of exurban development. This pattern of land use places housing within native habitats because natural landscapes are viewed by many homeowners as desirable (Rudzitis 1999, Rasker and Hansen 2000). This perforation creates an extensive interface

between natural bear habitat and housing. Our results demonstrated such land use patterns facilitate interactions between bears and humans in exurban areas.

In Missoula, Montana, the probability of human-black bear conflict locations was positively related to intermediate housing density and proximity to large ($>100 \text{ km}^2$) forest patches (Merkel et al 2011). Inconsistency in predictors between Connecticut and Montana likely reflects differences in land use patterns. Housing in Connecticut is typical of exurban land use, which perforates rather than fragments a continuous forest canopy (Fig 2a.). Much of the non-urban residential area in Connecticut included a predominance of intermixed (WUI classification) land use (Fig. 1.2b), indicating forest cover was ubiquitously distributed among housing (and vice versa). With houses located extensively within forests that are suitable bear habitat (Garshelis and Pelton 1981, Rogers 1987, Powell et al. 1997, Mitchell et al. 2002), the local abundance and structure of forest at a given location determined conflict intensity rather than forest proximity. Further, conflict intensity increased with housing density because these locations were largely surrounded by forest. In both Montana and Connecticut, conflicts between black bears and humans occurred at the interface of housing and natural land cover. Differences in significant predictors illustrate the importance of local land use patterns in facilitating conflicts between humans and black bears.

We believe the positive effect of mean household income on the intensity of human-bear conflict in the most supported non-spatial model, and a spatial model with more support than the top-ranked natural habitat model, suggested residents of high income areas had an increased propensity for reporting incidents. The reduced importance, as indicated by model weight, of income in spatial compared to non-spatial models suggests income may be associated with spatial autocorrelation of conflict locations – a result consistent with changes in rates of

reporting. We reached this conclusion because although high income areas may contain unique bear attractants such as orchards, vineyards, beehives, or livestock, only 2.5% of conflicts involved damage to these items, indicating such features did not play a major role in attracting bears to high income properties.

One possible explanation for increased reporting rates in high-income census tracts is the potentially high monetary value of damaged property in these areas. The cost of wildlife damage can decrease tolerance for wildlife on and around private property (Conover 1998), and generate demand for management efforts such as lethal control (Bangs and Shivik 2001, Decker et al. 2006, Muhly and Musiani 2009). Therefore, greater cost of bear damage could increase the likelihood of complaints. However, 82% of damage reports in Connecticut involved bears rummaging in garbage or destroying bird feeders, making damage expense an unlikely explanation for reporting rates.

Instead, we suggest that high-income areas in Connecticut may have lower black bear acceptance capacity (Decker and Purdy 1988). Previous studies have found that citizens' perception and attitudes toward wildlife can vary according to a wide variety of social factors including demographics, occupation, education level, media exposure, and the nature of interactions with wildlife (Kaltenborn et al. 1999, Bright et al. 2000, Naughton-Treves et al. 2003, Gore et al. 2007, Siemer et al. 2007, Don Carlos 2008). Public tolerance for wildlife is a function of the balance of perceived benefits and costs presented by wildlife populations (Conover 2001, Decker et al. 2002, 2006); therefore, bears are likely viewed as a potential risk with little benefit by residents of high-income census tracts. Our results highlight the potential need to consider spatial variation in stakeholder attitudes when making and evaluating black bear

management decisions (Gore 2006) because social carrying capacity may change over small spatial scales.

Variation in social carrying capacity will be important to consider when managing bears in an exurban context because of potentially opposing views toward management actions. For example, bear hunting can reduce human-bear conflicts by limiting the size of bear populations and re-enforcing wariness of humans (Brody and Pelton 1989, Mattson 1990). However, the institution of bear hunting can be a socially contentious issue (Harker and Bates 2007). In exurban and suburban contexts, hunting over bait may be the only applicable method to implement harvest (Hristienko and MacDonald 2007) because of the relatively close spacing of housing, division of private lands, firearm discharge restrictions, and trespassing laws. If support of hunting for bear management changes at the scale of census tracts, localized decisions regarding acceptable methods will be needed to preserve its viability as a management option across a wider range of landscapes.

Likewise, high-risk areas with low support for lethal management can be targeted for education programs and local legislation aimed at modifying human behavior (e.g., town garbage ordinances). Such practices can be effective at preventing conflicts at localized scales (MacArthy and Seavoy 1994, Peine 2001), minimizing the need for responsive management actions (e.g., translocation and aversive conditioning) that can involve substantial resource requirements (Rauer et al. 2003). Identification of high-risk and high-demand areas would allow managers to focus human behavior modification strategies where there is the greatest potential for return on investment.

IMPLICATIONS

As black bear range continues to expand in the northeast United States, our model can be used to proactively reduce the potential for conflict between bears and humans by informing housing development and targeting preventative management actions. Housing built within natural settings is generally seen as an amenity of exurbia, but our results demonstrate this arrangement comes with increased risk of conflicts with bears. Our findings suggest that a more distinct segregation of forest cover and housing would likely reduce conflicts. These patterns should be considered in areas where minimizing bear damage is a high priority and/or opposition to management actions is strong. The variables associated with high conflict intensity identified in our model also indicate areas of Connecticut with high potential for human-black bear conflict not yet reporting incidents. Such areas should be targeted for proactive measures such as public education programs and garbage ordinances, particularly those at the leading edge of bear range in Connecticut.

CHANGES IN BEAR DENSITY WITH DEVELOPMENT

INTRODUCTION

Understanding the consequences of changing land-use patterns on ecological processes is critical to the conservation of natural resources (Ricketts & Imhoff, 2003), as urban areas are growing on average twice as fast as their human populations (Seto *et al.*, 2011). In the United States exurban development has been the fastest growing pattern of land-use (Brown *et al.*, 2005). Broadly defined as 6 – 50 houses/km² (Theobald, 2004), exurban development is distinguished from urban and suburban development by greater preservation of natural land cover around houses (Theobald, 2001; Clark *et al.*, 2009). This intermixing of development and natural land cover blurs traditional urban-rural distinctions, and these landscapes are increasingly being studied as intermixed ecosystems (Zipperer *et al.*, 2000). The effects of such intermixed land-use on wildlife have yet to be fully articulated, benefiting some species and hindering others (Hansen *et al.*, 2005; Bar-Massada *et al.*, 2014). Quantifying the response of wildlife to new patterns of land-use will help anticipate the impact of future development on wildlife populations and plan conservation strategies.

Intermixed ecosystems have led to a proliferation of synanthropic wildlife – species that exhibit positive demographic or numeric responses in developed areas (Johnston, 2001; McKinney, 2006). The benefits of anthropogenic resources and refuge (Waite *et al.*, 2007) can lead to increased survival and reproduction (Marzluff & Ewing, 2001; DeStefano & DeGraaf, 2003; Gehrt *et al.*, 2010). While many carnivores avoid development (Cardillo *et al.*, 2004), a number of species have increased densities in developed landscapes (see Bateman *et al.*, 2012 for a review). Carnivore cohabitation with humans spans a gradient from avoidance, to ‘urban adapters’ that tolerate development and rely on natural resources, to synanthropes with positive

association with development (McKinney, 2006). These relationships are likely influenced by the specific pattern of development, and identifying landscape characteristics affecting species' distributions, will be important to anticipate how changing land-use patterns affect the abundance and distribution of carnivore populations. Relationships between density and land-use patterns can distinguish between avoidance, tolerance, and synanthropy.

The American black bear (*Ursus americanus*) has become a species at the center of urban-wildlife research. Once extirpated from much of North America, populations have been recolonizing the former range over the last several decades (Garshelis & Hristienko, 2006). Black bear have traditionally been considered to require large amounts of natural land cover – including forest, shrubland, and wetland habitats (Powell *et al.*, 1997) - and to be negatively affected by anthropogenic disturbance (Dixon *et al.*, 2007; Brodeur *et al.*, 2008). However, populations are expanding into developed areas, often exploiting anthropogenic foods (Ranglack *et al.*, 2009; Merkle *et al.*, 2013; Johnson *et al.*, 2015). In urban-rural systems, bears select high quality natural resources when available, indicating tolerance of development (Baruch-Mordo *et al.*, 2014; Johnson *et al.*, 2015). However, bears are increasingly recolonizing exurban areas (Ellingwood, 2003; Evans *et al.*, 2014), and use of these intermixed ecosystems may differ from urban or suburban landscapes.

The recent re-establishment of a black bear population in Connecticut presents an opportunity to understand how expanding carnivore populations respond to emerging development patterns. Bear range in the state encompasses a spectrum of housing densities, including primarily intermixed exurban and suburban development, with patches of rural and urban areas. In this context, changes in black bear density can be quantified across a gradient of development patterns. If bears are urban adapters, tolerating development, we would expect to

find an inverse relationship between development intensity and bear densities. Conversely, elevated densities in and around development would provide evidence that bears are synanthropic, benefiting by living in intermixed ecosystems in close proximity to humans. Finally, uniform bear densities across this landscape would indicate a generalist strategy (Rosenzweig, 1981). As exurban development proliferates, these distinctions will be important for predicting the persistence of these large carnivores, and identifying the degree to which intermixed ecosystems support the occurrence of bears and people.

Here we rank competing hypotheses about which characteristics of intermixed ecosystems were associated with variations in black bear density. We hypothesized that the degree of interspersed housing and forest cover would determine bear density, and predicted that the Wildland-Urban Interface classification (Radeloff *et al.*, 2005) would best explain variation in bear density. Our second objective was to identify land-use patterns that maximize bear density, including thresholds at which densities change drastically. We hypothesized that intermixed land-use would elevate bear densities by providing forest cover and additional anthropogenic foods (Mazur & Seher, 2008; Greenleaf *et al.*, 2009). We also hypothesized that the numerical response of black bear to development would differ between males and females, due to differences in dispersal (Moyer *et al.*, 2006; Costello *et al.*, 2008) and behavior at range peripheries between the sexes (Beckmann & Berger, 2003b; Sato *et al.*, 2011).

METHODS

Study Area and Sample Collection

We used non-invasive hair corrals (Woods *et al.*, 1999) to collect hair samples from black bears in northwest Connecticut. Corrals consisted of two strands of barbed wire spaced at 30 cm and 45 cm off of the ground, creating an enclosure of ~5x5 m. We used non-nutritional scent

lures applied to log piles at the center of corrals, and rags hung over corrals, to attract bears to sampling locations while minimizing the potential for a trap-happy response. We used multiple, intensive (Wilton *et al.*, 2014) sampling grids to systematically distribute hair corrals across four study areas. Grids encompassed the entire reproductive range of black bear in western CT, and spanned the full gradient of housing densities therein (Fig. 2.1).

Grid cells were 2.5 km² to accommodate 3 – 4 sampling locations within an area the size of a female summer home range (approx. 30 km², CT DEEP unpublished data). North grid consisted of 49 sampling locations in the northwest corner of CT, and covered 271 km². Land cover on and around this grid was primarily forested, with an average housing density of 6.8 km⁻². East grid had 48 sampling locations across 215 km² of suburban and exurban areas of CT, with an average housing density of 83.6 km⁻². South grid was 220 km² containing 50 sampling sites. This grid was located in an attempt to span the southern extent of reproductive bear range. Average housing density within South grid was 23.2 km⁻². Barkhamsted grid consisted of 25 sites over 95 km². Barkhamsted grid was similarly forested but contained higher housing densities (mean = 37.3 km⁻²) than North grid.

Bear hair was collected over two sampling years during June – August, 2013 and 2014. Hair samples were collected from corrals and stored in individually labeled coin envelopes weekly, producing 12 sampling occasions in 2013 and 11 occasions in 2014. Corrals on Barkhamsted grid were only operated during 2014 and only the northernmost 25 corrals were operated in South grid in 2014. All hairs deposited on a single barb were considered a single sample. New scent lure was applied at each visit. We used four different scents over the course of each sampling season to increase trap novelty and minimize a behavioral response to previous detection. Within a sampling occasion, the same lure was applied at all sites.

Genetic Methods

We extracted DNA from hair follicles using the InstaGene Matrix (Bio-Rad Laboratories, Hercules, CA) following the protocol of Eggert *et al.* (2005). We assessed restriction fragment length polymorphisms at the cytochrome b region following digestion with DdeI and ApoI to confirm species identification. We compared amplified fragment sizes to positive controls of black bear, raccoon (*Procyon lotor*), domestic dog (*Canis familiaris*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), and white-tailed deer (*Odocoileus virginianus*) eliminating all samples not producing a positive bear genotype.

To identify individuals we amplified extracted DNA from all bear samples at seven polymorphic microsatellite loci (G1A, G10B, G10L, G10P, G1D, G10M, G1C; Paetkau & Strobeck, 1994, 1998). We determined individual sex by amplifying the Amelogenin gene (Carmichael *et al.*, 2005). We used the redesigned primer pairs of Kristensen *et al.* (2011) to increase genotyping efficiency using low concentration and potentially degraded DNA. All PCR reactions were performed in a UV-sterilized hood, following the multiplex genotyping protocol of Puckett *et al.* (2014). Each 96-well plate contained extracted DNA from a bear handled by CT DEEP during den visits as a positive control. Products were separated in a DNA Analyzer (ABI 3730, Applied Biosystems, Waltham, MA, USA) at the University of Missouri DNA Core Facility (Columbia, MO). We scored the size of fluorescently labeled DNA fragments against size standards (GeneScan 600 LIZ, Life Technologies, Waltham, MA, USA) to generate genotype data using GENEMARKER v1.97 (Soft Genetics, State College, PA).

We estimated P_{ID} and $P_{ID_{sibs}}$ (Waits *et al.*, 2001) in GenAlEx (Peakall & Smouse, 2006) to confirm sufficient power of our marker set to identify unique individuals. We used the multi-tubes approach (Taberlet *et al.*, 1996) to produce consensus genotypes, amplifying and scoring

up to five replicates of a sample to confirm heterozygous genotypes in at least two replicates, and homozygous genotypes three times. Samples were required to have consensus genotypes of at least 6 loci to be considered in further analyses. We used MICRO-CHECKER v2.2.3 (Van Oosterhout *et al.*, 2004) to test for deviations from Hardy-Weinberg equilibrium due to null alleles and scoring errors. To minimize the possibility for shadow effects (Mills *et al.*, 2000) to bias density estimation, we assessed genotyping error leading to misidentification of individuals using DROUPOUT v1.2 (McKelvey & Schwartz, 2005). We re-genotyped individuals that differed at 3 or fewer loci, and allowed a mismatch at 1 locus following this step when determining recaptures. Finally, to minimize the potential for biasing density estimates by erroneously considering dependent young as independent samples, we used ML-Relate (Kalinowski *et al.*, 2006) to identify parent-offspring pairs detected at a single hair corral at a single sampling occasion and treated these groups as a single individual.

Density Modeling

We used spatial mark-recapture (SMRC) methodology (Gardner *et al.*, 2009) to estimate bear population densities around each study grid, and across all study grids in western CT. This approach considers the observed history of individual detections and their locations as a function of two processes; the latent density of individual activity centers, and detection probability as a function of distance between activity centers to trap locations. Detection probability is described by two parameters; g_0 , which indicates the probability of detection for an individual with an activity center at a sampling site, and σ , which defines the rate of decline in detection probability as a function of distance from a sampling site. Additionally, the density of activity centers can be modeled as inhomogeneous poisson processes, varying according to spatial covariates. Models were implemented using the *secr* package (Efford, 2012) for Program R v

3.0.2 (R Development Core Team, 2014). To fit SMRC models, grids were buffered by 10 km. This distance was determined by the “suggest.buffer” function, which selects a distance beyond which further decline in detection probability is negligible. We refer to these buffered extents as North, East, South and Barkhamsted study areas, and the buffered extent of all sampling locations as the Combined study area.

We tested hypotheses regarding what landscape features correspond to variation in bear density by fitting inhomogeneous density models in which estimated bear density varied as a function of different landscape classifications. Each classification represented a different hypothesis regarding how intermixed landscapes affect the distribution of individuals (see Fig. S1). Classifications included forested vs. non-forested land cover (FOREST), level of development as indicated by housing density (DEV), and the Wildland-Urban Interface (WUI) land-use classification. These hypotheses were mutually exclusive, and therefore did not appear in models together. While currently limited to the western half of CT, black bear range has been expanding south following an initial recolonization in the northern part of the state (CT DEEP, unpublished data). Therefore, we considered the effect of a trend in densities according to latitude (Y), both alone and in addition to each of the land cover hypotheses.

We created the FOREST classification by reclassifying 30 m NLCD 2010 (Fry *et al.*, 2011) land cover data. All forest classes, forested wetlands, and emergent wetland classes were combined into a single ‘forest’ class, and all other categories comprised ‘non-forested’ land cover. We used Wildland-Urban Interface data to derive our DEV classification. We aggregated census blocks into rural (< 6 houses/km²), exurban (6 – 49 houses/km²), suburban (50 – 750 houses/km²), and urban (> 750 houses/km²) areas. These bins are used by WUI to define subcategories of land-use, and correspond with previous land-use definitions (U.S. Census

Bureau, 2000; Theobald, 2001). We also created the WUI classification from Wildland-Urban Interface data, aggregating census blocks classified as vegetated, intermix, interface, and developed land-use. Intermixed areas have $> 50\%$ forest cover and $6 - 750$ houses/km², thus including both exurban and suburban areas. We used the *maptools* (Bivand & Lewin-Koh, 2014) package to add the value of each of these spatial variables as ‘habitat’ covariates of points in mask objects used to fit and estimate models of inhomogeneous density in *secr*.

We used a two-stage approach to select the appropriate detection function, and then test hypothesized relationships between bear density and landscape composition. First, we fit a set of candidate models of homogenous density, and all combinations of detection probability covariates. We considered heterogeneity in detection probability among individuals as a function of previous capture history, and among trapping locations as a function of percent forest cover within 1 km². To account for potential differences in detection between sexes, and to estimate sex ratios, all detection models were fit as hybrid mixture models with sex as an individual covariate (using the “hcov” argument of the “secr.fit” function). We refer to these candidate sets as detection models, which were identical for all study areas (see Table S2.). We then evaluated the addition of variable density to the top ranked detection model in each study area. We considered the same candidate set of density hypotheses which included our classifications of FOREST, DEV, WUI, and a north-south trend (Y) (Table 2.1).

We evaluated model support in an information theoretic framework using Akaike’s Information Criterion adjusted for small sample size (AICc; Akaike, 1974; Burnham & Anderson, 2002). AICc weights were used to indicate relative model support and evaluate hypothesized relationships. We applied this approach to identify the best model of bear densities in each study area and across the Combined study area, as well as for males and females

separately within the Combined study area. Sex ratios were determined using the mixing proportion of males and females estimated from the top ranked model in each study area.

Differences in sex ratios were evaluated using a likelihood ratio test between the top model, and an identical model in which the mixing proportion was fixed. We used this approach to examine whether sex ratios differed from 50:50 in each study area, and whether sex ratios differed between study areas.

We used the top ranked model from each study area to estimate black bear densities and abundance in that study area using the “region.N” function in *secr*, which integrates estimated densities across a defined region. We used the top ranked model from the Combined study area to identify the extent of black bear range, to map the distribution of bear densities across western CT, and estimate bear abundance within that range. To produce a density map, we evaluated the top ranked model across the corresponding habitat mask bounded by Connecticut’s northern, western, and southern borders as well as the Connecticut River. We defined the southern extent of bear range in the state by the latitude at which estimated bear density declined to zero.

RESULTS

We collected 814 hair samples in 2013 and 1226 hair samples in 2014, of which 935 were genetically determined to be black bear. We successfully obtained individual genotypes from 734 samples. Our set of seven microsatellite loci provided sufficient power to distinguish unique individuals ($P_{ID} = 5.2 \times 10^{-10}$, $P_{IDsibs} = 1.5 \times 10^{-4}$). Micro-Checker did not indicate evidence of deviation from Hardy-Weinberg equilibrium due to null alleles or genotyping error at any loci. We found 11 instances of putative parent-offspring pairs detected at the same location within a sampling occasion. These detections included 17 genetic individuals which we functionally treated as 6 independent individuals.

We detected 235 unique individuals and determined sex of 198 bears (93 male, 105 female). We did not detect the same individual on multiple sampling grids within a year, but detected 3 individuals (1F, 2 M) on different sampling grids between years. On the North grid 48 of 49 sites produced bear hair, corresponding to 117 individuals. On the East grid, 62 individuals were detected at 37 out of 48 sites. On the Barkhamsted grid, 47 individuals were detected and at 22 out of 25 sites in 2014. Only 10 individuals were detected at 11 of the 50 South grid sites. This prevented reliable estimates of abundance or density within the South study area. For comparison between disparate landscape contexts, we report abundance and density estimates from North and East study areas, and include data from the South and Barkhamsted grids in our analyses for the Combined study area.

On North study area, we found a trap-happy behavioral response among individuals, with g_0 increasing and sigma decreasing following first encounter ($\omega_i = 0.999$). Using this detection function, a model of homogenous bear density had more support ($\omega_i = 0.903$) than any model including variable bear density (Table 2.1). Estimated bear density for this sampling area was $0.11 \pm 8.5 \times 10^{-3}$ individuals/km², resulting in estimated population sizes across the 10km buffered North study area of 86.4 ± 1.94 in 2013 and 102.2 ± 1.94 in 2014. Estimated sex ratio was 70:30 female to male ($pmix = 0.69 \pm 0.04$), and differed significantly from a 50:50 ratio ($\chi^2 = 9.95$, $df = 1$, $P = 0.001$).

On East study area, detection probability was a function of percent forest cover ($\omega_i = 0.955$), with increasing g_0 and decreasing sigma with increasing forest cover. Both the DEV and FOREST hypotheses received AICc support greater than 0.10 (Table 2.1). We therefore used model averaged parameter values to estimate bear densities in East study area. Estimated bear density in areas of forest cover in East study area was $0.24 \pm 4.5 \times 10^{-2}$ individuals/km² and

approached zero in non-forest. Estimated population sizes across this study area were 180.1 ± 29.9 in 2013 and 165.2 ± 29.9 in 2014. Estimated sex ratio was 60:40 female to male ($pmix = 0.60 \pm 0.09$). This sex ratio in East study area differed from the estimated sex ratio in North study area ($\chi^2 = 96.45$, $df = 1$, $P < 0.001$).

Within the Combined study area, the percent forest cover detection function was the most supported detection model ($\omega_i = 0.999$). Both the DEV and DEV+Y hypotheses received AICc support greater than 0.10 (Table 2.1). Using model averaged parameters, the highest estimated densities of bear evaluated at the mean latitude in the Combined study area were in places of exurban housing density ($0.18 \pm 2.0 \times 10^{-2}$ individuals/km²). Estimated density in rural areas was $0.12 \pm 1.9 \times 10^{-2}$ individuals/km². Suburban areas had an estimated density of $0.02 \pm 3.8 \times 10^{-2}$ bears/km², and estimated bear density in urban areas was effectively zero (Table 2.2). Estimated population sizes across the Combined study area were 411.0 ± 29.7 in 2013 and 415.6 ± 29.7 in 2014. Estimated sex ratio was 66:34 female to male ($pmix = 0.66 \pm 0.05$), which was significantly different from 50:50 ($\chi^2 = 9.95$, $df = 1$, $P = 0.001$). Extrapolation of this top ranked model across western CT indicated bear densities were zero at the southern extent of our sampling area, and the population is effectively bounded by high density development along the Connecticut River (Fig. 2.2). Estimated bear abundance in western CT was 427.3 ± 29.7 .

After identifying housing density as the most supported landscape element corresponding to variations in bear density, we fit a *post hoc* model of bear density as a function of continuous housing density and a latitudinal trend to data from the Combined study area. This model included a squared housing density predictor, to accommodate the potentially quadratic relationship indicated by the results of our DEV model and used the top ranked detection function from the Combined study area. Because bear densities in suburban and urban density

housing areas were zero, we truncated housing density data at 50 houses/km² to quantify a relationship over the range of housing densities at which bears persisted. Maximum estimated bear density occurred at 13.2 houses /km² (95% CI = 7.5 – 18.2 houses/km²; Fig. 2.3).

Male and female data were too sparse to test models of variable density for each sex within North and East study areas. We proceeded with sex specific model fitting for the Combined study area. Females exhibited a trap-happy behavioral response ($\omega_i = 0.970$; Table 2.1), whereas detection probability of males was a function of percent forest cover surrounding hair corrals ($\omega_i = 0.997$; Table 2.1). For both sexes, we found two competing models of density, as both the DEV and DEV + Y hypotheses received greater than 0.10 of available AICc support. The order of support was reversed between sexes. DEV + Y was the most supported model of female density ($\omega_i = 0.687$) followed by DEV ($\omega_i = 0.235$), whereas among males DEV received greater support ($\omega_i = 0.622$) than DEV + Y ($\omega_i = 0.285$; Table 2.1).

Model averaged estimates of female bear densities evaluated at the mean latitude of the Combined study area were equal in exurban (0.100 ± 0.026 females/km²), and rural areas (0.095 ± 0.038 ; Table 2.2). Estimated male bear densities were higher in exurban (0.058 ± 0.022 males/km²), relative to rural areas (0.037 ± 0.018 males/km²). Estimates of male and female densities in both suburban and urban housing density areas (>50 houses/km²) were effectively 0 (Table 2.2).

DISCUSSION

Our results indicate that black bears exhibit a positive numerical response in exurban areas, thus suggesting a positive synanthropic relationship with this development pattern. We found strong evidence supporting the hypothesis that housing density, rather than forest cover, is the primary determinant of black bear density in intermixed ecosystems. Despite some similarity in

their categorization of our study area, we found a large gap in model support between the DEV and WUI hypotheses in all study areas (Table 2.1), and thus our hypothesis that the distinction between intermixed and interfaced development predicting bear density was not supported. We found that densities in exurban areas (6 – 49 houses/km²) were elevated relative to rural and undeveloped areas (< 6 houses/km²), with peak bear density occurring at 7.5 - 18.2 houses/km² (Fig. 2.3). These relationships predict expanding black bear populations recolonizing exurban areas, but a lack of persistence among more intense development.

Elevated black bear densities may constitute second order - home ranges within the population range (Johnson, 1980) – habitat selection for exurban areas. Bears densities may be elevated in this context because increased food availability can reduce intraspecific competition and increase fecundity (Powell, 1987; Moyer *et al.*, 2007; Mitchell & Powell, 2007; Hostetler *et al.*, 2009). Although we found no evidence of movements between grids within sampling periods, despite small distances between grids (Max = 16.5 km), we attribute this result to intentionally sampling during summer, when individuals occupy well-defined home ranges (DEEP unpublished data). However, particularly within East study area, housing densities in Connecticut change over a spatial scale within the extent of daily and summer movements (Powell, 1987; Dobey *et al.*, 2005). Finally, bears may move among grids during fall foraging movements to track seasonal mast production (Beeman & Pelton, 1980), and 3 individuals were detected on different grids in different years. Given the scale of variation in land-use patterns in Connecticut relative to black bear movement capabilities, we assume all areas were available to be used by the black bear population.

Black bears share many of the same behavioral traits as common synanthropes (Bateman and Fleming 2012), and our findings contribute to a growing body of research that human

development provides some benefit to ecologically flexible species. Large-bodied carnivores are likely able to evaluate landscapes at large spatial scales (Lidicker Jr, 1999), and movement capabilities enable these species to traverse hostile matrices (Gehrig & Swihart, 2003). However association with humans by large, obligate carnivores is often restricted to rural landscapes (Bateman & Fleming, 2012). As omnivores with high learning capacity and behavioral plasticity (Gilbert, 1989; Mazur & Seher, 2008), black bears can exploit novel resources (e.g.; garbage, bird feeders, etc.) in human-modified landscapes. While bears do not recognize the sharp delineations used to test hypotheses, our results reflect a difference in rates of black bear occurrence in rural, exurban, and suburban areas.

Differences between the DEV and WUI landscape classifications illustrate important thresholds determining bear densities in intermixed landscapes. The lack of support for the Wildland-Urban Interface model was surprising, as we expected both the intensity and arrangement of development relative to forest cover to be important. The primary difference between the two classifications was the intermixed WUI category (see Fig. S1), which include exurban and suburban areas with at least 50% forest cover (Radeloff *et al.*, 2005). In the Combined study area, a high portion of both exurban (94.2%) and suburban (72.36%) areas were intermixed. Greater support for DEV relative to WUI suggests that bear densities in areas with >50% forest cover differ when housing densities are above and below 50 houses/km².

In East study area, correlation between exurban areas and high forest cover was likely responsible for the model selection uncertainty between FOREST and DEV hypotheses. The majority of exurban census blocks (74.9%) had >75% forest cover. In contrast, while a high portion of suburban blocks were intermixed, only 38.4% were at least 75% forested. Therefore, non-forested areas in the East study area contained primarily suburban and urban housing

densities. Thus, East study area models indicating high bear densities in forested areas were indistinguishable from models indicating high bear densities in exurban areas. Models from the Combined study area contained areas of suburban with high forest and exurban with non-forest, and indicate that the DEV hypothesis is the best explanation of bear density

Our post-hoc model of bear density quantified the non-linear relationship between bear density and housing density and identified a development threshold to black bear synanthropy. Bear densities declined above 18.2 houses/km², falling to zero as housing density reached 35 – 50 km⁻² (Fig. 2.3). Although bears are regularly reported in intensely developed areas, our results suggest that populations are unlikely to persist in expanses of suburban housing. Bears using urban-wildland interfaces exhibit avoidance of highly developed areas, shift to nocturnal behavior (Beckmann & Berger, 2003a; Lyons, 2005) and reduce use of urban areas when natural foods are more available (Baruch-Mordo *et al.*, 2014). Our results help resolve positive and negative response to development in the literature by showing elevated bear densities in exurban areas, tolerance of suburban housing densities in certain landscape contexts, and evidence as to when development may preclude occurrence of bears and people.

Density is not necessarily an indicator of habitat quality (Van Horne, 1983), and black bears experience both positive and negative demographic responses to development (Beckmann & Berger, 2003a; Beckmann & Lackey, 2008; Hostetler *et al.*, 2009). Urban fringes support persistent male biased sex ratios, and skewed age distributions towards younger individuals (Beckmann & Berger, 2003b; Johnson *et al.*, 2015), and we found sex ratios become more male biased with increasing housing density (Fig. 2.2). In Connecticut, both housing density and increased male dispersal from core areas during range expansion (Swenson *et al.*, 1998; Sato *et al.*, 2011) likely contribute to these patterns. A population structure more skewed toward young

males can negatively impact population growth, as females drive reproduction (Powell *et al.*, 1996; Clark & Eastridge, 2006), and males can be a significant mortality source for juvenile bears (LeCount, 1987). Sex ratios, and reproductive rates should be monitored by managers to fully anticipate population level response of black bears to exurban development.

