Black bear recolonization patterns on human-dominated landscapes vary based on housing: New insights from spatially explicit density models.

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ABSTRACT

Housing development is often intermixed within natural land cover, creating coupled human-natural systems that benefit some species, while eliminating critical habitat for others. As carnivore populations recover and expand in North America, understanding how populations may recolonize human-dominated landscapes is an important goal for conservation. We empirically test whether a population of American black bear (*Ursus americanus*) recolonizing a developed landscape is responding to land cover, housing density, or the amount of intermixture between forest and housing as quantified by the Wildland Urban Interface. Housing density was the most supported spatially explicit mark-recapture model and indicated that bear density was highest among exurban housing densities. Mean estimated bear density in exurban areas (6 – 49 houses/km²) was 0.18 individuals/km² compared to 0.12 individuals/km² in rural areas (< 6 houses/km²). Bear densities also declined to zero as development approached 50 houses/km². We also tested for differences in sex ratio between more and less intensely developed areas, using hybrid mixture models. Sex ratios were significantly more male-biased in areas of higher housing density. Elevated bear densities provide evidence that exurban land-use can facilitate recolonization of black bears, yet high housing density may also limit the recovery of bear populations. Explicit relationships between land-use and bear density will allow managers to anticipate future population distribution, and areas where bears and people may come into frequent contact.

Key Words conservation; exurban; land-use; recolonization; spatially explicit mark-recapture; synanthropic

1. 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). Frequently this form of development integrates natural land cover and housing potentially increasing habitat for wildlife (Clark *et al.*, 2009; Theobald, 2001). This intermixing of development and natural land cover blurs traditional urban-rural distinctions, creating intermixed ecosystems (Zipperer *et al.* 2000). The Wildland Urban Interface (WUI) provides one way to describe these landscapes, using vegetated (i.e., little housing), intermixed (i.e., areas with where houses are located amidst natural cover), interfaced (i.e., areas where houses abut natural vegetation, and non-vegetated (i.e., houses and imperious surfaces) classifications (Radeloff *et al.*, 2005). Wildlife response to intermixed ecosystems can differ among taxa (Bar-Massada *et al.*, 2014; Hansen *et al.*, 2005), and are not fully understood for species recolonizing urbanizing landscapes.

Intermixed ecosystems have led to a proliferation of synanthropic wildlife – species that exhibit positive demographic or numeric responses in the presence of people (Johnston, 2001; McKinney, 2006). Wildlife may benefit from humans because the anthropogenic resources and refuges provided (Waite *et al.*, 2007) can increase survival and reproduction (DeStefano & DeGraaf, 2003; Gehrt *et al.*, 2010; Marzluff & Ewing, 2001). For example, while many carnivores avoid roads and houses (Cardillo *et al.*, 2004), a number of species have increased densities in urban landscapes (see Bateman *et al.*, 2012 for a review). Carnivore cohabitation with humans spans a gradient from avoidance, to urban adapters that tolerate development while

relying on natural resources, to exploiters (i.e., synanthropes) with positive association with people (McKinney, 2006). The recovery and expansion of carnivore populations across North America and Europe (Chapron *et al.*, 2014; Linnell *et al.*, 2001) has increased the presence of carnivores within human-modified landscapes, creating a need to understand how recolonizing populations respond to human activities.

Our goal was to understand how recolonizing wildlife populations respond to human-modified landscapes. Here we focus on the American black bear (*Ursus americanus*), a prominent species in 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 bears were thought to require large amounts of natural land cover – including forest, shrubland, and wetland habitats (Powell *et al.*, 1997) - and to be negatively affected by human activity (Brodeur *et al.*, 2008; Dixon *et al.*, 2007). However, populations are expanding into urban landscapes, often exploiting anthropogenic foods (Johnson *et al.*, 2015; Merkle *et al.*, 2013; Ranglack *et al.*, 2009). In landscapes classified as interface, bears select high quality natural land cover, and portions of the home range extend into urban areas, indicating urban avoidance (Baruch-Mordo *et al.*, 2014; Johnson *et al.*, 2015). This research has occurred primarily in the western United States. However, bears are increasingly recolonizing intermixed areas (Ellingwood, 2003; Evans *et al.*, 2014) throughout the eastern US, where there are no rural areas within entire bear populations and individual home ranges.

