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Acceptability of residential development in a regional landscape: Potential effects on wildlife occupancy patterns

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A B S T R A C T

The conversion of natural lands to developed uses may pose the single greatest human threat to global terrestrial biodiversity. Continued human growth and development over the next century will further exacerbate these effects of habitat loss and fragmentation. Natural resource managers are tasked with managing wildlife as a public trust, yet often have little say in land use decisions. Generally speaking, decision makers could benefit from an understanding of what different regulations mean in terms of wildlife distribution. In a previous paper (Bettigole et al., 2013), we surveyed town residents throughout Vermont to measure how respondents feel about a range of development levels within their town boundaries. We estimated the "social carrying capacity for development" – or SK_d – for 251 towns in Vermont. SK_d provides an estimate of the level of developed land cover classes that town residents deem "acceptable" within their town boundaries. In this paper, we design a framework for linking the town-specific SK_d estimates with the wildlife distribution patterns for three wide-ranging mammalian species: American black bear (*Ursus americanus*), fisher (*Martes pennanti*), and bobcat (*Lynx rufus*). We simulated landscape conditions at SK_d for each town in Vermont, and then used existing occupancy models for the three target species to spatially map and compare occupancy rates in the baseline year 2000 with occupancy rates at SK_d. With nearly 90% of Vermont towns willing to increase developed landcover classes within town boundaries compared to baseline levels, significant state-wide changes in occupancy rates were predicted for all three focal species. Average occupancy rates declined by −15.9% and −3.1% for black bear and bobcats, respectively. Average occupancy rates for fisher increased by 9.0%. This study provides a method for linking development standards within a town with wildlife occurrence. Across towns, the methodology spatially identifies areas that may be at risk of future development, as well as identifying areas where wildlife distribution patterns may face future change as a result of increased human population growth and development.

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1. Introduction

The conversion of natural lands to developed uses may pose the single greatest human threat to global terrestrial biodiversity (Vitousek, 1994). This form of conversion is almost always permanent, and occurs world-wide at an exponential rate. Loss of habitat affects species extinction rates (Hughes et al., 1997) as well as local extirpations, with nearly three quarters of mammals worldwide having lost at least 50% of their historic geographic range (Ceballos and Ehrlich, 2002). The loss of natural areas to development reduces the total amount of habitat available to wildlife and changes the arrangement of the remaining habitat. This reduces species richness, population abundance and distribution, decreases genetic diversity, and alters species interactions (Komonen et al., 2000; Schmiegelow and Monkkonen, 2002).

Natural resource managers, tasked with managing wildlife as a public trust, require techniques for predicting *how much* and *where* wildlife habitat is likely to be converted in the future. Yet, resource managers often have little say in directing landscape change outside the boundaries of protected areas. In Vermont, the focus of our work, these external areas are largely shaped by town and city planning commissions, who consider a myriad of physical, social,

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cultural, economic, and conservation values when establishing zoning and development regulations. Town sizes in Vermont range from 3.9 to 32.37 km^2.

One method for gauging citizens' perception of development within a town boundary is to survey residents and identify the amount of development that an average resident deems "acceptable" (Manning, 2007). In a companion paper, Bettigole et al. (2013), used this "social norms" approach to elicit the acceptability of various levels of town development for an average resident. Briefly, Bettigole et al. (2013) surveyed >4000 residents of Vermont, USA and asked respondents to rate the acceptability of a range of development scenarios in a hypothetical Vermont town, where acceptability was scored on a Likert scale, with −4 being very unacceptable and +4 being very acceptable. The core of the survey was a set of six, three-dimensional illustrations of a fictional Vermont town that displayed a gradient of housing development levels. The fictional town began as 83% forested, 12% agriculture, 3% water and 2% development (the lowest level found currently found in Vermont). Each image incremented housing levels exponentially, culminating in an image with ~49% development. Build out followed past trends in Vermont, occurring on 60% forest land and 40% agricultural lands; care was taken to hold the arrangements of habitats constant across images. Additionally, respondents provided their opinions on whether new development should replace forested lands or agricultural lands, the two dominant landcover types throughout the state. Bettigole et al. then analyzed responses and developed a mathematical model that identified on a town-by-town basis the level of development where "acceptability" moved from the acceptable realm to the unacceptable on a town-by-town basis (Fig. 1a). They defined this point as the social carrying capacity for development, or SK_d. SK_d identifies the percentage of developed lands within town boundaries that are acceptable to citizens. It is important to note that the SK_d represents acceptable levels of development within a given town; it does not necessarily predict how land use change will occur in the future. Many other techniques exist to predict land use change and population growth, such as past trends and multi-agent models (Parker et al., 2003; Theobald, 2005). Here, using SK_d, we have measured the potential (rather than a prediction) for growth.

SK_d is just one metric identifying resident's feelings towards development. Bettigole et al. (2013) also identified the average preferred level of development (preference), the average level of development where one would move from their town to another (displacement), and the average level of development where town planners should take action to curtail development (management). Any of these metrics could be used by town planners as a means for setting development guidelines.

Vermonters had an average SK_d of 9.1% development, which contrasts with the current town average of 5.4% development. Importantly, SK_d varied across towns, with some towns more accepting of development than others. Given a scenario where development levels within each town were at SK_d, Bettigole et al. (2013) predicted a 16,753.91 km^2 reduction in forested land statewide (−11.16%) and a 1,038.42 km^2 reduction in farmland (−60.45%), based on respondent preferences from the survey. From a conservation perspective, these outputs may be more meaningful if they were related to potential changes in wildlife distribution patterns in a quantitative manner. In the face of habitat reduction, species of high conservation concern that require forested, agricultural, or riparian areas to carry out their life cycles may be expected to decline. Such assessments could provide additional information to help land planners make more informed decisions.

