Density and distribution of a colonizing front of the American black bear Ursus americanus

Authors: Frary, Vincent J., Duchamp, Joseph, Maehr, David S., and Larkin, Jeffery L.

Source: Wildlife Biology, 17(4) : 404-416

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/09-103

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 09 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 17: 404-416 (2011)
DOI: 10.2981/09-103

www.wildlifebiology.com

Original article

Density and distribution of a colonizing front of the American black bear *Ursus americanus*

Vincent J. Frary, Joseph Duchamp, David S. Maehr† & Jeffery L. Larkin

Effective management of small expanding populations is aided by the availability of reliable estimates of distribution, as well as by demographic characteristics such as population density, genetic diversity and sex ratio. The range of the black bear *Ursus americanus* in the southeastern United States is expanding to include areas from which it has been extirpated for more than a century. Lack of baseline demographic data in recently reoccupied areas leaves little information on which to base emerging management needs. We estimated the current extent of expansion at the colonizing front of a black bear population in the central Appalachian Mountains and identified landscape-scale habitat characteristics affecting the expansion. In 2007, we genotyped hair samples collected throughout a 8,205-km^2 area at six microsatellite loci to identify individual black bears and estimate genetic diversity. We used capture-recapture and occupancy analyses to estimate density and distribution of black bears in our study area. Our results suggest that black bears were not uniformly distributed, but were localized to high elevations and protected public conservation lands. Limited availability of high elevations to the west, north and northeast of our study area may limit further expansion. Despite a limited distribution and low estimated population density (7.51 bears/100 km^2), genetic diversity at genotyped loci was high (mean $H_o = 0.81$). Until the population grows further, the small number of individuals in the region may be sensitive to management practices that result in mortalities, especially to females. Our research exemplifies the utility of remote genetic sampling to estimate population demographics of wide-ranging mammals throughout a large study area, particularly where private land ownership hinders intensive study.

Key words: capture-recapture, genetic, microsatellite, non-invasive, occupancy, United States of America

Vincent J. Frary, Joseph Duchamp & Jeffery L. Larkin, Department of Biology, Indiana University of Pennsylvania, USA - e-mail addresses: vfrary1@yahoo.com (V.J. Frary); larkin@iup.edu (J.L. Larkin); jduchamp@iup.edu (J. Duchamp)
David S. Maehr†, Department of Forestry, University of Kentucky, USA
† Deceased

Corresponding author: Vincent J. Frary

Received 26 November 2010, accepted 13 July 2011

Associate Editor: Olivier Gimenez

The spatial distribution and demographics of populations along the edge of a species' geographic range are often complex (Gaston 2003) and thus difficult to monitor. This task is made even more challenging if the focal species typically exists at low population densities (McDonald 2004). Moreover, logistical challenges associated with rugged, remote terrain, limited access to private land and economic cost also hinder research and monitoring of expanding populations (Flagstad et al. 2004). Nonetheless, the successful completion of conservation priorities such as predicting how species will be impacted by and respond to global climate change will be, in part, dependent on our ability to empirically characterize factors that drive population expansion. In recent years, non-invasive genetic sampling has become a valuable method for detecting rare and elusive species and estimating population demographics (Waits 2004). Moreover, several studies have shown that accurate demographic estimates across large spatial extents can be obtained via non-invasive sampling (Mowat & Strobeck 2000, Dixon et al. 2006, Schwartz & McKelvey 2009).

Monitoring colonizing fronts of expanding black bear *Ursus americanus* populations in remote regions of the Appalachian Mountains in the eastern

United States of America appears to be an excellent scenario for the use of non-invasive molecular techniques. Historically, the black bear was distributed throughout the forested portions of eastern North America including the Appalachian Mountains (Hall 1981). Black bears were extirpated throughout much of the eastern United States by the early 20th century due to unregulated hunting and large-scale habitat loss (Laliaberte & Ripple 2004). Although the black bear remains extirpated in portions of historically-occupied habitat, within the past several decades, populations have increased, and the species has reoccupied several states, from which it became absent (Pelton et al. 1998). This pattern of recovery contrasts with a general pattern of decline among the world's seven other bear species (Servheen et al. 1998).

Black bear reproduction was documented in Kentucky in 2003 after an absence of more than a century (Unger 2007). The return of the species to this portion of the Appalachian Mountains coincides with increasing bear populations in neighbouring areas (Virginia Department of Game and Inland Fisheries 2003, West Virginia Department of Natural Resources 2006), and indicates westward expansion by a regional population that extends from the southern Appalachians into the northeastern United States (Pelton 2003). Recolonization of historic range by the black bear reflects improved resource management and increased tolerance among people in such areas; however, recovery of any large carnivore species establishes the potential for wildlife/human interaction and conflict. Development of effective management strategies can be hindered by the lack of baseline demographic information, which can be particularly difficult to obtain in areas where private land ownership hinders intensive study or previous harvest data are unavailable.

While black bears have expanded into previously unoccupied regions and reproduction has been documented, anecdotal evidence suggests that population growth and continued expansion appears to be slower in southeastern Kentucky relative to adjacent areas of the Appalachian Mountains (Unger 2007). We initiated our study because little empirical information exists regarding the distribution and population density of black bears that comprise this colonization front. Additionally, no previous studies have identified landscape-scale factors that may be affecting the westerly expansion of the regional population.

To empirically address these questions, we used remote sampling and molecular genetic techniques to survey black bears throughout recently recolonized areas. We evaluated the genetic diversity of sampled individuals, and we used spatially explicit capture-recapture methods (SECR; Efford et al. 2009) to estimate density of black bears in our study area. Additionally, we applied occupancy models (MacKenzie et al. 2002) to evaluate black bear distribution in our study area and to identify factors affecting this distribution under an information-theoretic framework (Burnham & Anderson 2002).