The recent re-establishment of a black bear population in western Connecticut presents an opportunity quantify bear population distributions when recolonizing urbanized landscapes. While bear range in the state is composed primarily of forested land cover (i.e., National Land Cover Database; Fry *et al.* 2011), housing density within the range are predominantly exurban,

with small patches of rural and urban areas (U.S. Census, 2010), and the WUI map depicts Connecticut as 72% intermixed (Fig. 2). Our first objective was to use spatially explicit mark-recapture models to test competing hypotheses regarding whether bears densities vary with land cover, housing density, or the amount of intermixture between forest and housing as quantified by the Wildland Urban Interface. We hypothesized that both forest cover and housing density influence the spatial distribution of bears, and thus predicted that the WUI would best explain spatial variation in bear density.

Our second objective was to identify where black bear density is highest, by quantifying the relationship between bear density and identified landscape classifications. We expected bear densities would be highest in intermixed areas, because these landscapes contain both forest cover and anthropogenic foods such as garbage and bird feeders (Greenleaf *et al.*, 2009; Mazur & Seher, 2008). Finally, we expected this relationship to differ between males and females due to differences in dispersal (Costello *et al.*, 2008; Moyer *et al.*, 2006) and behavior at range peripheries between the sexes (Beckmann & Berger, 2003b; Sato *et al.*, 2011). Quantifying the response of expanding black bear populations to human-modified landscapes will help wildlife managers and land-use planners anticipate the future patterns of bear recolonization, and plan conservation strategies.

2. Methods

2.1. Study area and sample collection

Spatially explicit mark-recapture (SMRC) models (Gardner *et al.*, 2009) use the locations of individual detections to directly estimate population densities. We used non-invasive hair corrals (Woods *et al.*, 1999) to collect hair samples from black bears in northwest Connecticut, which provided genetic material used for individual identification. 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 attracted bears to corrals using non-nutritional scent lures applied to log piles at the center of corrals, and rags hung over corrals. Scent lures did not provide a food reward, minimizing the potential for bears becoming conditioned to return to corrals. 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. 1).

Grid cells were 2.5 km², with one hair corral per cell, to accommodate 3 – 4 corrals within an area the size of a female summer home range (approx. 30 km², CT DEEP unpublished data). North grid consisted of 49 corrals in the northwest corner of CT, and covered 271 km². Land cover on and around this grid was primarily mixed and deciduous forest as according to land cover maps (Fry *et al.* 2011), and confirmed during ground surveys, with an average housing density of 6.8 km⁻². East grid had 48 corrals 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 corrals. 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 corrals 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. 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. New scent lure was applied at each visit. We collected 814 hair samples in 2013 and 1226 hair samples in 2014. Hair samples were collected from corrals and

stored in small, paper 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.

2.2 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). One well on 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_{IDsibs} (Waits *et al.*, 2001) - the probability that two random individuals and two siblings can be genetically identical at a given a set of genetic markers - in GenAlEx (Peakall & Smouse, 2006). 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.

2.3. Density modeling

We used individual detection and re-detection data in SMRC models to estimate bear population densities around each study grid, and across all study grids in western CT. This approach considers the observed history and location of individual detections as a function of two processes; the latent density of individual activity centers, and individual detection

probability. Detection probability is modeled as a function of distance between activity centers and corral locations using two parameters; $g0$, representing the probability of detection for an individual with an activity center at a corral, and σ , defining the rate of decline in detection probability as individual activity centers are located farther from a corral (Fig. S1). The density of activity centers are estimated as the rate parameter of a spatial poisson process, which can be either constant, or variable 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 corral locations as the Combined study area (Fig. 2).

We tested hypotheses as to whether land cover, housing density, or both correspond to variation in bear density by fitting SMRC models with density varying as a function of different landscape classifications. In these models, different estimated rates of distribution of activity centers are maximized within different areas, according to categorization. Each classification represented alternative hypotheses regarding how human-modified landscapes affect the distribution of bears (see Fig. 2). Classifications included forested vs. non-forested land cover (COVER), housing density (HOUSE), and the Wildland-Urban Interface (WUI) classification. 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 landscape hypotheses.