Wildlife use of developed areas often leads to conflict between wildlife and humans (Kretser *et al.*, 2009; Evans *et al.*, 2014), and spatially explicit density estimates can be used to anticipate the future distribution of recolonizing populations. Our estimates of density at northern latitudes in CT (0.26 bears/km²) were similar to other black bear populations, such as upstate New York (0.2/km²; Gardner *et al.*, 2010), New Hampshire (0.15 – 0.25; Coster *et al.*, 2011), and Florida (0.12 – 0.14; Dobey *et al.*, 2005), indicating the population in northern Connecticut is near equilibrium. Our top ranked Combined study area model included a North-South density trend and we used the latitude at which estimated bear densities reached zero to define the current southern extent of recolonization (Fig. 2.2). This trend suggests that bear density may increase within central and southern latitudes in Connecticut, places that already receive many conflict reports.

IMPLICATIONS

Our results illustrate the fine line between beneficial and detrimental land-use patterns for recovering carnivore populations. Large carnivore abundances in North America and Europe have increased despite concurrent increases in human density (Linnell *et al.*, 2001; Chapron *et al.*, 2014). Our finding that bear densities were elevated in exurban, relative to rural areas suggests that as exurban development proliferates, high density bear populations may be expected to co-occur with people. Managers should anticipate increases in human-black bear conflict associated with exurban development (Evans *et al.*, 2014). Our results also indicate that

development above 50 houses/km² may create areas that bears traverse but do not persist within (Long *et al.*, 2010). Where black bear and human populations are simultaneously expanding, there is concern that increased development will reduce available habitat for bears (Bettigole *et al.*, 2014). Land-use planning considering conservation of carnivores should account for the likelihood of transitions beyond these thresholds, so that population growth and stability are not overestimated.

SPATIAL AND LANDSCAPE GENETICS

INTRODUCTION

As both intermixed ecosystems and carnivore populations expand across Europe and North America, carnivore populations are increasingly interacting with development (Chapron *et al.* 2014; Linnell *et al.* 2001). Recently, shifting land-use patterns towards diffuse, low-density exurban development (Brown *et al.* 2005) has changed the nature of these interactions. These land-use patterns are at times associated with loss of biodiversity and exotic species invasions (Hansen *et al.* 2005; Bar-Massada *et al.* 2014; Blair 2004), yet also provide habitat to human adapters, and synanthropic species (Johnston 2001; McKinney 2006). However, positive association of wildlife with development may mask changes to ecologically and evolutionarily important dynamics within populations occupying exurban landscapes (Van Horne 1983; Remeš 2000). It is therefore critical to the conservation and management of carnivores to understand how populations associated with development are maintained, predict detrimental genetic consequences, and identify the potential for ecological traps.

Historically, human land use has detrimentally affected wildlife populations by reducing and fragmenting habitat (Saunders *et al.* 1991; Fischer & Lindenmayer 2007; Didham *et al.* 2007), and large carnivores are particularly susceptible to these effects due to their low population densities, large spatial requirements, and long generation times (Noss *et al.* 1996). Despite high mobility and dispersal potential, many large carnivores naturally exhibit significant spatial genetic structure (Geffen *et al.* 2004; Rueness *et al.* 2003; Sacks *et al.* 2004). Both intrinsic and extrinsic factors contribute to this spatial organization. Many species exhibit male-biased dispersal and female natal philopatry (Waser & Jones 1983), creating genetic patterns of isolation by distance by which more distant individuals are less closely related (Wright 1943). In

addition, geographic, habitat, and anthropogenic barriers may restrict the movement of dispersing individuals (McRae *et al.* 2005; Riley *et al.* 2006; Millions & Swanson 2007).

While some carnivores cohabitate among development, at times reaching higher densities in developed areas (Harris 1981; Riley *et al.* 1998; Fedriani *et al.* 2001; Evans *et al.* In Review), the characteristics of these landscapes may alter dispersal and migration, which produce patterns of spatial genetic structure. Instead of removing habitat, exurban landscapes integrate low and medium density housing within natural landcover (Clark *et al.* 2009; Stewart *et al.* 2007; Rasker & Hansen 2000), presenting animals inhabiting these landscapes with resources and mortality sources that differ from binary urban-wildland systems. Roads are often of particular importance, functioning as barriers to movement and connectivity (Riley *et al.* 2006; Roever *et al.* 2010; Epps *et al.* 2005). Even if roads do not directly limit carnivore movement, they can be a source of additional mortality (Bateman & Fleming 2012), which may be biased towards individuals that move greater distances, such as males and dispersing juveniles (Baker *et al.* 2007). Thus, the outcome of a high prevalence of roads may be to functionally limit dispersal and/or shift demographic population structure. These potentially detrimental effects are of particular concern in exurban landscapes as this development pattern imbeds high densities of roads within natural landcover (Clark *et al.* 2009).

Spatial genetic patterns can indicate potentially detrimental effects of inhabiting intermixed ecosystems. The American black bear (*Ursus americanus*) is a prominent species occupying these landscapes. In addition to extensive use of development, elevated densities in exurban relative to rural areas have recently been documented (Baruch-Mordo *et al.* 2014; Johnson *et al.* 2015; Evans *et al.* In Review). However, intermixed ecosystems could alter the spatial genetic structure of bear populations in unpredictable ways, and the evolutionary

consequences of exurban synanthropy are unknown. Black bears typically exhibit female philopatry - clusters of closely related females resulting from male-biased dispersal (Rogers & Allen 1987; Schwartz & Franzmann 1992) – a behavior important in the avoidance of inbreeding (Moyer *et al.* 2006; Costello *et al.* 2008). The degree to which features of development in intermixed ecosystem disrupt dispersal is also important to the genetic health of populations (Dixon *et al.* 2006; Hostetler *et al.* 2009; Beckmann & Lackey 2008).

Spatial genetic patterns can also provide insight into the ecological processes contributing to patterns of cohabitation with development. Elevated densities may be maintained by an enrichment of anthropogenic resources leading to increased overlap of unrelated individuals, or reduced home range size (Horner & Powell 1990; Atwood & Weeks Jr. 2003; Mitchell & Powell 2007; Vanak *et al.* 2013). With an increase in overlap of ranges of unrelated individuals, patterns of isolation by distance are expected to be less pronounced. Additionally, relative rates of movement between more rural and more developed areas indicate whether subpopulations are sustained by immigration or recruitment. Even if densities are high, anthropogenic mortality may offset benefits provided by intermixed ecosystems, creating the potential for population sinks maintained by immigration (Beckmann & Lackey 2008). Alternatively, if resources provided by exurban development outweigh anthropogenic mortality, synanthropic subpopulations may be self-sustaining, and even serve as important sources of immigrants to the surrounding population (Hellgren *et al.* 2005; Sweanor *et al.* 2000; Weaver *et al.* 1996). Identifying asymmetrical immigration or emigration of individuals in intermixed ecosystems can identify source-sink dynamics, and is therefore an important component of predicting population persistence and vulnerability.

Our goal was to distinguish among mechanisms explaining patterns of black bear density across a gradient of development, and model the effect of intermixed landscapes on gene flow. Our first objective was to test the hypothesis that overlap of unrelated individuals, rather than reduced home range sizes, increases bear densities in exurban areas, by quantifying differences in patterns of isolation by distance. We predicted that female philopatry would be disrupted in a more developed landscape, due to the prevalence of housing and roads. We used a landscape genetics approach (Manel *et al.* 2003) – testing for correlation between genetic similarity of individuals and characteristics of the intervening landscape - to distinguishing among anthropogenic and natural features that limit or facilitate dispersal. Finally, we tested the hypothesis that populations in more developed areas are sustained by immigration by estimating the rate and directionality of black bear migration between land-use contexts.

METHODS

Sample Collection

We used non-invasive barbed wire hair corrals (Woods *et al.* 1999) to collect hair samples from black bears in northwest Connecticut (Evans *et al.* In Review). Corrals were created by two strands of barbed wire strung around trees at 30 cm and 45 cm off of the ground, creating an enclosure of ~5x5 m. We applied non-nutritional scent lures to log piles at the center of corrals, and to rags hung above corrals to attract bears to sampling locations. We distributed hair corrals across four study areas, which encompassed the majority of reproductive black bear range in western CT, as approximated by the Connecticut Department of Energy and Environmental Protection (DEEP). Grid cells were 2.5 km² to accommodate 3 – 4 sampling locations within an area the size of a female summer home range (approx. 30 km², CT DEEP unpublished data). North grid consisted of 49 sampling locations in the northwest corner of CT,

and covered 271 km². Landcover on and around North grid was primarily forested, with an average housing density of 6.8 km⁻². East grid had 48 sampling locations across 215 km² in and around suburban and exurban areas of CT, with an average housing density of 83.6 km⁻². South grid was 220 km² containing 50 sampling sites. This grid was located in an attempt to span the southern extent of reproductive bear range. Average housing density within the South grid was 23.2 km⁻². Barkhamsted grid was likewise located at the CT bear population's northern bound. This grid consisted of only 25 sites over 95 km². While similarly forested as North grid, Barkhamsted grid contained higher housing densities (mean = 37.3 km⁻²).

We collected bear hair weekly over two sampling years during June – August 2013 and 2014. We operated corrals on Barkhamsted grid only during 2014, and in this year only the 25 northernmost corrals on South grid. During weekly visits, we collected and stored all samples in individually labeled coin envelopes, considering all hairs deposited on a single barb as a single sample. New scent lure was applied at each visit. We used four different scents over the course of each sampling season (available upon request) to increase trap novelty and minimize trap avoidance following previous detection. Within a sampling occasion, we applied the same lure at all sites.

Genetic Methods

We extracted DNA from hair follicles using the InstaGene Matrix (Bio-Rad Laboratories, Hercules, CA) following the protocol of Eggert *et al.* (2005). We extracted DNA from a blood sample collected by CT DEEP from a bear handled by CT DEEP during den visits for use as a positive control using a DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) with the manufacturer's instructions. We confirmed species identity by amplifying a fragment of the mitochondrial cytochrome b gene using the primers HCarn200 (Bidlack *et al.* 2007) and

CanidL1 (Paxinos *et al.* 1997), followed by digestion with DDeII and APO I. We eliminated all samples not producing a positive bear genotype.

We identified unique individuals from all bear samples using seven polymorphic microsatellite loci (G1A, G10B, G10L, G10P, G1D, G10M, G1C; (Paetkau & Strobeck 1998; Paetkau & Strobeck 1994). We used the redesigned primer pairs of Kristensen *et al.* (2011) to increase genotyping efficiency using low concentration and potentially degraded DNA from hair samples. A 96-well PCR plate contained 94 samples, a negative control, and our positive control sample. All PCR reactions were performed in a UV-sterilized hood, following the multiplex genotyping protocol of Puckett *et al.* (2014). Products were separated in an ABI 3730 DNA Analyzer at the University of Missouri DNA Core Facility (Columbia, MO). We scored the size of fluorescently labeled DNA fragments against Genescan LIZ 600 size standards to generate genotype data using GENEMARKER v1.97 (Soft Genetics, State College, PA).

We estimated $P_{(ID)sibs}$ (Waits *et al.* 2001) in GENALEX (Peakall & Smouse 2006) to confirm sufficient power of our marker set to identify unique individuals. We used the multi-tubes approach (Taberlet *et al.* 1996) to produce consensus genotypes, amplifying and scoring up to five replicates of a sample to confirm heterozygous genotypes in at least two replicates, and homozygous genotypes three times. Samples were required to have consensus genotypes for at least 6 loci to be considered in further analyses. We then amplified DNA from unique individuals at an additional 6 loci (G10J, G10O, P2H03, Mu05, Mu23, Mu59) to provide greater resolution of genetic relationships. We used DROUPOUT (McKelvey & Schwartz 2005) to identify potential genotyping errors leading to misidentification of individuals. We re-genotyped individuals that differed at 3 or fewer loci, and allowed a mismatch at 1 locus following this step

when determining recaptures. We determined the sex of unique individuals by amplification of the Amelogenin gene (Carmichael *et al.* 2005).

We removed samples that produced a consensus genotype at fewer than 11 loci from further analysis. We used GENEPOP (Raymond & Rousset 1995) to test for deviation from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) among all loci within each study area. We used a Bonferroni correction of $\alpha < 0.004$ for HWE and $\alpha < 0.00091$ for LD. We checked for the presence of null alleles in each study area using MICROCHECKER (Van Oosterhout *et al.* 2004). We estimated expected (H_E) and observed (H_O) heterozygosity, allelic richness (A_R), and inbreeding (F_{IS}) within study areas, and calculated pairwise F_{ST} (Weir & Cockerham 1984) between each study area in FSTAT v2.9.3 (Goudet 1995).

Population Genetic Structure

We analyzed black bear population structure across northwest CT using the Bayesian assignment software STRUCTURE v2.3 (Pritchard *et al.* 2000). This program assigned individuals to one of K genetic groups by minimizing deviation from HWE within groups. To minimize the potential for dependent offspring to bias STRUCTURE analyses, we used ML-RELATE (Kalinowski *et al.* 2006) to identify putative parent-offspring pairs detected at the same sampling location on the same occasion, and removed one individual. We applied the admixture model with correlated allele frequencies option, and performed 10 repetitions at values of K between 1 and 8 with a 10^6 iteration burn-in followed by 10^6 sampling iterations. Replicates were averaged in CLUMPP v1.2 (Jakobssen and Rosenberg 2007). We evaluated support for the number of genetic groups present using the log probability of the data, $\text{LnP}(K)$ and the second-order derivative rate of change in log probability, DeltaK (Evanno *et al.* 2005) using STRUCTURE HARVESTER (Earl &

vonHoldt 2012). We interpreted individual assignments at successive numbers of genetic groups in the context of geographic patterns.

Recent Migration Rates

We initially estimated the rate and directionality of dispersal of individuals between study areas using the program BAYESASS 3.0 (Wilson & Rannala 2003), which applies a Bayesian Markov chain Monte Carlo (MCMC) analysis to estimate rates of recent immigration among putative populations from multilocus genotypes. We performed 10^6 iterations following a burn-in of 10^6 iterations, sampling the posterior distribution every 1000 iterations for all individuals, males, and females. To ensure consistent and accurate estimates, we varied initial seed numbers over the course of 10 independent MCMC runs and examined chain convergence by visually assessing of trace files, and comparing posterior mean parameter estimates for concordance. We adjusted the magnitude of proposed changes to parameter values for allele frequency, migration rate, and inbreeding coefficients at each iteration that lead to acceptance rates between 30% and 50% of total iterations. This rate ensured adequate exploration of mixing space, while sufficiently discriminating among estimated values (Rannala 2007). We assessed asymmetry in migration rates among genetic populations for males, females, and all individuals by comparing 95% confidence intervals around the posterior mean estimate.

Due to the potential for BAYESASS to produce spurious results when migration rates are high, or genetic differentiation is low (Faubet *et al.* 2007), we also quantified migration rates using BIMr 1.0 (Faubet & Gaggiotti 2008). The F model implemented in BIMr allows for departure from HWE within populations, improving estimation of allele frequencies and producing accurate estimates of migration rates between weakly differentiated ($F_{ST} > 0.01$) populations (Faubet & Gaggiotti 2008). BIMr assumes migration occurs prior to sampling,

therefore we use genetic groups indicated by STRUCTURE as putative populations (Andreasen *et al.* 2012). We ran 20 replicates, each of which included 20 pilot runs of 1000 iterations to optimize mixing parameters, followed by a 10^6 iteration burn-in. We then collected 10,000 samples from each replicate using a thinning interval of 1000 iterations, and examined parameter estimates from the run with the lowest Bayesian assignment deviance (D_{assign}). In addition to confidence interval overlap, we assessed migration asymmetry by measuring the proportion of post-burn in iterations at which a given migration rate estimate was greater than its reciprocal (Fordyce *et al.* 2011).

Spatial Genetic Structure

To identify the extent of spatial genetic structure and kin clustering within each study area, we analyzed spatial autocorrelation in the program GenAlEx v6.5 (Peakall & Smouse 2006). This approach used pairwise geographic and pairwise squared individual genetic distance matrices to calculate an autocorrelation coefficient (r) for each of a series of predetermined distance classes. We estimated the geographic locations of individuals using the centroid of the minimum convex polygon formed by all hair corral locations visited by each individual. We used random permutation, and bootstrap analyses to identify distance classes exhibiting significant, positive autocorrelation. The observed value of r was compared to a confidence interval formed by the calculation of r following 999 random permutations of genotypes among individual locations. We inferred significance if the observed r fell outside this confidence interval. Positive autocorrelation was inferred if the distribution of 10,000 bootstrap estimates of r did not include 0.

We also compared the average distance between female parent-offspring pairs. We used ML-RELATE to first identify pairs of individuals for which parent-offspring was the most likely

relationship. We then specified half-sibling as an alternative hypothesized relationship, and used a simulation based test to evaluate the probability of this alternative relationship. We used 999 random permutations and accepted pairs having a p-value below 0.10 as parent-offspring. We then used a t-test to compare mean dispersal distance between parent-offspring pairs on North and East grids.

Landscape Genetics

We applied a landscape genetics approach to identify features influencing the spatial genetic structure of female black bears in human-dominated landscapes. We limited this analysis to females because they are the philopatric sex. We used multiple regression on distance matrices (MRM) in a causal modeling framework (Cushman *et al.* 2006) to discriminate amongst natural and anthropogenic drivers of spatial genetic structure. We created resistance surfaces in ArcMAP 10.1 (ESRI, Redlands, CA) from reclassified land use and land cover data to represent landscape hypotheses. All rasters representing hypothesized resistance surfaces were composed of 100 x 100m cells. We considered the potential effects of forest cover, roads, housing density, and combinations of these features on black bear dispersal.

To represent the effect of resistance due to forest cover, we created rasters from the Wildland Urban Interface (Radeloff *et al.* 2005) polygons, which provides percent forest cover per census block. Percent forest cover was naturally bounded between 0.0 and 1.0, which we reclassified to a 0 to 100 integer scale. Areas of 0% forest cover were reclassified to a value of 1. Housing density was also rasterized using census block polygons from WUI data. We scaled housing density using four Gaussian distributions at which a peak raster value of 100 occurred at 0, 50, and 100 houses/km². This allowed us to evaluate the possibility that the effect of development on bear dispersal movements was most pronounced at intermediate housing

densities. The Gaussian distribution with peak value at zero was preferable to a linear relationship between landscape resistance and housing density, because we were able to represent housing densities above a threshold of approximately 250 houses/km² as affecting bear movement equally. This representation of housing density aligns with our previous research defining the relationship between bear density and development in CT (Evans *et al.* In Review), and knowledge of black bear space use around urban areas (Merkle *et al.* 2011; Johnson *et al.* 2015; Beckmann & Berger 2003).

To represent hypotheses regarding the effects of roads on bear dispersal, we created rasters from TIGER (U.S. Census Bureau) line shapefiles. We considered the effects of primary and secondary roads (TIGER Feature Classes S1100 & S1200) as potential barriers to black bear movements. Primary roads represent divided interstate and state highways accessible by interchange, and secondary roads are major arteries in the U.S., state, or county highway systems. Restricting our analysis to these types of roads eliminated local neighborhood, rural, and city streets as potential barriers. These smaller road types are highly correlated with housing density and are unlikely barriers in and of themselves, as they occur frequently within bear home ranges in CT (DEEP unpublished data). We considered three possible effects of primary and secondary roads on bear movement: both road types having equal effect on bear movement (Rd_100_100), primary roads more strongly affecting movement (Rd_100_50), and only primary roads affecting movement (Rd_100_1; Table 3.1). For each of these hypotheses, primary roads were assigned a resistance value of 100, and secondary roads were alternatively assigned resistances of 100, 50, and 1. The surrounding matrix within the study area had a resistance value of 1 in each case.

For each landscape hypothesis, we considered each feature of interest as potentially facilitating and inhibiting movement. Therefore, in addition to the hypothesized effects of each feature described above, we also created rasters representing the inverse of each of these relationships. This was done to accommodate the possibility that landscape features seen as inhospitable by bears might either be avoided, or moved through rapidly. We denote the inverse of restriction, conductance, for each hypothesis with a “C” (Table 3.1). We considered the additive effects of all possible combinations of each landscape hypothesis by combining resistance rasters, creating a total of 146 resistance surfaces.

We used the program CIRCUITSCAPE v4.0 (Shah & McRae 2008) to calculate the total resistance distances between all pairs of females across each of the 146 resistance surfaces, creating pairwise resistance distance matrices. Individual locations were represented by centroids of minimum convex polygons encompassing all detection locations. We chose to use landscape resistance, as opposed to least-cost path analysis, because landscape resistance accounts for spatial heterogeneity in landscape composition, the possibility of multiple paths between two locations, and represents landscapes as continuous surfaces (McRae & Beier 2007). It is more likely that bears experience landscapes as gradients of varying quality and movement resistance, rather than patch-matrix mosaics (Manning *et al.* 2004, McGarigal & Cushman 2005).

To evaluate the effect of landscape structure on bear dispersal movements, we compared the strength of relationships between pairwise Rousset’s a_r (Rousset 2000) and resistance distance using multiple regression on distance matrices (Lichstein 2007). MRM models were implemented in Program R (R Core Team) using the *ecodist* package. We used 1000 random permutations of the genetic distance matrix to assess significance of correlations. We constructed models of genetic distance as a function of each resistance distance matrix created

representing all 146 landscape hypotheses. To account for the effect of geographic distance in determining genetic distance, we constructed an identical set of landscape resistance models including the effect of pairwise geographic distances as well. Finally, we included a model of genetic distance as a function of geographic distance alone. This modeling procedure was performed for females detected on North and East grid, as these areas represented the most disparate development contexts, and had multiple years of data. For a landscape factor to be considered to have affected bear dispersal, we required a priori that the variable appear in a model(s) with a significant F-test ($p < 0.05$), an R^2 value greater than the geographic distance model, and a significant ($p < 0.05$) beta parameter on the variable of interest.

RESULTS

We collected 814 hair samples in 2013 and 1226 hair samples in 2014, 935 of which were genetically determined to be black bear. Of these black bear samples, we successfully obtained individual genotypes for 734 samples. Our initial set of seven microsatellite loci provided sufficient power to distinguish unique individuals ($P_{ID} = 5.2 \times 10^{-10}$, $P_{IDsibs} = 1.5 \times 10^{-4}$).

We identified 235 unique individuals, and determined the sex of 198 bears (93 male, 105 female). Detections varied among sampling grids. 48 of 49 sites produced bear hair on North grid, corresponding to 117 individuals (56 female, 47 male). On the East grid, detections at 37 out of 48 sites corresponded to 62 individuals (29 female, 21 male). On Barkhamsted grid, 47 individuals (16 female, 20 males) were detected and bear hair was collected at 22 out of 25 sites in 2014. Only 11 of the 50 South grid sites produced bear samples corresponding to 10 individuals (3 females, 6 males, 1 unknown). Due to the limited sample size, we do not report results for South grid. We did not detect the same individual on multiple sampling grids within a

year. We detected one female and one male on East and Barkhamsted grids and one male on East and North grids between years.

Two loci differed significantly from HWE in all study areas (P2H03, and G10L), and we eliminated these from further analysis. Additionally, two loci differed significantly from HWE within the North grid only (Mu59; $p = 0.001$, and G10P; $p = 0.003$). As this pattern of nonrandom assortment appeared in only one study area, we retained these loci for all analyses. Estimates of F_{IS} were 0.029 ($p = 0.041$) on North grid, 0.006 ($p = 0.473$) on East grid, and -0.009 ($p = 0.391$) on Barkhamsted grid. Genetic diversity was similar among study areas (North; $A_R = 6.85$, $H_E = 0.683$, East; $A_R = 5.54$, $H_E = 0.6614$, Barkhamsted; $A_R = 5.48$, $H_E = 0.654$). No loci used in analyses exhibited significant linkage disequilibrium. MICROCHECKER did not indicate evidence of deviation from Hardy-Weinberg equilibrium due to null alleles or genotyping error at any loci.

Population Structure

We found 11 instances of putative parent-offspring pairs detected at the same location within a sampling occasion, and eliminated 6 individuals prior to analysis in STRUCTURE. STRUCTURE results indicated support for $K = 2$ and $K=5$ genetic clusters within the population of black bears in western Connecticut (Fig 1). At $K = 2$, individuals from East grid grouped as one genetic cluster, and individuals from Barkhamsted grid grouped as a second cluster. Individuals captured on North grid grouped with either the East or Barkhamsted clusters, with little admixture (Fig 1). At $K = 3$, each grid was comprised primarily of individuals from clusters predominantly unique to those areas (Fig. 3.1). This pattern persisted to $K=5$, with single individuals assigning to additional groups. All three study areas were significantly differentiated from each other at the Bonferroni corrected $\alpha < 0.0167$, and exhibited sufficient genetic

differentiation to estimate recent migration rates (F_{ST} : 0.011 – 0.018). Peak support for the number of unique clusters of females occurred at $K = 4$. Each grid grouped as a unique genetic cluster, with single individuals assigned to a fourth group (Fig. 3.1). We therefore used three populations in analyses of recent migration rates among all individuals and females. Among males, $K = 2$ was most supported at which unique clusters corresponded to Barkhamsted and East grid, and individuals captured on North grid grouped with either cluster. Among males, we estimated rates of migration between these two clusters.

Recent Migration Rates

Migration rates among all individuals estimated by BAYESASS were asymmetric from Barkhamsted to East, indicated by non-overlapping 95% CIs (0.14 – 0.31, and 0.02 – 0.11). Barkhamsted grid was the largest source of migrants to North, (0.17, 95% CI = 0.07 – 0.23) and East grids (0.24, 95% CI = 0.14 – 0.31). Estimate migration between North and South grids were also asymmetric (0.08 – 0.26, and 0.00 – 0.06). Male migration rates were asymmetrical from Barkhamsted to East (95% CI = 0.19 – 0.32, and 0.00 – 0.14). The directionality of movement for females was opposite of males. Female migration was asymmetrical from East to Barkhamsted (95% CI = 0.23 – 0.36, and 0.00 – 0.07) and from East to North (95% CI = 0.26 – 0.34, and 0.00 – 0.09). Per generation, 0.95 (95% CI = 0.88 – 1.0) of individuals detected on the East grid originated in East grid. Additionally, East grid was the greatest source of female migrants to both Barkhamsted (0.30, 95% CI = 0.23 – 0.36) and North (0.30, 95% CI = 0.26 – 0.34) study areas.

Estimates of migration rates were consistent among the 10 BIMr runs with the lowest Bayesian deviance (coefficient of variation for rates of all individuals: 0.005 – 0.028, females: 0.009 – 0.026, males: 0.007 – 0.024). Migration rates between grids among all individuals

ranged from 0.14 (North to South) to 0.46 (Barkhamsted to East). Confidence intervals surrounding estimates were large, and there were no pairwise population migration rates among all individuals, males, or females with non-overlapping 95% CIs. Probability that migration from Barkhamsted to East grid was asymmetrical among all individuals was 0.88, and 0.83 from North to South (Fig. 3.2a). Estimated migration rates for females ranged from 0.18 (North to East), to 0.50 (East to Barkhamsted). Probability of migration asymmetry was 0.90 from East to North, 0.83 from North to Barkhamsted, and 0.98 from East to Barkhamsted (Fig. 3.2c). Among males, estimated migration rates were 0.12 (East to Barkhamsted) and 0.51 (Barkhamsted to East). Probability of asymmetry was 0.91 (Fig. 3.2b).

Spatial Genetic Structure

Spatial autocorrelation of genetic relatedness revealed differences in the extent of kin clustering between study areas and sexes. Black bears within North grid exhibited greater spatial genetic structure, compared to the East grid. Within North grid, there was a significant relationship between geographic distance and genetic distance ($R^2 = 0.15$, $p = 0.001$) among females. We found significant, positive correlation among North grid females with detection centers within 4km (Fig. 3). Females detected within the East grid did not exhibit significant spatial autocorrelation of relatedness ($R^2 = 0.00196$, $p = 0.32$), and none of the tested distance classes had significant positive autocorrelation (Fig. 3.3). Males exhibited little spatial genetic structure in either study area. Spatial autocorrelation among males was weak and not significantly different from a random distribution of individuals on both North ($R^2 = 0.0098$, $p = 0.12$) and East ($R^2 = 0.01$, $p = 0.34$) study areas. Males on North and East grids exhibited significant positive correlation only within the closest (1km) distance class considered (Fig 3.) We identified 41 female parent-offspring pairs on North grid, and 21 on East grid. Mean

distance was higher ($p = 0.07$) on East grid (7557 m, $\sigma^2 = 4450$ m) than North grid (6556 m, $\sigma^2 = 4393$ m).

Landscape Genetics

On North grid, eight MRM models of genetic distance (Rousset's a_r) as a function of geographic distance that met criteria for identifying important drivers of spatial genetic structure (significant F-tests, greater correlation with genetic distance than geographic distance alone, and significant beta parameters). The three most strongly correlated models included an effect of roads providing resistance to black bear dispersal, and five models included an effect of housing density conducting dispersal (Table 3.2). Finally, two significant models included the effect of forest cover resisting dispersal.

On East grid, four MRM models met our significance criteria, and exhibited higher correlation between landscape features and female spatial genetic structure than North grid models. All four models included an effect of housing density. Housing density conducting dispersal (HDC) was included in three models with the strongest correlation between hypothesized landscape resistance and genetic distance. Equal conductance across primary and secondary roads (Rd100_100C) appeared in one model meeting significance criteria, in conjunction with HDC. A model of housing density resisting dispersal (HDR100) met significance criteria. The sign of the correlation coefficient for this model was negative, indicating decreasing genetic distance as resistance distance increased, which is equivalent to a positive correlation between genetic distance and an HDC hypothesis.

DISCUSSION

The spatial genetic structure of carnivore populations provides insight into how land use affects gene flow, and ultimately evolutionary dynamics. We found female philopatry to be disrupted by increasing development among American black bear, and anthropogenic landscape features associated with increased dispersal movements. Greater distances between parent-offspring pairs in a more developed context indicates the observed lack of structure resulted from greater interspersions of unrelated individuals. While increased housing density was associated with increased gene flow in both rural and developed contexts, roads were associated with restricted gene flow only within the more rural study area. Finally, asymmetrical female emigration from the more developed study area indicated that exurban areas exhibiting high bear densities act as a source of migrants. Together, these findings suggest that spatial genetic structure is disrupted by development, and that elevated densities in exurban areas may be maintained by increased home range overlap, and local recruitment.