We predicted that the density of black bears in our study area was low, but because of the abundance of forested habitat in the region, the species would be evenly distributed. We also expected that since evidence suggests that black bears in Kentucky represent an extension of a larger regional population, genetic diversity would be high. Black bear recolonization of this portion of the Appalachian Mountains provides a rare opportunity to study how large carnivores colonize vacant habitats. Non-invasive surveys at large spatial scales combined with statistical modeling are a logical first step in large mammal conservation planning (Larkin et al. 2004, Dixon et al. 2006). As such, our methodologies and general findings should be applicable to other carnivore species colonizing remote, difficult-to-survey areas.

Material and methods

Study area

Our study area included an 8,205-km^2 area in the southeastern portion of the state of Kentucky, USA. The average elevation of our study area was 450 m a.s.l. Several high-elevation areas (i.e. Pine, Black and Cumberland Mountains) were included in the southeastern extent of our study area where elevations reached 1,262 m a.s.l. (Homer et al. 2004). Our study area also included a portion of the northern Cumberland Plateau of the Appalachian Plateau physiographic province, which is characterized by forested hills and deep, narrow valleys (Thornbury 1965). Elevations in this area generally ranged from 300 to 500 m a.s.l. (Homer et al. 2004).

The study area was predominantly (89%) composed of mesophytic forests, which are characterized by nearly 30 dominant tree species (Ricketts et al. 1999). Common trees include maples *Acer* spp., oaks *Quercus* spp., hickories *Carya* spp., magnolias *Magnolia* spp. and birches *Betula* spp. (Barbour &

Davis 1973). Common understory shrubs throughout the study area included mountain laurel *Kalmia latifolia* and rhododendron *Rhododendron* spp. (Barbour & Davis 1973). Active and reclaimed coal surface mines accounted for approximately 6% of the land cover (Sayler 2006). The remaining portions of the landscape (5%) were mainly agricultural and developed land (Sayler 2006). Land ownership in the study area was 6% public and 94% private.

Sampling design

We overlaid a grid composed of 313 contiguous sampling cells across our study area. Each cell was 25 km^2, which approximated the smallest known summer black bear home range of individuals in our target population (Unger 2007). This ensured that at least one sampling site was placed in each potential black bear home range (Woods et al. 1999). Due to resource constraints and our desire to maximize detection of black bears in our study area, we omitted four cells within this grid because they were > 80% non-forested and thus likely constituted little potential habitat for black bears. We omitted an additional six cells, because we could not obtain permission from landowners for access.

Within each of the remaining 303 sampling cells, we subjectively selected areas most likely to constitute black bear habitat (i.e. including remote, contiguously forested habitat containing mast-producing trees; Brody & Pelton 1989, Vaughan 2002, Pelton 2003) to maximize the probability of detecting our target species in each cell if present (Mowat & Strobeck 2000). We identified these areas using topographical maps, land cover data and visual reconnaissance of sampling areas. Field technicians surveyed each suitable area until they located an appropriate location for installation of a hair-snare (i.e. 3-5 trees capable of holding two strands of barbed-wire and enclosing an area of approximately 15 m^2). Since the majority (72%) of the cells were located on private property, our access to an entire cell was occasionally limited because of the inability to gain the landowner's consent. In these situations, we selected the best potential site within a cell to which we could gain access. However, because forest was extensive throughout the study area, we rarely encountered an occasion in which only one location within a cell constituted potential bear habitat.

Our snares were similar to those described by Woods et al. (1999). Each snare consisted of two strands of barbed wire, wrapped parallel to the ground around 3-5 trees. A strand of barbed wire was placed 25 and 50 cm above ground level to allow sampling of both adult and subadult black bears. We baited snares with two 4.25 oz cans of sardines and checked for the presence of black bear hair every eight days. Each hair snare was active for five 8-day sampling sessions between 15 May and 29 June 2007. Samples collected at hair snares were individually stored in kraft paper envelopes and placed in containers of silicone desiccant to preserve the integrity of genetic material.

Genetic analysis

We pre-screened all samples collected at hair snares using a dissecting microscope to exclude any samples that were not uniformly black with white root tips, indicating a non-target species (Hausman 1920). Remaining samples were analyzed by Wildlife Genetics International (WGI, Nelson, British Columbia, Canada). WGI genotyped all hair samples at six nuclear microsatellite loci (G10H, G10M, G10L, G10C, G1A and G1D) using the methods described in Woods et al. (1999) to identify individual black bears. WGI employed genotyping quality assurance and error-checking recommendations described in Paetkau (2003) to ensure confident identification of individuals. This included reanalyzing individual genotypes that matched at all but one or two loci (1MM and 2MM pairs, respectively). We calculated the probability of identity (PI), or the probability that a multi-locus genotype was shared by > 1 individual for our genotyping results (Paetkau & Strobeck 1994). We considered an overall PI < 0.01 to be an acceptable level at which we would conclude proper identification of individuals (Mills et al. 2000). WGI used a single sample from each individual to assign gender based on size polymorphism at the amelogenin gene (Ennis & Gallagher 1994). WGI used a mitochondrial test to confirm species (D. Paetkau, WGI, pers. comm.) in samples where microsatellite DNA was insufficient to identify individuality, which allowed the sample to be used to document black bear occupancy.

WGI provided measures of genetic diversity including mean expected and observed heterozygosity, and the mean number of unique alleles at each locus. We used genotyping results to complete tests for a Hardy-Weinberg Equilibrium between genotypes and linkage equilibrium between gene loci to identify evidence of non-random mating (Frankham et al. 2002). We performed these tests ($\alpha = 0.05$) using program Genepop 3.4 over 20 batches of 5,000 iterations (Raymond & Rousset 1995).