We created the COVER 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 housing densities from 2010 census block data to derive our HOUSE 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 in conjunction with forest cover to define subcategories of intermix and interface areas in the Wildland-Urban Interface classification, and correspond with previous land-use definitions (; Theobald, 2001; U.S. Census Bureau, 2000). We created the WUI classification from Wildland-Urban Interface data, which includes both housing density and percent forest cover per census block, thus representing the combined effects of the COVER and DEV hypotheses. We aggregated non-WUI vegetated, intermix, interface, and developed categories. 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 variable 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 probability 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 “secur.fit ” function). We refer to these candidate sets as detection models, which were identical for all study areas (see Table S1 in supporting information). 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 COVER, HOUSE, WUI, and a north-south trend (Y) (Table 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 (ω_i) were used to indicate relative model support. We considered models with $\omega_i < 0.10$ as unsupported, and multiple models with $\omega_i > 0.10$ as competing (Burnham and Anderson, 2002). In cases in which a single model was supported, we refer to this model as top-ranked. When multiple models in a candidate set were supported, we used model averaging to obtain parameter estimates. We applied this approach to identify supported models 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 proportion of male and female individuals, accounting for differences in detection probability, (p_{mix}) estimated from top ranked model in each study area. We tested whether sex ratios differed from 50:50 in each study area, and between study areas, using a likelihood ratio test between the top model, and an identical model in which the mixing proportion was fixed to either 0.50, or that of a comparison study area.

We used parameters from supported models from each study area to estimate black bear densities as bears per km^2 , and applied the “region.N” function in *secur*, which integrates estimated densities across a defined region, to estimate abundance in a given study area. For

both measures we report mean estimates and standard errors. For comparison between disparate landscape contexts, we report abundance and density estimates from North and East study areas. 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.

3. Results

We genetically determined 935 hair samples 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 the sex of 198 bears (93 male, 105 female). There were no differences in number of detections among lure types used ($F_{3,7} = 0.203$, $p = 0.89$). 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.

On North study area, a single detection model was supported ($\omega_i = 0.999$), and indicated an individual behavioral response to previous detection, with $g0$ increasing and σ decreasing following first encounter. 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 1). Estimated bear density for this sampling area was $0.11 \pm 8.5 \times 10^{-3}$ individuals/km² (Table 4), 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, one detection model was supported ($\omega_i = 0.955$), indicating detection probability was a function of percent forest cover, with increasing $g0$ and decreasing σ with increasing forest cover. Both the HOUSE and COVER hypotheses received AICc support greater than 0.10 (Table 2). 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 (Table 4). 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 HOUSE and HOUSE+Y hypotheses received AICc support greater than 0.10 (Table 3). 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 4). 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 ($p_{mix} = 0.66 \pm 0.05$), 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 urbanization along the Connecticut River (Fig. 3). 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 HOUSE 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. 4).

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 3), whereas detection probability of males was a function of percent forest cover surrounding hair corrals (ω_i

= 0.997; Table 1). For both sexes, we found two competing models of density, as both the HOUSE and HOUSE + Y hypotheses received greater than 0.10 of available AICc support. The order of support was reversed between sexes. HOUSE + Y was the most supported model of female density ($\omega_i = 0.687$) followed by HOUSE ($\omega_i = 0.235$), whereas among males HOUSE received greater support ($\omega_i = 0.622$) than HOUSE + Y ($\omega_i = 0.285$; Table 3).

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). 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 4).

4. Discussion

We found strong evidence that in intermixed landscapes black bear densities vary with housing density, rather than forest cover, or a measure of intermixture. Despite some similarity in their categorization of our study area, we found a large gap in model support between the HOUSE and WUI hypotheses in all study areas (Table 1), and thus our hypothesis that the distinction between intermixed and interface areas 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. 4). These relationships suggest expanding black bear populations may recolonize exurban areas, and initially avoid more intense housing. This positive numerical response in exurban areas supports the conceptualization of recolonizing black bears as urban adaptors.

Elevated black bear densities may constitute second order habitat selection (i.e.; home ranges within the population range; Johnson, 1980) for exurban areas. 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. Housing densities in Connecticut change over a spatial scale within the extent of daily and summer bear movements (Dobey *et al.*, 2005; Powell *et al.* 1997). 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, 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. The housing categories used to test hypotheses do not represent delineations recognized by bears. Bear density certainly does not change discretely between rural, exurban, and suburban areas, but our results reflect a difference in rates of black bear occurrence as a function of housing density at a scale relevant to their movement capabilities.

Our post-hoc model identified a non-linear relationship between bear density and continuously measured housing density, indicating an upper limit to the amount of housing tolerated by bears. Bear densities declined above 18.2 houses/km², falling to zero as housing density reached 35 – 50 km⁻² (Fig. 4). Although bears are regularly reported among higher housing densities, our results suggest that recolonizing populations are unlikely to establish in expanses of suburban housing. Bears using interface areas 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 human-modified landscapes 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 housing densities may preclude occurrence of bears and people.