Differences in spatial genetic structure between female bears on East and North grid support the hypothesis that high bear densities in exurban areas are facilitated by greater home range overlap, rather than reduced home range sizes. The lack of a relationship between geographic and genetic distances among female bears in East grid (Fig. 3.3) indicates greater interspersions of unrelated individuals, relative to North grid, where the expected pattern of isolation by distance, indicating female philopatry, was observed. These patterns suggest elevated densities in exurban areas are facilitated by greater home range overlap among unrelated individuals, which could arise from larger dispersal movements, and/or larger home range sizes. Philopatry often evolves when habitat within the natal range is sufficiently productive, such that the potential fitness benefits of finding alternative habitat are outweighed

by dispersal costs (Waser & Jones 1983; Rogers 1987). Additionally, differences in average female parent-offspring distances indicate longer dispersal on East grid. Therefore, spatial overlap of unrelated individuals may reflect greater spatial requirements to meet resource needs among individuals occupying developed landscapes.

The finding that black bears separated by areas of high housing density were closely related presents an additional potential mechanism leading to the breakdown of kin clustering. Significant correlation between matrices of genetic distance and resistance distance constructed with high housing density facilitating gene flow in both North and East grids (Table 3.2), indicates that increasing housing density increased contemporary gene flow. On North grid, we found a lack of distinction among housing density conductance hypotheses (HDC50, HDC100, HDC). Only one census block within North grid had housing density > 100 houses/km², and an area of only 13.7km² had greater than 50 houses/km². Therefore, resistance surfaces with maximum conductance at intermediate values were essentially equivalent to the surface with highest conductance at maximum housing density.

It is important to consider that spatial patterns of relatedness are determined by dispersal, the outcome of which is affected by both movement decisions and resulting fitness consequences. Therefore our results suggest a tendency for young individuals to move quickly through development during dispersal – a response that may diminish with age as bears become more adept at navigating intermixed ecosystems (Johnson *et al.* 2015). More rapid movement through development during dispersal may explain greater interspersions of unrelated bears in East grid, relative to North grid, due to the greater prevalence of high housing densities. This finding also suggests that bears may perceive medium to high intensity development as hostile or inhospitable habitat - despite the propensity of bears to live in and around developed areas. This

is consistent with recent research demonstrating a preference for natural resources when available by bears utilizing urban areas (Johnson *et al.* 2015; Baruch-Mordo *et al.* 2014; Merkle *et al.* 2013).

In intermixed ecosystems, roads can be the biggest contributor to fragmentation (Hawbaker *et al.* 2006), yet our results indicate that even large roads do not present a dispersal barrier in this context. On East grid, road barrier hypotheses were not supported (Table 3.2), suggesting roads did not pose a significant enough fitness cost or behavioral barrier to dispersal. In contrast, we found that bear dispersal in more rural areas was limited by the presence of major roadways. The significant positive correlation of both road limiting models (Rd100_50 and Rd100_100; Table 3.2) in North grid suggests that major roads restrict dispersal movements, either by acting as barriers, demarcate home range boundaries (Coster & Kovach 2012), or elevating mortality. Black bears avoid high traffic volume roads (Carter *et al.* 2010; Brody & Pelton 1989; Reynolds-Hogland & Mitchell 2007), often in response to increased vulnerability to hunting. As there is currently no bear hunting in CT, North grid individuals may avoid roads due to alternative costs, such as vehicle collisions (Beckmann & Lackey 2008). The contrasting effects of roads on dispersal suggest that in more developed contexts black bears either acclimate to roads - possibly learning favorable crossing behavior from adults (Lewis *et al.* 2011; Mazur & Seher 2008) - or experience high enough dispersal pressure that roads cannot be avoided. Mammalian dispersal is often density dependent (Matthysen 2005), with populations at lower densities exhibiting less dispersal (Busch *et al.* 2009). Increased dispersal pressure as a result of elevated bear density within exurban areas is consistent with reduced spatial genetic structure on East grid, and could also contribute to greater gene flow across roads. Given the high density of roads associated with suburban and exurban land use, it is likely both factors are at play.

Elevated densities in developed areas may be supported by immigration of males, as indicated by the high rates of immigration from Barkhamsted grid to East grid, and low male recruitment rates within East grid (Fig. 3.3a) estimated by both BAYESASS and BIMr. These movement patterns align with previous findings of sex ratios significantly more skewed towards males in developed areas (Beckmann & Lackey 2008; Evans *et al.* In Review). Among the population as a whole, recent emigration was highest from the northernmost (Barkhamsted) study area (Fig. 3.2). Recolonization of Connecticut by black bear is considered to have originated from Massachusetts, and the pattern of estimated migration rates supports the theory of a North to South recolonization process.

Estimates of recent migration rates did not support the hypothesis that exurban sub-populations are potential population sinks. Both methods indicated that East grid had the highest rates of female recruitment relative to immigration (BAYESASS: 0.95, 95% CI = 0.88 – 1.00, BIMr: 0.5, 95% CI = 0.16 – 0.79). Both analyses indicated high, asymmetrical rates of emigration of females from East grid (Fig 2), indicating the most developed portion of black bear range acts as a source of females for the rest of the western Connecticut population. In addition to population viability, asymmetrical gene flow can affect evolutionary processes such as local adaptation (Lenormand 2002). Among black bears inhabiting intermixed ecosystems, if anthropogenic foraging is in part socially learned (Mazur & Seher 2008; Breck *et al.* 2009) or heritable, the emigration of individuals from developed contexts could accelerate propagation of nuisance behaviors throughout bear range. Additionally, a learned or selected propensity to cross roads among ‘urban-adapted’ bears could facilitate asymmetrical movement of females from developed to less developed areas.

Genetic clustering assignment of individuals indicated distinct genetic clusters on East and Barkhamsted grids, with individuals detected on North grid grouping with either cluster, or a third unique cluster when three clusters were assumed (Fig. 3.1). This pattern could be produced by the primarily unidirectional immigration of females from East to North grid. It also suggests that the movement of males from Barkhamsted to East may be ineffective. Females are more important in determining reproductive and population growth rates. Alternatively, the predominance of East grid individuals grouping with a single cluster could reflect a founder effect following establishment by individuals originating from either North or Barkhamsted. Given the finding that, the low rate of female movement otherwise (max = 0.03), and in conjunction with previous estimates of density in these areas (Evans *et al.* In Review), we consider East to North migration the more plausible scenario.

IMPLICATIONS

Both in North America and globally, the division between society and nature is decreasingly clear. Human populations continue to expand while large carnivores increasingly persist in intermixed ecosystems, outside of protected areas (Linnell *et al.* 2001; Chapron *et al.* 2014). Our findings suggest that intermixed land use did not fragment a recolonizing population of black bears, yet still altered the spatial ecology of bears in important ways. Bears in a more developed context dispersed greater distances, including crossing major roadways, and provided a substantial source of female immigrants to surrounding parts of the population. Source-sink dynamics are important to consider among wildlife populations in intermixed ecosystems, due to the volatility of land-use patterns, and potential anthropogenic mortality sources. Under continued development, exurban areas are often converted to suburban, with an associated loss of natural landcover (Clark *et al.* 2009; Bettigole *et al.* 2014). If exurban areas act as sources,

such loss of habitat could have cascading consequences for the surrounding population. These dynamics will affect how bears recolonize human-dominated landscapes as populations expand, and could have important implications for the management of conflict with humans.

STEP SELECTION MOVEMENT MODELS

INTRODUCTION

The global proliferation of developed landscapes has the potential to significantly impact the ecology and persistence of wildlife populations (DeStefano and DeGraaf, 2003; Shochat et al., 2006; Gehrt et al., 2010). Wildlife often change behaviors in response to development (Tuomainen and Candolin, 2011). While some species avoid developed areas, others are able to exploit novel resources associated with human activity (Bateman and Fleming, 2012; Merkle et al., 2013), leading to the emergence of ‘urban adapted’ wildlife (McKinney, 2006). However, positive numerical association with development does not necessarily equate to long-term fitness benefits, or increased population viability (Van Horne, 1983; Remeš, 2000). Development often modifies environmental conditions faster than evolutionary processes, creating the potential for maladaptive responses and ecological traps (Robertson et al., 2013). For instance, attractive habitat patches with negative impact on demographic rates can produce population sinks (Delibes et al., 2001; Naves et al., 2003). The expansion of novel, human-modified landscapes has created the need to integrate behavior into wildlife conservation and management (Anthony and Blumstein, 2000).

Movement behaviors and space use in and around human development can reflect trade-offs between the perceived benefits of exploiting anthropogenic resources, and risks associated with human activity (Frid and Dill, 2002; Baruch-Mordo et al., 2014; Johnson et al., 2015). The risk-disturbance hypothesis (Frid and Dill, 2002) postulates that animals will exhibit behaviors similar to predator avoidance in the face of development. Animals can incur fitness costs when individuals overestimate the risk associated with human disturbances. Avoidance behaviors around anthropogenic landscape features among urban associated species have indicated

perceived risk of utilizing urban environments, even among urban adapters (Riley et al., 2003; Kertson et al., 2011; Gehrt et al., 2011). Understanding how animals perceive and manage trade-offs within developed landscapes is important to understanding the cumulative effects of development on wildlife ecology. Elucidating the behavioral response of wildlife to development has become particularly important for some large carnivores, which increasingly interact with human development as populations have recovered (Linnell et al., 2001; Chapron and Lopez-Bao, 2014), and can be a polarizing source of conflict with people (Treves et al., 2006).

Among American black bears (*Ursus americanus*), use of anthropogenic resources can be temporally dynamic, with selection for developed areas occurring during times when natural food sources are more 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). Despite these patterns, conflicts related to American black bears (*Ursus americanus*) utilizing developed areas have increased over time (Hristienko and McDonald Jr, 2007). The risk allocation hypothesis (Lima and Bednekoff, 1999) states that animals will decrease anti-predator effort in response to increasingly frequent high-risk situations (i.e. habituation) (Rodriguez-Prieto et al., 2009). Some research suggests that there are ‘nuisance’ bears, which have modified foraging behavior to target anthropogenic food sources (Messmer, 2009), and there is evidence that such foraging behavior is learned (Mazur and Seher, 2008; Hopkins, 2013). Identifying patterns and predictors of variation in selection for anthropogenic resources can help wildlife managers to effectively reduce human-carnivore conflicts in developed landscapes.

Changes in preferences as a function of changes in habitat or resource availability (i.e., functional responses) can provide insight into the cumulative effects of human development

(Matthiopoulos et al., 2011). Throughout the United States, the proliferation of exurban land use (Brown et al., 2005) has created intermixed ecosystems (Zipperer et al., 2000) completely integrating anthropogenic features and natural land cover. These landscapes may elicit different behavioral responses than urban-wildland dichotomies, as the arrangement of resources and food items influences the space use of wildlife, especially solitary species exhibiting well-defined home-ranges, such as black bears (Horner and Powell, 1990; Mitchell and Powell, 2007). In Connecticut, portions of a recolonizing population of black bears now occupy home ranges with ubiquitous distribution of houses, while other bears are able to occupy almost exclusively forested home ranges. We recently demonstrated that black bear occur at highest densities within exurban development (Evans et al., In Review). This context provides an opportunity to identifying trends in behavioral response to development, and quantify the amount of phenotypic variation within a bear population occupying an intermixed ecosystem. These patterns are of particular importance to management and conservation of wildlife in developed contexts (Groffman et al., 2006).

Here, we evaluate the risk-disturbance hypothesis by measuring changes in black bear selection for anthropogenic resources across intensities of development. Our first objective was to quantify the functional response in avoidance/selection among bears occupying a range of housing densities. If bears have habituated to development, we would expect bears to increase selection for anthropogenic features with increasing development. Alternatively, the risk-disturbance hypothesis predicts consistent selection or a negative functional response to increasing development. Our second objective was to compare selection among seasons and between females differing in reproductive status. Bears overcome winter food shortages by intense late summer feeding, or hyperphagia, followed by hibernation (Nelson et al., 1983;

Powell et al., 1997). We expected bears to exhibit low avoidance/high selection for anthropogenic features during hyperphagia, because the increased cost of forgoing foraging opportunities. We predicted that females with cubs would exhibit strong avoidance of anthropogenic features relative to females without cubs, due to the high cost associated with losing a dependent offspring in risky conditions (Dahle and Swenson, 2003; Rode et al., 2006). Finally, we sought to identify patterns of behavioral plasticity, by evaluating changes in selection for anthropogenic features during different times of day. We provide insight into how individual black bears respond to features of development (e.g., houses vs. highways), the degree of variation within a recolonizing population, and discuss how these patterns may affect population growth and viability.

METHODS

Data Collection

The global proliferation of developed landscapes has the potential to significantly impact the ecology and persistence of wildlife populations (DeStefano and DeGraaf, 2003; Shochat et al., 2006; Gehrt et al., 2010). Wildlife often change behaviors in response to development (Tuomainen and Candolin, 2011). While some species avoid developed areas, others are able to exploit novel resources associated with human activity (Bateman and Fleming, 2012; Merkle et al., 2013), leading to the emergence of ‘urban adapted’ wildlife (McKinney, 2006). However, positive numerical association with development does not necessarily equate to long-term fitness benefits, or increased population viability (Van Horne, 1983; Remeš, 2000). Development often modifies environmental conditions faster than evolutionary processes, creating the potential for maladaptive responses and ecological traps (Robertson et al., 2013). For instance, attractive habitat patches with negative impact on demographic rates can produce population sinks

(Delibes et al., 2001; Naves et al., 2003). The expansion of novel, human-modified landscapes has created the need to integrate behavior into wildlife conservation and management (Anthony and Blumstein, 2000).

Movement behaviors and space use in and around human development can reflect trade-offs between the perceived benefits of exploiting anthropogenic resources, and risks associated with human activity (Frid and Dill, 2002; Baruch-Mordo et al., 2014; Johnson et al., 2015). The risk-disturbance hypothesis (Frid and Dill, 2002) postulates that animals will exhibit behaviors similar to predator avoidance in the face of development. Animals can incur fitness costs when individuals overestimate the risk associated with human disturbances. Avoidance behaviors around anthropogenic landscape features among urban associated species have indicated perceived risk of utilizing urban environments, even among urban adapters (Riley et al., 2003; Kertson et al., 2011; Gehrt et al., 2011). Understanding how animals perceive and manage trade-offs within developed landscapes is important to understanding the cumulative effects of development on wildlife ecology. Elucidating the behavioral response of wildlife to development has become particularly important for some large carnivores, which increasingly interact with human development as populations have recovered (Linnell et al., 2001; Chapron and Lopez-Bao, 2014), and can be a polarizing source of conflict with people (Treves et al., 2006).

Among American black bears (*Ursus americanus*), use of anthropogenic resources can be temporally dynamic, with selection for developed areas occurring during times when natural food sources are more 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). Despite these patterns, conflicts related to American black bears (*Ursus americanus*) utilizing

developed areas have increased over time (Hristienko and McDonald Jr, 2007). The risk allocation hypothesis (Lima and Bednekoff, 1999) states that animals will decrease anti-predator effort in response to increasingly frequent high-risk situations (i.e. habituation) (Rodriguez-Prieto et al., 2009). Some research suggests that there are ‘nuisance’ bears, which have modified foraging behavior to target anthropogenic food sources (Messmer, 2009), and there is evidence that such foraging behavior is learned (Mazur and Seher, 2008; Hopkins, 2013). Identifying patterns and predictors of variation in selection for anthropogenic resources can help wildlife managers to effectively reduce human-carnivore conflicts in developed landscapes.

Changes in preferences as a function of changes in habitat or resource availability (i.e., functional responses) can provide insight into the cumulative effects of human development (Matthiopoulos et al., 2011). Throughout the United States, the proliferation of exurban land use (Brown et al., 2005) has created intermixed ecosystems (Zipperer et al., 2000) completely integrating anthropogenic features and natural land cover. These landscapes may elicit different behavioral responses than urban-wildland dichotomies, as the arrangement of resources and food items influences the space use of wildlife, especially solitary species exhibiting well-defined home-ranges, such as black bears (Horner and Powell, 1990; Mitchell and Powell, 2007). In Connecticut, portions of a recolonizing population of black bears now occupy home ranges with ubiquitous distribution of houses, while other bears are able to occupy almost exclusively forested home ranges. We recently demonstrated that black bear occur at highest densities within exurban development (Evans et al., In Review). This context provides an opportunity to identifying trends in behavioral response to development, and quantify the amount of phenotypic variation within a bear population occupying an intermixed ecosystem. These patterns are of

particular importance to management and conservation of wildlife in developed contexts (Groffman et al., 2006).

Here, we evaluate the risk-disturbance hypothesis by measuring changes in black bear selection for anthropogenic resources across intensities of development. Our first objective was to quantify the functional response in avoidance/selection among bears occupying a range of housing densities. If bears have habituated to development, we would expect bears to increase selection for anthropogenic features with increasing development. Alternatively, the risk-disturbance hypothesis predicts consistent selection or a negative functional response to increasing development. Our second objective was to compare selection among seasons and between females differing in reproductive status. Bears overcome winter food shortages by intense late summer feeding, or hyperphagia, followed by hibernation (Nelson et al., 1983; Powell et al., 1997). We expected bears to exhibit low avoidance/high selection for anthropogenic features during hyperphagia, because the increased cost of forgoing foraging opportunities. We predicted that females with cubs would exhibit strong avoidance of anthropogenic features relative to females without cubs, due to the high cost associated with losing a dependent offspring in risky conditions (Dahle and Swenson, 2003; Rode et al., 2006). Finally, we sought to identify patterns of behavioral plasticity, by evaluating changes in selection for anthropogenic features during different times of day. We provide insight into how individual black bears respond to features of development (e.g., houses vs. highways), the degree of variation within a recolonizing population, and discuss how these patterns may affect population growth and viability.

Individual Step Selection

We used step-selection functions (SSF) to measured selection and avoidance of features associated with human development as a bear moves within its home range (Rhodes et al., 2005; Coulon et al., 2008). Steps were the unit of analysis and defined as the straight line between successive GPS relocations. We compared habitat characteristics between each observed step and 20 simulated steps, and therefore the analysis was a used-availability design (Manly et al., 2002; Lele et al., 2013) evaluating 4th order selection (Johnson, 1980). We generated simulated steps at each location using the Geospatial Modeling Environment, drawing 20 random length values from a bear's empirical step length distribution. To account for potential directional persistence in movements, each length was paired with a random turn angle from the empirical turn angle distribution for that bear. The log odds of an observed step were estimated as a function of landscape covariates using conditional logistic regression in the *mclogit* package (Elff, 2013) for program R.

For each bear, we fit a base SSF model consisting of natural landscape features. We derived topographic variables from 30m National Elevation Dataset digital elevation models (available from the USGS), extracting elevation (m) at step endpoints, and length weighted mean slope along step lengths. We reclassified 30m National Land Cover Dataset data (Fry et al., 2011) to delineate 6 land cover classes relevant to black bear habitat selection: forest, grassland, shrub, wetland, low intensity development, and high intensity development. Distance from streams was measured at 30m resolution using Connecticut and Massachusetts hydrography line files. We tested predictor variables for correlation ($r > 0.6$), and univariate significance ($p < 0.05$), and included all independent, significant covariates in the base model for each bear.

We suggest that bears move through development by responding to two types of anthropogenic variables. The housing hypothesis is that bears predominately respond to buildings, where people and human food resources are located. The highway hypothesis is that bears predominately respond to roads with high traffic volumes that are the primary source of mortality for bears. For each bear, we expressed these *a priori* hypotheses as the base model with the addition of relevant anthropogenic variables (Roever et al., 2010; Thurfjell et al., 2014). The housing hypothesis model included a categorical variable (Dev) with three levels indicating whether a step ended in high intensity development (High), low intensity residential areas (Res), or undeveloped land cover (Non), and a 30m resolution measure of distance (km) to local and neighborhood roads (RDist). Development categories were represented by NLCD developed landcover classes. We combined medium and high intensity development into the High development category. These classes consist of areas with > 50% impervious surface cover, and typically represent commercial areas or urban housing densities. We combined the developed open space, and low intensity development classes into the Res development category. These classes have < 50% impervious surface cover, and typically include single family housing units and parks. We used local and neighborhood roads as a proximate measure of housing and human food sources (garbage cans, bird feeders, etc.), since accurate GIS layers of house locations were not available. Highway hypothesis models included an indicator variable as to whether a step crossed a highway (HXing), and a 30m resolution measure of distance (km) to highways (HDist). Distances to roads and highways were calculated 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.

To test the hypothesis that bear movements change according to human activity throughout a day, we also included candidate models that contained interaction terms between anthropogenic variables and time of day. We used traffic data collected by Connecticut Department of Transportation to identify daily periods of increased traffic volume. Based on these peaks, we created a categorical Time variable including day (09:00 to 15:00), night (18:00 to 07:00), and rush hour (07:00 to 08:59 and 15:01 to 17:59) periods. In total, our candidate model set for each bear included Base, Highway, Highway*Time, Housing, and Housing*Time models. We fit this candidate model set to separate summer, hyperphagia, and pre-denning datasets for each bear-year, to account for seasonal and annual changes in movement.

We used Akaike's Information Criterion corrected for small sample size (AICc; Akaike, 1974; Burnham and Anderson, 2002) to evaluate model support. We considered models with $\Delta\text{AICc} > 2$ as unsupported, and multiple models with $\Delta\text{AICc} < 2$ as competing (Burnham and Anderson, 2002). In cases in which a single model was supported, we refer to this model as top-ranked. To describe variation in model importance among individuals, we report the proportions of datasets for which different types were either top-ranked, or supported. We report these proportions aggregating the two housing models (e.g. Housing & Housing*Time) and the two highway models, to indicate which landscape features were important to bears. We also report proportions aggregating models with a time interaction and those without.

Changes in Selection Among Bears

We extracted a single set of beta coefficients, standard error estimates, and z-scores for anthropogenic variables from supported models for each bear. We ordered levels of Time such that interaction coefficients represented the change in selection from day to night (Night), and day to rush hour (Rush). In models including time interactions, the coefficient on an

anthropogenic variable, then, measured selection during the day period. Therefore, when the most supported model included a time interaction (e.g. Housing*Time), in addition to the parameters from that model, we took parameter estimates of the anthropogenic variable from a model without time (e.g. Housing). These represented average response to the variable across time of day, and allowed comparison with datasets for which an interaction with time was not supported. We refer to z-scores from interaction terms with time as Δz for rush hour and night, respectively. We applied the same protocol if competing models represented the same anthropogenic hypothesis (e.g. Highway and Highway*Time). If competing models were of different types, we extracted model-averaged parameter estimates and standard errors based on AIC weights.

We used linear mixed effects models including only an intercept, and individual random effects to determine whether the population mean beta coefficients for Res, RDist, HDist, and HXing were positive or negative. We assessed whether intercepts differed from zero using a Wald chi-square test. We used standardized z-scores as the response variable in analyses testing for differences in selection for anthropogenic variables by home range housing density (HRHD), reproductive status, and season. To assess differences in selection for development according to season and reproductive status, we fit linear mixed models comparing z-scores with fixed effects on season, reproductive status, and an interaction term, and a random effects on season nested within individuals, and reproductive status nested within individuals. Season and reproductive status were repeated measures categorical variables with summer vs. hyperphagia vs. pre-denning, and yes vs. no levels. To test for changes in selection as a function of land use context, we fit linear mixed models of z-scores as a function of log HRHD, including a random intercept for individuals. We used the natural logarithm of home range housing density, as this

transformation produced a normal distribution and a linear relationship with z-scores. We additionally considered models with fixed effects interactions between log HRDH and season, and log HRHD and reproductive status, with random effects on season or reproductive status nested within individual, respectively.

To test the effects of home range housing density, reproductive status, and season on changes in movement behavior with time, we performed a similar modeling procedure using Δz -scores for rush hour and night as response variables. These estimated the change in selection from day to rush hour, and day to night for all anthropogenic variables. We tested differences in changes in movement behavior with time of day among seasons and by reproductive status. We fit linear mixed models with fixed effects on season, reproductive status, and an interaction term, and a random effects on season and reproductive status nested within individual. To evaluate whether diel changes varied with development, we fit linear mixed models including fixed effects on log HRHD, an interaction with season, and a random effect on season within individuals. We also fit models including fixed effects on log HRHD, an interaction with reproductive status, and a random effect on reproductive status within individuals. We report the slope of these relationships by season and reproductive status only in cases in which a significant interaction was found. Otherwise, overall slope is reported.

All mixed models were fit using the “lmer” function in the *lme4* package (Bates et al. 2015) for program R, maximizing the full log-likelihood. We examined model residuals for departures from normality by inspecting Q-Q plots and plots of residuals against predicted values. We tested statistical significance of fixed effects with Wald chi-square tests, using a cutoff of $p > 0.10$ (i.e. $> 90\%$ of bootstrapped estimates were non-zero) to infer significant difference from zero. We assessed Type III sum of squares for interaction terms, and in the

absence of a significant interaction, Type II sum of squares on main effects. Significance tests were implemented using the “Anova” function in the *car* package in program R.

RESULTS

We collected 68 bear-years of GPS locations from a total of 35 female bears. Home range housing density ranged from 0.51 to 214.43 houses/km². HRHD did not differ between bears with cubs and those without cubs ($t_{\text{paired}} = 0.86$, $df = 14$ $p = 0.43$), or among seasons ($F_{2,43} = 0.86$, $p = 0.423$). Step lengths were longest during hyperphagia ($t = 2.39$, $p < 0.001$) and when bears were without cubs ($t_{\text{paired}} = 5.95$, $df = 14$ $p = 0.02$). A total of 83 ear-tagged bears were reported in nuisance incidents to DEEP from 2012 to 2015, 35 of which were collared females included in this study. Mean selection for low intensity residential areas was higher ($t_{\text{one-tailed}} = 2.58$, $df = 32$, $p = 0.006$) among bears with > 5 complaints ($\bar{\beta} = 0.50$, $\sigma = 0.53$), than for bears with < 5 complaints ($\bar{\beta} = -1.22$, $\sigma = 1.12$). Mean avoidance of local roads was higher ($t_{\text{one-tailed}} = 3.44$, $df = 30$, $p = 0.002$) among bears with > 5 complaints ($\bar{\beta} = 1.78 \times 10^{-3}$, $\sigma = 1.45 \times 10^{-3}$), than for bears with < 5 complaints ($\bar{\beta} = 7.5 \times 10^{-4}$, $\sigma = 1.11 \times 10^{-3}$). We found no significant differences in avoidance of highways, or selection for crossing highways.

Model Selection

We fit candidate SSF models to 66 summer, 61 hyperphagia, and 57 pre-denning GPS datasets from 67 bear-years. 28 bear-years were from females with cubs, 27 from females without cubs, and 12 from females of unknown reproductive status. Highway models were top-ranked for the majority of bears during summer (66.67%), and hyperphagia (74.19%). During pre-denning, housing and highway models were top ranked for an equal proportion of bears (38.6%), and 21.1% had support for both hypotheses. Top-ranked models included an

interaction with time of day for the majority of bears during summer (60.6%), and hyperphagia (54.1%). During pre-denning, the largest portion of bears had top-ranked models without an interaction with time (47.4%), and for 35.1% of bears, models with and without an interaction with time competed. Top-ranked models changed seasonally for 43 bears. Of these, 62.8% of bears switched from highway to housing hypotheses as top-ranked over the course of the year, whereas 18.6% changed from housing to highway. The remaining 18.6% changed back and forth.

Housing

Bears for which housing models were supported ($\Delta AICc < 2$), avoided local roads, indicated by a mean selection coefficient ($\bar{\beta}_{(RDist)} = 9.0 \times 10^{-4}$, $\sigma = 1.22 \times 10^{-3}$) greater than zero (Fig. 4.1). Black bear avoidance of local roads increased with HRHD ($\chi^2 = 7.06$, $p = 0.008$; Fig. 4.2). Bears increasingly avoided local roads as HRHD increased during summer ($\beta_{(HRHD)} = 0.566$), hyperphagia ($\beta_{(HRHD)} = 0.453$), and pre-denning ($\beta_{(HRHD)} = 0.317$), although the relationship was not statistically significant during pre-denning ($p = 0.125$; Table 4.3). Bears selected against steps ending in low intensity residential areas, indicated by a mean selection coefficient less than zero ($\bar{\beta}_{(LowDev)} = -0.67$, $\sigma = 0.76$; Fig. 4.1). Black bear selection for low intensity residential areas did not vary significantly with HRHD ($\chi^2 = 7.06$, $p = 0.008$; Fig. 4.2).

The interaction of reproductive status and season was significant in predicting selection for steps ending in low intensity residential areas ($\chi^2 = 2.50$, $p = 0.08$). Bears without cubs increased selection between summer and hyperphagia, whereas bears without cubs decreased selection between these seasons (Fig. 4.3). Reproductive status was important in predicting avoidance of local roads ($\chi^2 = 10.67$, $p = 0.001$), and bears with cubs avoided roads more than

bears without cubs (Fig. 4.3). In addition, bears avoided local roads less during hyperphagia than during summer or pre-denning ($\chi^2 = 2.88, p = 0.093$)

Bears for which top ranked models included an interaction between Time and Housing avoided local roads more at night ($\Delta\bar{z} = 0.47, \sigma = 1.83$) and during rush hour ($\Delta\bar{z} = 0.06, \sigma = 1.93$) than during the day. The elevated avoidance of local roads at night decreased as HRHD increased ($\beta_{(\text{HRHD.Night})} = -0.217, \chi^2 = 4.57, p = 0.033$). These bears selected steps ending in low intensity residential areas more at night ($\bar{\Delta}z = 0.51, \sigma = 2.32$) and less during rush hour ($\bar{\Delta}z = -0.07, \sigma = 0.93$) than during the day. Bears decreased selection for low intensity residential areas from day to night more during hyperphagia, than summer or pre-denning (Fig. 4.4).

A significant interaction between HRHD and reproductive status (Fig. 4.4), indicated that bears without cubs increased selection at night as HRHD increased ($\beta_{(\text{HRHD.NoCubs})} = 0.150$), whereas bears with cubs decreased selection from day to night as HRHD increased ($\beta_{(\text{HRHD.Cubs})} = -0.146$). A significant interaction between HRHD and seasons ($\chi^2 = 8.98, p = 0.01$) indicated that during hyperphagia and pre-denning, bears decreased selection of low intensity residential areas from day to night as HRHD increased ($\beta_{(\text{HRHD.Hyperphagia})} = -0.122, \beta_{(\text{HRHD.Pre-den})} = -0.156$), and increased selection from day to night during the summer ($\beta_{(\text{HRHD.Summer})} = 0.17$).

Highways

Bears for which highway models were supported ($\Delta\text{AICc} < 2$) neither avoided nor selected steps closer to highways, as the mean selection coefficient ($\bar{\beta}_{(\text{HDist})} = 5.91 \times 10^{-5}, \sigma = 1.18 \times 10^{-3}$) was statistically indistinguishable from zero (Fig. 4.1). Bears selected steps crossing highways, indicated by a mean selection coefficient greater than zero ($\bar{\beta}_{(\text{HXing})} = 0.47, \sigma = 1.07$; Fig. 4.1).