One method for estimating the landscape capacity for wildlife species is occupancy modeling (MacKenzie et al., 2006). Wildlife occupancy modeling takes inputs in the form of detection and non-detection data of target species at multiple sites, and allows researchers to estimate the probability of occurrence (ψ) at any number of locations, given the characteristics of the site. Occupancy models in Vermont for American black bear (*Ursus americanus*), fisher (*Martes pennanti*), and bobcat (*Lynx rufus*) (Long et al., 2010) were developed by surveying sites with non-invasive techniques (e.g. hair traps, remote cameras, scat detection dogs). Each of these species exhibits some sensitivity to the amount of habitat (e.g., forest) within a given area. For example, in Vermont, black bear occurrence (ψ) was very sensitive to changes in forest cover within a 5 km radius of a site (Fig. 1b), with a sharp decline in occupancy as forest habitat drops from 85% to 40%.

In this paper, we design a framework for linking the social carrying capacity for development (SK_d) within towns with the capacity of a landscape to host three wide-ranging mammalian species: American black bear, fisher, and bobcat. Our objectives were to (1) transform the results from town level norm curve analysis into a spatially explicit land use scenario that represents landscape conditions at SK_d, (2) adapt existing occupancy models for black bear, fisher, and bobcat to predict species occurrence under present landscape conditions (year 2000) and landscape conditions associated at SK_d, and (3) compare species occurrence at the town scale between present conditions and at SK_d.

2. Materials and methods

2.1. Study area

Our study area included the entire state of Vermont (24,963 km^2). Mean elevation was 370 m, ranging from 30 m in

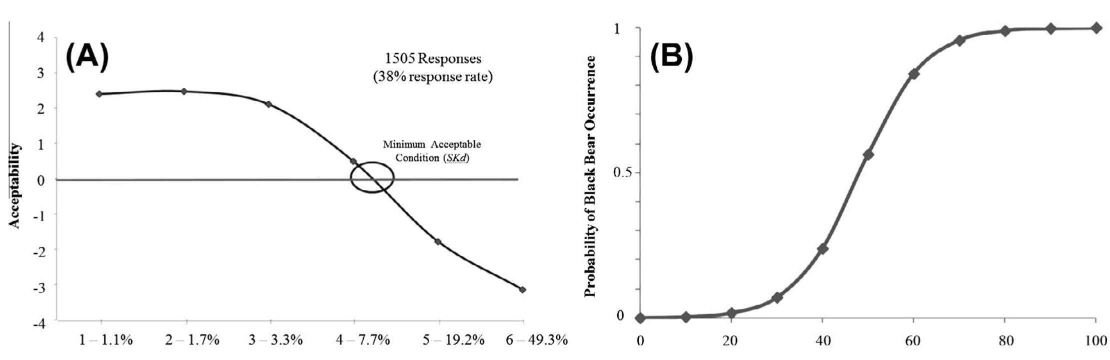

Fig. 1. (A) Average acceptability curve across all towns in Vermont, USA. As percent developed shown in each of the six illustrations increases, mean acceptability ratings decrease (housing density = $1.707 * 2.68^{(\text{Illustration\#1})}$, percent developed = 0.0075 + 0.0021 * housing density). Acceptability moves from the positive realm to the negative at 9.1% development, which is the state-wide average SK_d. (B) Response of black bear occurrence to varying levels of percent forest within 5 km of a location (30 m^2 pixel) in Vermont.

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the Champlain Valley in the northwest of the state, to 1339 m at Mount Mansfield, the highest point of the Green Mountains, a mountain range stretching the length of the state. Vermont's landscape is roughly 77% forested, 14% agricultural, 5% developed, and 4% water (NOAA Coastal Services Center, 2011). Most of Vermont's forests are composed of northern hardwood species (i.e., sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*), and American beech (*Fagus grandifolia*)), although upper elevations are dominated by montane spruce-fir forests (e.g., red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*)).

2.2. Study species

We selected three wide-ranging, territorial mammals for this study: black bear, fisher, and bobcat. While these species are all sensitive to human disturbance and land use change, they exhibit variation in habitat requirements, food use, and the degree of their response to human intrusion (Long et al., 2010). When analyzed together, this suite of focal species provides insight into how development levels at the social carrying capacity may affect broader mammalian populations in Vermont.

The American black bear is one of the most common large mammalian species in North America. Ideal habitats for black bear contain large blocks of intact forest, preferably remote areas with low human and road densities (Rudis and Tansey, 1995). Black bears, as omnivores, generally prefer forests containing multiple stages of succession, and a wide variety of food resources (Clark et al., 1993).

Fisher, once extirpated from Vermont and much of the northeast due to habitat loss, occur throughout the state at their highest levels since the mid 19th century (Trombulak and Royar, 2001). Fisher rely on dense coniferous or mixed forests with continuous canopy cover for habitat, and forage on a variety of small animals (Allen, 1983).

Bobcats are one of the most widely distributed carnivores in the contiguous United States, with populations in nearly every state (Hall, 1981). Bobcats inhabit a wide range of habitat types (Litvaitis et al., 1986), and although forested habitats are preferred, they are not averse to using open or shrubby areas (Rolley and Warde, 1985). Within home ranges, bobcats occupy habitats that have high amounts of shrub, deciduous, coniferous forest, and wetland cover types within 1 km (Donovan et al. 2011).

2.3. SK_d to land use. (Objective 1)

Assuming that development reached SK_d within each town across the state of Vermont, we developed landscape scenarios based on town-specific SK_d estimates for: (1) percent development and the ratio of residential development to commercial development, (2) relative reductions in forest cover and agriculture in response to increases in development, and associated reduction of deciduous, mixed and coniferous forest types, and (3) reductions in percent core forest in response to increased development. We assumed that wetlands, forested wetlands, conserved lands, and large roads would remain constant under social carrying capacity conditions. We also assumed that towns with no social capacity for growth in the future (SK_d less than current level of development) would not change in their landscape condition. We describe our analytical approach in detail below.