Occupancy

We used genotyping results to develop a black bear detection history for each sampling cell. We used occupancy models developed by MacKenzie et al. (2002) to estimate black bear distribution across our study area. We interpreted our estimates as cells 'used' instead of cells 'occupied' following suggestions in MacKenzie (2006) for situations in which geographic and demographic closure are not met for each sampling unit, as we expected in our study. We performed our computations using program MARK (White & Burnham 1999).

Habitat variables

In order to refine our estimates of black bear use, we identified landscape-scale habitat variables that may have either affected our ability to detect black bears using our sampling methods, or may be influencing black bear distribution throughout our study area (Table 1). All habitat variables were represented as raster data sets in ArcGIS 9.x Geographic Information System (Environmental Systems Research Institute, Redlands, California).

Detection probability

In order to properly incorporate detection probability (p) in our occupancy models, we tested a null model of constant detection probability against three additional models while keeping probability of use constant. First, we tested a model that accounted for variation among our sampling periods. This model allowed for temporal variation in detection probability by estimating a unique probability for each sampling session. This reflected our prediction that weather or natural seasonal changes in black bear activity may have affected detection probability.

We predicted that our probability of detecting black bears may be greater in or near public

Table 1. Source, resolution, range and overall mean and standard deviation across our study area of GIS habitat variables. Habitat variables were used to estimate detection probability and probability of black bear use of eastern Kentucky in 2007.

Variable	Description	Resolution	Data source	$\bar{x}$	Range	SD
Percent forest (perfor)	Percent forested landscape within each 25-km^2 sampling cell	30 m	National landcover data set (Homer et al. 2004)	82.0%	50.0 - 96.4	8.7
Elevation (elev)	Mean elevation within each 25-km^2 sampling cell	30 m	National landcover data set (Homer et al. 2004)	481.93 m	272.17 - 1042.30	114.3
Percent slope (slope)	Mean percent slope within each 25-km^2 sampling cell	30 m	National landcover data set (Homer et al. 2004)	21.67%	10.40 - 26.06	2.61
Human population density (pop)	Mean human population density within each 25-km^2 sampling cell	100 m	GeoLytics (2003)	25.5 people/km^2	3.4 - 101.8	16.44
Distance from nearest road (road)	Mean distance to nearest road from each 30 m raster pixel within each 25-km^2 sampling cell	30 m	United States Census Bureau (2000)	497.61 m	195.43 - 1551.66	240.92
Distance from nearest forest edge (edge)	Mean distance to nearest forest/nonforest edge from 30 m raster pixels within each 25-km^2 sampling cell	30 m	National landcover data set (Homer et al. 2004)	172.52 m	60.70 - 681.42	87.64
Distance from nearest public conservation land (pub)	Mean distance to nearest public conservation land (e.g. state park, state wildlife management area) from 30 m raster pixels within each 25-km^2 sampling cell	30 m	Kentucky Department of Fish and Wildlife Resources Information System (2001)	7287.13 m	0.0 - 25754.60	6040.72
Distance from colonization source (colo)	Mean distance to nearest known black bear colonization source population from 30 m raster pixels within each 25-km^2 sampling cell	30 m	Kentucky Department of Geographic Information (2005)	18799.75 m	612.06 - 46437.0	11497.6

conservation lands vs private lands for several reasons. First, accessibility to public lands was essentially unlimited, and thus, we had no limitations when selecting ideal sampling locations within these areas. Secondly, several ongoing studies of black bear have occurred on public lands in our study area. Some of these studies have involved baiting bears to trap sites, which we predicted may have habituated some bears in these areas to human food. In order to explicitly address this possibility, we tested models that constrained detection probability to be a function of the mean distance from each sampling cell to the nearest public conservation land (habitat variable 'pub'; see Table 1). Finally, we tested a model that specified a relationship between detection probability and additive effects of temporal variation and variation due to proximity to public lands.

We ranked all candidate models according to their Akaike's Information Criterion (AIC; Akaike 1973) value corrected for small sample size (AIC_c; Burnham & Anderson 2002) and regarded the model with the lowest AIC_c value as our best model. We used the overall detection probability formula $1 - \prod_{i=1}^{k} (1 - p_i)$ to calculate the probability of detecting black bear at least once during $k = 5$ sampling sessions (MacKenzie 2006).

Probability of use

We tested a candidate set of 13 *a priori* models that constrained probability of use (Ψ) to be a function of various additive and interactive combinations of site-specific habitat variables (see Table 1). Several models included variables that addressed fundamental factors affecting the quality of black bear habitat, including the availability and contiguity of forests (Pelton 2003). Since human activity and accessibility have been shown to affect black bear habitat use (Brody & Pelton 1989, Kasworm & Manley 1990, VanderHeyden & Meslow 1999), we considered models that tested the influence of roads and human populations in our study area. We also tested models that represented the prediction that higher elevations and rugged terrain may be of particular importance in our study area by limiting development and human access (Nelleman et al. 2007). We included several models that addressed our prediction that forest protection measures on public conservation lands may serve as black bear refugia from other areas where anthropogenic disturbance is more prevalent. Finally, we tested models that represented the prediction that patterns of black bear use of our study were a function of a population in the early stages of recolonization of the state (i.e. the population has simply not had adequate time to expand far from its source population).

We ranked all candidate models according to AIC_c values, and regarded the model with the lowest AIC_c value as our best model. We considered models that were ranked within four AIC_c values of the best model to be competing, and we averaged parameter estimates from competing models using program MARK. We averaged beta-coefficients and standard errors of all covariates included in competing models (Burnham & Anderson 2002), which allowed us to assess the relative strength of each variable in predicting black bear use. We also assessed the overall support for each variable included in competing models by summing the AIC_c weights of competing models in which that variable was included (Burnham & Anderson 2002). We calculated the probability of use for each 25-km^2 sampling cell using the logistic model described in MacKenzie et al. (2002).