A significant interaction between season and HRHD (Fig. 4.2) indicated that during summer, bears increasingly avoided highways in areas of higher housing density ($\beta_{\text{HRHD.Sum}} = 0.36$), and that this avoidance response was less acute during hyperphagia ($\beta_{\text{HRHD.Hyperphagia}} = 0.10$) and pre-denning ($\beta_{\text{HRHD.Pre-den}} = 0.01$; Table 4.3). We found no differences in black bear avoidance of highways among seasons, or by reproductive status (Fig. 4.3). A significant interaction between season and reproductive status ($\chi^2 = 20.86, p < 0.001$) indicated that bears without cubs decreased selection for steps crossing highways from summer to hyperphagia, whereas bears with cubs increased selection between these seasons (Fig. 4.3).

Among bears for which top ranked models included an interaction between Time and Highways, mean selection for steps crossing highways was lower at night ($\overline{\Delta z} = -0.51, \sigma = 1.34$) and greater during rush hour ($\overline{\Delta z} = 0.324, \sigma = 0.93$) than during the day. These bears also avoided highways more during rush hour ($\overline{\Delta z} = 0.73, \sigma = 1.94$) and at night ($\overline{\Delta z} = 0.51, \sigma = 2.32$).

A significant interaction between season and reproductive status ($\chi^2 = 16.5, p < 0.001$), indicated that bears without cubs increased selection for steps crossing highways from day to rush hour during summer ($\overline{\Delta z} = 1.04, \sigma = 0.97$) and decreased selection during hyperphagia ($\overline{\Delta z} = -0.20, \sigma = 0.77$), whereas bears with cubs exhibited no change (Fig. 4.5). The interaction between season and reproductive status was also important in explaining changes in bear selection for steps crossing highways from day to night ($\chi^2 = 6.60, p < 0.04$). Bears without cubs increased selection from day to night during summer ($\overline{\Delta z} = 0.26, \sigma = 1.76$), and decreased selection during hyperphagia ($\overline{\Delta z} = -1.34, \sigma = 1.03$), whereas bears with cubs exhibited consistent reduced selection from day to night ($\overline{\Delta z} < 0$) across seasons (Fig. 4.5). A significant interaction between HRHD and reproductive status ($\chi^2 = 7.50, p = 0.006$), indicated that bears without cubs increased selection for highway crossings at night as HRHD increased

($\beta_{(\text{HRHD.Hyperphagia})} = 0.277$), whereas bears with cubs decreased selection of highway crossings at night ($\beta_{(\text{HRHD.Cubs})} = -0.188$) in areas of higher housing density.

Bears avoided steps near highways more at night ($\overline{\Delta z} = 0.51$, $\sigma = 2.32$) and during rush hour ($\overline{\Delta z} = 0.373$, $\sigma = 1.94$) than during the day. Avoidance at night differed among seasons ($\chi^2 = 16.81$, $p < 0.001$), with bears avoiding at night more during summer ($\overline{\Delta z} = 0.57$, $\sigma = 2.19$) and hyperphagia ($\overline{\Delta z} = 0.59$, $\sigma = 2.89$) than pre-denning ($\overline{\Delta z} = 0.36$, $\sigma = 1.77$; Fig. 4.6). Avoidance during rush hour differed by season and reproductive status ($\chi^2 = 5.46$, $p = 0.065$). Bears without cubs increased avoidance of highways at rush hour during summer ($\overline{\Delta z} = 0.27$, $\sigma = 1.90$) and decreased avoidance during hyperphagia ($\overline{\Delta z} = -0.03$, $\sigma = 1.87$), while bears with cubs increased avoidance from summer to hyperphagia (Fig. 4.5). A significant interaction between HRHD and season ($\chi^2 = 17.90$, $p < 0.001$) indicated that during summer, bears decreased avoidance of highways at night as HRHD increased ($\beta_{(\text{HRHD.Summer})} = -0.108$), and even more acutely during hyperphagia ($\beta_{(\text{HRHD.Hyperphagia})} = -1.06$). During pre-denning, bears change in avoidance from day to night did not vary with housing density ($\beta_{(\text{HRHD.Pre-den})} = 0.05$; Fig. 4.6).

DISCUSSION

Our results provide support for the risk-disturbance hypothesis among American black bears inhabiting developed landscapes. Black bears exhibited stronger avoidance of houses (indicated by proximity to local roads) and highways in areas of higher housing density. Additionally, bears generally increased avoidance for houses and highways when with cubs. These changes corresponded to expected patterns if development was perceived as risky habitat. We found no support for population level habituation to development, as bears did not decrease avoidance of houses and highways in more highly developed areas. Additionally, we found evidence of behavioral plasticity indicating bears alter movement behaviors in response to

perceived risk among development, changing avoidance between seasons and with time of day. These findings contribute to a growing body of literature indicating that use of development by black bears is not necessarily preferred, and potentially dynamic. Movement behavior was highly variable among individuals, indicating capacity for future changes in population-level response to development. As behavioral traits, and response to risk, affect fitness (Anthony and Blumstein, 2000), patterns of bear movement in developed landscapes may be an important determinant of population growth, and future behavioral phenotypes in these contexts.

Changes in avoidance of housing and highways as a function of HRHD, and reproductive status were consistent with the risk-disturbance hypothesis. Black bears increasingly avoided houses and highways as they occupied areas of higher housing density (Fig. 4.2), indicating that in general bears did not show habituation to development, but rather perceived these landscapes as risky. Selection for low intensity residential areas was negative overall, and did not change as a function of housing density, indicating consistent avoidance of residential areas across development contexts (Fig. 4.2). Females bears with cubs often exhibit more risk avoidant movement behaviors (Dahle and Swenson, 2003; Beckmann and Berger, 2003a; Rode et al., 2006), as overestimation of risk is especially advantageous when underestimation can result in death of offspring. Accordingly, bears with cubs were more avoidant of housing (Fig 3). Additionally, bears without cubs made significantly longer steps than those with cubs, demonstrating greater rates and/or distances of movement among un-reproductive individuals. Each of these patterns represents females with dependent offspring making less risky movements than those without cubs.

The decreases in avoidance of development during hyperphagia further indicate the perception of development as risky, and also suggest bears in developed landscapes are able to

shift behaviors in accordance with increased caloric requirements. Overall, bears decreased avoidance of housing and highways from summer to hyperphagia (Fig. 4.3), and increases in avoidance with HRHD were more acute in summer than during hyperphagia (Fig. 4.2). Animals must often choose between foraging and risk avoidance, when these behaviors cannot occur simultaneously (Fortin et al., 2004), generally overestimating, rather than underestimating risk. While overestimation results in a lost foraging opportunity, underestimation can result in death (Frid and Dill, 2002). Under historical selective regimes, risk avoidant strategies would be advantageous, producing net benefits to fitness. However, developed landscapes may represent altered selective regimes, to which historically advantageous behaviors could be maladaptive (Schlaepfer et al., 2002; Sih et al., 2004). For example, avoidance of development may be a case of overestimating risk, if use of anthropogenic resources does not result in death.

Changes in avoidance of housing and highways with time of day further indicate behavioral plasticity in response to perceived risk associated with developed landscapes. Changes in daily movement patterns to minimize risk exposure can be a sign of behavioral adaptation to human disturbance (Ditchkoff et al., 2006). Bears in areas of higher housing density exhibited lower avoidance of highways at night relative to day, especially during pre-denning (Fig. 4.6), as well as local roads. Similarly, females with cubs increased avoidance of highways during rush hour in hyperphagia (Fig. 4.5). 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 movements at night, or both. Shifts to more nocturnal behavior among black bears have been observed in other urban areas (Beckmann and Berger, 2003b), and we found greater selection of residential areas at night by bears without cubs living in more highly developed areas (Fig. 4.4). Together, our results suggest that bears in developed

areas may alter avoidance of highways corresponding to traffic patterns, and become less avoidant of housing at night. This behavioral alteration may be adaptive, indicating local selection, or simply represent phenotypic plasticity (Lowry et al., 2013).

Furthermore, the more pronounced response of bear movement to roads and highways suggest changes in avoidance of development may be in relation to traffic, more so than land cover. Highway hypothesis models were supported among more bears than housing models (Table 4.1), and relationships indicating increased avoidance with greater housing density primarily involved road related variables (Fig. 4.2). These findings indicate greater variability in response to roads, relative to more consistent avoidance of residential areas (i.e., suburban housing and open spaces). In the context of risk avoidant behavior within development, one possible explanation for this distinction is that sound is an important source of disturbance and perceived risk among wildlife. Chronic noise exposure associated with development can be a severe threat to a range of taxa, impacting foraging and predator avoidance behavior, among other behaviors (Francis and Barber, 2013). Behavior may be modified due to acute auditory disturbances (Darrow and Shivik, 2009), impeded communication, or masking of sounds (Barber et al., 2010). 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 anthropogenic foraging opportunities.

The nature of interactions between season and reproductive status on black bear step selection could potentially have important effects on population growth. Female survivorship and fecundity are the most important life history transitions determining population growth in bears (Powell et al., 1996; Clark and Eastridge, 2006). We found that females with cubs

decreased selection for residential areas from summer to hyperphagia, and similarly, increased selection for steps crossing highways (Fig. 4.3). 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. 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 could predominate in bear populations within relatively short ecological time. Similarly, maladaptive risk avoidance could rapidly decrease in frequency within bear populations inhabiting developed landscapes. Therefore, even small changes to either of these demographic rates may have cascading effects on population growth and viability.

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 is a well-recognized phenomenon, including differences in sets of correlated behavioral traits, creating ‘personalities’ (Slater, 1981; Dall, 2004). Temperament may cause individuals to distribute themselves in a non-random way, in response to disturbance, such that more risk-tolerant individuals colonize and populate more developed areas (Martin and Réale, 2008). Among black bears, individual differences in use of urban areas according to age and gender have been documented (Johnson et al., 2015), and the variability in response to development measured in this study demonstrates a range of behaviors among individuals within the study population (Fig. 4.1). This diversity of movement behaviors provides potential for the recently re-colonized Connecticut black bear population to undergo selection, resulting in future shifts in mean behaviors. 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).

IMPLICATIONS

Balance between human land use and conservation of wildlife requires understanding of levels of development at which anthropogenic disturbance has a pronounced effect on wildlife populations, and the conditions that modify this behavior. Our results suggest managers can anticipate increased black bear use of areas near housing and highways, and potentially increased anthropogenic foraging, during hyperphagia and when bears are without cubs. Our findings also indicate that bear habituation to development and human activity does not initially occur at a population level, but rather is a variable individual characteristic. We found a distribution of movement behaviors ranging from selection to avoidance, and identified problem bears that exhibited significantly higher selection for residential areas than the rest of the population. In the context of minimizing nuisance behavior in intermixed landscapes, these patterns suggest a relationship between individual avoidance and proclivity to conflict. Therefore, preventative measures reducing the proliferation of bold individuals may be effective in Connecticut, and places with recently established bear populations. For example, lethal management actions – whether hunting or targeted removal – specifically targeting individuals exhibiting bold or nuisance behavior may further reduce the possibility of shifts in mean population behavior toward habituation.

SUMMARY

I combined non-invasive genetic, global positioning system (GPS), and public report data to measure changes in interrelated facets of bear ecology in response to human land use patterns. I used spatially explicit mark recapture (SMRC) analyses to show that bear densities were associated with housing density, and elevated in exurban areas. Likewise, the spatial distribution of reports of property damage indicated that exurban development promoted conflicts between bears and people. Spatial genetic analyses demonstrated female philopatry, and kin clustering to be disrupted within more developed areas, and suggested that the prevalence of housing and roads in these landscapes are associated with this pattern. Estimates of recent migration rates identified asymmetries in the frequency of bear movement between land-use contexts, with greater emigration of females out of more developed areas, and greater immigration of males into these areas. Finally, hourly movement patterns demonstrated that bears increasingly avoided anthropogenic landscape features with increased intensity of development, and that individual behavior in response to anthropogenic landscape features was highly variable within the population. Here, I discuss implications arising from interactions among these results, and important directions for future research.

Predicting Future Black Bear Distributions

SMRC models identified the density of houses as more strongly associated with changes in black bear density in intermixed landscapes than forest cover, or degree of intermixture. SMRC analyses also quantified the relationship between human housing density and the density of black bears, indicating peak bear densities in areas between 7.5 – 18.2 houses/km². By providing an understanding of the relationship between bear density and land-use patterns in intermixed ecosystems, this analysis enabled a limited prediction of future bear distributions in

Connecticut. Density estimates at lower latitudes within the study area, and the importance of a North to South trend indicate ecological carrying capacity for bears has not yet been reached in Connecticut. Extrapolating density estimates in each development category along Connecticut's northern border (Fig. 5.1) produces a future population estimate of ~ 1164 in western Connecticut. This simple projection does not account for future landscape change, and the estimate is substantially less than abundance estimates from similar areas in northwest New Jersey (~3,000 individuals; McBride pers. comm.) and western Massachusetts (2,950 individuals, (Spencer et al., 2007). These discrepancies suggest additional capacity for further increases in density and abundance in Connecticut.

Habitat Selection

Differences in bear densities among development classes, in combination with observed distances between genetically identified parent-offspring pairs, indicate habitat selection for exurban development. Habitat selection has been defined as any process or processes by which individuals preferentially use, or occupy one of a set of available habitats (Morris, 2003). In this context, heterogeneous spatially explicit density estimates are an implicit measure of selection, given equal availability of different habitat types. Generally, available habitat constitutes those areas that could potentially be encountered by an animal (Lele et al., 2013). At a population level, available habitats can be conceptualized as areas available for home range establishment by dispersing individuals. The location of observed parent-offspring pairs can therefore be used to indicate the extent of habitat available to a population. In this study, mean parent offspring distances ($\bar{x} = 15.24$ km) were greater than the scale of variability in land use types (Fig. 5.2). Furthermore, pairs spanned study areas with relatively high frequency ($n = 57$). These patterns indicate rural, exurban, and suburban areas have been available to the sampled Connecticut black

bear population for establishment of home ranges. With increasing prevalence of SMRC analyses in wildlife research, models are being extended to incorporate other ecological processes (Royle et al., 2013a; Royle et al., 2013b). When SMRC models are fit to detection data produced by individual genotypes (Kery et al., 2010), genetic data can simultaneously be used to estimate the extent of dispersal movements, and availability of landscape scale habitats. These results illustrate that SMRC models can be used in a framework to estimate habitat selection

Tolerance of Development

The quadratic relationship between black bear density and development indicates that bears in Connecticut are currently an urban tolerant species. This characterization has been used to describe wildlife for which developed landscapes are utilized, but not preferred, where abundance is expected to be highest in areas of intermediate development (McKinney, 2006). The patterns of density found in Connecticut closely match these expectations. Further, results from landscape genetic, and step selection analyses provided additional evidence that bears inhabiting developed landscapes perceive increasingly developed areas as un-preferred or marginal habitat. Comparison of fine scale spatial genetic structure between bears occupying more developed and more rural landscapes indicated that development disrupted the spatial and social organization of black bears. While urban adapters often exhibit decreased home range size and increased clustering in higher density populations, spatial genetic analyses revealed decreased clustering in populations occupying a more developed landscape, reflecting greater home range overlap among unrelated individuals.

This spatial genetic pattern was explained, in-part, by results from landscape genetic analyses, which associated increasing housing and road densities with greater dispersal. These

results suggest a model of bear dispersal in which anthropogenic landscape features are avoided, inducing longer movements through developed areas. Step-selection analyses provided direct support for this hypothesis. Step-selection results confirmed that female bears avoided developed landcover, roads, and highways, and indicated that this avoidance increased in areas of more intense development. Not only do these results indicate a mechanism by which dispersing bears ultimately move farther away from natal ranges in developed areas, but also provide more direct evidence that many bears perceived developed landscapes, and anthropogenic landscape features, as risky. Together, these analyses provide a hierarchical explanation of how individual movement decisions at small scales may manifest during dispersal, affecting population level patterns of relatedness.

Male Biased Sex Ratios

Results from SMRC models also indicated more male-biased sex ratios among bears in more developed areas. Recent migration rate and step selection analyses suggested mechanisms by which this pattern may be generated, and maintained. Elevated male densities in the more developed study area could be supported by the net immigration of males into developed areas, and the simultaneous emigration of females out of developed areas. These asymmetries could be related to range expansion, and the propensity of males to dominate range peripheries (Swenson et al., 1998; Sato et al., 2011). However, given the high densities of females in rural and exurban areas surrounding these places, and frequent sightings of females with cubs in suburban towns, it is likely the Connecticut bear population is established in these areas. Furthermore, female emigration from the more developed study area also suggests colonization has occurred by both sexes.

The altered sex ratios found among development in Connecticut may reflect differences in risk tolerance and boldness between sexes. Step selection analyses indicated overall avoidance of development by females, and estimates of recent migration rates indicated female emigration from more developed areas. Previous studies of bear behavior have indicated that males are often more aggressive, or bolder, than females (Swenson et al. 2001; Schwartz et al. 2006). In many places, this has resulted in males being more often involved in conflicts with humans (Hristienko & McDonald 2007). In the context of risk perception, mammalian sexual selection theory predicts that in polygynous, dimorphic species males may be more risk tolerant (Sukumar 1991; Ahlering et al 2011). The expectation that male bears are more tolerant of development was supported by recent migration rates showing immigration of males into more developed areas of Connecticut. Sex specific differences in behavior and risk tolerance may be contributing to the differences in patterns of recent migration between males and females. Together, these analyses findings provide a potential mechanism by which altered sex ratios among development are generated and maintained.

Preventing Human-Bear Conflict

Predicted density distributions produced by extrapolating SMRC models can be used in conjunction with the model of relative human-bear conflict risk to further focus targeted conflict reduction strategies. By considering both land-use configurations that facilitate conflict between black bears and people, and an anticipated distribution of bear densities, managers can identify areas that may be both prone to conflict due to the configuration of landscape features, that are also likely to have high bear densities (Fig. 5.3a). Identification of at-risk areas may be further aided by considering changes in current and predicted bear abundance, in relation to landscape configuration (Fig. 5.3b). As management budgets are limited, there is an impetus to use

resources effectively. These tools can be used by managers and towns to focus preventative efforts, such as waste disposal strategies, and public education in areas with the greatest potential impact.

Furthermore, an integration of behavior can help managers to identify best practices for reducing conflict with bears. As movement behaviors among bear within development indicated avoidance of housing among the population as a whole, targeted reduction of anthropogenic food sources may be particularly effective in reducing the potential for habituation as bears extend their population range.

Future Research Directions

The relatively recent recolonization of Connecticut by black bears is important to consider in the context of evaluating responses to development. Continued range expansion, in combination with potential changes in mean population behavior may alter the patterns of density, dispersal, and conflict. In particular, decreases in avoidance of developed areas, which may be induced by habituation, social transmission, or human induced selection, would increase the propensity/tolerance of bears to occupy more developed areas. Our results demonstrate suburban areas of black bear range in Connecticut currently hold the lowest densities of bears. Decreased avoidance and/or increased tolerance within the population would presumably elevate densities in these areas. This may provide one potential mechanism by which the Connecticut population could reach the previously reported abundances in western Massachusetts and New Jersey. Furthermore, continued asymmetry in migration between sexes could indicate that personality types are still in the process of equilibrating with the distribution of perceived risk. Therefore, even in the absence of changes in mean population response, densities and conflicts have the potential to increase in more developed parts of bear range.

From both a theoretical perspective, and practical management of black bear populations, it will be important to quantify demographic rates, especially survival and recruitment, across the gradients of development in this study. Measures of reproductive success are necessary to anticipate the potential evolutionary impacts of habitat selection (Morris 2003), and to elucidate the net effects of occupation of intermixed ecosystems on long term black bear population growth and sustainability. Recent migration rates indicated the potential for bears near development to act as population sources. Mortality and reproductive rates would confirm these hypothesized dynamics, and enable the creation of population projection models. Furthermore, as habituation to humans among bears may be socially transmitted (Mazur & Seher, 2008), differences in reproductive rates among land use contexts, in conjunction with asymmetrical migration, may affect the spread of nuisance behavior to new areas of the population range.

Another important area of research will need to focus on landscape genomics, adaptive genetic patterns, and the potential for human-induced evolution (Andrew et al., 2013). Several of the results from this study indicated behavioral differences between bears occupying different land-use contexts, and among individuals within more developed landscapes. Especially among large carnivores, movement and activity patterns change in response to development (Ditchkoff et al., 2006). These patterns may be the result of behavioral plasticity, or local adaptation, and human-induced evolution is beginning to be recognized as a significant consequence of development (Ashley et al. 2003). Studies across taxa have indicated the potential for rapid microevolutionary responses to human-induced environmental changes (Kettlewell, 1961; Losos, 2001; Hessenauer et al., 2015). In addition to identifying factors predicting which species succeed and don't succeed in urban landscapes, this research supports the growing importance of distinguishing why *individuals* succeed. Research identifying local adaptation and selection will

require an integration of behavioral or phenotypic measures along with quantification of patterns of genetic diversity (Eckert et al., 2010; Parchman et al., 2012). Ideally, these patterns of variation would be associated with individual fitness. The ability to identify human-induced variation in behavior and fitness will allow wildlife conservation and management to account for the effect of development patterns not only on population ecology, but evolutionary trajectories.

REFERENCES

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions On Automatic Control* 19, 716-723.
- Ahlering, M.A., Millspaugh, J.J., Woods, R.J., Western, D., Eggert, L.S. 2011. Elevated levels of stress hormones in crop raiding male elephants. *Animal Conservation*, 14(2), 124-130.
- Andreasen A.M. Stewart K.M., Longland W.S., Beckmann J.P., Forister M.L. 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. *Molecular Ecology*, 21, 5689-5701.
- Andrew, R.L., Bernatchez, L., Bonin, A. *et al.* 2013. A road map for molecular ecology. *Molecular Ecology*, 22(10), 2605-2626.
- Anthony, L.L., Blumstein, D.T. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce Ne. *Biological Conservation*, 95, 303-315.
- Atwood T.C., Weeks Jr. H.P. 2003. Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. *Canadian Journal of Zoology*, 81, 1589-1597.
- Baddeley, A., Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. *Journal of Statistical Software* 12, 1–42.
- Baker, P.J., Dowding, C.V., Molony, S.E., White, P.C., Harris, S. 2007. Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behavioral Ecology* 18, 716-724.

- Baldwin, R. A., Bender, L.C. 2012. Estimating population size and density of a low-density population of black bears in Rocky Mountain National Park, Colorado. *European Journal of Wildlife Research* 58, 557–566
- Bangs, E. E., Shivik, J. 2001. Managing wolf conflict with livestock in the Northwestern United States. *Carnivore Damage Prevention News* 3, 2–5.
- Bar-Massada, A., Radeloff, V.C., Stewart, S.I. 2014. Biotic and abiotic effects of human settlements in the wildland–urban interface. *Bioscience*, 64, 429-437.
- Barber, J.R., Crooks, K.R., Fristrup, K.M. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* 25, 180-189.
- Baruch-Mordo, S., S. W. Breck, K. R. Wilson, and D. M. Theobald. 2008. Spatiotemporal distribution of black bear-human conflicts in Colorado, USA. *Journal of Wildlife Management* 72, 1853–1862.
- Baruch-Mordo, S., Wilson, K.R., Lewis, D.L., Broderick, J., Mao, J.S., Breck, S.W. 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human-bear conflicts. *PloS One* 9, e85122.
- Bateman, P., Fleming, P. 2012. Big city life: carnivores in urban environments. *J. Zool.* 287, 1-23.
- Bates, D., Maechler, M., Bolker, B. Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48.
- Beckmann, J.P., Berger, J., 2003a. Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy* 84, 594-606.

- Beckmann, J.P., Berger, J. 2003b. Rapid ecological and behavioral changes in carnivores: the response of black bears to (*Ursus americanus*) to altered food. *Journal of Zoology* 261, 207-212.
- Beckmann, J.P., Lackey, C.W. 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. *Human-Wildlife Conflicts*, 2, 168-174.
- Beeman, L.E. & Pelton, M.R. 1980. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. *Bears: Their Biology and Management*, 4, 141-147.
- Bettigole, C.A., Donovan, T.M., Manning, R., Austin, J., Long, R. 2014. Acceptability of residential development in a regional landscape: potential effects on wildlife occupancy patterns. *Biological Conservation*, 169, 401-409.
- Beyer, H.L. 2014. Geospatial modeling environment (Version 0.7.4).
<<http://www.spataleecology.com/gme>>.
- Bidlack, A.L., Reed, S.E., Palsboll, P.J., Getz, W.M. 2007. Characterization of a western North American carnivore community using PCR-RFLP of cytochrome b obtained from fecal samples. *Conservation Genetics*, 8, 1511-1513.
- Bivand, R., Lewin-Koh, N. 2014. Maptools: tools for reading and handling spatial objects. R package version 0.8-29. (<http://cran.r-project.org/web/packages/maptools>).
- Blair, R. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society*, 9, 2.
- Boyce, M. S., Vernier, P. R., Nielsen, S. E., Schmiegelow, K. A. 2002. Evaluating resource selection functions. *Ecological Modeling* 157, 281–300.
- Bradley, E. H., Pletscher, D.H. 2005. Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. *Wildlife Society Bulletin* 33, 1256–1265.

- Breck, S.W., Lance, N., Seher, V. 2009. Selective foraging for anthropogenic resources by black bears: Minivans in Yosemite National Park. *Journal of Mammalogy*, 90, 1041-1044.
- Bright, A. D., Manfredo, M.J., Fulton, D.C. 2000. Segmenting the public: an application of value orientations to wildlife planning in Colorado. *Wildlife Society Bulletin* 28, 218–226.
- Brodeur, V., Ouellet, J., Courtois, R., Fortin, D. 2008. Habitat selection by black bears in an intensively logged boreal forest. *Canadian Journal of Zoology*, 86(11), 1307-1316.
- Brody A.J., Pelton M.R. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin*, 17, 5-10.
- Brown, D.G., Johnson, K.M., Loveland, T.R., Theobald, D.M., 2005. Rural land-use trends in the conterminous United States, 1950-2000. *Ecol. Appl.* 15, 1851-1863.
- Burnham, K.P., Anderson, D.R. 2002. *Model Selection and Multi-model Inference: A Practical Information Theoretic Approach*. New York, Springer.
- Busch, J.D., Waser, P.M., DeWoody, J.A. 2009. The influence of density and sex on patterns of fine-scale genetic structure. *Evolution*, 63, 2302-2314.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J., Mace, G.M. 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biology*, 2(7), e197.
- Carmichael, L.E., Krizan, P., Blum, S.P., Strobeck, C. 2005. Genotyping of pseudohermaphrodite polar bears in Nunavut and advances in DNA sexing techniques. *Journal of Mammalogy*, 86, 160-169.
- Carter, N.H., Brown, D.G., Etter, D.R., Visser, L.G. 2010. American black bear habitat selection in northern Lower Peninsula Michigan, USA, using discrete-choice modeling. *Ursus*, 21, 57-71.

- Chapron, G., Lopez-Bao, J.V., 2014. Conserving carnivores: politics in play. *Science* 343, 1199-1200.
- Clark, J.D., Eastridge, R., 2006. Growth and sustainability of black bears at White River National Wildlife Refuge, Arkansas. *Journal of Wildlife Management* 70, 1094-1101.
- Clark, J.K., McChesney, R., Munroe, D.K., Irwin, E.G. 2009. Spatial characteristics of exurban settlement pattern in the United States. *Landscape and Urban Planning*, 90(3), 178-188.
- Costello, C.M., Creel, S.R., Kalinowski, S.T., Vu, N.V., Quigley, H.B. 2008. Sex-biased natal dispersal and inbreeding avoidance in American black bears as revealed by spatial genetic analyses. *Molecular Ecology*, 17, 4713-4723.
- Coster, S.S., Kovach, A.I., Pekins, P.J., Cooper, A.B., Timmins, A. 2011. Genetic mark-recapture population estimation in black bears and issues of scale. *The Journal of Wildlife Management*, 75(5), 1128-1136.
- Coster, S.S., Kovach, A.I. 2012. Anthropogenic influences on the spatial genetic structure of black bears. *Conservation Genetics*, 13, 1247-1257.
- Cushman, S.A., McKelvey, K.S., Hayden, J., Schwartz, M.K. 2006. Gene Flow in Complex Landscapes: Testing Multiple Hypotheses with Causal Modelling. *The American Naturalist*, 168, 486-499.
- Conover, M. R. 1998. Perceptions of American agricultural producers about wildlife on their farms and ranches. *Wildlife Society Bulletin* 26:597–604.
- Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J., Hewison, A.J.M., 2008. Inferring the effects of landscape structure on roe deer movements using a step selection function. *Landscape Ecology* 23, 603-614.

- Dahle, B., Swenson, J.E. 2003. Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology*, 72, 660-667.
- Dall, S.R. 2004. Behavioural biology: fortune favours bold and shy personalities. *Current Biology*, 14, 470-472.
- Darrow, P.A., Shivik, J.A. 2009. Bold, shy, and persistent: variable coyote response to light and sound stimuli. *Applied Animal Behavior Science*, 116, 82-87.
- Decker, D. J., Jacobson, C.A., Brown, T.L. 2006. Situation-specific "impact dependency" as a determinant of management acceptability: insights from wolf and grizzly bear management in Alaska. *Wildlife Society Bulletin* 34, 426–432.
- Decker, D. J., Purdy, K.G. 1988. Toward a concept of wildlife acceptance capacity in wildlife management. *Wildlife Society Bulletin* 15, 53–57.
- Delibes, M., Gaona, P., Ferreras, P. 2001. Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist*, 158, 277-285.
- DeStefano, S., DeGraaf, R.M. 2003. Exploring the ecology of suburban wildlife. *Frontiers in Ecology and the Environment*, 1, 95-101.
- Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, 22, 489-496.
- Ditchkoff, S.S., Saalfeld, S.T., Gibson, C.J. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems*, 9, 5-12.
- Dixon, J.D., Oli, M.K., Wooten, M.C. *et al.* 2006. Genetic consequences of habitat fragmentation and loss: the case of the Florida black bear (*Ursus americanus floridanus*). *Conservation Genetics*, 8, 455-464.

Dobey, S., Masters, D.V., Scheick, B.K., Clark, J.D., Pelton, M.R., Sunquist, M.E. 2005.

Ecology of Florida Black Bears in the Okefenokee-Osceola Ecosystem. Wildlife Monographs, 158(1), 1-41.

Earl, D.A., vonHoldt, B.M. 2011. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources, 4, 359-361.

Efford, M. 2012. secr: spatially explicit capture-recapture models. R package version 2.3.2. (<http://cran.r-project.org/web/packages/secr>).

Eiler, J.H., Wathen, W.G., Pelton, M.R. 1989. Reproduction in black bears in the southern Appalachian Mountains. The Journal of Wildlife Management, 353-360.

Eggert, L.S., Maldonado, J.E., Fleischer, R.C. 2005. Nucleic acid isolation from ecological samples—animal scat and other associated materials. Methods in Enzymology, 395, 73-82.