First, given SK_d estimates from Bettigole et al. (2013), we partitioned total development into one of two types: commercial development and residential development. Here, we used data from the Coastal Change Analysis Program, (CCAP) (National Oceanic and Atmospheric Administration Costal Services Center, 2011). CCAP analyzes changes in the National Land Cover Database (Fry et al, 2011) and estimates conversion probabilities from one land cover type to another over five year increments from 1996 to 2006. We examined every cell statewide at a 30 m^2 resolution that changed from non-developed to developed land uses to estimate the proportion of land use change allocated to commercial (2%) versus residential (98%) development. For example, if the SK_d for a given town suggests that development can increase by 10%, roughly 9.8% of this would be allocated to residential and 0.2% to commercial uses.

Second, we used respondents' preferences from Bettigole et al. (2013) to reduce forested or agricultural lands in response to new development. For example, if the SK_d for a given town suggested that development could increase by 10%, then, agriculture and/or forested lands would decrease by 10% to accommodate this new development. Vermont residents preferred that 43% of this would occur on agricultural land, and 57% would occur on forested land. In many towns, there was less existing agriculture than the amount needed for development. In such cases, we allocated as much development as possible to agricultural uses (removing all agriculture from the town) and the remainder transferred to development of forested land.

Third, given a reduction in total forest in response to the social carrying capacity of the landscape, we analyzed development trends between 1996 and 2006 (National Oceanice and Atmospheric Administration Costal Services Center, 2011) to allocate the loss of forest into deciduous, mixed, or coniferous forest landcover types. We used these trends to partition overall decreases in forested land into decreases in these three categories: 19% of total forest loss in deciduous, 62% in mixed, and 19% in coniferous forests.

Fourth, in towns where forest decreases were expected in response to the social carrying capacity scenario, we estimated the reduction in core forest (forest >100 m from an edge) that would result from increased development, using transition histories from the Coastal Change Analysis Program (NOAA Coastal Services Center, 2011) between 1996 and 2006. Given a certain reduction in forest land, this allowed us to predict the relative reduction in core forest. For every 10 km^2 of forest converted to development, we predicted a loss of roughly 1.5 km^2 of core forest.

The final products of this multi-step process were percentage values for %commercial development, %residential development, %deciduous forest, %evergreen forest, %mixed forest, and %forest core at the town scale across the entire state of Vermont. These values were then prepared as spatial inputs for predicting the wildlife capacity of the landscape in response to the social carrying capacity (Objective 2).

2.4. Predicting species occurrence (Objective 2)

We used Long et al. (2010) occupancy models for black bear, fisher, and bobcat to compare current probability of occurrence (year 2000) versus probabilities of occurrence associated with the landscapes at their SK_d. Between May and August of 2003, Long et al. (2010) sampled 168 sites throughout Vermont with detection dogs, hair snares and remote cameras, testing for the presence or absence of these three focal species. Likelihood-based occupancy modeling (MacKenzie et al., 2006) was used to estimate ψ (probability that the species occurred at a site) and p (probability that the species was detected if present). The coefficients from the top models were weighted and averaged (Burnham and Anderson, 2002) to develop unique parameter coefficients for each of the relevant covariates for the three species (Table 1). For example, the probability of occurrence for black bear was most strongly influenced by two covariates: %developed within 5 km, and %forest within 5 km (see also Fig. 1b). The high absolute value of these coefficients reflects a

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strong influence on occupancy probability. The negative coefficient for %developed implies that as development increases within a 5 km radius of a site, ψ for black bear declines, while if %forest increases within a 5 km radius of a site, ψ for black bear will increase. Predictor variables for fisher and bobcat were much weaker in terms of effect sizes. The strongest predictor variables for fisher were %residential development within 5 km (positive), %commercial development within 5 km (negative), and %wetland within 1 km (negative). For bobcat, the strongest covariates were %forested wetland within 1 km, and %mixed forest within 1 km (Long et al., 2010).

To map the present wildlife capacity of the landscape for our focal species, we applied model averaged parameter estimates in Table 1 to covariates at a 30 m^2 resolution for the state of Vermont. We did not modify predictor variables held constant (i.e. %wetland, %conserved) between time steps.

To map the wildlife capacity of the landscape when it is at the social carrying capacity, we used the outputs of our landscape change scenario (Objective 1). We used a moving window analysis to transform the outputs of the landscape change scenario from percentages at the town level so that each 30 m^2 pixel yielded the percent within 5 km (or 1 km) as required by the occupancy models. We used the Spatial Analyst tool in ArcGIS (ESRI, 2009) to compute the mean values (i.e., %deciduous forest, %commercial development, etc.) from pixels within 5 km of each grid cell statewide. The output of these analyses was a suite of 30 m^2 raster maps, where pixel values represented covariate percentage values within a 5 km or 1 km radius of conditions under SK_d. We then used the model-averaged coefficients developed by Long et al. (2010), along with the social carrying capacity rasters, to calculate ψ for each 30 m^2 grid cell in Vermont.

2.5. Comparing occupancy between present conditions and social carrying capacity (Objective 3)

We categorized each town under present conditions into one of four town development types: "urban" (less than 0.1 ha per housing unit), "suburban" (between 0.1–0.68 ha per unit), "exurban" (between 0.68–16.18 ha per unit), or "rural" (greater than 16.18 ha per unit) (Theobald, 2004). We then categorized town level forest cover under present conditions as low (less than 40%), medium (between 40% and 85%), and high (greater than 85%), and analyzed how changes in occupancy differed among these three categories of percent forest cover and four development types. We performed a repeated measures ANOVA for each focal species to test for differences in the average occupancy rate between present conditions and under social carrying capacity, where each town represented a sample. Analyses were performed in JMP (JMP, 1989–2007).