We assessed goodness-of-fit for occupancy models using the median c-hat test in program MARK. This test is not available for models that include individual covariates, so we tested the most fully-parameterized models that did not include any of our habitat variables (i.e. model: $p(t)\Psi(.)$). Regardless, this technique provides an acceptable measure of model goodness-of-fit, as model fit will only improve with the inclusion of additional covariates (G.C. White, Colorado State University, pers. comm.).

Density

We used the results of genetic analysis to assemble capture-recapture encounter histories for each individual black bear sampled in our study. The simplest method to estimate population density from capture-recapture data is to first estimate capture probability and abundance using one of a variety of applicable models (Otis et al. 1978, Williams et al. 2002), and divide abundance estimates by the size of the study area. However, this approach poses several problems. First, this method requires that the area occupied by the target species is known. Second, the majority of these models assume that a population is closed to demographic changes during at least a portion of the study duration, which is unlikely in many ecological investigations and can bias estimates (Kendall 1999, Boulanger & McLellan 2001).

To avoid these potential confounding issues, we employed spatially explicit capture-recapture (SECR) methods (Efford 2004). SECR estimates population density explicitly based on capture-recapture encounter histories and home ranges inferred from the spatial location of captured individuals (Efford 2004, Royle & Young 2008, Obbard et al. 2010). SECR models do not make inferences based on trap layout, and thus do not require ad-hoc definition of the 'effective study area'. Furthermore, demographic closure is not an assumption of the SECR approach. SECR models estimate three main parameters: the magnitude of the capture probability (g_0), the spatial extent over which capture probability declines (σ) and population density ($\hat{D}$).

We used SECR models to estimate population density for all sampling cells within our study area where black bear occupancy was estimated to be ≥ 0.25. We utilized a maximum likelihood approach at fitting SECR models (Efford et al. 2009) using program DENSITY (Efford 2008). We assumed a Poisson distribution of home range centers and a half normal spatial capture probability function. We developed a suite of models *a priori* that specified combinations of different forms of variation in g_0 and σ. We considered models that kept both g_0 and σ constant. We also considered models that allowed g_0 and σ to vary temporally among sampling sessions. We considered a behavioural response for both parameters since we were using a caloric reward as bait. Finally, we considered models that modeled g_0 and σ with heterogeneity in a two-point mixture.

We ranked all candidate models according to support given to our data using AIC_c values. The model with the lowest AIC_c value was considered to be our best model, and density estimates were used from our best model. We extrapolated overall abundance ($\hat{N}$) as $\hat{N} = \hat{D}$ x the size of our study area.

Results

Field sampling and genetic analyses

We collected a total of 1,402 hair samples from 254 hair snares, with the remaining 49 snares collecting no hair. Of the 1,402 collected samples, 328 samples exhibited microscopic characteristics of black bear hair (Hausman 1920), and were submitted to WGI for genotyping. Of these 328 samples, we discarded 134 because of lack of a sufficient number of follicles for DNA extraction ($N = 131$), or because they were from non-target species ($N = 3$). A total of 194 samples collected from 36 unique hair snares were positively identified as black bear (Fig. 1). Of these, 192 were matched to 54 individuals, including 20 males and 34 females. From these individuals, 38 were snared during only one sampling session, 10 were snared twice, five were snared three times and one was snared four times.

Genetic variability within hair samples was high, with mean observed (H_O) and expected (H_E) heterozygosities calculated as 0.81 (SD = 0.05) and 0.80 (SD = 0.06), respectively. Mean number of observed alleles at each locus was 7.5 (SD = 1.76). Deviations from the Hardy-Weinberg equilibrium were not detected at any loci ($P > 0.08$). Linkage disequilibrium was detected between one pair of loci (G1A, G10M; $P = 0.003$), although considering the high genetic diversity suggested by other measures, this is likely because of a recent admixture of alleles as opposed to non-random mating (Frankham et al. 2002).

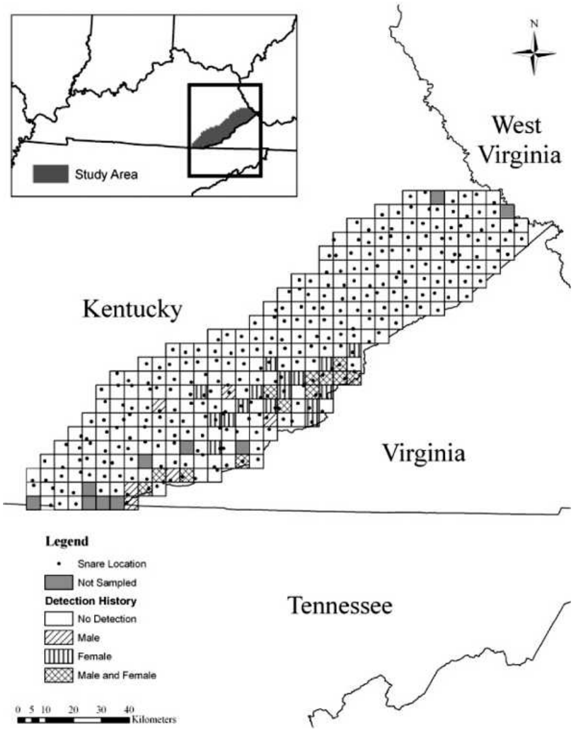

Figure 1. Sampling grid used to estimate probability of use by the black bear in eastern Kentucky in 2007. A single hair-snare was constructed and monitored in each grid cell and locations of detected black bears are shown. Note the limited geographic extent in which black bears were detected.

Table 2. Rankings of 2007 eastern Kentucky black bear occupancy models that allowed for different forms of variation in detection probability (p) while keeping occupancy constant. Our best model suggested a positive relationship between detection probability and proximity to public conservation lands as well as temporal variation across sampling periods.