Elff, M. 2014. mclogit: Mixed conditional logit. R package version 0.3-1. <https://CRAN.R-project.org/package=mclogit>.

Ellingwood, M. 2003. Nuisance black bear habitat use and activity patterns. New Hampshire Federal Aid Grant Report W-89-R-3, Concord, NH, USA.

Epps, C.W., Palsbøll, P.J., Wehausen, J.D., Roderick, G.K., Ramey, R.R., McCullough, D.R. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters, 8, 1029-1038.

Evanno, G., Regnaut, S., Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology, 14, 2611-2620.

Evans, M.J., Hawley, J.E., Rego, P.W., Rittenhouse, T.A.G. 2014. Exurban land use facilitates human-black bear conflicts. The Journal of Wildlife Management, 78(8), 1477-1485.

- Evans, M.J., Hawley, J.E., Rego, P.W., Rittenhouse, T.A.G., In Review. Variable densities indicate thresholds to development limiting and facilitating recolonization of a large carnivore. *Landscape and Urban Planning*.
- Faubet, P., Waples, R.S., Gaggiotti, O.E. 2007. Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. *Molecular Ecology*, 16, 1149-1166.
- Faubet, P., Gaggiotti, O.E. 2008. A New Bayesian Method to Identify the Environmental Factors That Influence Recent Migration. *Genetics*, 178, 1491-1504.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography*, 24, 325-331.
- Fischer, J., Lindenmayer, D.B. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, 16, 265-280.
- Fortin, D., Boyce, M.S., Merrill, E.H., Fryxell, J.M. 2004. Foraging costs of vigilance in large mammalian herbivores. *Oikos* 107, 172-180.
- Francis, C.D., Barber, J.R. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment* 11, 305-313.
- Frid, A., Dill, L.M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6, 11.
- Fry, J.A., Xian, G., Jin, S., Dewitz, J.A., Homer, C.G., LIMIN, Y., Barnes, C.A., Herold, N.D., Wickham, J.D. 2011. Completion of the 2006 national land cover database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing*, 77, 858-864.
- Gardner, B.J., Royle, A., Wegan, M.T. 2009. Hierarchical models for estimating density from DNA mark-recapture studies. *Ecology*, 90(4), 1106-1115.

- Gardner, B.J., Royle, A., Wegan, M.T., Rainbolt, R.E., Curtis, P.D. 2010. Estimating black bear density using DNA data from hair snares. *The Journal of Wildlife Management*, 90(2), 318-325.
- Garshelis, D.L., Noyce, K.V., Ditmer, M.A. 2012. Ecology and population dynamics of black bears in Minnesota. *Summaries of wildlife research findings*. Minnesota DNR, St. Paul, MN, USA.
- Geffen, E., Anderson, M.J., Wayne, R.K. 2004. Climate and habitat barriers to dispersal in the highly mobile grey wolf. *Molecular Ecology*, 13, 2481-2490.
- Gehrt, S.D., Brown, J.L., Anchor, C. 2011. Is the urban coyote a misanthropic synanthrope? The case from Chicago. *Cities and the Environment*, 4, 3.
- Gehrt, S.D., Riley, S.P., Cypher, B.L. 2010. *Urban carnivores: ecology, conflict, and conservation*, Johns Hopkins University Press, Baltimore, MD.
- Gilbert, B. 1989. Behavioral plasticity and bear-human conflicts. In M. Bromley (Ed.), *Bear–people conflicts: proceedings of a symposium on management strategies*. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Glennon, M. J., Porter, W.F. 2005. Effects of land use management on biotic integrity: an investigation of bird communities. *Biological Conservation*, 126, 499–511.
- Gore, M. L., Knuth, B.A., Curtis, P.D., J. E. Shanahan, J.E. 2006. Education programs for reducing American black bear-human conflict: indicators of success? *Ursus* 17, 75–80.
- Goudet, J. 1995. FSTAT (version 1.2): a computer program to calculate F-statistics. *Journal of Heredity*, 86, 485-486.

- Greenleaf, S.S., Matthews, S.M., Wright, R.G., Beecham, J.J., Leithead, H.M. 2009. Food habits of American black bears as a metric for direct management of human-bear conflict in Yosemite Valley, Yosemite National Park, California. *Ursus*, 20(2), 94-101.
- Groffman, P.M., Baron, J.S., Blett, T., *et al.* 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems*, 9, 1-13.
- Hansen, A.J., Knight, R.L., Marzluff, J.M. *et al.* 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications*, 15, 1893-1905.
- Harker, D., Bates, D.C. 2007. The black bear hunt in New Jersey: a constructionist analysis of an intractable conflict. *Society and Animals* 15, 329–352.
- Harris, S. 1981. An estimation of the number of foxes (*Vulpes vulpes*) in the city of Bristol, and some possible factors affecting their distribution. *Journal of Applied Ecology*, 18, 455-465.
- Hawbaker, T.J., Radeloff, V.C., Clayton, M.K., Hammer, R.B., Gonzalez-Abraham, C.E. 2006. Road development, housing growth, and landscape fragmentation in northern Wisconsin: 1937-1999. *Ecological Applications*, 16, 1222-1237.
- Hellgren, E.C., Onorato, D.P., Skiles, J.R. 2005. Dynamics of a black bear population within a desert metapopulation. *Biological Conservation*, 122, 131-140.
- Hessenauer, J-M., Vokoun, J.C., Suski, C.D., Davis, J., Jacobs, R., O'Donnell, E. 2015. Differences in the metabolic rates of exploited and unexploited fish populations: a signature of recreational fisheries induced evolution? *PloS One* 10(6), e0128336.

- Hilderbrand, G.V., Jenkins, S.G., Schwartz, C.C., Hanley, T.A., Robbins, C.T. 1999. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology*, 77, 1623-1630.
- Hopkins, J.B. 2013. Use of genetics to investigate socially learned foraging behavior in free-ranging black bears. *Journal of Mammalogy*, 94, 1214-1222.
- Horner, M.A., Powell, R.A. 1990. Internal structure of home ranges of black bears and analyses of home-range overlap. *Journal of Mammalogy*, 71, 402-410.
- Hostetler, J.A., McCown, J.W., Garrison, E.P., *et al.* 2009. Demographic consequences of anthropogenic influences: Florida black bears in north central Florida. *Biological Conservation*, 142, 2456-2463.
- Howe, E. J., Obbard, M.R., Black, R., Wall, L.L. 2010. Do public complaints reflect trends in human-bear conflict? *Ursus* 21(2), 131-142
- Hristienko, H., McDonald Jr, J.E. 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus* 18, 72-88.
- Hulbert, I.A.R, French, J. 2001. The accuracy of GPS for wildlife telemetry and habitat mapping. *Journal of Applied Ecology*, 38, 869-878.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65-71.
- Johnson, H.E., Breck, S.W., Baruch-Mordo, S., Lewis, D.L., Lackey, C.W., Wilson, K.R., Broderick, J., Mao, J.S., Beckmann, J.P. 2015. Shifting perceptions of risk and reward:

Dynamic selection for human development by black bears in the western United States.

Biological Conservation, 187, 164-172.

Johnston, R.F. 2001. Synanthropic birds of North America. In: *Avian ecology and conservation in an urbanizing world* (eds Marzluff JM, Bowman R, Donnelly R), pp. 49-67. Springer, New York, New York, USA.

Kalinowski, S.T., Wagner, A.P., Taper, M.L. 2006. ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes*, 6, 576-579.

Kaltenborn, B., Bjerke, T., Vitterso, J. 1999. Attitudes toward large carnivores among sheep farmers, wildlife managers, and research biologists in Norway. *Human Dimensions of Wildlife* 4, 57-73.

Kertson, B.N., Spencer, R.D., Marzluff, J.M., Hepinstall-Cymerman, J., Grue, C.E. 2011. Cougar space use and movements in the wildland-urban landscape of western Washington. *Ecological Applications*, 21, 2866-2881.

Kery, M., Gardner, B., Stoeckle, T., Weber, D., Royle, J.A. 2010. Use of spatial capture-recapture modeling and DNA data to estimate densities of elusive animals. *Conservation Biology*, 25(2), 356-364.

Kettlewell, H.B.D. 1961. The phenomenon of industrial melanism in *Lepidoptera*. *Annual Review of Entomology*, 6, 245-262.

Kretser, H.E., Curtis, P.D., Francis, J.D., Pendall, R.J., Knuth, B.A. 2009. Factors affecting perceptions of human-wildlife interactions in residential areas of northern New York and implications for conservation. *Human Dimensions of Wildlife*, 14(2), 102-118.

- Kristensen, T.V., Faries, K.M., White, Jr. D., Eggert, L.S. 2011. Optimized methods for multiplex genotyping analysis of hair samples for American black bears (*Ursus americanus*). *Wildlife Biology in Practice*, 7, 123-128.
- LeCount, A.L. 1987. Causes of black bear cub mortality. *Bears: Their Biology and Management*, 7, 75-82.
- Lele, S.R., Merrill, E.H., Keim, J., Boyce, M.S. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *Journal of Animal Ecology*, 82, 1183-1191.
- Lenormand, T. 2002. Gene flow and the limits to natural selection. *TRENDS in Ecology & Evolution*, 17, 183-189.
- Lewis, J.S., Rachlow, J.L., Horne, J.S. *et al.* 2011. Identifying habitat characteristics to predict highway crossing areas for black bears within a human-modified landscape. *Landscape and Urban Planning*, 101, 99-107.
- Lichstein, J.W. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecology*, 188, 117-131.
- Lidicker Jr., W.Z. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology*, 14(4), 333-343.
- Lima, S.L., Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649-659.
- Linnell, J.D., Swenson, J.E., Anderson, R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, 4, 345-349.

- Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J., Buzas, J.S. 2010. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landscape Ecology*, 26(3), 327-340.
- Losos, J.B., Schoener, T.W., Warheti, K.I., Creer, D. 2001. Experimental studies of adaptive differentiation in Bahamian *Anolis* lizards. *Genetica*, 8, 399.
- Lowry, H., Lill, A., Wong, B. 2013. Behavioural responses of wildlife to urban environments. *Biological Reviews* 88, 537-549.
- Lyons, A.J. 2005. Activity patterns of urban American black bears in the San Gabriel Mountains of southern California. *Ursus*, 16(2), 255-262.
- MacKenzie, K. G. 2003. Nuisance vs. non-nuisance bears: seasonal movement and home range utilization of female New Jersey black bears (*Ursus americanus*). Thesis, East Stroudsburg State University, East Stroudsburg, Pennsylvania, USA.
- Manel, S., Schwartz, M.K., Luikart, G., Taberlet, P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, 18, 189-197.
- Manly, B., McDonald, L., Thomas, D., McDonald, T., Erickson, W. 2002. Resource selection by animals: statistical analysis and design for field studies. Nordrecht, the Netherlands, Kluwer
- Manning, A.D., Lindenmayer, D.B., Nix, H.A. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos*, 104, 621-628.
- Martin, J.G., Réale, D. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behavior* 75, 309-318.
- Marzluff, J.M., Ewing, K. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology*, 9(2), 280-292.

- Matthiopoulos, J., Hebblewhite, M., Aarts, G., Fieberg, J. 2011. Generalized functional responses for species distributions. *Ecology* 92, 583-589.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. *Ecography*, 28, 403-416.
- Mattson, D. J. 1990. Human impacts on bear habitat use. *Bears: Their Biology and Management*, 8, 33–56.
- Mazur, R., Seher, V. 2008. Socially learned foraging behavior in wild black bears, *Ursus americanus*. *Animal Behaviour*, 75, 1503-1508.
- McGarigal, K., Cushman, S.A. 2005. The gradient concept of landscape structure. In: *Issues and perspectives in landscape ecology* (eds Wiens J, Moss M), pp. 112-119. Cambridge University Press, Cambridge, UK.
- McKelvey, K., Schwartz, M. 2005. dropout: a program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. *Molecular Ecology Notes*, 5, 716-718.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247-260.
- McRae, B., Beier, P., Dewald, L., Huynh, L., Keim, P. 2005. Habitat barriers limit gene flow and illuminate historical events in a wide-ranging carnivore, the American puma. *Molecular Ecology*, 14, 1965-1977.
- McRae, B.H., Beier, P. 2007. Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 19885-19890.

- Merkle, J.A., Krausman, P.R., Decesare, N.J., Jonkel, J.J. 2011. Predicting spatial distribution of human-black bear interactions in urban areas. *Journal of Wildlife Management*, 75, 1121-1127.
- Merkle, J.A., Robinson, H.S., Krausman, P.R., Alaback, P. 2013. Food availability and foraging near human developments by black bears. *Journal of Mammalogy*, 94, 378-385.
- Messmer, T.A., 2009. Human–wildlife conflicts: emerging challenges and opportunities. *Human Wildlife Conflicts* 3, 10-17.
- Michalski, F. R., Boulhosa, L.P., Faria, A., Peres, C.A. 2006. Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Animal Conservation*, 9, 179–188.
- Miller, J. R., Hobbs, R.J.. 2002. Conservation where people live and work. *Conservation Biology* 16, 330–337.
- Millions, D.G., Swanson, B.J. 2007. Impact of natural and artificial barriers to dispersal on the population structure of bobcats. *The Journal of Wildlife Management*, 71, 96-102.
- Mills, L.S., Citta, J.J., Lair, K.P., Schwartz, M.K., Tallmon, D.A. 2000. Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. *Ecological Applications*, 10(1), 283-294.
- Millsbaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, Sheriff, S.L. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management*, 70, 384–395
- Mitchell, M. S., Zimmerman, J.W., Powell, R.A. 2002. Test of a habitat suitability index for black bears in the southern Appalachians. *Wildlife Society Bulletin*, 30, 794–808.

- Mitchell, M.S., Powell, R.A. 2007. Optimal use of resources structures home ranges and spatial distribution of Black Bears. *Animal Behaviour*, 74, 219-230.
- Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136, 1-13.
- Moyer, M.A., McCown, J.W., Eason, T.H., Oli, M.K. 2006. Does genetic relatedness influence space use pattern? A test on Florida black bears. *Journal of Mammalogy*, 87, 255-261.
- Moyer, M.A., McCown, J.W., Oli, M.K. 2007. Factors influencing home-range size of female Florida black bears. *Journal of Mammalogy*, 88(2), 468-476.
- Muhly, T. B., Musiani, M. 2009. Livestock depredation by wolves and the ranching economy in the Northwestern U.S. *Ecological Economics* 68, 2439–2450.
- Naughton-Treves, L., Grossberg R., Treves, A. 2003. Paying for tolerance: the impact of depredation and compensation payments on rural citizens' attitudes toward wolves. *Conservation Biology*, 17, 1500–1511.
- Naves, J., Wiegand, T., Revilla, E., Delibes, M. 2003. Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. *Conservation Biology*, 17, 1276-1289.
- Nellemann, C., Støen, O., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B.P., Martin, J., Ordiz, A. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation*, 138, 157-165.
- Nelson, R.A., Folk, J., G.E., Pfeiffer, E.W., Craighead, J.J., Jonkel, C.J., Steiger, D.L. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: Their Biology and Management* 5, 284-290.

- Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., Paquet, P.C. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, 10, 949-963.
- Ordiz, A., Støen, O., Delibes, M., Swenson, J.E. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, 166, 59-67.
- Paetkau, D., Strobeck, C. 1998. Ecological genetic studies of bears using microsatellite analysis. *Ursus*, 10, 299-306.
- Paetkau, D., Strobeck, C. 1994. Microsatellite analysis of genetic variation in black bear populations. *Molecular Ecology*, 3, 489-495.
- Parchman, T.L., Gompert, Z., Mudge, J., Schilkey, F.D., Benkman, C.W., Buerkle, C. 2012. Genome-wide association genetics of an adaptive trait in lodgepole pine. *Molecular Ecology*, 21(12), 2991-3005.
- Paxinos, E., McIntosh, C., Ralls, K., Fleischer, R. 1997. A noninvasive method for distinguishing among canid species: Amplification and enzyme restriction of DNA from dung. *Molecular Ecology*, 6, 483-486.
- Peakall, R., Smouse, P.E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes*, 6, 288-295.
- Peine, J. D. 2001. Nuisance bears in communities: strategies to reduce conflict. *Human Dimensions of Wildlife* 6, 223-237.
- Powell, R.A., Zimmerman, J.W., Seaman, D.E. 1997. Ecology and behaviour of North American black bears: home ranges, habitat, and social organization, Springer Science & Business Media, New York, NY.

- Powell, R.A., Zimmerman, J.W., Seaman, D.E., Gilliam, J.F. 1996. Demographic analyses of a hunted Black Bear population with access to a refuge. *Conservation Biology*, 10, 224-234.
- Pritchard, J.K., Stephens, M., Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics*, 155, 945-959.
- Puckett, E.E., Kristensen, T.V., Wilton, C.M. *et al.* 2014. Influence of drift and admixture on population structure of American black bears (*Ursus americanus*) in the Central Interior Highlands, USA, 50 years after translocation. *Molecular Ecology*, 23, 2414-2427.
- R Development Core Team. 2014. *R: A language and environmental for statistical computing version 3.0.2*. R Foundation for Statistical Computing (<http://www.R-project.org/>).
- Radeloff, V.C., Hammer, R.B., Stewart, S.I. *et al.* 2005. The wildland-urban interface in the United States. *Ecological Applications*, 15, 799-805.
- Ranglack, D., Signor, K., Bunnell, K., Shivik, J. 2009. Black bear activity and visitation patterns at human food sources in Utah. In J.R. Boulanger (Ed.), *Proceedings of the 13th Wildlife Damage Management Conferences* (Paper 144).
- Rasker, R., Hansen, A.J. 2000. Natural amenities and population growth in the Greater Yellowstone region. *Human Ecology Review*, 7, 30-40.
- Rauer, G., Kaczensky, P., Knauer, F. 2003. Experiences with aversive conditioning of habituated brown bears in Austria and other European countries. *Ursus*, 14, 215–224.
- Raymond, M., Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, 86, 248-249.
- Remeš, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics? *Oikos*, 91, 579-582.

- Reynolds-Hogland, M.J., Mitchell, M.S. 2007. Effects of roads on habitat quality for bears in the southern Appalachians: A long term study. *Journal of Mammalogy*, 88, 1050-1061.
- Ricketts, T., Imhoff, M. 2003. Biodiversity, urban areas, and agriculture: locating priority ecoregions for conservation. *Ecology and Society*, 8, 1.
- Rhodes, J.R., McAlpine, C.A., Lunney, D., Possingham, H.P. 2005. A spatially explicit habitat selection model incorporating home range behavior. *Ecology*, 86, 1199-1205.
- Riley, S.P., Hadidian, J., Manski, D.A. 1998. Population density, survival, and rabies in raccoons in an urban national park. *Canadian Journal of Zoology*, 76, 1153-1164.
- Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., Wayne, R.K. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology*, 17, 566-576.
- Riley, S.P., Pollinger, J.P., Sauvajot, R.M. *et al.* 2006. FAST-TRACK: A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology*, 15, 1733-1741.
- Robertson, B.A., Rehage, J.S., Sih, A. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution*, 28, 552-560.
- Rode, K.D., Farley, S.D., Robbins, C.T. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology*, 87, 2636-2646.
- Rodriguez-Prieto, I., Fernández-Juricic, E., Martín, J., Regis, Y. 2009. Antipredator behavior in blackbirds: habituation complements risk allocation. *Behavioral Ecology*, 20, 371-377.
- Roever, C.L., Boyce, M.S., Stenhouse, G.B. 2010. Grizzly bear movements relative to roads: application of step selection functions. *Ecography*, 33, 1113-1122.

- Rogers, L.L., Allen, W. 1987. Habitat suitability index models: black bear Upper Great Lakes Region. U.S. Fish and Wildlife Service Biology Report 82(10.144).
- Rogers, L.L. 1987. Factors influencing dispersal in the black bear. In: *Mammalian dispersal patterns* (eds Chepko-Sade BD and Halpin ZT), pp. 75-84. University of Chicago Press, Chicago, Illinois.
- Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology*, 62(2), 327-335.
- Rousset, F. 2000. Genetic differentiation between individuals. *Journal of Evolutionary Biology*, 13, 58-62.
- Royle, J.A., Chandler, R.B., Gazenskik, K.D., Graves, T.A. 2013. Spatial capture-recapture models for jointly estimating population density and landscape connectivity. *Ecology*, 94(2), 287-294.
- Royle, J.A., Chandler, R.B., Sun, C.C., Fuller, A.K. 2013. Integrating resource selection information with spatial capture-recapture. *Methods in Ecology and Evolution*, 4(6), 520-530.
- Rudzitis, G. 1999. Amenities increasingly draw people to the rural West. *Rural Development Perspectives*, 14, 9-13.
- Rueness, E.K., Stenseth, N.C., O'Donoghue, M. *et al.* 2003. Ecological and genetic spatial structuring in the Canadian lynx. *Nature*, 425, 69-72.
- Sacks, B.N., Brown, S.K., Ernest, H.B. 2004. Population structure of California coyotes corresponds to habitat-specific breaks and illuminates species history. *Molecular Ecology*, 13, 1265-1275.
- Sato, Y., Itoh, T., Mori, Y., Satoh, Y. & Mano, T. 2011. Dispersal of male bears into peripheral habitats inferred from mtDNA haplotypes. *Ursus*, 22(2), 120-132.

- Saunders, D.A., Hobbs, R.J., Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5, 18-32.
- Schlaepfer, M.A., Runge, M.C., Sherman, P.W. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution*, 17, 474-480.
- Schwartz, C.C., Franzmann, A.W. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *The Journal of Wildlife Management*, 56, 426-431.
- Seto, K.C., Fragkias, M., Guneralp, B., Reilly, M.K. 2011. A meta-analysis of global urban land expansion. *PLoS ONE*, 6(8), e23777.
- Shah, V., McRae, B. 2008. Circuitscape: a tool for landscape ecology. In: *Proceedings of the 7th Python in Science Conference* (eds Varoquaux G, Vaught T, Millman J), pp. 62-66.
- Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E., Hope, D. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, 21, 186-191.
- Siemer, W. F., Hart, P.S., Decker, D.J., Shanahan, J.E. 2009. Factors that influence concern about human-black bear interactions in residential settings. *Human Dimensions of Wildlife: An International Journal*, 14(3), 185–197.
- Sih, A., Bell, A., Johnson, J.C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372-378.
- Slater, P. 1981. Individual differences in animal behavior, in: *Anonymous Perspectives in ethology*. Springer, pp. 35-49.
- Stewart, S.I., Radeloff, V.C., Hammer, R.B., Hawbaker, T.J. 2007. Defining the wildland–urban interface. *Journal of Forestry*, 105, 201-207.

- Sukumar, R. 1991. The management of large mammals in relation to male strategies and conflict with people. *Biological Conservation*, 55, 93-102.
- Sweanor, L.L., Logan, K.A., Hornocker, M.G. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology*, 14, 798-808.
- Swenson, J.E., Sandegren, F., SO-Derberg, A. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology*, 67(5), 819-826.
- Spencer, R.D., Beausoleil, R.A., Martorello, D.A. 2007. How agencies respond to human-black bear conflicts: a survey of wildlife agencies in North America. *Ursus* 18, 217-229.
- Taberlet, P., Griffin, S., Goossens, B. *et al.* 1996. Reliable Genotyping of Samples with Very Low DNA Quantities Using PCR. *Nucleic acids research*, 24, 3189-3194.
- Theobald, D. M. 2001. Land-use dynamics beyond the American urban fringe. *Geographical Review*, 91(3), 544–564.
- Theobald, D.M. 2004. Placing exurban land-use change in a human modification framework. *Frontiers in Ecology and the Environment*, 2(3), 139-144.
- Thurfjell, H., Ciuti, S., Boyce, M. 2014. Applications of step-selection functions in ecology and conservation. *Movement Ecology*, 2, 4.
- Treves, A., Wallace, R.B., Naughton-Treves, L., Morales, A. 2006. Co-managing human–wildlife conflicts: a review. *Human Dimensions of Wildlife*, 11, 383-396.
- Tuomainen, U., Candolin, U. 2011. Behavioural responses to human-induced environmental change. *Biological Reviews*, 86, 640-657.
- United States Census Bureau. 2011. Selected economic characteristics, 2007–2011. U.S. Census Bureau, Washington, D.C., USA.

- United States Census Bureau. 2012 Annual estimates of the populations for the United States, regions, states, and Puerto Rico: April 1, 2012 to July 1, 2012. U.S. Census Bureau, Washington, D.C., USA.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*, 893-901.
- Van Oosterhout, C., Hutchinson, W.F., Wills, D.P., Shipley, P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, 4, 535-538.
- Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., Slotow, R. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, 94, 2619-2631.
- Vogel, W. O. 1989. Response of deer to density and distribution of housing in Montana. *Wildlife Society Bulletin* 17, 406–413.
- Waite, T.A., Chhangani, A.K., Campbell, L.G., Rajpurohit, L.S., Mohnot, S.M. 2007. Sanctuary in the city: urban monkeys buffered against catastrophic die-off during ENSO-related drought. *EcoHealth*, 4(3), 278-286.
- Waits, L.P., Luikart, G., Taberlet, P. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Molecular Ecology*, 10, 249-256.
- Waser, P.M., Jones, W.T. 1983. Natal philopatry among solitary mammals. *Quarterly Review of Biology*, 58, 355-390.
- Weaver, J.L., Paquet, P.C., Ruggiero, L.F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology*, 10, 964-976.

- Weir, B.S., Cockerham, C.C. 1984. Estimating F-statistics for the analysis of population structure. *Evolution*, 38, 1358-1370.
- West, B. C., Parkhurst, J.A. 2002. Interactions between deer damage, deer density, and stakeholder attitudes in Virginia. *Wildlife Society Bulletin*, 30, 139–147.
- Wilton, C.M., Puckett, E.E., Beringer, J., Gardner, B., Eggert, L.S, Belant, J.L. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. *PLoS ONE*, 9(10), e111257.
- Wilson, G.A., Rannala, B. 2003. Bayesian Inference of Recent Migration Rates Using Multilocus Genotypes. *Genetics*, 163, 1177-1191.
- Wilson, S. M., Madel, M.J., Mattson, D.J., Graham, J.M, Merrill, T. 2006. Landscape conditions predisposing grizzly bears to conflicts on private agricultural lands in the western USA. *Biological Conservation*, 130, 47–59.
- Woods, J.G., Paetkau, D., Lewis, D., McLellan, B.N., Proctor, M., Strobeck, C. 1999. Genetic tagging of free-ranging black and brown bears.
- Wright S. 1943. Isolation by distance. *Genetics*, 28, 114-138.
- Young, D. D., Beecham, J.J. 1986. Black bear habitat use at Priest Lake, Idaho. *Bears: Their Biology and Management*, 6, 73–80.
- Zipperer, W.C., Wu, J., Pouyat, R.V., Pickett, S.T., 2000. The application of ecological principles to urban and urbanizing landscapes. *Ecological Applications*, 10, 685-688.

TABLES

Table 1.1. Summary of spatial model-selection procedure examining variables affecting spatial intensity of human-black bear conflicts in Connecticut during 2008–2012. We report Akaike’s Information Criterion (AIC), relative difference in AIC value compared to the top-ranked model (Δ AIC), AIC model weight (ω), and the number of model parameters (K). Variables included percent forest cover within 1 km² (%Forest), proportion of forest edge within 1 km² (%Edge), distance to wetlands (Wet), distance to streams (Stream), distance to forest (ForDist), housing density (Housing), and household income (Income). All models included an autoregressive term that is not displayed in the table.

Model	K	AIC	Δ AIC	ω
Natural habitat + anthropogenic				
%Forest, (%Forest) ² , %Edge, Wet, Wet ² , Stream, Housing	8	−24,237.9	0	0.73
%Forest, (%Forest) ² , %Edge, Wet, Wet ² , Stream, Housing, Income	9	−24,235.0	2.9	0.17
%Forest, (%Forest) ² , %Edge, Wet, Wet ² , Stream	7	−24,232.6	5.3	0.05
%Forest, (%Forest) ² , %Edge, Wet, Wet ² , Stream, Income	8	−24,232.4	5.5	0.05
Natural habitat				
%Forest, (%Forest) ² , %Edge, Wet, Wet ² , Stream	7	−24,232.6	0	0.86
%Forest, (%Forest) ² , %Edge, Wet, Wet ² , Stream, ForDist	8	−24,229.9	3.7	0.14
%Forest, (%Forest) ² , %Edge	4	−24,219.2	13.4	0.001
%Forest, (%Forest) ² , %Edge, ForDist	5	−24,218.5	15.1	<0.001
Wet, Wet ² , Stream, ForDist	5	−24,202.0	30.6	<0.001
Wet, Wet ² , Stream	4	−24,174.4	58.2	<0.001

Table 1.2. Parameter estimates (β) and standard error (SE) for significant predictor variables in top-ranked spatial model of human-black bear conflicts in Connecticut during 2008–2012.

Variable	β	SE	<i>P</i>
Edge density	0.014	0.004	<0.001
Forest cover	0.067	0.009	<0.001
Forest cover ²	−0.044	0.009	<0.001
Distance to main stream (m)	4.96E−04	1.55E−04	0.001
Distance to wetland (m)	0.00267	8.76E−04	0.002
Distance to wetland ² (m)	−3.99E−04	1.56E−07	0.01
House density	2.74E−06	1.01E−06	0.007

Table S1.1. Results of model-selection procedure evaluating characterization of percent forest cover (%For), forest edge density (%Edge), and streams in explaining human-black bear conflicts in Connecticut during 2008–2012. We report the number of model parameters (K), Akaike's Information Criterion (AIC), and relative difference in AIC value compared to the top-ranked model (Δ AIC).

Model	K	AIC	Δ AIC
%For			
1-km ²	1	565.2	0
500-m ²	1	572.0	6.8
250-m ²	1	573.0	7.8
%Edge			
1-km ²	1	590.5	0
500-m ²	1	592.2	1.7
250-m ²	1	596.2	5.7
Streams			
Main Stem	1	605.4	0
All	1	609.3	3.9

Table S1.2. Results of model-selection procedure comparing quadratic versus linear relationships between selected landscape variables and spatial intensity of human-black bear conflicts in Connecticut during 2008–2012. We report the number of model parameters (K), Akaike’s Information Criterion (AIC), and relative difference in AIC value compared to the top-ranked model (Δ AIC).

Model	K	AIC	Δ AIC
Distance to Wetlands			
Wet	1	597.5	0
Wet, (Wet) ²	2	577.0	20.5
Percent Forest Cover			
%For	1	565.2	0
%For, (%For) ²	2	553.0	12.2

Table S1.3. Results of non-spatial model-selection procedure evaluating variables affecting human-black bear conflict intensity in Connecticut during 2008–2012. We report the number of model parameters (K), Akaike’s Information Criterion (AIC), relative difference in AIC value compared to the top-ranked model (ΔAIC), and AIC model weight (ω). Significant ($P < 0.05$) Lagrange Multiplier test statistics (LM_{error}) indicate spatial dependencies and improved parameter estimation using a spatial error model. Variables are the same as in Table 1.