3. Results

3.1. Landscape change scenario (Objective 1)

Because current development levels within 86% (216/251) of towns in Vermont are below development levels associated with SK_d, large reductions in forest habitat, core habitat, and agricultural lands are expected if towns develop to their social carrying capacity. On average, to achieve their social carrying capacity for development, Vermont towns increased levels of development by 4.7%, with 4.6% in residential and 0.1% in commercial land uses (Fig. 2). In response to increased development, total forest was expected to decline by 2.7%, with a loss of 0.6% in deciduous, 1.6% in mixed, and 0.5% in coniferous forest types. Within towns, total forest loss ranged from 0.1% to 5.4%. On average, core habitat declined statewide by 2.3%, ranging from 0.1% to 4.3%.

3.2. Occupancy modeling (Objective 2)

We estimated the average occupancy rate within each town for our three focal species under both present and SK_d conditions. Average current occupancy estimates were 76% for black bear, 73% for fisher, and 35% for bobcat. Town level black bear occupancy ranged from 0% to 99.8%; fisher 11.3% to 92.7%; and bobcat 1.6% to 81.9%. Black bear current probability of occurrence (ψ) was high throughout the state of Vermont, with the exception of the Champlain Valley in the northwest, and within 5–15 km of large urban centers (e.g. Burlington, Rutland, Newport) (Fig. 3a). Fisher ψ was likewise high throughout the state, with lower values in the Champlain Valley (Fig. 3b). Bobcat ψ was highest in some eastern portions and the northeast of the state, with patches of high occurrence in the south and northwest (Fig. 3c).

Average occupancy values under the landscape social carrying capacity scenario were 64.6% for black bear, 83.2% for fisher, and 32.8% for bobcat (Fig. 3). Town level ψ for black bear ranged from 0.0% to 95.7%; fisher from 14.5% to 97.1%; and bobcat from 1.6% to 78.8%. Black bear ψ was relatively high in most of the state, with lowest values in the Champlain Valley and proximal lower ranges of the Green Mountains (Fig. 3d). Fisher ψ was high throughout the state, with lowest values in the southern and northern sections of the Champlain Valley (Fig. 3e). Bobcat ψ was highest in some eastern portions and the northeast of the state, with patches of high occurrence in the south and northwest (Fig. 3f).

All three focal species exhibited significant differences between current landscape conditions and landscape conditions at SK_d (Fig. 3g–i). Across the board, occupancy for black bear and bobcat declined as development increased under the social carrying capacity landscape scenario. Across towns, black bear occupancy dropped by an average of 15.9%, with a maximum decline of 55.5% (Fig. 3g). Black bear occurrence changed most drastically in

Table 1
Model-averaged estimates of coefficients for covariates in occupancy models, based on Long et al. (2010). Coefficients are in logit (log odds) space, and were re-estimated to reflect raw (untransformed) covariate scores. Positive coefficient values reflect a positive relationship between probability of occupancy and the covariate; negative values reflect a negative relationship.

Black bear		Fisher		Bobcat	
Intercept	−7.1855	Intercept	−0.2311	Intercept	−3.8587
%Forest-5 K	0.1410	%Forest-lK	0.0120	%Forest-lK	0.0027
%Deciduous-5 K	0.0010	%Conifer-lK	0.0305	%Mixed-lK	0.1035
%Core-5 K	0.0002	%Core-5 K -0.0020 %Core-5 K	0.0025		
%Conserved-5 K	−0.0003	%Conserved-lK	0.0097	%Conserved-lK	0.0030
%Wetland-5 K	0.0704	%Wetland-lK	−0.1940	%Forestedwetland-IK	0.3223
%Developed-5 K	−0.4050	%Residential-5 K 0.1613 Largeroads-5 K	−1.3407		
Largeroads-5 K	0.6519	%Commercial-5 K	−0.6767	Smallroads-5 K	9.0429
		North	0.0000		

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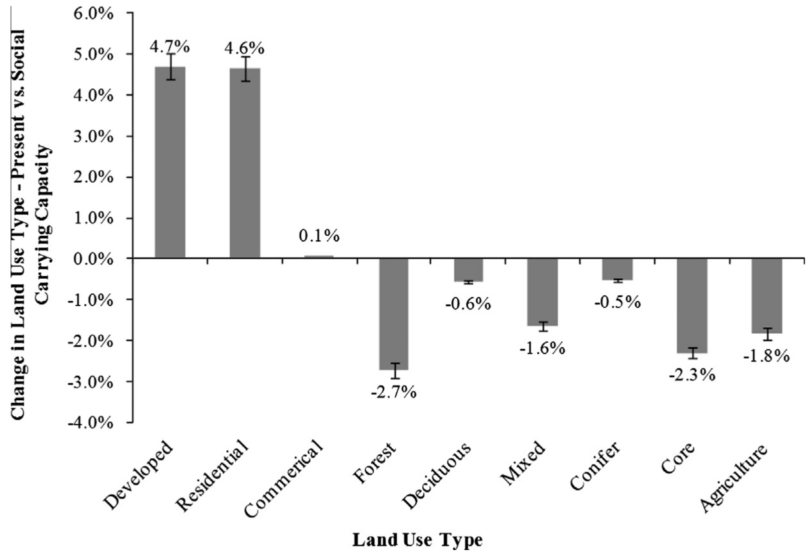

Fig. 2. Change in percent land use type between present conditions and social carrying capacity of the landscape. Negative values reflect land use types which were lower under social carrying capacity, while positive values (developed uses only) reflect land use types which were higher under social carrying capacity. Bars reflect 95% confidence intervals.

two areas: in moderately forested areas on the fringe of the Champlain Valley; and in the north of the state around Newport. The probability of occurrence for bobcat dropped by an average of 3.1%, with the largest decline of 7.6% (Fig. 3h). Change in bobcat ψ was largely sporadic throughout the state, with isolated patches of change in the southern Green Mountains and in portions of the northeast. Fisher occupancy increased in all towns with projected development, averaging 9.0%, with a maximum rate of increase of 19.1% (Fig. 3i). Fisher ψ changed most along the western edge of the state: in the Champlain valley in the northwest, and the Taconic valley in the southwest.