Our findings contribute to a growing body of research that human-modified landscapes can benefit ecologically flexible species. Association with humans by large, obligate carnivores is often restricted to rural areas (Bateman & Fleming, 2012). However, large-bodied mammals are able to evaluate landscapes at large spatial scales (Lidicker Jr, 1999), and long distance movement capabilities enable these species to traverse hostile matrices (Gehrig & Swihart, 2003). As omnivores with high learning capacity and behavioral plasticity (Gilbert, 1989; Mazur & Seher, 2008), black bears also share many of the same behavioral traits as smaller mammalian synanthropes (Bateman and Fleming 2012), able to exploit novel resources (e.g.; garbage, bird feeders, etc.) in human-modified landscapes. Bear densities may be elevated in exurban, relative to rural, contexts because increased food availability can reduce intraspecific competition and increase fecundity (Hostetler *et al.*, 2009; Moyer *et al.*, 2007; Mitchell & Powell, 2007).

Differences between the HOUSE, WUI, and COVER landscape classifications help discern the relationships between housing density, land cover, and bear densities in intermixed ecosystems. The lack of support for the Wildland-Urban Interface model was surprising, as we expected housing density and forest cover to be important. The primary difference between the two classifications was the intermixed WUI category (see Fig. 2), which includes exurban and suburban areas with at least 50% forest cover (Radeloff *et al.*, 2005). In the Combined study area, both exurban (94.2%) and suburban (72.36%) areas were primarily intermixed, and thus stronger support for HOUSE relative to WUI indicates the housing density distinction was

important. Estimated densities derived from the HOUSE model suggests that bear densities differ between exurban and suburban housing densities, even within > 50% forest cover.

In East study area, correlation between exurban areas and high forest cover was likely responsible for the model selection uncertainty between COVER and HOUSE hypotheses. The majority of exurban census blocks (74.9%) were also classified as forested. In contrast, while a high portion of suburban blocks were intermixed, only 38.4% were 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. However, forested areas in the Combined study area contained both rural and exurban areas (Fig. 2), and support for the HOUSE hypothesis here, in conjunction with the lack of support for the COVER hypothesis, indicating differences in bear density between rural and exurban housing densities.

Density is not necessarily an indicator of habitat quality (Van Horne, 1983), and black bears experience both positive and negative demographic responses to human activities (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. 3). In Connecticut, both housing density and increased male dispersal from core areas during range expansion (Sato *et al.*, 2011; Swenson *et al.*, 1998) likely contribute to these patterns. A population structure more skewed toward young males can negatively impact population growth, as females drive reproduction (Clark & Eastridge, 2006; Powell *et al.*, 1996), 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 black bear population recolonization patterns in human-modified landscapes.

Use of human-modified landscapes by large mammals often leads to conflict with humans (Evans *et al.*, 2014; Kretser *et al.*, 2009), and spatially explicit density estimates can be used to anticipate the future distribution of recolonizing populations. 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. 3). Additionally, estimates of density at northern latitudes in CT (0.26 bears/km^2) were similar to established black bear populations in other parts of the species' range, such as upstate New York ($0.2/\text{km}^2$; Gardner *et al.*, 2010), New Hampshire ($0.15 - 0.25$; Coster *et al.*, 2011), and Florida ($0.12 - 0.14$; Dobey *et al.*, 2005). This result, in combination with the support for a latitudinal trend, suggests that bear density may increase within central and southern latitudes in Connecticut, places that already receive many conflict reports.

5. Conclusions

Our results illustrate the effect of different patterns of human landscape modification on recovering black bear populations. Large carnivore abundances in North America and Europe have increased despite concurrent increases in human density (Chapron *et al.*, 2014; Linnell *et al.*, 2001). Our finding that bear densities were elevated in exurban, relative to rural areas suggests that as exurban land use 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 land use (Evans *et al.*, 2014). Our results also indicate that housing densities above 50 houses/km^2 may create areas that bears traverse but do not persist within (Long *et al.*, 2010). Where black bear and human populations are simultaneously expanding,

413 there is concern that increased development will reduce available habitat for bears (Bettigole *et*
414 *al.*, 2014). Land-use planning considering conservation of carnivores should account for the
415 likelihood of transitions beyond these densities, so that population growth and stability are not
416 overestimated.