Model	AIC_c	Δ AIC_c	AIC_c weight	Model likelihood	Number of parameters	Deviance
p(t + pub)	430.51	0.00	0.81	1.00	7	416.13
p(pub)	433.45	2.94	0.19	0.23	3	427.37
p(t)	457.67	27.16	0.00	0.00	6	445.39
p(.)	460.82	30.31	0.00	0.00	2	456.78

The overall probability of identity using the frequency of alleles at genotyped loci suggested that the likelihood of two individuals sharing the same genotype was extremely low (PI = 4.70E-30). The high level of variability within genotypes, along with the infrequency of 1MM (N = 1) and 2 MM (N = 5) suggested high accuracy of genotyping results.

Probability of use

When considering detection probability alone, all of our *a priori* models ranked higher than our null model (Table 2). Our best model suggested that black bears were more likely to be detected in close proximity to public conservation lands (β=-1.66, SE =0.33), and that detection probability varied among sampling periods (Table 3).

Three of our *a priori* occupancy models were found to be competing (Table 4). After averaging parameter estimates from competing models, black bear use was found to be correlated most strongly with higher elevations (ELEV: $\beta = 2.43$, SE = 0.68). The sum of competing model weights indicating a positive relationship between elevation and black bear use of our study area was 0.9, suggesting strong evidence for this relationship. Elevation in areas that we predicted to have ≥ 0.25 probability of being occupied by black bears averaged 659 m (range: 481-1,042 m), in contrast to an average elevation of 445 m (range: 272-653 m) in areas that we predicted to have < 0.25 probability of being occupied.

Out of three competing models, two suggested that black bears were more likely to use areas close to public conservation lands (PUB: $\beta = -1.80$, SE = 0.83). The summed weights of these two competing models was 0.79, indicating a moderate to strong relationship between black bear use of our study area and proximity to public conservation lands. One competing model suggested that black bear use was negatively correlated with the percent of forest cover (PERFOR: β=-0.086, SE=0.19). Considering standard error, lack of support of this variable in multiple models, and low summed model weights supporting this variable (0.11), we considered the importance of PERFOR to be negligible. Using model-averaged results, overall detection probability was 0.68 (SE=0.07). A median c-hat test based on model p(t)Ψ(.) suggested adequate model fit for these data (c-hat=0.976). Calculation of site-specific

Table 3. Rankings of the 2007 eastern Kentucky spatially explicit capture-recapture models of black bear population density. All models were fit using maximum-likelihood in program DENSITY (Efford 2008).

Model [a]	Number of parameters	Log likelihood	AIC	AIC_c	Deviance
g_0 (h) σ (h)	5	-212.27	434.53	436.00	341.771
g_0 (.) σ (h)	4	-214.41	436.82	437.77	346.053
g_0 (b) σ (h)	5	-231.81	473.63	475.09	380.865
g_0 (b) σ (.)	3	-236.58	479.15	479.71	390.390
g_0 (t) σ (.)	3	-236.94	479.88	480.44	391.120
g_0 (t) σ (h)	5	-236.21	482.42	483.88	389.654
g_0 (.) σ (.)	3	-240.60	487.19	487.75	392.737
g_0 (h) σ (.)	5	-239.30	488.61	490.07	390.153
g_0 (t + h) σ (.)	6	-239.27	490.54	492.64	390.089
g_0 (b + h) σ (.)	6	-239.42	490.84	492.94	390.390
g_0 (t + h) σ (h)	7	-239.21	492.42	495.29	389.963
g_0 (b + h) σ (h)	7	-239.40	492.80	495.67	390.347

[a] Candidate models included multiple forms of variation in g_0 and σ the constant (.) and with heterogeneity (h), trap response (b) and temporal variation (t).

Table 4. Rankings of the 2007 eastern Kentucky black bear occupancy models. The models included different combinations of site-specific habitat variables as covariates affecting occupancy (Ψ). Only the top three models were competing, and beta estimates from these models were used to calculate site-specific probability of black bear use across our study area.

Model[a]	AIC$_c$	AIC$_c$	AIC$_c$ weight	Parameters	Deviance
Ψ (pub + elev)	353.39	0.00	0.55	9	334.77
Ψ (elev + pub + perfor)	355.00	1.62	0.24	10	334.25
Ψ (edge + elev + edge*elev)	356.63	3.24	0.11	10	335.87
Ψ (elev)	357.52	4.13	0.07	8	341.03
Ψ (perfor + elev)	359.39	6.00	0.03	9	340.77
Ψ (colo)	397.15	43.76	0.00	8	380.66
Ψ (edge)	410.05	56.67	0.00	8	393.56
Ψ (perfor + edge)	412.17	58.78	0.00	9	393.55
Ψ (pub + edge + pub*edge)	412.95	59.57	0.00	10	392.20
Ψ (pop)	428.51	75.12	0.00	8	412.02
Ψ (.)	430.51	77.13	0.00	7	416.13
Ψ (road)	431.40	78.01	0.00	8	414.91
Ψ (slope)	432.27	78.89	0.00	8	415.78

[a] All models included the most appropriate form of detection probability [p(t + pub)] as determined in the first step of fitting occupancy models (see methods).

(25-km^2 sampling cells) probabilities of use by black bear using model-averaged beta estimates suggested that high probabilities of black bear use were localized to southeastern portions of our study area (Fig. 2).