3.3. Comparing occupancy between present landscape conditions (Year 2000) and landscape conditions at SK_d. (Objective 3)

Changes in wildlife occupancy rates in response to the social carrying capacity for development within Vermont towns occurred only in exurban ($n = 149$) and rural ($n = 101$) towns (Fig. 4a). In general, occupancy rates did not change between time periods in urban and suburban towns. Black bear exhibited greater declines in occupancy in exurban versus rural towns, although not significantly so ($p = 0.1550$). Fisher and bobcat displayed greater changes in ψ between current conditions and social carrying capacity in rural towns over exurban towns, but for different reasons. Average town ψ level for fisher was expected to increase by roughly 10% in rural towns compared to 7% in exurban towns in response to SK_d (Fig. 4a). In contrast, average town ψ levels for bobcat was expected to decrease in rural towns by roughly 4% in rural areas and by 3% in exurban areas (Fig. 4a; fisher: $p < 0.0001$, bobcat: $p < 0.0001$).

Change in black bear occupancy rates between current conditions and SK_d varied significantly by towns depending on low ($n = 24$), medium ($n = 130$), or high ($n = 96$) levels of forest ($p < 0.0001$). Black bear ψ decreased the most in towns with medium percent forest under current conditions (mean difference = −0.217, 95% CI: −0.237, −0.197), followed by high percent forest (mean = −0.109, 95% CI: −0.132, −0.088), with relatively little change in towns with low percent forest (mean = −0.012, 95% CI: −0.055, 0.030) (Fig. 4b).

Although change in fisher occupancy in response to towns' social carrying capacity did not vary significantly between forest types ($p = 0.080$), mean change was highest in towns with high percent forest under current conditions (mean = 0.097, 95% CI: 0.088, 0.105), followed by medium percent forest (mean = 0.083, 95% CI: 0.076, 0.091), and low percent forest (mean = 0.075, 95% CI: 0.060, 0.091). Bobcat displayed small changes in occupancy between current conditions and social carrying capacity, which varied significantly between forest types ($p < 0.0001$). Occupancy for bobcat changed the most in towns with high percent forest (mean = −0.045, 95% CI: −0.049, −0.042), followed by medium percent forest (mean = −0.026, 95% CI: −0.029, −0.022), and low percent forest (mean = −0.005, 95% CI: −0.012, 0.001).

4. Discussion

This paper, in concert with Bettigole et al. (2013), provides a powerful methodology to: (a) measure the social carrying capacity for development within a landscape, and predict how these social norms vary with changing demographic parameters; (b) transform these social norms into a land use scenario under SK_d; and (c) assess how these social norms and corresponding social carrying capacity land uses potentially affect wildlife occupancy for a suite of focal species. The techniques developed here not only set a baseline for repeated study in the future, but offer a scale-able and spatially transferable methodology for linking the relationship between social carrying capacity for development with the capacity of the landscape to host wildlife species.

Although we use SK_d as the standard for maximum development within a town boundary, town planners could use other metrics from the norm curve (see Bettigole et al., 2013), results from land use change and population growth models, or other approaches for establishing standards (Walters, 2007). It may be reasonable for planners to assume that their town will eventually build out based on what the zoning standards allow. What is important here is the linking of a standard with the potential change in wildlife distribution patterns, which may enable town planners to make a more informed decision when establishing land use standards for their community.

While Vermont remains a largely rural state, and population growth projections are modest (Brown, 2012), Vermont's social capacity for development among residents is greater than what currently exists. In Vermont, as in many states, land use decisions are made from the ground-up on a community scale, and it is important to provide town, regional, and state level predictive