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Tables

Table 1. 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	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3817.23	0.00	0.736
	Different in Rural, Low, and Med/High Development	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3819.37	2.13	0.253
	North-South Trend & Different in Natural, Intermixed, Interface, and Developed Land Use	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3827.27	10.04	0.005
	Different in Natural, Intermixed, Interface, and Developed Land Use	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3827.27	10.04	0.005
	North-South Trend	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3831.40	14.17	0.001
	Homogenous Density	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3853.13	35.89	0.000
	Difference between forest vs. non-forest	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3835.05	17.81	0.000
	North-South Trend & Difference between forest vs. non-forest	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3833.62	16.39	0.000
Detection	Homogenous	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+\text{Forest}]$	3853.13	0.00	1.000
	Homogenous	$g0[\text{Sex}+b], \sigma[\text{Sex}+b]$	3885.92	32.80	0.000
	Homogenous	$g0[\text{Sex}+\text{Forest}], \sigma[\text{Sex}+b]$	3893.65	40.53	0.000
	Homogenous	$g0[], \sigma[\text{Sex}+b]$	3901.67	48.54	0.000
	Homogenous	$g0[\text{Sex}+\text{Forest}], \sigma[]$	3924.20	71.08	0.000
	Homogenous	$g0[\text{Sex}+b], \sigma[]$	3932.26	79.14	0.000
	Homogenous	$g0[], \sigma[]$	3933.04	79.92	0.000
	Homogenous	$g0[], \sigma[\text{Sex}+\text{Forest}]$	3970.43	117.30	0.000
	Homogenous	$g0[\text{Sex}+b], \sigma[\text{Sex}+\text{Forest}]$	3971.81	118.69	0.000

Table 2. 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 3. 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	Δ AICc	ω_i
	North Study Area				
Density	Homogenous	g0[Sex+b], σ [Sex+b]	2718.39	0.00	0.903
	North-South Trend	g0[Sex+b], σ [Sex+b]	2739.24	20.85	0.000
	North-South Trend & Difference between forest vs. non-forest	g0[Sex+b], σ [Sex+b]	2722.85	4.46	0.097
	Different in forest vs. non-forest	g0[Sex+b], σ [Sex+b]	2740.77	22.39	<0.001
	Different in Rural, Low, and Med/High Development	g0[Sex+b], σ [Sex+b]	2740.97	22.59	<0.001
	Different in Natural, Intermixed, Interface, and Developed Land Use	g0[Sex+b], σ [Sex+b]	2763.29	44.90	<0.001
	North-South Trend & Different in Rural, Low, and Med/High Development	g0[Sex+b], σ [Sex+b]	2765.44	47.05	<0.001
	North-South Trend & Different in Natural, Intermixed, Interface, and Developed Land Use	g0[Sex+b], σ [Sex+b]	2773.00	54.61	<0.001
Detection	Homogenous	g0[Sex+b], σ [Sex+b]	2718.39	0.00	1.000
	Homogenous	g0[], σ [Sex+b]	2738.25	19.86	<0.001
	Homogenous	g0[Sex+Forest], σ [Sex+b]	2740.36	21.97	<0.001
	Homogenous	g0[Sex+Forest], σ [Sex+Forest]	2757.98	39.60	<0.001
	Homogenous	g0[], σ [Sex+Forest]	2760.32	41.93	<0.001
	Homogenous	g0[b], σ [Sex+Forest]	2762.32	43.93	<0.001
	Homogenous	g0[], σ []	2764.35	45.96	<0.001
	Homogenous	g0[Sex+Forest], σ []	2764.48	46.10	<0.001
	Homogenous	g0[Sex+b], σ []	2766.10	47.72	<0.001

Table 4 Estimated values, standard error and t-values for paramaters 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.

Fig.1 Placement of sampling grids across western Connecticut spans urban to rural housing density. Grids encompassed the majority of the area in the state where adult females live with cubs, as determined from public sighting reports to Department of Energy and Environmental Protection. Grids also cover the full range of housing densities found in CT in non-urban areas.

Fig. 2 Landscape classifications representing hypothesized relationships between (a) land cover, (b) housing density, and (c) wildland-urban interface categories 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. The rate of a non-constant spatial poisson process representing rate of black bear activity centers varied between categories within a classification.

Fig. 3 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 (< 6 houses/km²), exurban ($6 - 49$ houses/km²), suburban ($50 - 750$ houses/km²), and urban (> 750 houses/km²) housing 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, with standard error bars shown.

Fig. 4 Quadratic relationship between bear density and continuous 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).