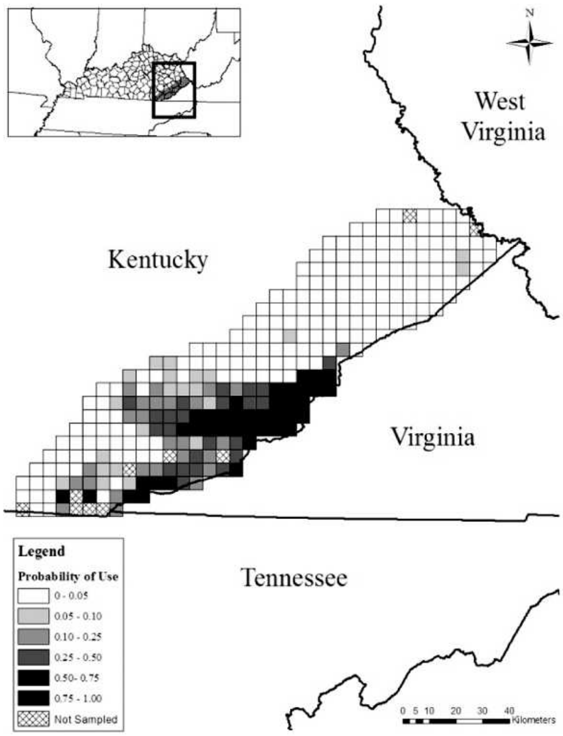

Figure 2. Estimated probability of black bear use of each sampling cell in eastern Kentucky in 2007. Calculations were based on averaged beta estimates from competing occupancy models.

Density

Our best SECR model of population density included heterogeneity with both g_0 and σ (see Table 2). Our best model estimated density as 7.51 bears/100 km^2 (95% C.I.: 5.37-9.66 bears/100 km^2). The mixing proportion was 0.99. Estimates of g_0 and σ under this model were 0.18 (SE = 0.06) and 1,610 m (SE = 300 m), respectively. Density estimates corresponded to an estimated abundance of 130 bears (95% C.I.: 92-165 bears).

Discussion

Our results suggest that contrary to our expectation, the black bear appears to be limited in its distribution to the southeastern portion of our study area, with the probability of encountering a black bear decreasing drastically as one travels west and northeast (see Fig. 2). The lack of evidence suggesting that the black bear colonization has proceeded further west and north may reflect the population existing below saturation density in areas currently used by the species (Sinclair 1992). Indeed, the apparent female-biased sex ratio found through our sampling was similar to reports from expanding bear populations elsewhere (Swenson et al. 1998, Bales et al. 2005), and combined with high fecundity (Unger 2007) suggests that the number of black bears in our study area is likely to increase. Furthermore, the estimated current density of black bears that comprise the colonization front that we studied fell well below population densities in other regions of the Appalachian Mountains. For example, population density of black bears in the Smoky Mountains of Tennessee has been estimated at 9-35 bears/100 km^2 (McLean & Pelton 1994). In North Carolina and Virginia, black bear population density at several intensively-studied areas has been estimated to range from 46 to 130 bears/100 km^2 (Tredick & Vaughan 2009). Therefore, if black bear habitat exists in even moderate quality in our study area relative to elsewhere in the region, it is likely that over time, the current habitat will become saturated and westerly colonization will proceed.

However, if indeed the lack of further westerly expansion of the black bear population to date is simply dependent on the population existing below saturation density in currently used areas, we would expect males to dominate the periphery of these areas (Swenson et al. 1998) with dispersing males distributed throughout our study area (Rogers 1987). Instead, we found limited evidence of black bear dispersal of either sex away from extreme southeastern portions of our study area (see Fig. 1). Further, home ranges measured in previous studies of the population that we sampled did not extend outside of areas we predicted to have a high probability of use by black bears (Unger 2007). Also, we found no support for our model predicting that black bear use was simply a function of the distance from the colonization source. Therefore, although an increase in abundance is probable in current black bear habitat throughout our study area, the future trajectory of the black bear range expansion remains uncertain.

It is possible that barriers, in the form of changes in habitat and/or terrain that occur outside the occupied area, are limiting dispersal away from currently used areas (Gaston 2003, Onorato et al. 2004). We found that black bear use of our study area was most strongly correlated with high elevation. Although high elevation is not a requirement of black bear use throughout the species' range, it does appear to influence black bear ecology in portions of the Appalachian Mountains. For example, despite an available elevational range of 260-2,025 m, the majority (83%) of black bear winter dens located in Great Smoky Mountain National Park, Tennessee, were at elevations $> 1,000$ m (Pelton et al. 1980). Elevation also influenced seasonal differences in the establishment of home-range activity centers in the same study area, and likely reflected seasonal variation in food availability between elevations (Garshelis & Pelton 1981). Black bear home ranges in Great Smoky Mountain National Park during the spring/summer period, which coincided with the season in which our hair snares were active, averaged 980 m (range: 690-1,350 m; Garshelis & Pelton 1981). In our study area, only elevations in areas that we predicted to have ≥ 0.25 probability of being occupied overlapped the range of elevations of summer black bear home ranges reported by Garshelis and Pelton (1981), whereas areas that we predicted to have < 0.25 of being occupied by black bears were found at lower elevations.

In our study area, high elevations are associated with large tracts of relatively contiguous forest. Areas of higher elevation also receive less human use than do lower elevations where transportation networks have been developed and most people live. Roads and associated developments can be semi-permeable barriers for black bear dispersal (Berringer et al. 1998, Larkin et al 2004). The permeability of these land uses is dependent on the degree of human activity, traffic volume and road type (Brody & Pelton 1989, Larkin et al. 2004). Additionally, public conservation lands, which we found to be moderately important to black bears, coincide with high elevations in our study area. These conservation areas included State and National Forests, National Parks, State Nature Preserves and State Wildlife Management Areas. The designation of such areas mandates wildlife and forest stewardship that may be absent on privately-owned lands that are more subject to disturbance and driven by different management philosophies. In Tennessee, Pelton et al. (1980) suggested that the availability of tree dens, an important factor of female and cub survival, may be limited outside protected areas due to differences in forest management practices. This finding may help explain the lack of a relationship between black bear use and the abundance and/or contiguity of forests in our study, characteristics that are generally thought to influence the distribution of black bears (Pelton 2003). It is possible that although forests are widespread throughout our study area, public forest management has resulted in more favourable conditions (e.g. greater availability of mast and availability of den sites) than those found in privately-owned areas. Such stewardship and rugged terrain may have created a network of bear refuges that has resulted in the disproportionate distribution of black bear in the most mountainous portion of our study area.