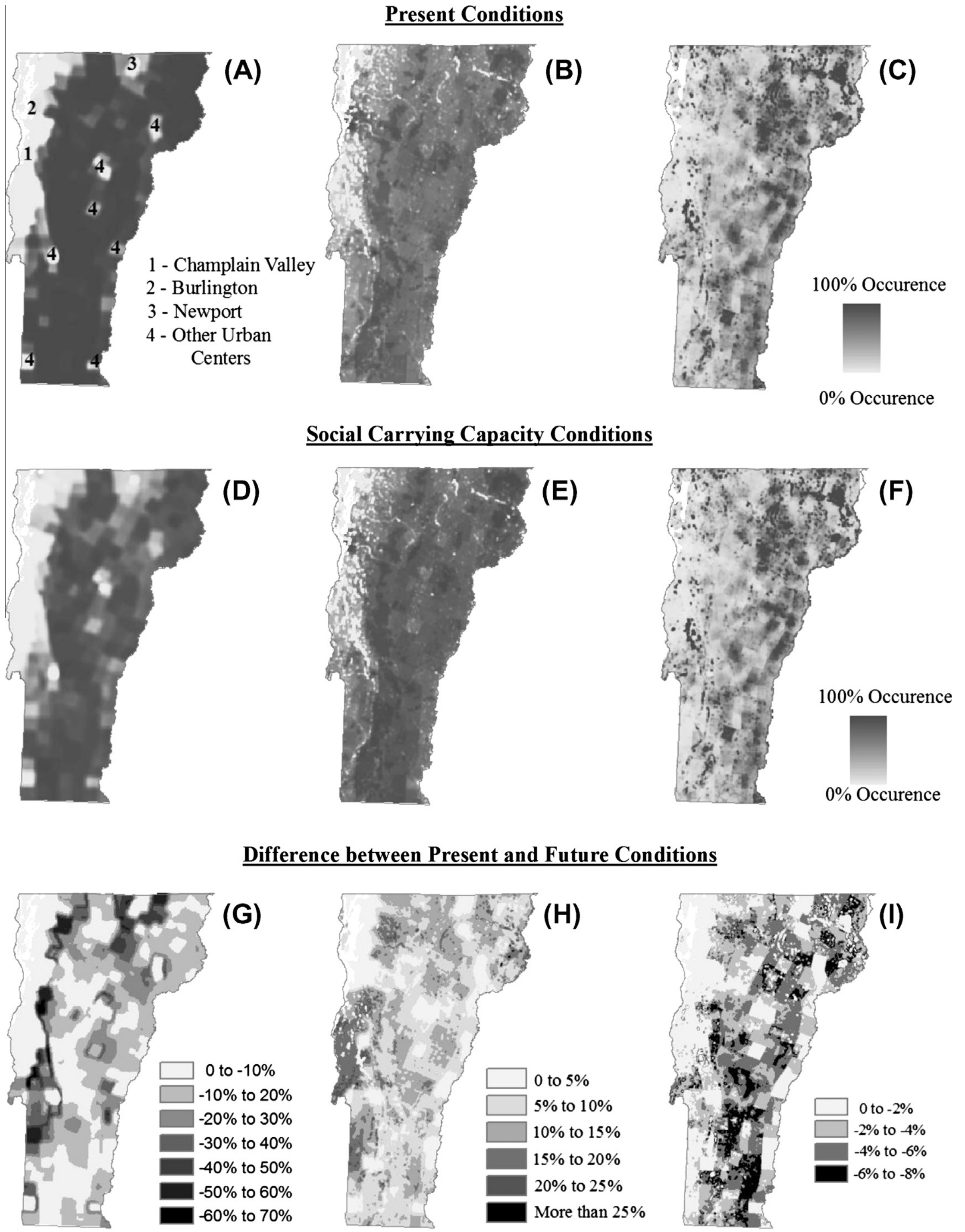

Fig. 3. Occupancy models under present conditions and conditions at social carrying capacity for black bear (a and d), fisher (b and e) and bobcat (c and f). Darkly shaded areas exhibit high probability of occurrence, while lightly shaded areas exhibit low probabilities of occurrence. Difference between present conditions and social carrying capacity for black bear (g), fisher (h), and bobcat (i). Note that bear and bobcat show higher occupancy under present conditions than carrying capacity conditions, while fisher shows higher occupancy under carrying capacity conditions.

models to ensure that decisions are made with attention to a variety of spatial scales. Government and private programs aimed at providing guidance and assistance to town planning and conservation commissions can benefit from this information by using it to illustrate the biological consequences of land use decisions. For example, for towns undergoing development, technical assistance can provide guidance on where new development can occur in a way that minimizes loss to biodiversity. Moreover, towns with similar attitudes for development can be prioritized for technical assistance depending on their current contribution to wildlife occurrence. Conversely, natural resource managers can pinpoint those towns where even small changes in development can result in large declines of target wildlife species.

We carefully selected our set of focal species to represent a broad range of life requisites, allowing them to serve as surrogates for the ranges and life histories of many species (Reining et al., 2006). Wide-ranging mammals are generally sensitive to changes in human land uses because of their low fecundity and limited ability to disperse across developed landscapes (Carroll et al., 2001). Because of their large home ranges, the conservation and