Model	K	AIC	ΔAIC	ω	LM_{error}	P
%For, (%For) ² , %Edge, Wet, Wet ² , Stream, Income	7	-11687.1	0	0.75	20978.4	≤ 0.001
%For, (%For) ² , %Edge, Wet, Wet ² , Stream	6	-11684.0	3.1	0.18	21209.5	≤ 0.001
%For, (%For) ² , %Edge, Wet, Wet ² , Stream, Housing, Income	8	-11681.3	5.8	0.05	20879.7	≤ 0.001
%For, (%For) ² , %Edge, Wet, Wet ² , Stream, Housing	7	-11680.9	6.2	0.04	21134.4	≤ 0.001
%For, (%For) ² , %Edge, Wet, Wet ² , Stream, ForDist, Housing, Income	9	-11680.0	7.1	0.02	19936.2	≤ 0.001

Table 2.1 AICc weights for candidate spatial mark-recapture model sets fit to detection data from East, North and the Combined study areas. Data from Combined study area were analyzed by male and female individuals and all together.

Hypothesized Variation in Bear Density	Combined study area			North	East
	All	Female	Male		
North-South Trend & Rural, Low, Medium and High Density Housing	0.736^a	0.687^a	0.285^a	<0.001	0.234^a
Rural, Low, Medium and High Density Housing	0.253^a	0.235^a	0.622^a	<0.001	0.010
North-South Trend & Natural, Intermixed, Interface, and Developed Land-use	0.005	<0.001	<0.001	<0.001	0.065
Natural, Intermixed, Interface, and Developed Land-use	0.005	0.027	0.025	<0.001	0.004
North-South Trend & Forest vs. Non-forest	<0.001	0.019	0.030	0.0969	0.567^a
Different in Forest vs. Non-forest	<0.001	0.015	0.030	<0.001	0.012
North-South Trend	<0.001	0.017	0.007	<0.001	0.121^a
Homogenous Density	<0.001	0.001	0.001	0.903^a	0.003
Detection Model					
$g0^b[\text{Sex}^d + \text{Forest}^e], \sigma^c[\text{Sex}^d + \text{Forest}^e]$	0.999^a	0.105^a	0.997^a	<0.001	0.942^a
$g0[\text{Sex} + b^f], \sigma[\text{Sex} + b^f]$	<0.001	0.870^a	0.002	0.999^a	<0.001
$g0[\text{Sex} + \text{Forest}], \sigma[\text{Sex} + b]$	<0.001	<0.001	<0.001	<0.001	0.011
$g0[\text{Sex}], \sigma[\text{Sex} + b]$	<0.001	0.017	<0.001	<0.001	<0.001
$g0[\text{Sex} + \text{Forest}], \sigma[\text{Sex}]$	<0.001	0.007	<0.001	<0.001	0.034
$g0[\text{Sex} + b], \sigma[\text{Sex}]$	<0.001	<0.001	<0.001	<0.001	<0.001
$g0[\text{Sex}], \sigma[\text{Sex} + \text{Forest}]$	<0.001	<0.001	<0.001	<0.001	<0.001
$g0[\text{Sex} + b], \sigma[\text{Sex} + \text{Forest}]$	<0.001	<0.001	<0.001	<0.001	<0.001
$g0[\text{Sex} + b + \text{Forest}], \sigma[\text{Sex}]$	<0.001	<0.001	<0.001	<0.001	<0.001
$g0[\text{Sex}], \sigma[\text{Sex} + b + \text{Forest}]$	<0.001	<0.001	<0.001	<0.001	<0.001
$g0[\text{Sex} + b + \text{Forest}], \sigma[\text{Sex} + b + \text{Forest}]$	<0.001	<0.001	<0.001	<0.001	<0.001
$g0[\text{Sex}], \sigma[\text{Sex}]$	<0.001	<0.001	<0.001	<0.001	<0.001

^a Bold weights indicate models with support > 0.10.

^b Baseline detection probability ($g0$)

^c Dispersion parameter (σ) of detection function.

^d Effect of individual gender (Sex) on detection function.

^e Effect of percent forest cover at detection site (Forest) on detection function.

^f Effect of previous encounter (b) on detection function.

Table 2.2 Estimated values, standard error and t-values for parameters included in top ranked spatial mark-recapture models of black bear density (individuals/km²) on North, East, and the Combined study areas.

Density Covariate ^a		β^b	Std. Error	<i>t-value</i>
Combined study area				
All Individuals	Density: Rural	0.125	0.019	6.579
	Density: Exurban	0.182	0.020	9.100
	Density: Suburban	0.023	0.049	0.478
	Density: Urban	0.000	-	-
	Latitude	0.103	0.016	6.510
Females	Density: Rural	0.100	0.026	3.825
	Density: Exurban	0.095	0.038	2.452
	Density: Suburban	0.000	-	-
	Latitude	-3.99E-05		
Males	Density: Rural	0.037	0.018	1.979
	Density: Exurban	0.058	0.022	2.607
	Density: Suburban	0.000	-	-
	Latitude	7.54E-05	1.01E-04	0.747
East Study Area				
	Density: Forest	0.246	0.045	5.467
	Density: Non-Forest	8.86E-11	1.81E-11	4.899
	Latitude	0.037	0.017	2.121
North Study Area				
	Density	0.110	0.008	12.968

^aDensity modeled as function of spatial covariates using identity link.

^b β parameter equivalent to density estimate in land-use/land cover categories.

Table S2.1. Full AICc model selection results for spatial mark-recapture models fit to detection data from Combined study area in northwest Connecticut 2013 - 2014. The top ranked detection model was identified first, and subsequently used in all models of variable bear density. Covariates of detection included individual sex (Sex), a behavioral response to prior detection (b), and percent forest cover at a sampling site (Forest).

	Hypothesized Bear Density	Detection Model	AICc	$\Delta AICc$	ω_i
Combined Study Area					
Density	North-South Trend & Different in Rural, Low, and Med/High Development	g0[Sex+Forest], σ [Sex+Forest]	3817.23	0.00	0.736
	Different in Rural, Low, and Med/High Development	g0[Sex+Forest], σ [Sex+Forest]	3819.37	2.13	0.253
	North-South Trend & Different in Natural, Intermixed, Interface, and Developed Land Use	g0[Sex+Forest], σ [Sex+Forest]	3827.27	10.04	0.005
	Different in Natural, Intermixed, Interface, and Developed Land Use	g0[Sex+Forest], σ [Sex+Forest]	3827.27	10.04	0.005
	North-South Trend	g0[Sex+Forest], σ [Sex+Forest]	3831.40	14.17	0.001
	Homogenous Density	g0[Sex+Forest], σ [Sex+Forest]	3853.13	35.89	0.000
	Difference between forest vs. non-forest	g0[Sex+Forest], σ [Sex+Forest]	3835.05	17.81	0.000
	North-South Trend & Difference between forest vs. non-forest	g0[Sex+Forest], σ [Sex+Forest]	3833.62	16.39	0.000
Detection	Homogenous	g0[Sex+Forest], σ [Sex+Forest]	3853.13	0.00	1.000
	Homogenous	g0[Sex+b], σ [Sex+b]	3885.92	32.80	0.000
	Homogenous	g0[Sex+Forest], σ [Sex+b]	3893.65	40.53	0.000
	Homogenous	g0[], σ [Sex+b]	3901.67	48.54	0.000
	Homogenous	g0[Sex+Forest], σ []	3924.20	71.08	0.000
	Homogenous	g0[Sex+b], σ []	3932.26	79.14	0.000
	Homogenous	g0[], σ []	3933.04	79.92	0.000
	Homogenous	g0[], σ [Sex+Forest]	3970.43	117.30	0.000
	Homogenous	g0[Sex+b], σ [Sex+Forest]	3971.81	118.69	0.000

Table S2.2. Full AICc model selection results for spatial mark-recapture models fit to detection data collected 2013 - 2014 from East study area in northwest Connecticut. The top ranked detection model was identified first, and subsequently used in all models of variable bear density. Covariates of detection included individual sex (Sex), a behavioral response to prior detection (b), and percent forest cover at a sampling site (Forest).

	Hypothesized Bear Density	Detection Model	AICc	$\Delta AICc$	ω_i
	East Study Area				
Density	North-South Trend & Difference between forest vs. non-forest	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	967.98	0.00	0.567
	North-South Trend & Different in Rural, Low, and Med/High Development	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	969.75	1.77	0.234
	North-South Trend	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	971.06	3.08	0.121
	North-South Trend & Different in Natural, Intermixed, Interface, and Developed Land Use	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	972.31	4.33	0.065
	Difference between forest vs. non-forest	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	975.70	7.72	0.012
	Different in Rural, Low, and Med/High Development	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	976.11	8.13	0.010
	Different in Natural, Intermixed, Interface, and Developed Land Use	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	978.00	10.03	0.004
	Homogenous Density	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	978.36	10.38	0.003
Detection	Homogenous	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	978.36	0.00	0.942
	Homogenous	$g0[\text{Sex}+\text{Forest}], \sigma[]$	985.02	6.66	0.034
	Homogenous	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+b]$	987.34	8.98	0.011
	Homogenous	$g0[], \sigma[\text{Sex}+\text{Forest}]$	994.45	16.09	0.000
	Homogenous	$g0[\text{Sex}+b], \sigma[\text{Sex}+\text{Forest}]$	996.02	17.66	0.000
	Homogenous	$g[], \sigma[]$	1002.74	24.38	0.000
	Homogenous	$g0[], \sigma[\text{Sex}+b]$	1004.50	26.14	0.000
	Homogenous	$g0[\text{Sex}+b], \sigma[]$	1004.57	26.21	0.000
	Homogenous	$g0[\text{Sex}+b], \sigma[\text{Sex}+b]$	1004.79	26.43	0.000

Table S2.3. Full AICc model selection results for spatial mark-recapture models fit to detection data collected 2013 – 2014 from North study area in northwest Connecticut. The top ranked detection model was identified first, and subsequently used in all models of variable bear density. Covariates of detection included individual sex (Sex), a behavioral response to prior detection (b), and percent forest cover at a sampling site (Forest).

	Hypothesized Bear Density	Detection Model	AICc	$\Delta AICc$	ω_i
North Study Area					
Density	Homogenous	$g0[Sex+b], \sigma[Sex+b]$	2718.39	0.00	0.903
	North-South Trend	$g0[Sex+b], \sigma[Sex+b]$	2739.24	20.85	0.000
	North-South Trend & Difference between forest vs. non-forest	$g0[Sex+b], \sigma[Sex+b]$	2722.85	4.46	0.097
	Different in forest vs. non-forest	$g0[Sex+b], \sigma[Sex+b]$	2740.77	22.39	<0.001
	Different in Rural, Low, and Med/High Development	$g0[Sex+b], \sigma[Sex+b]$	2740.97	22.59	<0.001
	Different in Natural, Intermixed, Interface, and Developed Land Use	$g0[Sex+b], \sigma[Sex+b]$	2763.29	44.90	<0.001
	North-South Trend & Different in Rural, Low, and Med/High Development	$g0[Sex+b], \sigma[Sex+b]$	2765.44	47.05	<0.001
	North-South Trend & Different in Natural, Intermixed, Interface, and Developed Land Use	$g0[Sex+b], \sigma[Sex+b]$	2773.00	54.61	<0.001
Detection	Homogenous	$g0[Sex+b], \sigma[Sex+b]$	2718.39	0.00	1.000
	Homogenous	$g0[], \sigma[Sex+b]$	2738.25	19.86	<0.001
	Homogenous	$g0[Sex+Forest], \sigma[Sex+b]$	2740.36	21.97	<0.001
	Homogenous	$g0[Sex+Forest], \sigma[Sex+Forest]$	2757.98	39.60	<0.001
	Homogenous	$g0[], \sigma[Sex+Forest]$	2760.32	41.93	<0.001
	Homogenous	$g0[b], \sigma[Sex+Forest]$	2762.32	43.93	<0.001
	Homogenous	$g0[], \sigma[]$	2764.35	45.96	<0.001
	Homogenous	$g0[Sex+Forest], \sigma[]$	2764.48	46.10	<0.001
	Homogenous	$g0[Sex+b], \sigma[]$	2766.10	47.72	<0.001

Table 3.1. Notation and description of landscape factors used to model landscape resistance to dispersal movement among American black bear in western CT. Resistance surfaces were created for each landscape factor, and all combinations of factors in addition to pairwise geographic distance.

Factor & Hypothesis	Code	Description
Land Cover		
Forest Resistance	FR	High resistance at high forest cover
Forest Conductance	FC	High resistance at low forest cover
Housing		
Housing Density Resistance	HDR	High resistance at maximum housing density
Housing Density Conductance	HDC	High resistance at minimum housing density
50 houses/km2 Resistance	HDR50	High resistance at 50 houses/km2
100 houses/km2 Resistance	HDR100	High resistance at 100 houses/km2
50 houses/km2 Conductance	HDC50	Minimum resistance at 50 houses/km2
100 houses/km2 Conductance	HDC100	Minimum resistance at 100 houses/km2
Roads		
Primary Roads Resistance	Rd100_1	High resistance at primary roads
Unequal Roads Resistance	Rd100_50	High resistance at primary roads; intermediate resistance at secondary roads
Equal Roads Resistance	Rd100_100	High resistance at primary & secondary roads
Primary Roads Conductance	Rd100_1C	Minimum resistance at primary roads
Unequal Roads Conductance	Rd100_50C	Minimum resistance at primary roads; intermediate resistance at secondary roads
Equal Roads Conductance	Rd100_100C	Minimum resistance at primary & secondary roads

Table 3.2. Results of multiple regression on distance matrices evaluating relationships between landscape resistance hypotheses and spatial patterns of genetic variation among American black bears in western CT. Only models exhibiting stronger correlation with pairwise genetic distance than geographic distance alone and significant beta parameters for the hypothesized surface are displayed. Analyses were performed among female individuals in North and East study areas.

Landscape Model		R	F	$\beta_{SURFACE}$	β_{GEO}
East Grid	HDC,FR + Geo	0.335**	25.471**	-36.128**	8.677E-5
	HDC,FR	0.323**	47.072**	-34.826**	
	HDC + Geo	0.315*	22.146*	-1.174**	6.50E-5
	HDC	0.308*	42.194*	-11.556*	
	HDC, R100_100C + Geo	0.289*	18.308*	-21.290*	1.00E-4
	HDC, R100_100C	0.270*	31.840*	-19.760*	
	HDC100 + Geo	0.240	12.350	-15.255*	2.80E-4*
	HDR100	-0.188*	14.837*	1.744*	
North Grid	HDC,Rd100_100	0.156**	35.72**	15.75**	
	Rd100_100	0.154**	34.65**	0.15**	
	Rd50_100	0.153**	34.26**	0.15**	
	HDC100	0.151**	33.56**	0.66**	
	HDC50	0.150**	32.98**	0.28**	
	HDR,FR	0.131**	24.97**	0.02**	
	HDC	0.130**	24.08**	0.67**	
	FR, Rd100_100	0.125**	22.83**	0.04**	

* $p < 0.05$

** $p < 0.01$

Table 4.1. Model selection results for competing step selection functions fit to hourly black bear movement data, showing frequencies of datasets for which a model type was supported ($AICc < 2$). Datasets were defined as GPS locations produced by an individual bear in each season. Datasets for with competing hypotheses were model averaged, indicated with a (+) sign. Housing and Housing*Time models are collapsed into the Housing category, likewise for Highway. Models with a Time interaction are collapsed into the Time category.

Model Category	Summer	Hyperphagia	Pre-denning
Base	1	0	0
Housing	12	11	22
Highway	43	46	22
Housing + Highway	10	5	12
No Time	5	12	27
Time	40	33	10
Time + No Time	21	16	20

Table 4.2. Results from linear mixed models of black bear selection for anthropogenic variables as a function of fixed effects on home range housing density, season, and reproductive status. Variables included distance from local roads (RDist), low intensity residential areas (Res), distance from highways (HDist), and highway crossing (H-Xing). Wald's chi-square tests on all fixed effects are displayed, with significant effects ($p < 0.10$) in bold. Beta coefficients are reported for relationships between housing density and selection for each season. Bold values indicate significant ($p < 0.10$) results.

	RDist	Res	HDist	H-Xing
Log Home Range Housing Density	$\chi^2 = \mathbf{10.24}$ $p = \mathbf{0.001}$	$\chi^2 = 1.61$ $p = 0.20$	$\chi^2 = \mathbf{5.76}$ $p = \mathbf{0.02}$	$\chi^2 = 0.03$ $p = 0.87$
Log Home Range Housing Density * Season	$\chi^2 = 1.68$ $p = 0.43$	$\chi^2 = 4.06$ $p = 0.13$	$\chi^2 = \mathbf{4.47}$ $p = \mathbf{0.10}$	$\chi^2 = 3.25$ $p = 0.20$
Season	$\chi^2 = \mathbf{2.88}$ $p = \mathbf{0.09}$	$\chi^2 = 0.578$ $p = 0.447$	$\chi^2 = 1.131$ $p = 0.25$	$\chi^2 = \mathbf{39.82}$ $p < \mathbf{0.001}$
Reproductive Status	$\chi^2 = \mathbf{10.67}$ $p = \mathbf{0.001}$	$\chi^2 = \mathbf{3.99}$ $p = \mathbf{0.04}$	$\chi^2 = 0.18$ $p = 0.67$	$\chi^2 = \mathbf{23.81}$ $p < \mathbf{0.001}$
Season*Reproductive Status	$\chi^2 = 0.086$ $p = 0.96$	$\chi^2 = \mathbf{2.50}$ $p = \mathbf{0.08}$	$\chi^2 = 0.051$ $p = 0.82$	$\chi^2 = \mathbf{20.86}$ $p < \mathbf{0.001}$

Table 4.3. Relationship between black bear selection for anthropogenic variables and home range housing density, estimated by beta coefficients from linear mixed models. Relationships are reported for models fit to summer, hyperphagia, pre-denning data, and to bears with and without cubs. Variables included distance from local roads (RDist), low intensity residential areas (Res), distance from highways (HDist), and highway crossing (H-Xing). Bold values indicate significant ($p < 0.10$) results.

	RDist	Res	HDist	H-Xing
Summer	$\beta = \mathbf{0.566}$ $p < \mathbf{0.001}$	$\beta = 0.118$ $p < 0.252$	$\beta = \mathbf{0.341}$ $p = \mathbf{0.009}$	$\beta = 0.484$ $p < 0.257$
Hyperphagia	$\beta = \mathbf{0.453}$ $p < \mathbf{0.001}$	$\beta = -0.124$ $p < 0.248$	$\beta = 0.070$ $p < 0.484$	$\beta = 0.034$ $p < 0.913$
Pre-denning	$\beta = 0.317$ $p < 0.125$	$\beta = 0.140$ $p < 0.253$	$\beta = -0.072$ $p < 0.720$	$\beta = -0.320$ $p < 0.175$
Cubs	$\beta = \mathbf{0.558}$ $p = \mathbf{0.002}$	$\beta = -0.105$ $p = 0.375$	$\beta = 0.158$ $p = 0.538$	$\beta = 0.102$ $p = 0.625$
Without Cubs	$\beta = \mathbf{0.554}$ $p = \mathbf{0.003}$	$\beta = 0.067$ $p = 0.745$	$\beta = \mathbf{0.366}$ $p = \mathbf{0.063}$	$\beta = 0.480$ $p = 0.505$

FIGURES

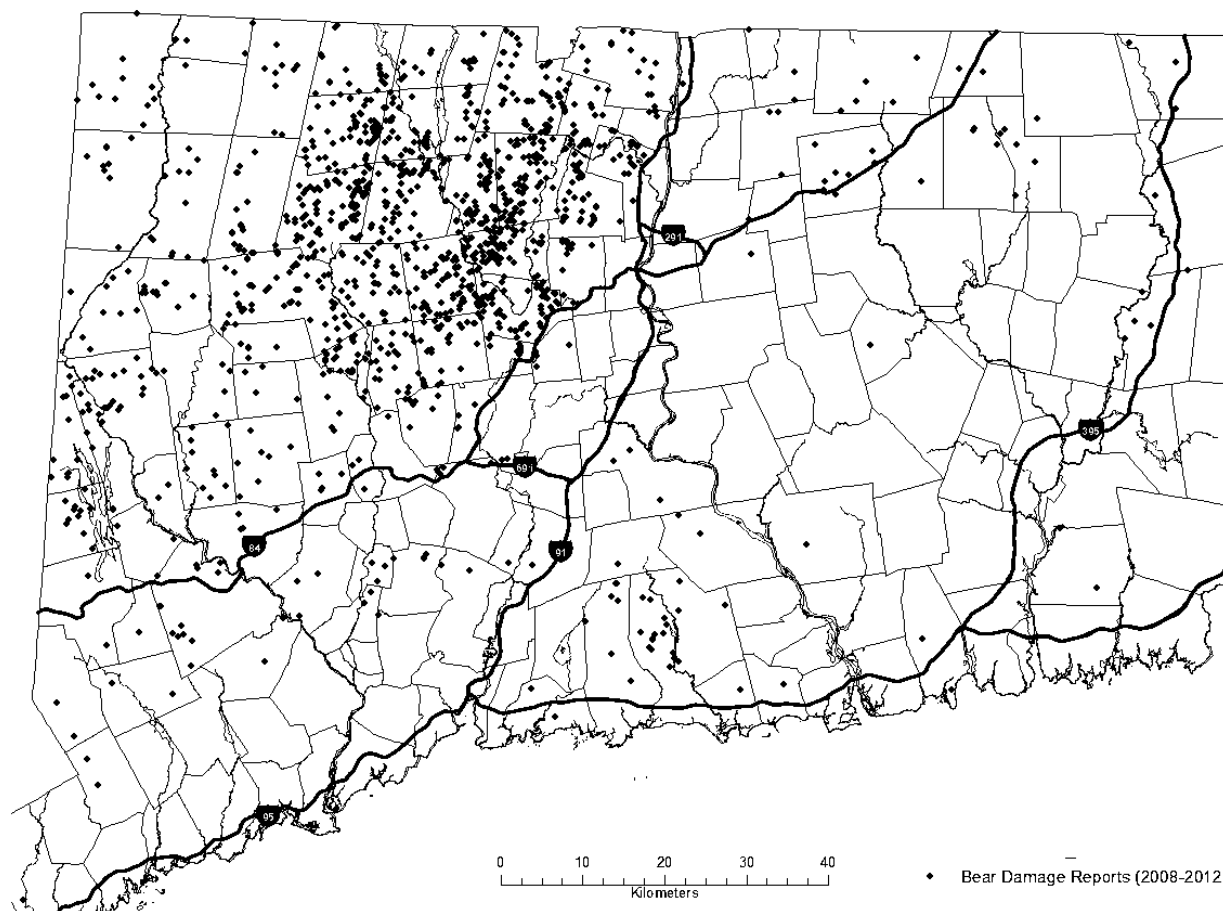


Fig. 1.1 Human-black bear conflict locations reported to Connecticut Department of Energy and Environmental Protection from 2008 to 2012. Borders for all 166 Connecticut towns are displayed, which may appear similar to county lines in other states.

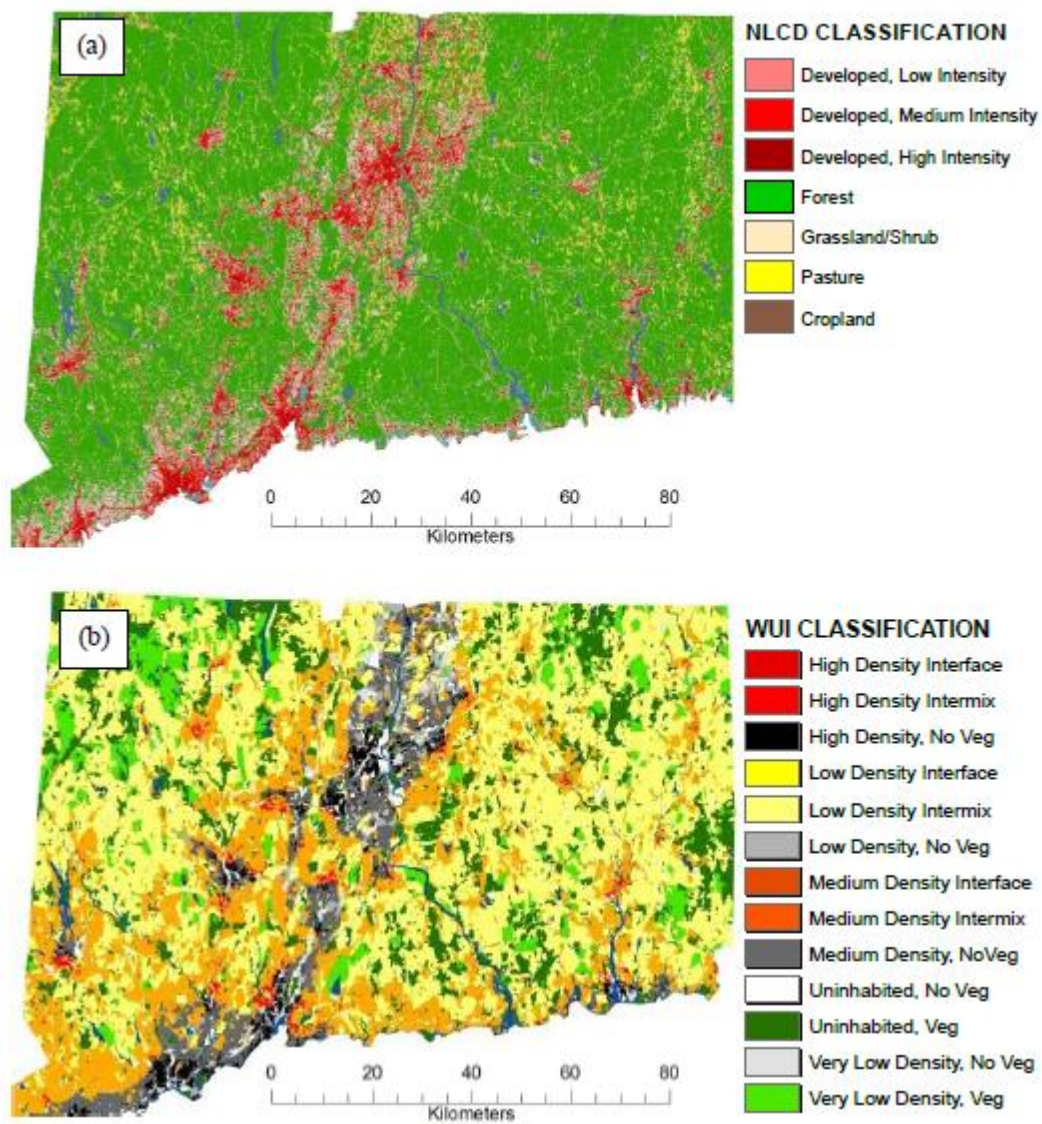


Fig. 1.2 2006 National Landcover Database (NLCD) landcover and 2005 Wildland-Urban Interface (WUI) classification for Connecticut showing a) predominant forest cover in green and b) intermixed land use (>1 house/16 ha and >50% forest cover) in yellow.

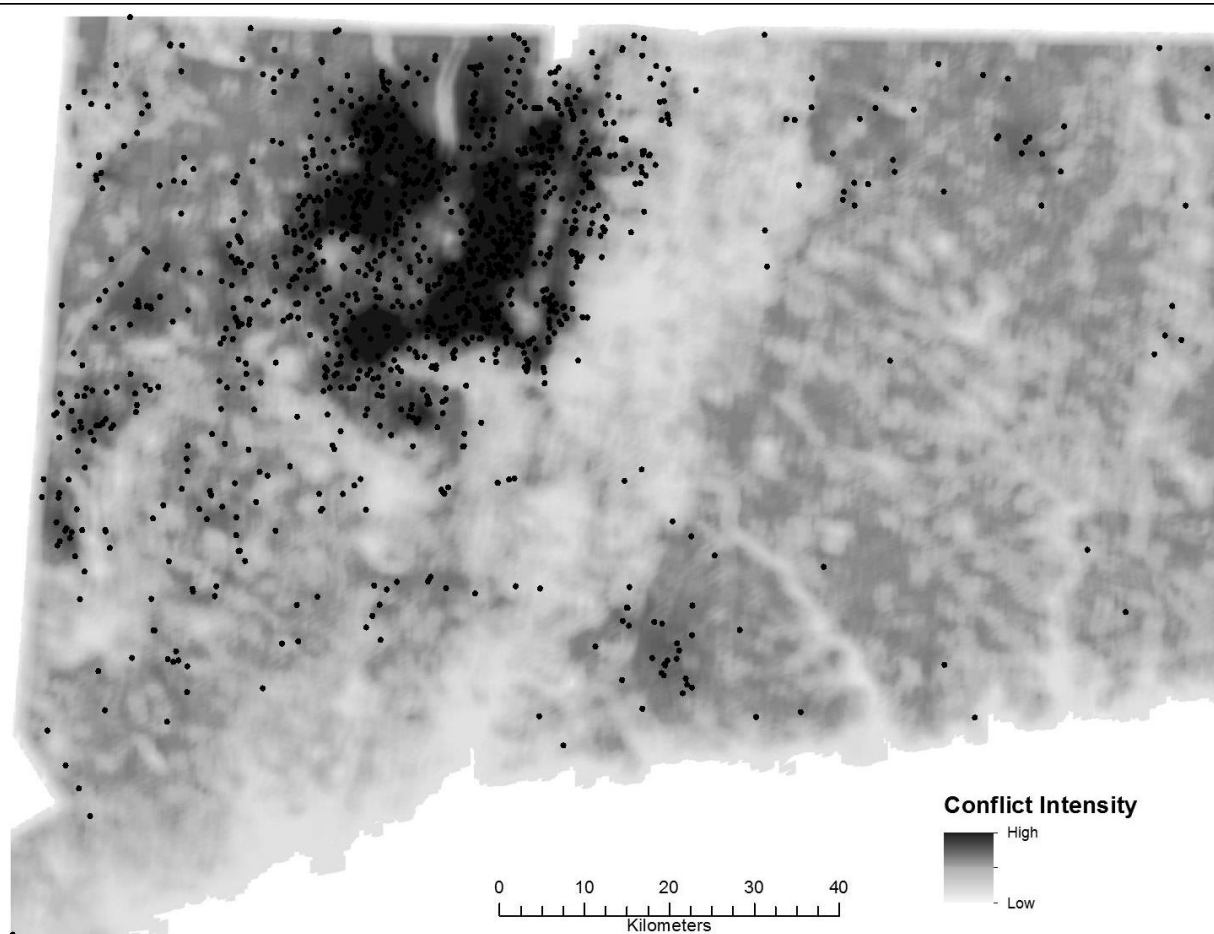


Fig. 1.3 Spatial distribution of risk of human-black bear conflict, if bears were present throughout Connecticut. We calculated relative risk of human-bear conflict at a location using values of landscape variables included in our top-ranked spatial model. These variables were percent forest cover, forest edge density, distance to main streams, distance to wetlands, and housing density. Locations of bear conflicts reported during 2008–2012 are displayed as points.