Although public conservation lands are available to the west, north and northeast of our study area, high elevation areas are not (Fig. 3). Thus, if landscape use by black bears is indeed dictated most strongly by habitat characteristics associated with high elevation areas, the lack of these areas to the west, north and northeast may inhibit further expansion. Under this scenario, since high elevations are unavailable, public conservation lands may provide critical habitat to colonizing individuals.

A loss of genetic diversity can occur when a new population is founded by a small number of individuals from a larger source population (Mayr 1963). Low genetic diversity can lead to inbreeding and a decrease in population viability (Frankham et al. 2002). Despite a relatively low population density and limited distribution, our results suggest that genetic diversity in the population of black bears that we sampled is high. Expected and observed heterozygosity, and mean number of alleles at genotyped loci are similar to the highest levels of genetic diversity reported in other bear populations where many of the same loci were examined (Paetkau et al. 1998, Belant et al. 2005, Dixon et al. 2007). This result supports our original prediction, as high genetic diversity would be expected if black bears in our study area indeed represent a western expansion front of a continuous regional population that includes bears in neighbouring states.

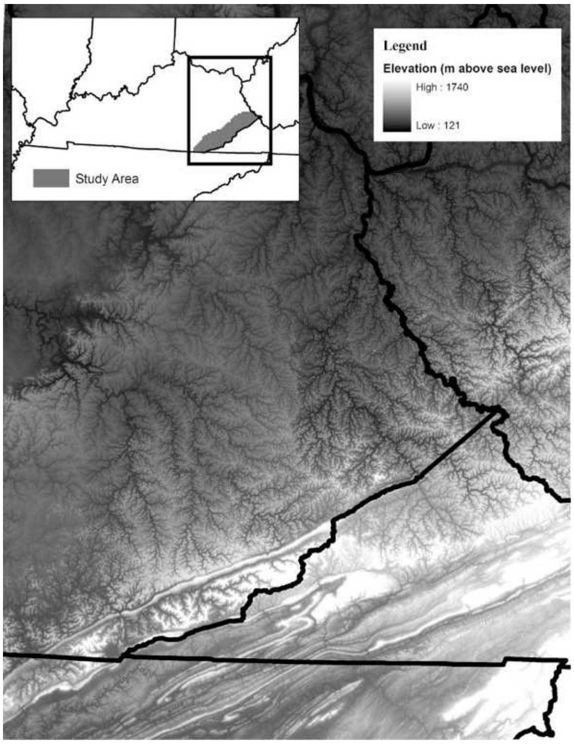

Figure 3. Elevation above sea level in and around our study area. According to occupancy modeling, high elevations are the strongest predictor of black bear use of our study area. The lack of high elevations to the west, north and northeast of our study area may constrain further expansion into the state of Kentucky.

Our study provides the first empirical estimate of the extent of the recolonization of historic range by the black bear into a large portion of the central Appalachian Mountains. Previous efforts aimed at assessing demographic information of the black bear in our study area which were hindered due to the wide area thought to be occupied by the species, and the difficulty in gaining permission to conduct sampling on private land. Through this study, we found that the use of hair snares or other remote sampling tools may be a particularly useful tool for monitoring wildlife populations on private land, as their passive operation, simple and temporary setup and the overall short duration required for sampling generally led to wide acceptance by landowners.

To date, no reliable method exists to define the spatial extent of a sampled population, or an 'effective study area' when using classical capture-recapture methods to estimate population density (Efford 2004). Furthermore, the assumption of closure in classical capture-recapture models is difficult to meet in many ecological studies (Boulanger & McLellan 2001, Mulders et al. 2007), and biases resulting from the violation of these assumptions can be substantial (Kendall 1999). SECR, therefore, provides a useful alternative approach for the estimation of population density where classical capture-recapture assumptions are unlikely to be met. SECR models do rely upon assumptions including the statistical distribution of capture probability and the spatial distribution of home ranges (Efford 2004). However, SECR models are generally thought to be very robust to relaxation of these assumptions in studies of many species including black bears (Obbard et al. 2010). Thus, we expect that our estimates of black bear population density are accurate. For our occupancy models, we clearly exceeded the suggested overall $P \geq 0.50$ threshold and employed > 3 sampling sessions beyond which parameters are generally estimated without bias (MacKenzie & Royle 2005).

Management implications

At this time, although it appears that the population density of black bears in our study area is lower than populations in other portions of the Appalachian Mountains, an unassisted increase in the number of black bears may be likely. However, until an increase in black bear abundance occurs, this expanding population may be sensitive to management activities that result in black bear mortality (e.g. hunting), particularly to females. At this time, the population does not appear to suffer any threat of genetic isolation, although maintenance of high genetic diversity may rely on the identification and preservation of linkages connecting black bears in our study area with the greater Appalachian population.

Our analysis suggests that the highest elevations and conservation lands may at present represent the 'best' black bear habitat in our study area. The current self-sustaining nature of the population and further geographic and demographic expansion may depend on protection of bears and their habitat in these areas (Berringer et al. 1998). Elevations of the magnitude in currently occupied areas do not exist to the north and west. Thus, further westerly black bear colonization may be reliant on the preservation and connectivity of the conservation land network or may require the use of landscapes that are not currently being utilized. Periodic hair snare surveys will likely be an important tool in understanding black bear dispersal and colonization behaviour and the factors that have, thus far, limited a more uniform distribution across this mountainous region.