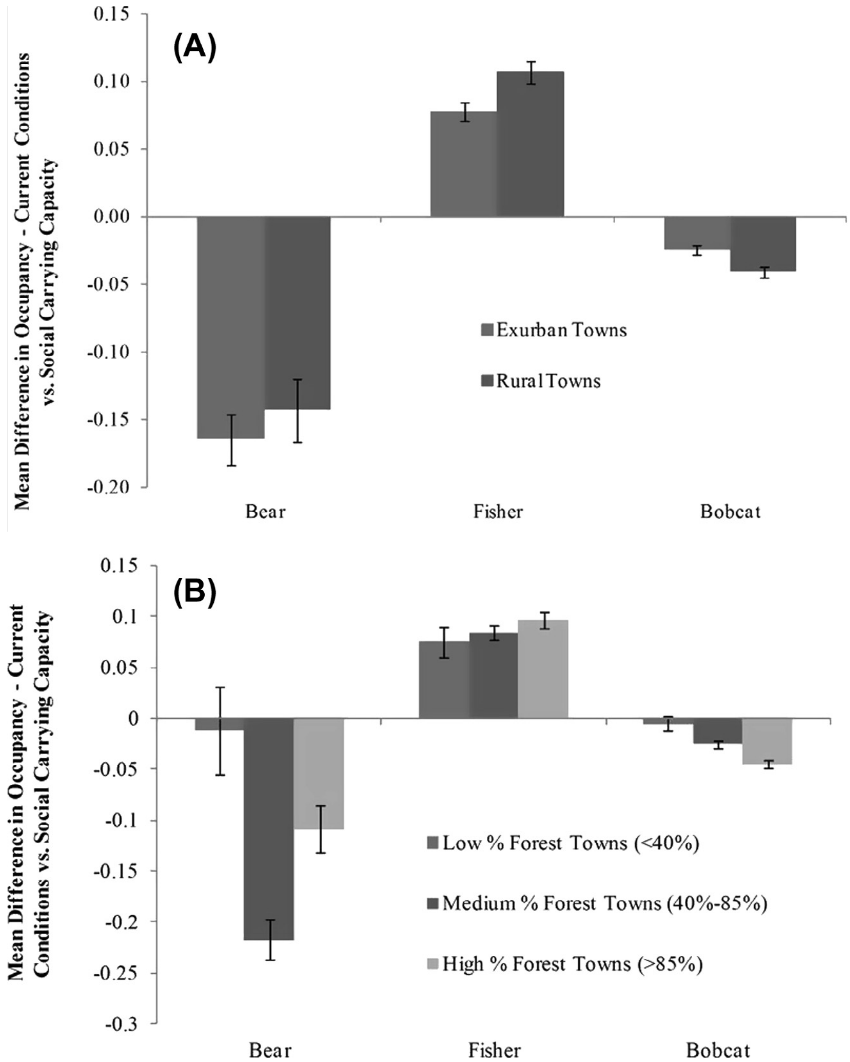

Fig. 4. (A) Change in occupancy between present conditions and social carrying capacity by intensity of town level development. "Exurban" towns have densities between 0.68–16.18 ha per housing unit (149 towns in Vermont), "rural" is classified as densities greater than 16.18 ha per housing unit (101 towns in Vermont). Bars reflect 95% confidence intervals. (B) Change in occupancy between present conditions and social carrying capacity by percent forest. Towns were classified based on current percent forest cover: low (less than 40%), medium (between 40% and 85%), and high (greater than 85%). Bars reflect 95% confidence intervals.

management of these species may require coordinated efforts across town boundaries to ensure their persistence. Many wildlife species experience a threshold where small reductions in available habitat (usually at low levels of habitat availability) precipitate large reductions in population size or occupancy (Fahrig, 2001). These species specific thresholds are dictated by: (a) the reproductive rate of the organism; (b) the rate of emigration; (c) habitat pattern; and (d) matrix quality (the ability of a species to survive outside of core habitat). If the long term persistence of the widest ranging mammals can be assured, then they may act as an umbrella species: if enough habitat is protected for viable populations of large carnivores, then species with smaller range requirements will also be protected (Noss et al., 1996).

Of the three focal species, our black bear occupancy model showed the largest threshold response to reductions in forest habitat (Fig. 1b); if existing habitat is between 40% and 85%, small reductions in forest result in large decreases in occupancy. We therefore observed the largest decreases in occupancy between current conditions and SK_d in those towns where current forest levels fall within this range. Towns with medium amounts of forested land (exurban) were likely to see the most dramatic changes in bear occurrence rate as development increased almost statewide in the SK_d landscape; highly forested towns (rural) are buffered from these effects because of large core habitat patches, and towns with low forest habitat (suburban and urban) already have insignificant bear occupancy levels.

We did not observe dramatic declines in response to SK_d for fisher and bobcat. This could be an indication that black bears are more sensitive to habitat loss than our other two focal species, which may be able to maintain stable populations in a more developed future, see also (Carroll et al., 2001). Additionally, the slight increase in fisher occupancy under SK_d could result from fisher's ability to occupy residential areas in Vermont (Long et al., 2010), which is the landcover type that was increased for towns whose SK_d exceeded their current levels of development. There may be many other factors influencing the behavior of fisher and bobcat that were not captured in the occupancy analysis that explain how they are able to survive in areas with more development than black bears.

In predicting the changes in distribution patterns of our three target species, several caveats are critical to keep in mind. First, wildlife populations are fundamentally dynamic, with the possibility for abundances and distributions to change drastically from year to year (MacKenzie et al., 2006). Occupancy models rely on empirical data (field observations); surveys conducted in a suboptimal year may produce overall low, patchy levels of occurrence, while surveys conducted at the same sites in a banner year may produce widely distributed, high levels of occurrence, with detection in sub-quality habitats (Fretwell and Lucas, 1970).

Second, the method of surveying carries great consequences for occurrence mapping. For example, Long et al. (2010) found much higher rates of detection for black bear and fisher compared to bobcats using scat detection dogs. Wide ranging mammals are, in general, elusive, and low detection probabilities lead to less precise occupancy estimates. Methodology can also affect the maximum likelihood (point) estimate of occupancy for a species. For example, habitat suitability models of bobcats in Vermont based on GPS data (Donovan et al., 2011) displayed significantly different patterns of bobcat distribution with stronger predictor variables than those found by Long et al. (2010). As such, planners should evaluate the consequences of SK_d under a range of estimates to reflect this uncertainty, or focus on species that have high detection rates and hence, provide more precise estimates of occupancy (e.g., Schwenk and Donovan, 2011).

Third, occupancy probabilities do not reflect population viability: areas of high occurrence do not necessarily indicate source habitat. Ecological theory suggests that local habitats may be sinks: local subpopulations whose mortality rate exceeds birth rate, yet persists due to constant immigration, (Pulliam, 1988). Moreover, some habitats may exhibit high population size because there are insufficient habitats elsewhere, or because they are ecological traps, possessing cues that draw individuals there but do not offer sufficient resources to promote population viability (Schlaepfer et al., 2002).

Fourth, while occupancy maps may be widely used in wildlife science, they do not reveal the population size that a landscape is capable of supporting. Probabilities are notoriously hard to interpret, and humans tend to dismiss small changes (Cosmides and Tooby, 1996), such as the relatively small decline in predicted occupancy pattern of bobcat in this study. However, new techniques that use maximum clique analysis (a branch of graph theory) can translate occupancy rasters into an estimate of N_k, defined as the maximum number of non-overlapping territories that a landscape is capable of supporting (Donovan et al., 2011). Using maximum clique analysis, Brown (2012) showed that small declines in occupancy probabilities can lead to very large changes in actual population size. In using the results of this study, it is important to understand that reductions or increases in occupancy for our focal species may not be in proportion to changes in species abundance. Overall, we recommend caution in assuming that these wide-ranging carnivores are capable of surviving in the long-term with less, more fragmented habitat.