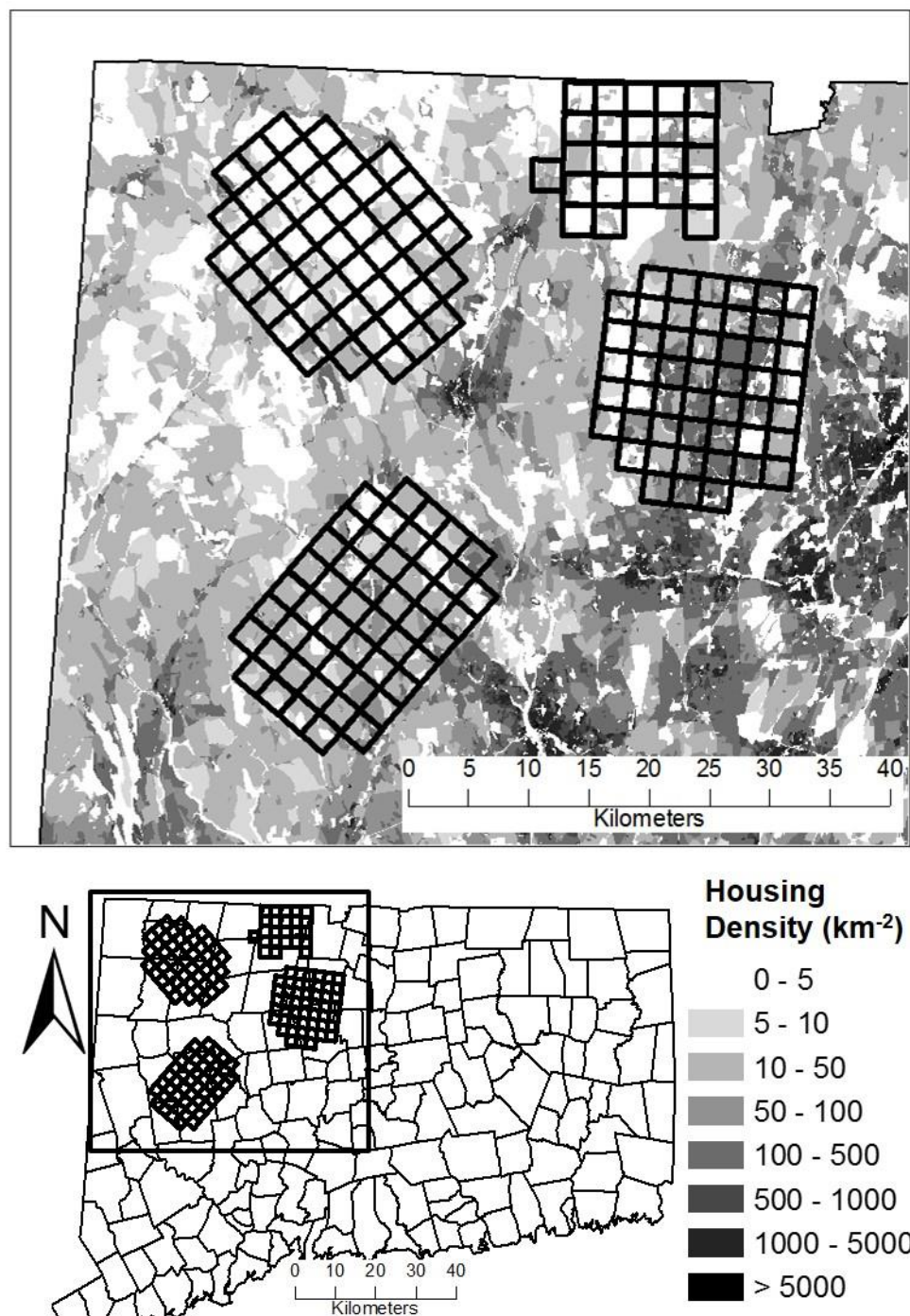


Fig. 2.1 Distribution of sampling grids across western Connecticut. Grids encompassed the majority of reproductive bear range in the state, and the range of housing densities found in CT in non-urban settings.

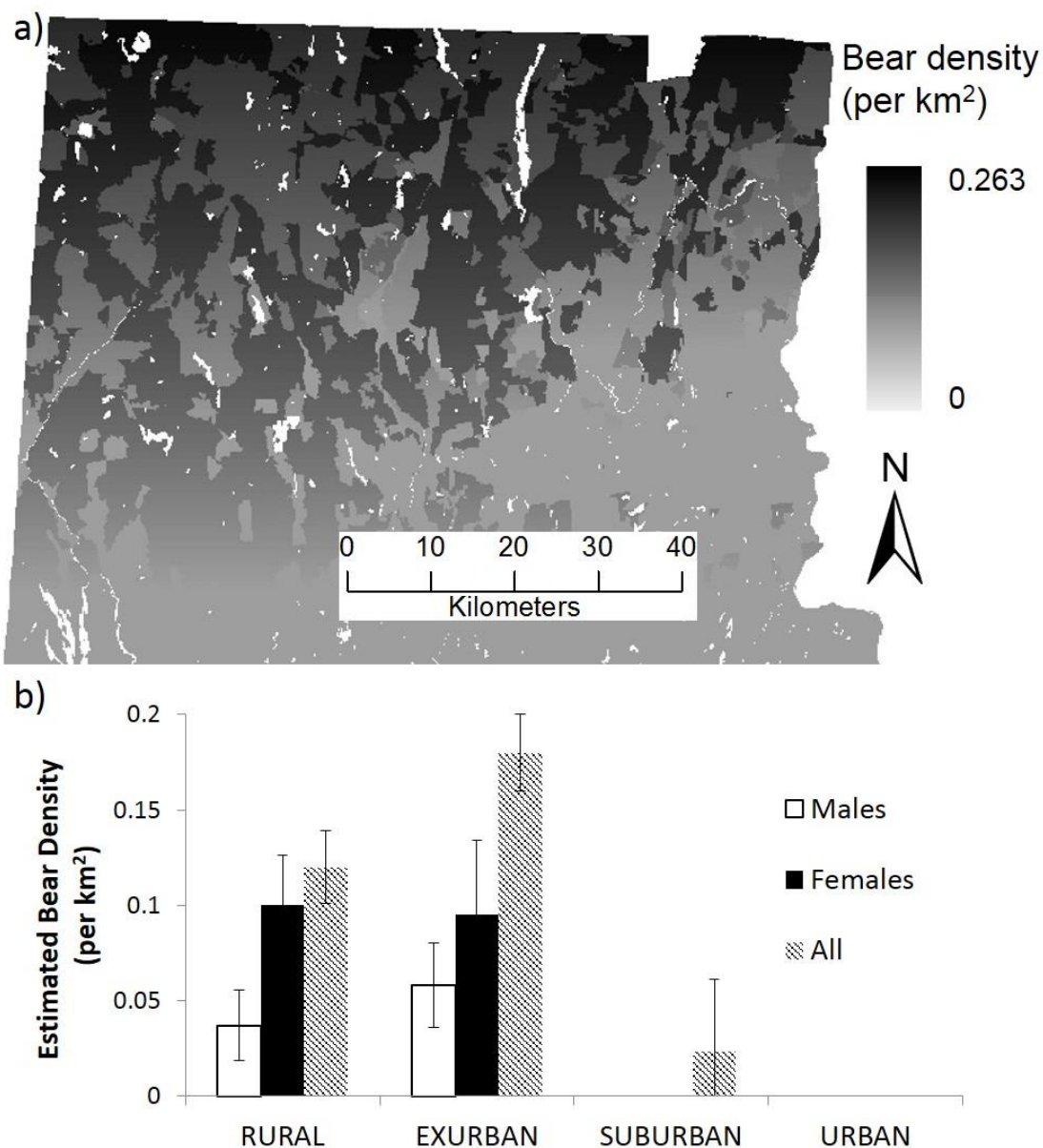


Fig. 2.2 Estimated black bear densities in western Connecticut. (a) Density estimated using the top ranked model of all individuals from the Combined study area across an area bounded by Connecticut's northern and western state boundaries, the Connecticut River and the southern latitude at which bear density declined to zero. (b) Mean bear density in rural, exurban, suburban, and urban development categories estimated by top-ranked models of all individuals, males, and females. Estimated values are at the average scaled latitude (0) for the Combined study area.

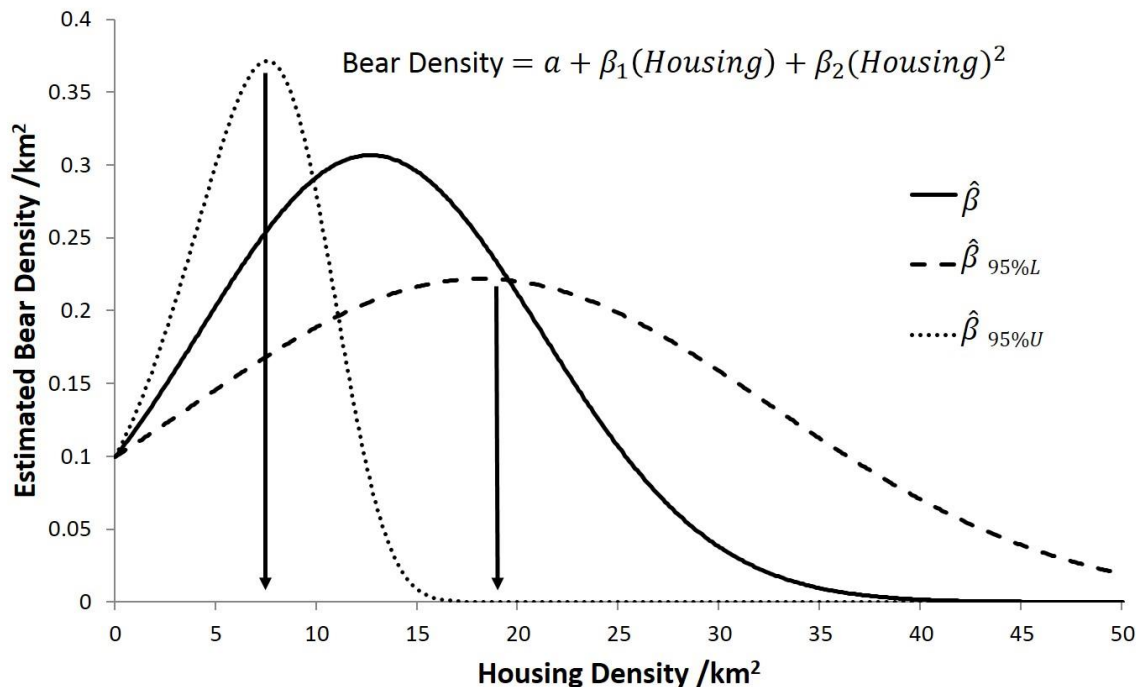


Fig. 2.3 Quadratic relationship between bear density and housing density, as estimated by a spatial mark-recapture model of density as a linear function of housing density + (housing density)² + latitude. Estimated values are at the average scaled latitude (0) for the Combined study area. Dotted and dashed curves were calculated using the upper and lower bounds of the beta parameters for housing density and squared housing density, the maxima of which (arrows) are used to indicate a 95% CI encompassing housing densities within which maximum bear density occurred (7.5 – 18.2 houses/km²)

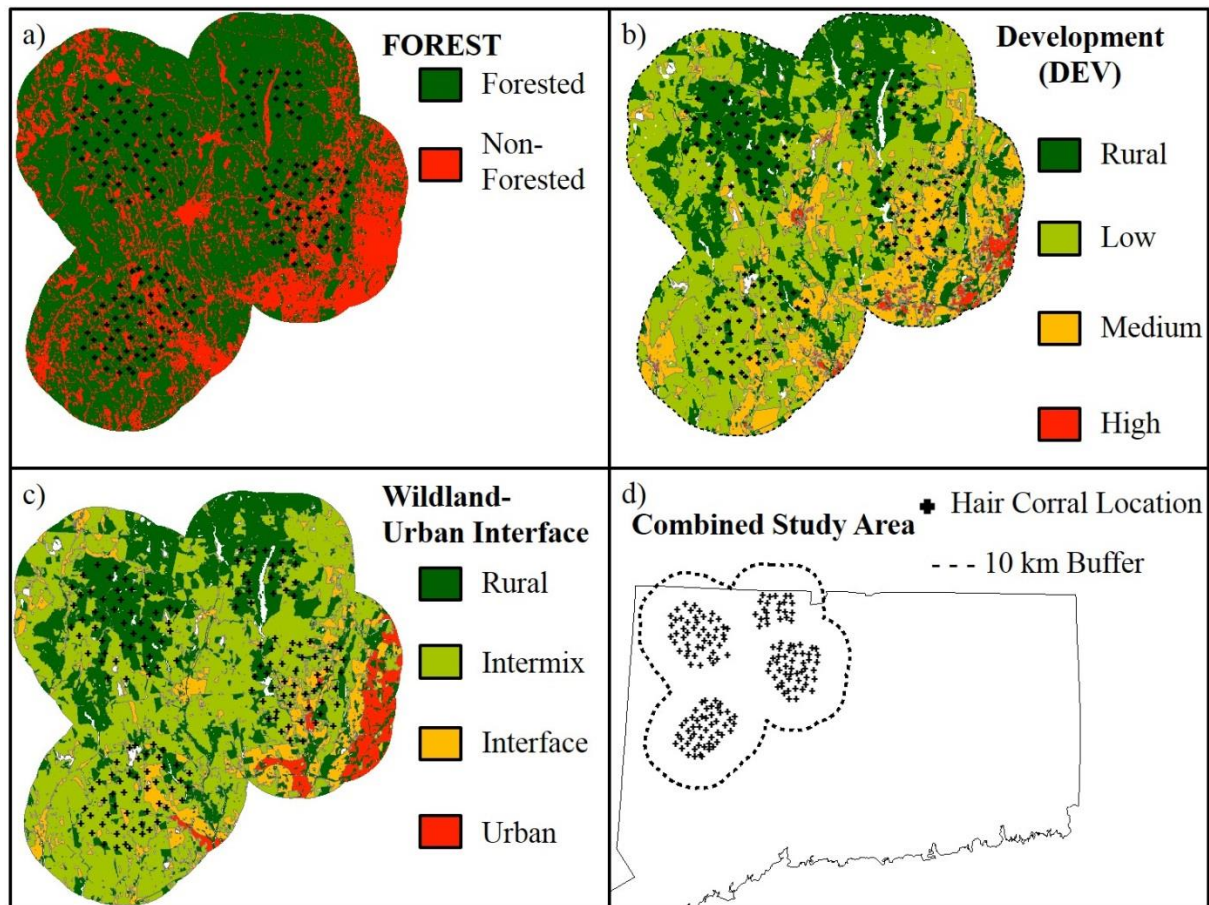


Fig. S2.1 Landscape classifications representing hypothesized relationships between (a) forest cover, (b) level of development, and (c) wildland-urban interface category and variation in black bear density within the (d) Combined Study Area in northwest Connecticut, USA. Landscapes were used as spatial covariates of density in spatially explicit mark-recapture models in which the rate of a heterogeneous poisson process representing rate of black bear activity centers varied between categories within a classification.

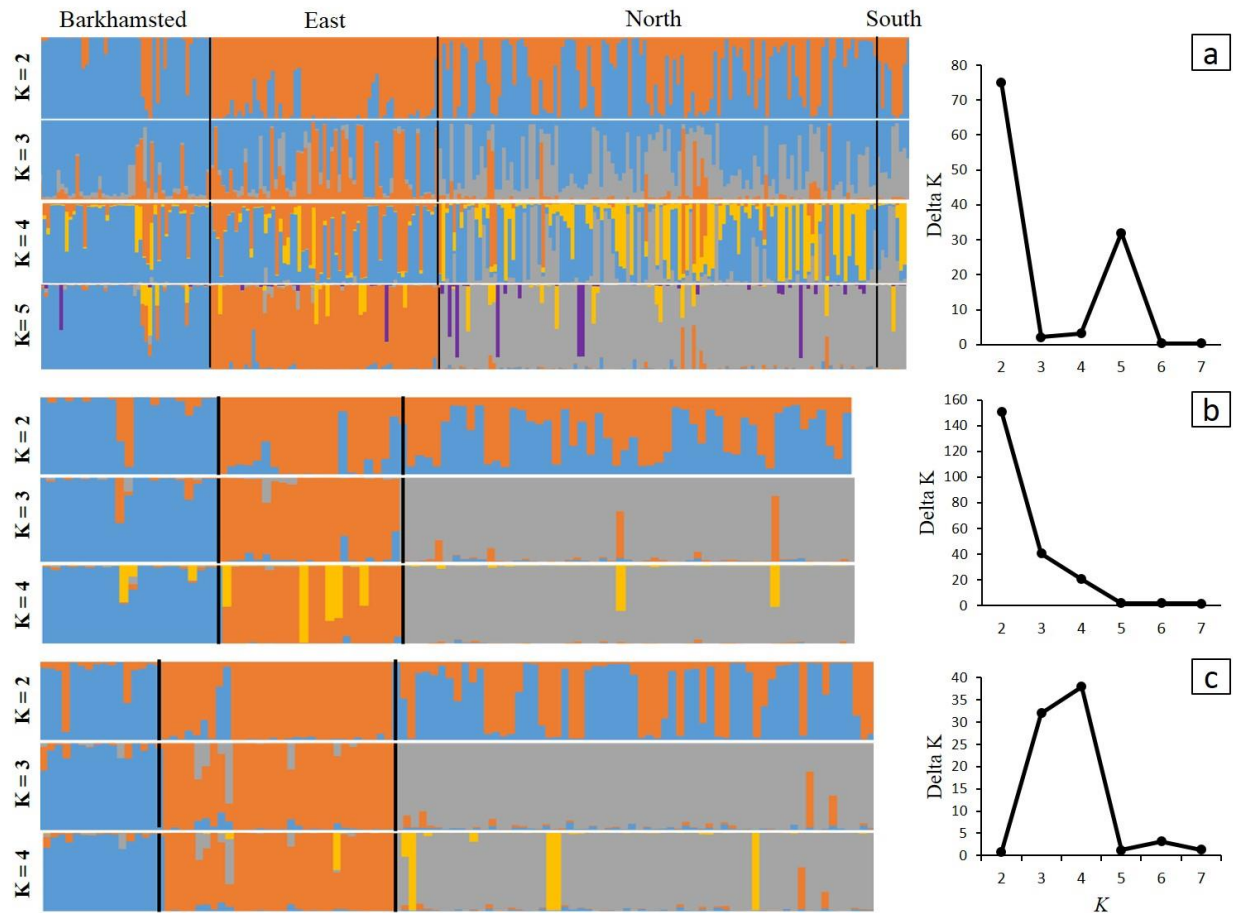


Fig. 3.1 Population assignment probabilities to an a priori number of genetic clusters (K) produced by STRUCTURE for (a) all black bears, (b) male individuals, and (c) female individuals detected in northwest Connecticut 2013 – 2014. Vertical black bars separate individuals detected on Barkhamsted, East, North, and South study grids. Delta K values indicate the most likely number of clusters.

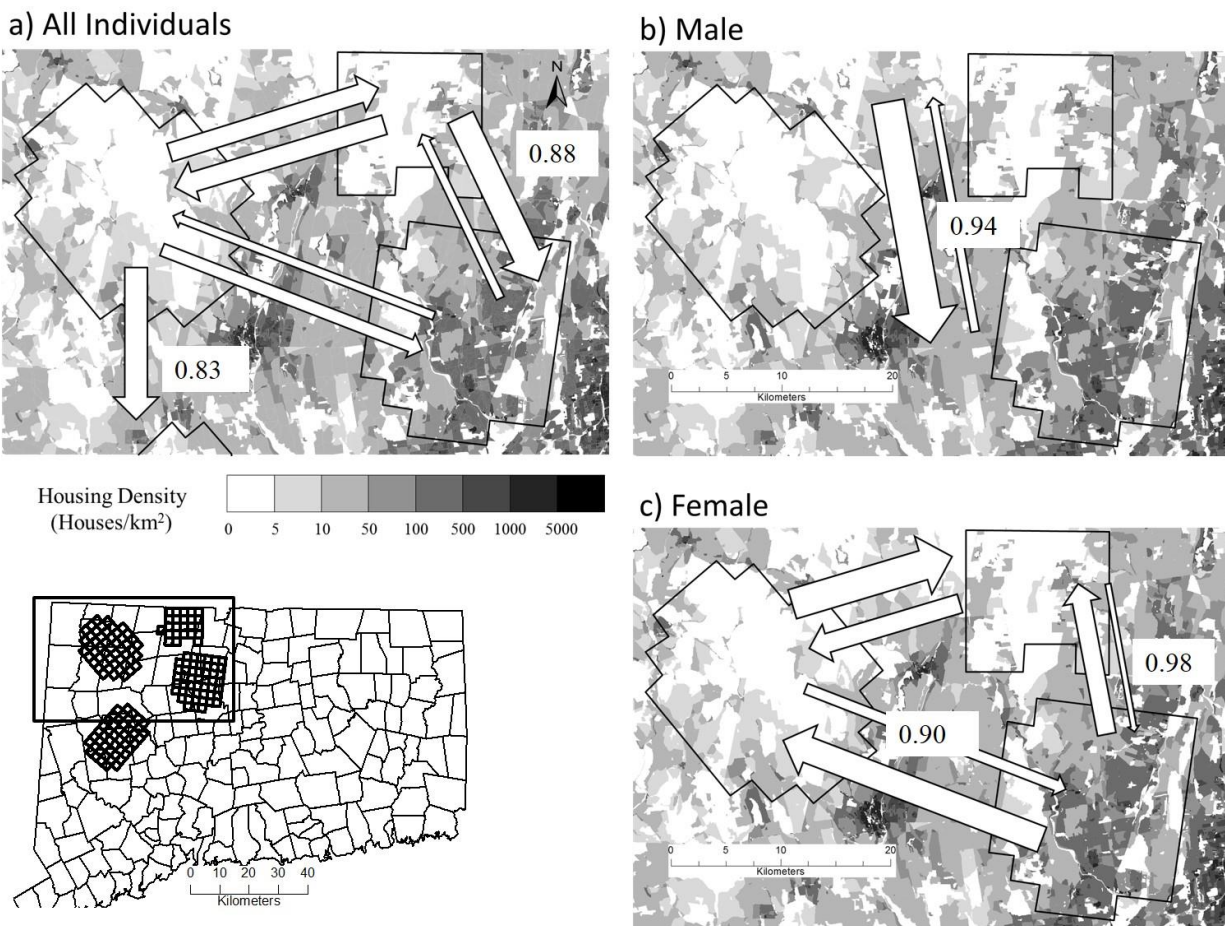


Fig. 3.2 Black bear migration rates among all individuals, males, and females between study areas in northwest CT. Probability of asymmetry values estimated by BIMr are displayed for comparisons with non-overlapping 95% CIs estimated by BAYESASS. Arrow sizes are proportional to BIMR estimated migration rates. Only rates greater than 0.10 are depicted. Rates among males were estimated between two genetic clusters indicated by STRUCTURE results.

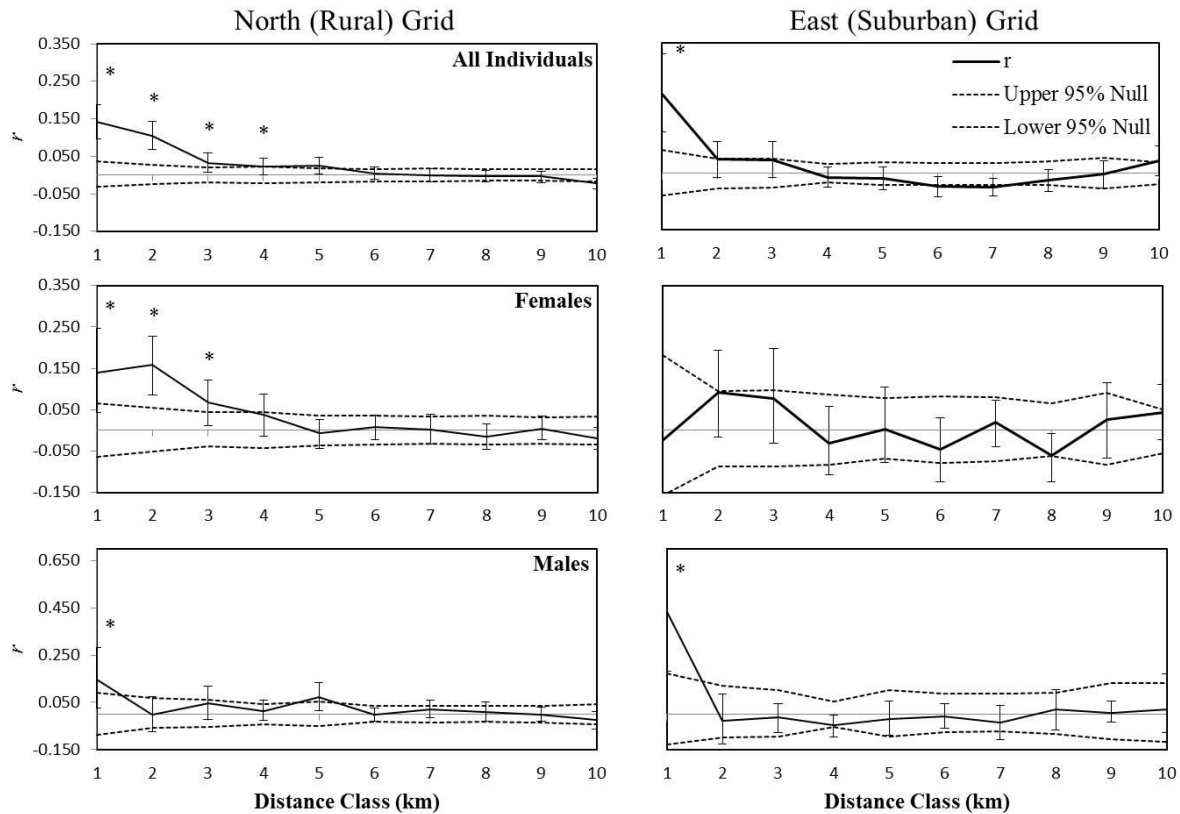


Fig. 3.3 Correlelogram plots depicting spatial autocorrelation of relatedness among black bears detected on North and East grid in 2013 and 2014. Dashed lines indicate a 95% CI surrounding the null hypothesis of randomly distributed genotypes, and vertical bars correspond to 95% error bars surrounding estimates of autocorrelation, obtained by bootstrapping. Significant, positive autocorrelation (*) inferred by estimates falling outside of the null hypothesis CI, and error bars that do not overlap zero (solid gray line).

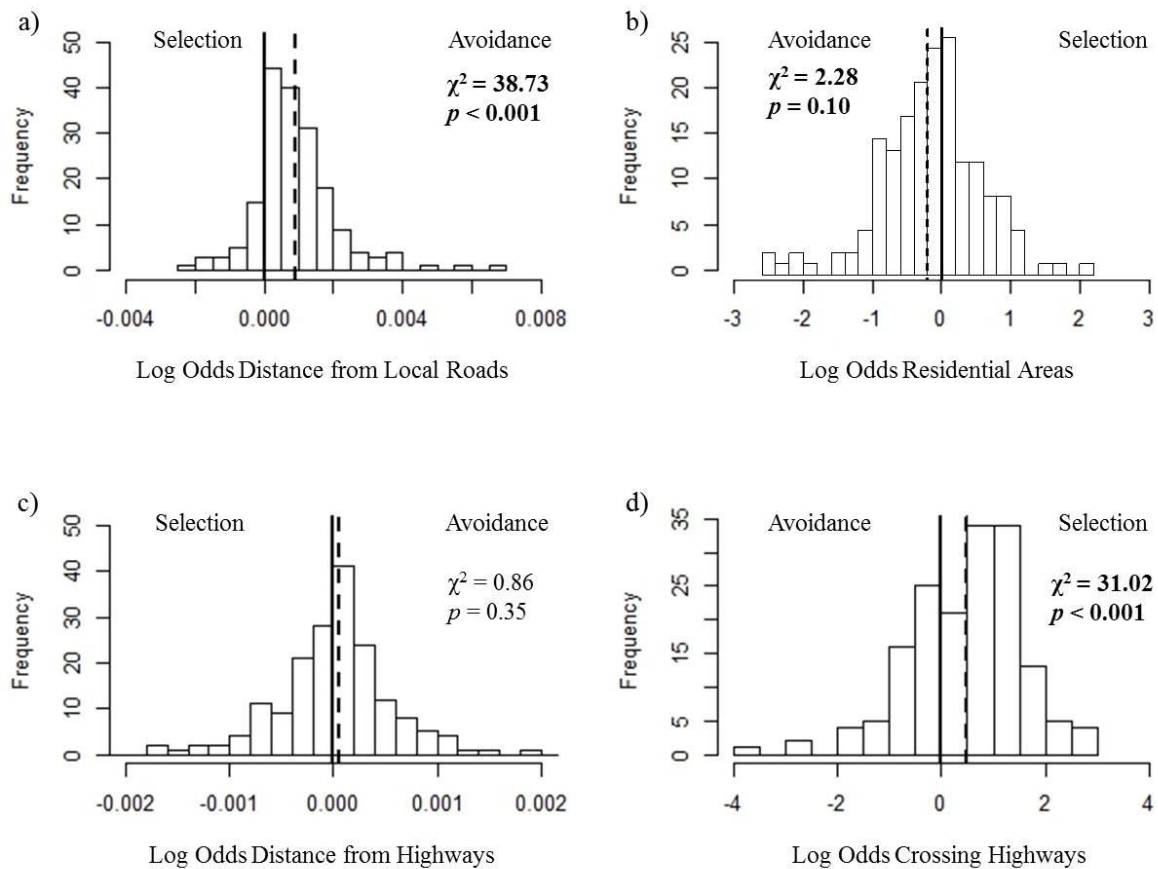


Fig. 4.1 Distribution of beta coefficients from top-ranked step selection models of black bear movement. Values indicate log odds of steps a) increasing distance from local roads b) ending in low intensity residential areas c) increasing distance from highways and d) crossing highways. Solid vertical lines at zero delineate regions indicating selection or avoidance of landscape features. Dashed vertical lines indicate the mean of the observed distribution. Wald's chi-square test on intercepts from linear mixed models indicate whether distribution means differ from zero.