Finally, in this study, we analyzed responses to land use change in three forest dwelling mammals, and although these may serve as focal species for other wildlife, many species in Vermont do not rely on forested habitats. It is important to note that what may be detrimental to one suite of species, may be largely beneficial to another. Even among our small sample forest dwelling carnivores, fisher showed a positive response to increased residential development, an indication that some species may respond positively to the increased edge effects and open land associated with development. These byproducts of forest loss and fragmentation may produce more conducive habitats for certain birds, small mammals, reptiles, and amphibians (Fahrig, 2003). However, direct human disturbance, increased road mortality from new roads and higher vehicular traffic (Forman et al., 2003), and a wealth of other human related factors (e.g., increased predation from domestic cats (Lepczyk et al., 2004)) may counteract these positive effects of openness. While our analysis of three focal species does capture a degree of variation in mammalian response to forest loss, it is important to understand that habitat requirements, food sources, and home ranges differ drastically for vertebrates throughout Vermont and the northern forest.

Paired with detailed land use change models, and town, state, and federal level planning, this research can facilitate targeted, spatially explicit conservation efforts. Additionally, by feeding probability based occupancy models into a maximum clique framework, managers can provide comprehensible, quantitative scenarios to clearly illustrate the effects of land use change on wildlife species.

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References

Allen, A.W. 1983. Habitat suitability index models: fisher. Page 19 pp. United States Fish and Wildlife Service-82/10.45. pp. 19.

Brown, M., 2012. Predicting Impacts of Future Human Population Growth and Development on Occupancy Rates and Landscape Carrying Capacity of Forest-Dependent Birds. M.S. Thesis. University of Vermont, Burlington.

Bettigole, C.A., Donovan, T.M., Manning, R., Austin, J. 2013. Normative standards for land use in Vermont: implications for biodiversity. Biol. Conserv.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. Springer, New York.

Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the rocky mountain region. Ecol. Appl. 11, 961–980.

Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. Science 296, 904–907.

Clark, J.D., Dunn, J.E., Smith, K.G., 1993. A multivariate model of female black bear habitat use for a geographic information system. J. Wildlife Manage. 57, 519–526.

Cosmides, L., Tooby, J., 1996. Are humans good intuitive statisticians after all? Rethinking some conclusions from the literature on judgment under uncertainty. Cognition 58, 1–73.

Donovan, T.M., Freeman, M., Abouelezz, H., Royar, K., Howard, A., Mickey, R., 2011. Quantifying home rang ehabitat requirements for bobcats (Lynx rufus) in Vermont USA. Biol. Conserv. 144, 2799–2809.

ESRI, 2009. Arcgis 9.3. ESRI, Redlands, CA.

Fahrig, L., 2001. How much habitat is enough? Biol. Conserv. 100, 65–74.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversiy. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC.

Fretwell, S.D., Lucas, H.J., 1970. On territorial behavior and other factors influencing habitat distributions in birds. Acta Biotheoretica. 19, 16–36.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 national land cover database for the conterminous United States. Photogrammetric Eng. Remote Sens. 77, 858–864.

Hall, E.R., 1981. The Mammals of North America. John Wiley and Sons, New York.

Hughes, J.B., Daily, G.C., Ehrlich, P.R., 1997. Population diversity: its extent and extinction. Science 278, 689–692.

JMP, 1989–2007. Version 7. SAS Institute Inc., Cary, NC.

Komonen, A., Penttilae, R., Lindgren, M., Hanski, I., 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90, 119–126.

Lepczyk, C.A., Mertig, A.G., Liu, J., 2004. Landowners and cat predation across rural-to-urban landscapes. Biol. Conserv. 115, 191–201.

Litvaitis, J.A., Sherburne, J.A., Bissonette, J.A., 1986. Bobcat habitat use and home range size in relation to prey density. J. Wildlife Manage. 50, 110–117.

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 Ecol. 26, 327–340.

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MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling – Inferring Patterns and Dynamics of Species Occurrence. Elsevier, Burlington, MA.

NOAA Coastal Services Center, 2011. NOAA coastal change analysis program (C-CAP) regional land cover database: data collected 1995–2006. National Oceanic and Atmospheric Administration Coastal Services Center, Charleston, SC.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., Paquet, P.C., 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conserv. Biol. 10, 949–963.

Parker, D.C., Manson, S.M., Janssen, M.A., Hoffmann, M.J., Deadman, P., 2003. Multi-agent systems for the simulation of land-use and land-cover change: a review. Ann. Assoc. Am. Geograph. 93, 314–337.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Naturalist 132, 652–661.

Manning, R.E., 2007. Parks and Carrying Capacity: Commons Without Tragedy. Island Press, Washington, DC.

Reining, C., K. Beazley, P. Doran, and C. Bettigole. 2006. From the adirondacks to acadia: a wildlands network design for the Greater Northern Apalachians. The Wildlands Project Special Paper #7. The Wildlands Project, Richmond, VT.

Rolley, R.E., Warde, W.D., 1985. Bobcat habitat use in Southeastern Oklahoma. J. Wildlife Manage. 49, 913–920.

Rudis, V.A., Tansey, J.B., 1995. Regional assessment of remote forests and black bear habitat from forest resource surveys. J. Wildlife Manage. 59, 170–180.

Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. Trends Ecol. Evol. 17, 474–480.

Schmiegelow, F.K.A., Monkkonen, M., 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecol. Appl. 12, 375–389.

Schwenk, W.S., Donovan, T.M., 2011. A multi-species framework for landscape conservation planning. Conserv. Biol. 25, 1010–1021.

Theobald, D.M., 2004. Placing exurban land-use change in a human modification framework. Frontiers Ecol. Environ. 2, 139–144.

Theobald, D.M., 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. Ecol. Soc. 10, 32.

Trombulak, S.C., Royar, K., 2001. Restoring the wild: species recovery and reintroduction. In: Klyza, C.M. (Ed.), Wilderness Comes Home: Rewilding the Northeast. University Press of New England, Hanover, NH.

Vitousek, P.M., 1994. Beyond global warming: ecology and global change. Ecology 75, 1861–1876.

Walters, D., 2007. Designing Community, Charrettes, Masterplans and Form-based Codes. Oxford, UK.