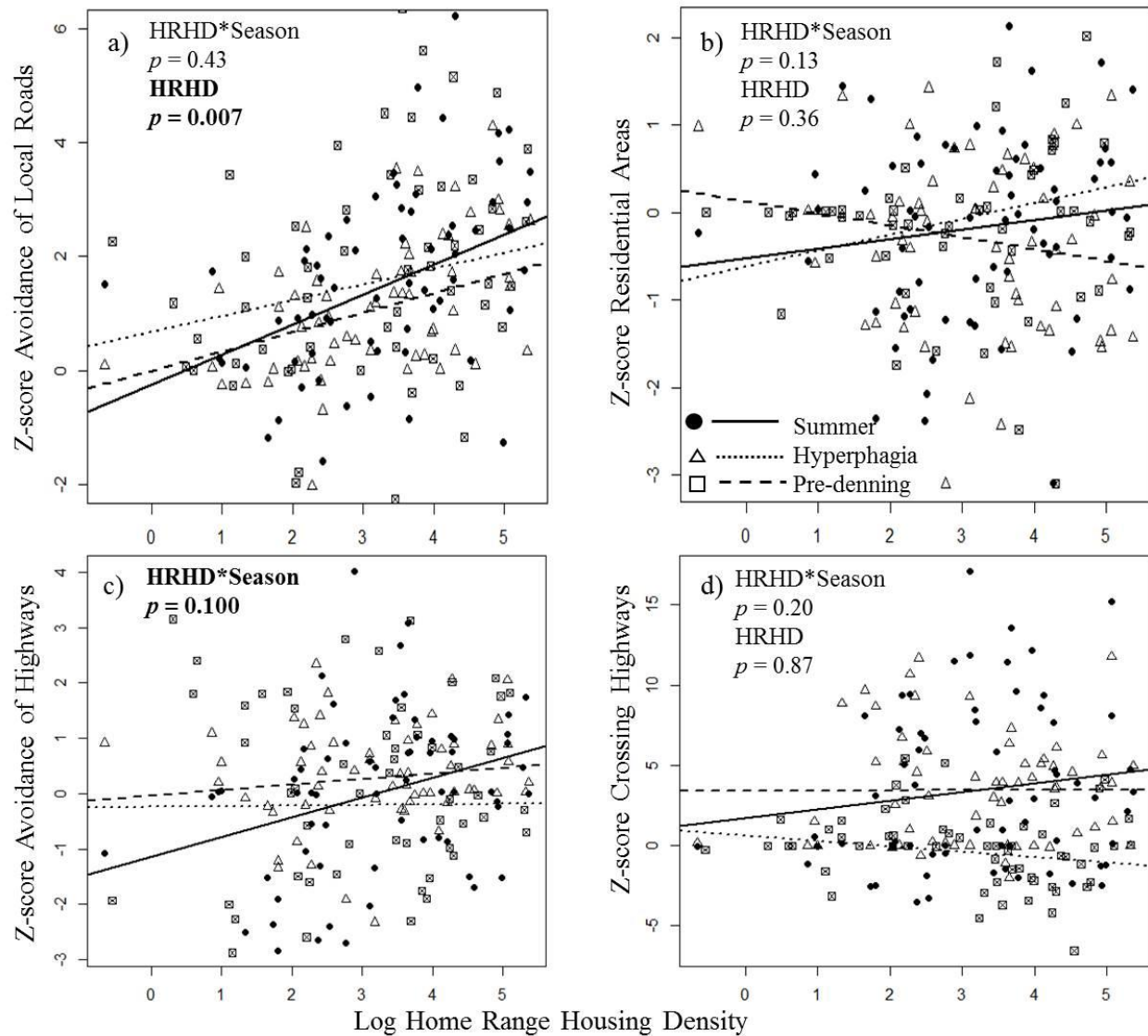


Fig. 4.2 Linear relationships between log home range housing density and z-scores estimating a) avoidance of local roads b) selection for steps in low intensity residential areas c) avoidance of highways and d) selection for steps crossing highways among individual black bears. Plots display relationships during summer (solid lines; solid dots), hyperphagia (dashed lines; triangles), and pre-denning (dotted lines; squares) separately. Test of significance for main effect of housing density (HRHD), and interaction between HRHD and season are displayed, with significant factors ($p < 0.10$) show in bold.

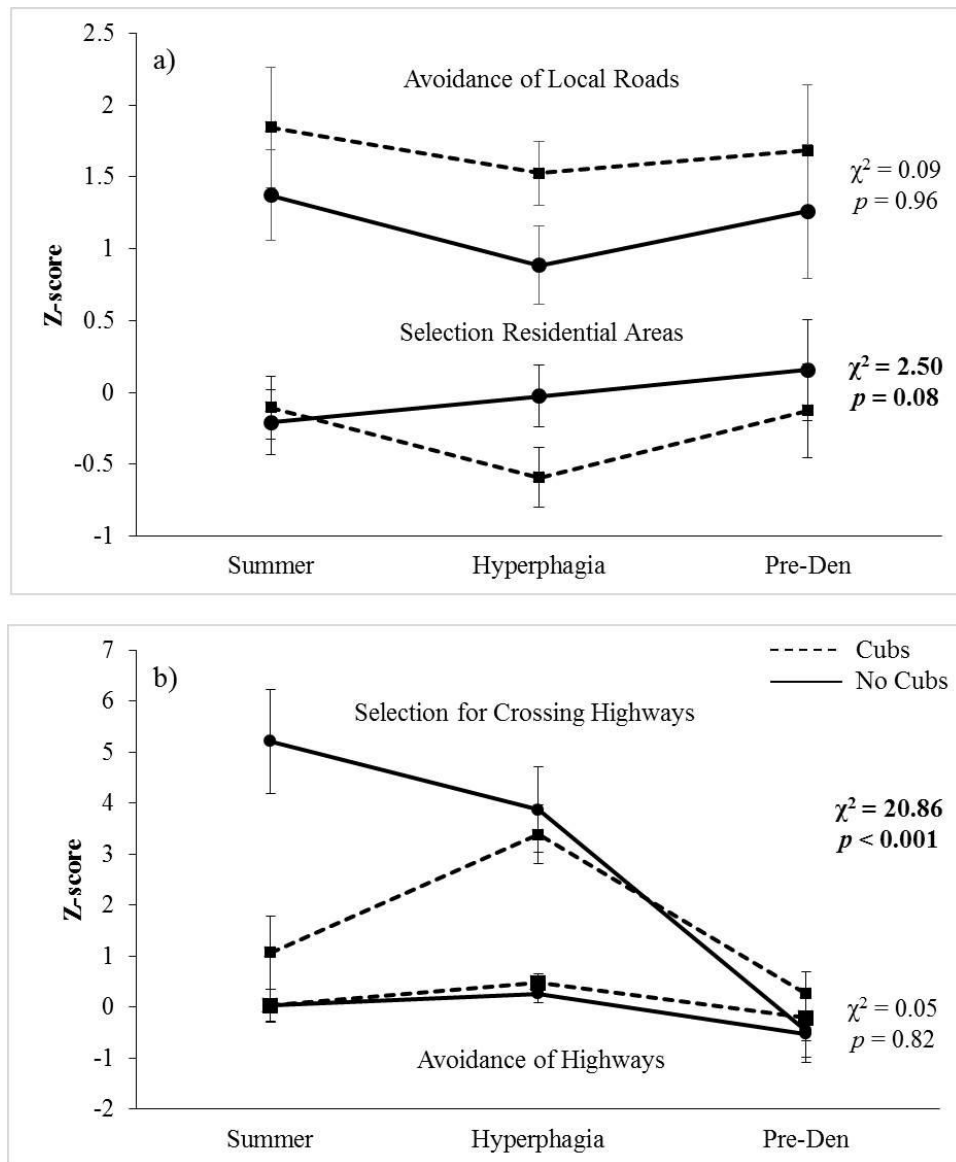


Fig. 4.3 Mean z-scores from black bear step selection functions for a) housing variables b) highway variables, by season and reproductive status. Z-scores for bears with cubs are shown by boxes and dashed lines, and by circles and solid lines for bears with cubs. Wald's chi-squared test on an interaction between season and reproductive status reported, with significant ($p < 0.10$) tests shown in bold.

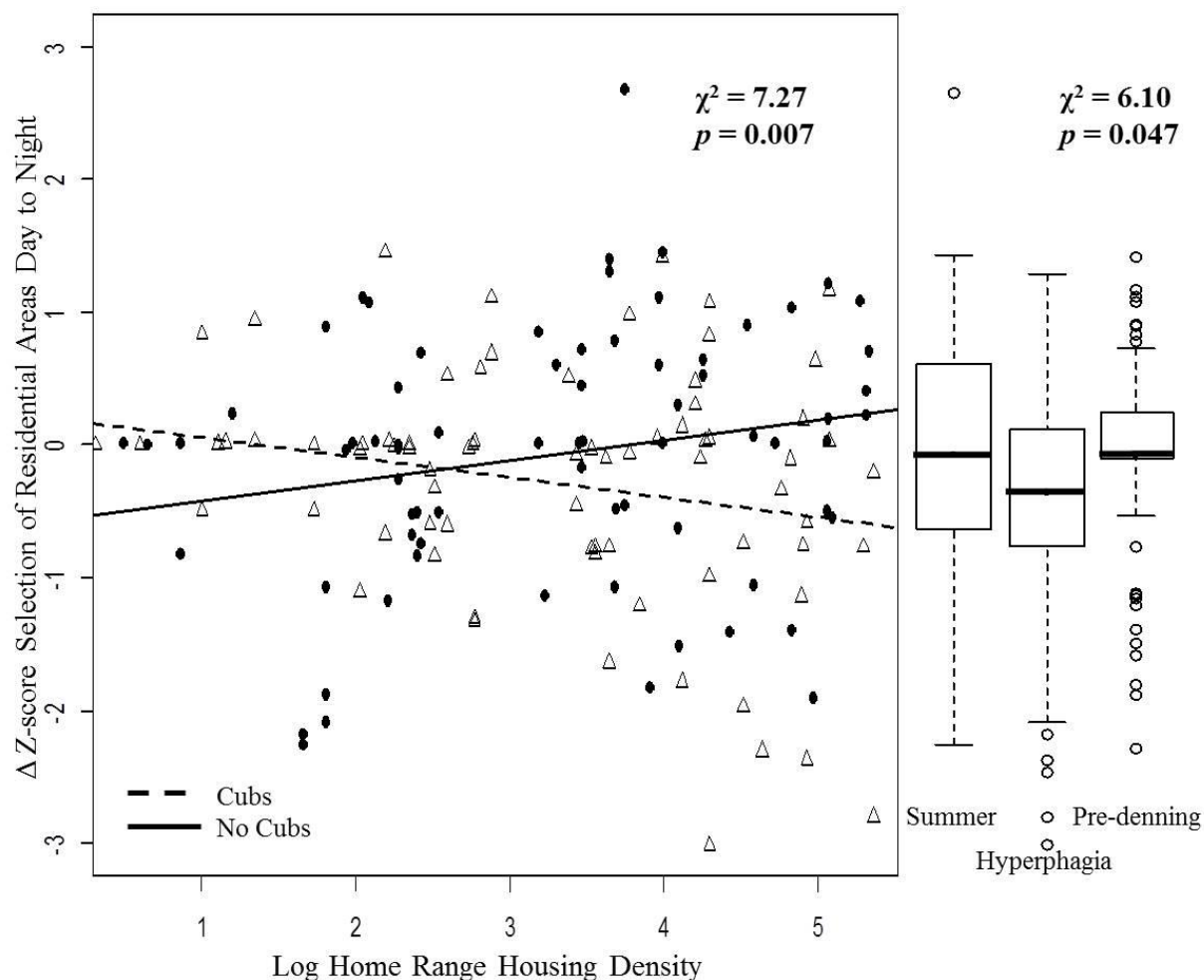


Fig. 4.4 Changes in selection for low intensity residential areas between day and night (Δz -score) as a function of home range housing density (HRHD). Plot displays relationships for female bears without cubs (solid lines), and with cubs (dashed lines) separately. Wald's chi-squared test on an interaction between log HRHD and reproductive status reported. Boxplots display significant differences in the change in z-score from day to night among seasons.

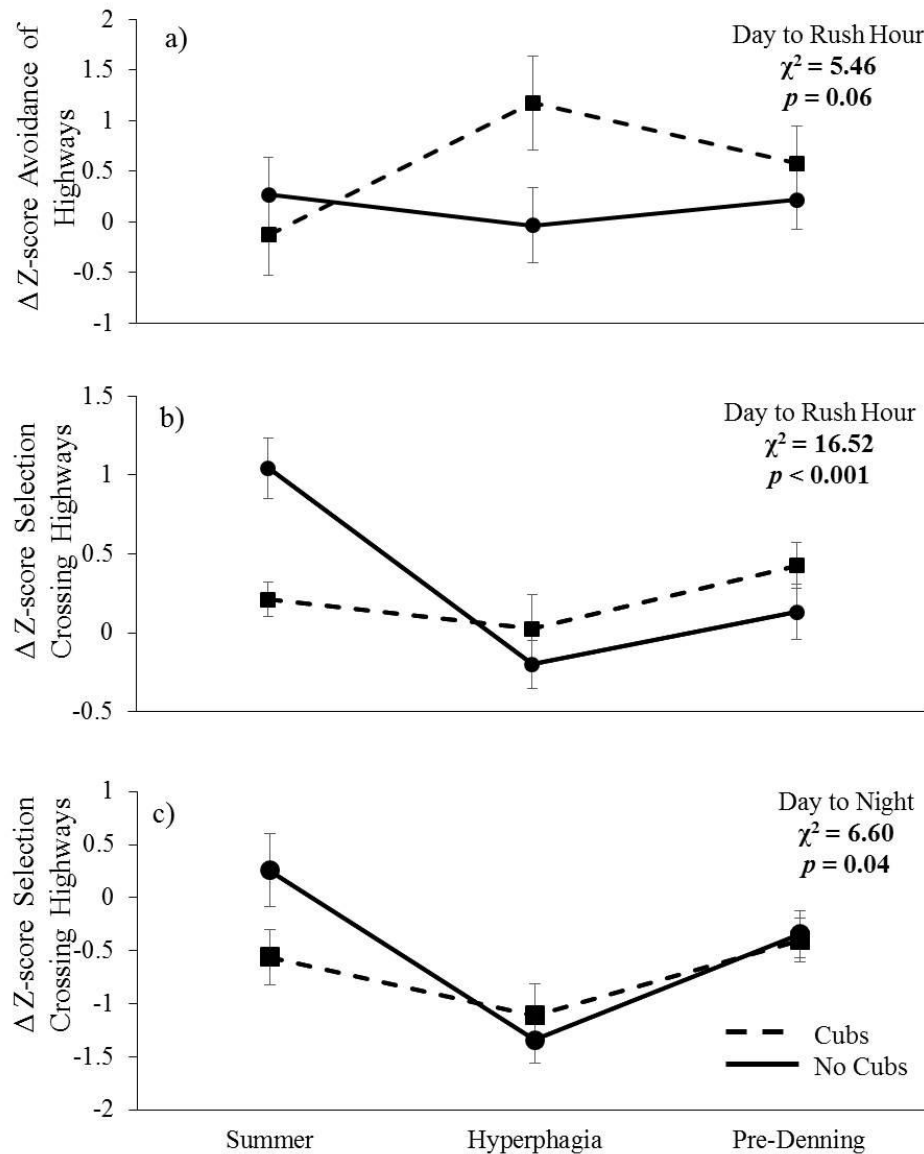


Fig. 4.5 Mean Δz -scores between times of day estimated by black bear step selection functions by season and reproductive status. Plots show changes in a) avoidance of highways between day and rush hour, b) selection for crossing highways between day and rush hour, and c) selection for crossing highways between day and night. Δz -scores for bears with cubs are shown by boxes and dashed lines, and by circles and solid lines for bears with cubs. Wald's chi-squared test for interactions between season and reproductive status displayed.

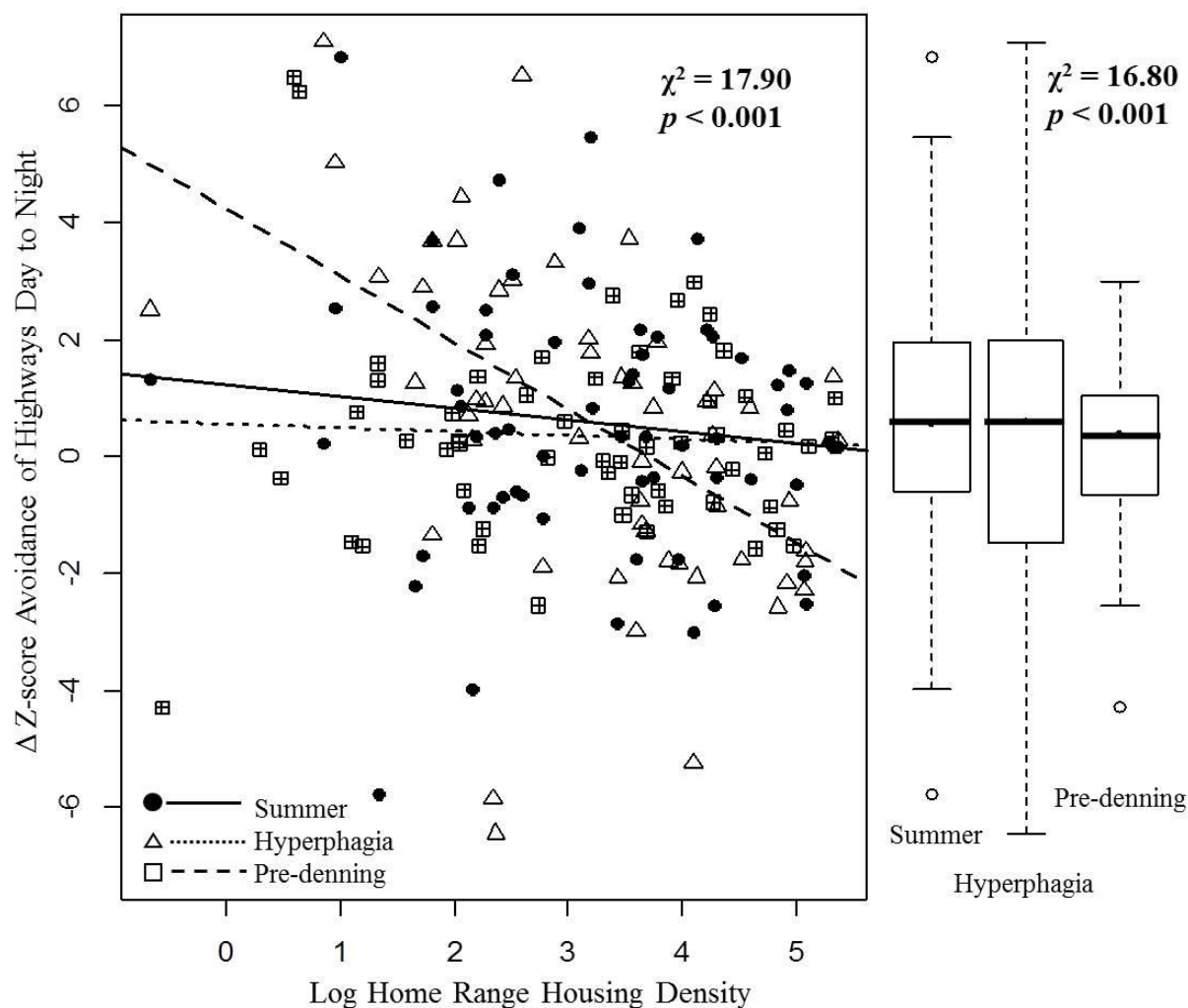


Fig. 4.6 Changes in avoidance of highways between day and night (ΔZ -score) as a function of home range housing density (HRHD). Plot displays relationships during summer (solid lines), hyperphagia (dashed lines), and pre-denning (dotted lines) separately. Wald's chi-squared test on an interaction between log HRHD and season reported. Boxplots display significant differences between seasons in changes in selection. Chi-squared statistic for the interaction between season and log home range housing density displayed.

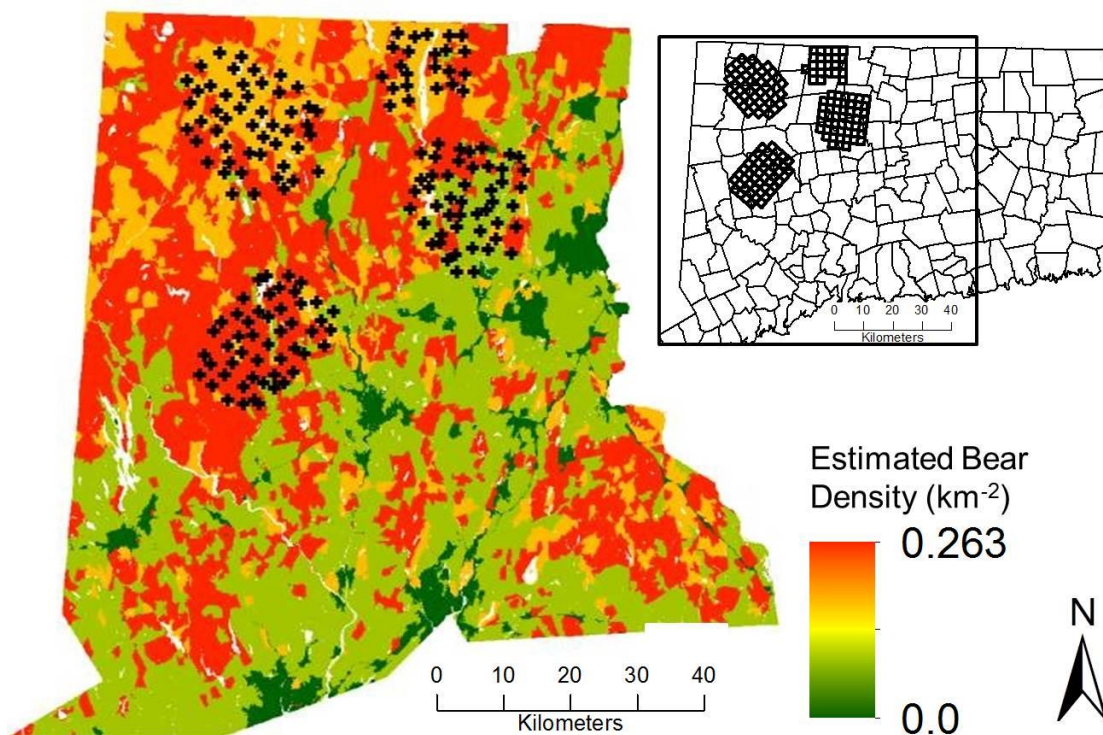


Fig. 5.1 Projected estimates of black bear density across western Connecticut. Estimated densities were obtained from the top-ranked spatial mark-recapture model, which indicated bear densities varied among rural, exurban, and suburban housing densities. This model also included a decline in density as a function of decreasing latitude, and projected densities were produced using northernmost estimated bear densities in each development category.

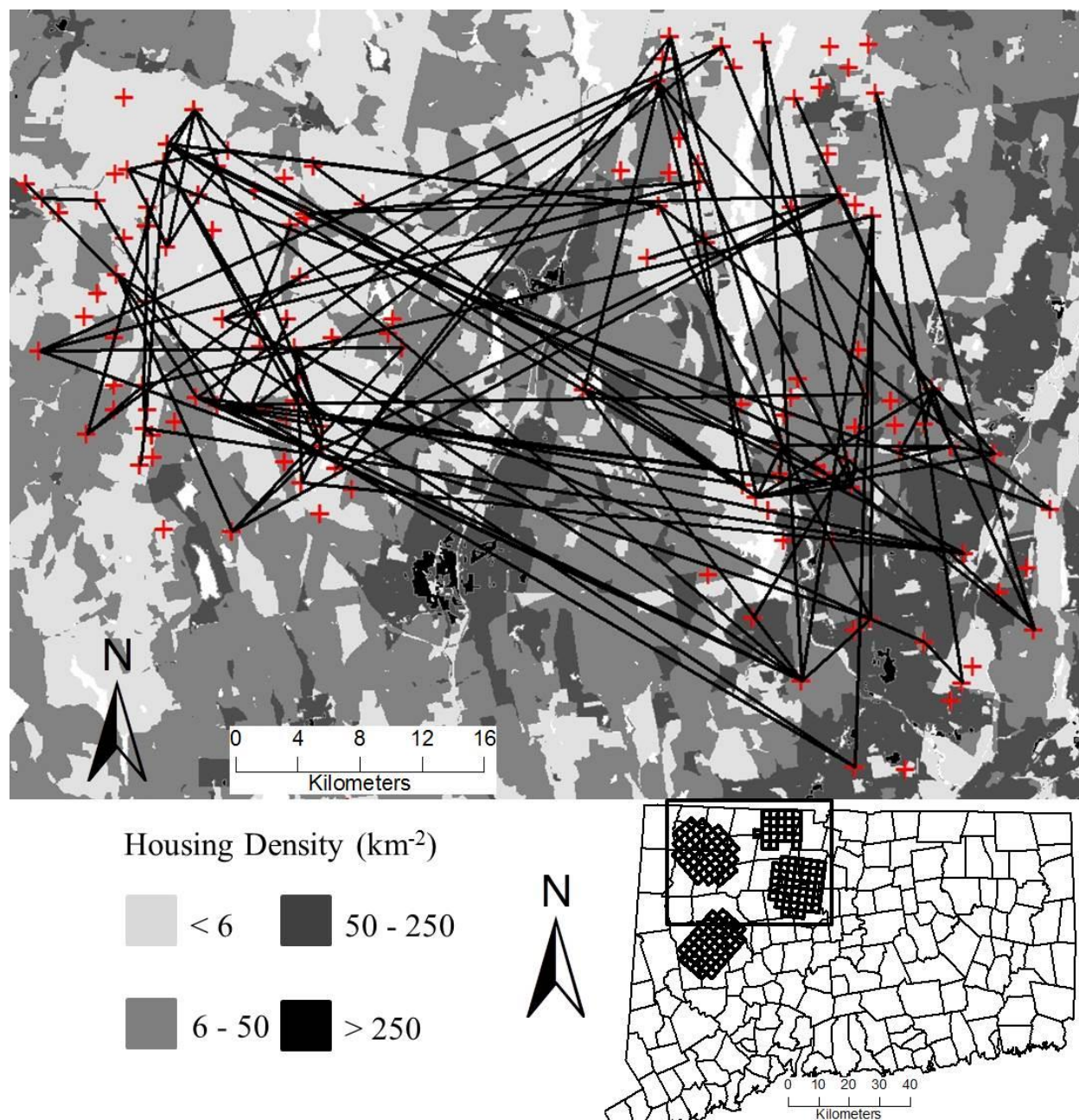


Fig. 5.2 Distribution of female parent-offspring black bear pairs across the study area in western Connecticut. Individual locations (red crosses) were approximated using the centroid of all sampling locations at which an individual was detected. Black lines connect pairs of individuals for which analyses of relatedness indicated parent-offspring was the most likely relationship.

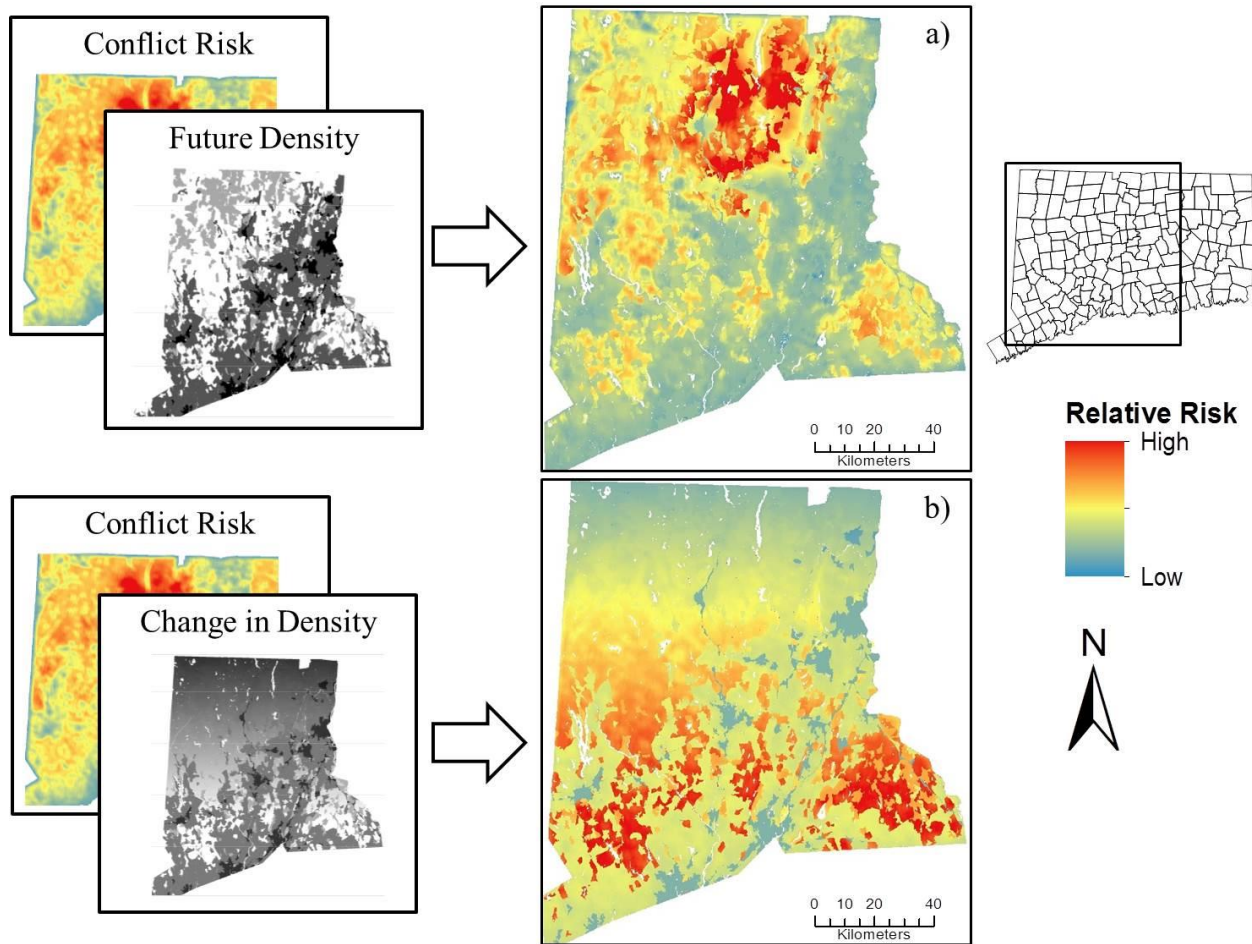


Fig. 5.3 Models of predicted human-black bear conflict in western Connecticut produced by combining spatial mark-recapture models of bear density with a model of conflict as a function of landscape variables. Maps highlight areas a) likely to experience the greatest rates of human-bear conflict, and b) likely to experience the greatest increase in conflicts. Predictions were produced by combining estimated conflict intensity using coefficients from a top ranked model of black bear conflict and projected future bear densities, and changes in density.