Acknowledgements - we dedicate this manuscript to our friend and co-author, Dr. David Maehr, who was killed on 20 June 2008 while conducting a black bear telemetry flight in Florida. Dr. Maehr's insight and dedication to the conservation and restoration of wildlife and their habitats will be missed. We thank Dr. K. Murphy, S. Rosenstock and Dr. M. Dzialak for providing reviews on this and previous manuscript drafts. We thank Indiana University of Pennsylvania, University of Kentucky, Kentucky Department of Fish and Wildlife Resources and Shikar Safari Foundation International for financial and logistical support. We also thank all those who granted access to property including Cumberland Gap National Historic Park, Big South Fork National Recreation Area, Kentucky State Nature Preserves Commission, Kentucky Division of Forestry, Kentucky Division of Parks, USDA Forest Service Daniel Boone District, Kentucky Department of Fish and Wildlife Resources, Eastern Kentucky University, The David School, Alice Lloyd College and hundreds of private landowners. Field assistance was provided by Dr. D. Unger, M. Nickols, A. Whittle, K. Kingsland, N. Dryer, T. Gieder, G. Grisdale and C. Lindbeck.

References

Akaike, H. 1973: Information theory and an extension of the maximum likelihood principle. - In: Petrove, B.N. & Csaki, F. (Eds.); Proceedings of the 2nd International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary, pp. 267-281.

Bales, S.L., Hellgren, E.C., Leslie, D.M., Jr. & Hemphill, J., Jr. 2005: Dynamics of a recolonizing population of black bears in the Ouachita Mountains of Oklahoma. - Wildlife Society Bulletin 33(4): 1342-1351.

Barbour, R.W. & Davis, W.H. 1973: Trees and shrubs of Kentucky. - University Press of Kentucky, Lexington, Kentucky, USA, 321 pp.

Belant, J.L., Van Stappen, J.F. & Paetkau, D. 2005: American black bear population size and genetic diversity at Apostle Islands National Lakeshore. - Ursus 16(1): 85-92.

Berringer, J., Seibert, S.G., Reagan, S., Brody, A.J., Pelton, M.R. & Vangilder, L.D. 1998: The influence of a small sanctuary on survival rates of black bears in North Carolina. - Journal of Wildlife Management 62(2): 727-734.

Boulanger, J. & McLellan, B. 2001: Closure violation in DNA-based mark-recapture estimation of grizzly bear populations. - Canadian Journal of Zoology 79(4): 642-651.

Brody, A.J. & Pelton, M.R. 1989: The effects of roads on black bear movements in western North Carolina. - Wildlife Society Bulletin 17(1): 5-10.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical-theoretic approach. 2nd edition. - Springer-Verlag, New York, New York, USA, 496 pp.

Dixon, J.C., Oli, M.K., Wooton, M.C., Eason, T.H., McCowan, J.W. & Paetkau, D. 2006: Effectiveness of a Regional Corridor in Connecting Two Florida Black Bear Populations. - Conservation Biology 20(1): 155-162.

Dixon, J.D., Oli, M.K., Wooten, M.C., Eason, T.H., McCowan, J.W. & Cunningham, M.W. 2007: Genetic consequences of habitat fragmentation and loss: the case of the Florida black bear (*Ursus americanus floridanus*). - Conservation Genetics 8(2): 455-464.

Efford, M. 2004: Density estimation in live-trapping studies. - Oikos 106(3): 598-610.

Efford, M.G. 2008: Density 4.3: software for spatially explicit capture-recapture. - Available at: http://www.otago.ac.nz/density (Last accessed on 10 November 2010).

Efford, M.G., Borchers, D.L. & Byrom, A.E. 2009: Density estimation by spatially explicit capture-recapture: likelihood-based methods. - In: Thompson, D.L., Cooch, E.G. & Conroy, M.J. (Eds.); Demographic processes in marked populations. - Springer, New York, New York, USA. pp. 255-269.

Ennis, S. & Gallagher, T.F. 1994: PCR based sex determination assay in cattle based on the bovine amelogenin locus. - Animal Genetics 25(6): 425-427.

Flagstad, O., Hedmark, E.A., Landa, A., Broseth, H., Persson, J., Anderson, R., Segerstrom, P. & Ellegen, H. 2004: Colonizing History and Noninvasive Monitoring of a reestablished Wolverine Population. - Conservation Biology 18(3): 676-688.

Frankham, R., Ballou, J. & Briscoe, D. 2002: Introduction to conservation genetics. - Cambridge University Press. New York, New York, USA, 624 pp.

Garshelis, D.L. & Pelton, M.R. 1981: Movements of black bears in the Great Smoky Mountain National Park. - Journal of Wildlife Management 45(4): 912-925.

Gaston, K.J. 2003: The structure and dynamics of geographic ranges. - Oxford University Press, New York, New York, USA, 266 pp.

GeoLytics. 2003: 2000 Population Density by Block for the Conterminous United States [GIS Data]. - GeoLytics Incorporated, Brunswick, New Jersey, USA.

Hall, E.R. 1981: The mammals of North America. 2nd edition. - John Wiley and Sons, New York, New York, USA, pp. 1181.

Hausman, L.A. 1920: Structural characteristics of the hair of mammals. - American Naturalist 54(635): 496-523.

Homer, C., Huang, C., Yang, L., Wylie, B. & Coan, M. 2004: Development of a 2001 national landcover database for the United States. - Photogrammetric Engineering and Remote Sensing 70(7): 829-840.

Kasworm, W.F. & Manley, T.L. 1990: Road and trail influences on grizzly bears and black bears in northwest Montana. - In: Darling, L.M. & Archibald, W.R. (Eds.); Bears: Their Biology and Management. Proceedings of the 8th International Conference. International Association for Bear Research and Management, Victoria, British Columbia, Canada, pp. 79-84.

Kendall, W.L. 1999: Robustness of closed-capture methods to violation of the closure assumption. - Ecology 80(8): 2517-2525.

Kentucky Department of Geographic Information. 2005: County boundary polygons of Kentucky [GIS Data]. - Commonwealth Office of Technology, Frankfort, Kentucky, USA.

Kentucky Fish and Wildlife Information System. 2001: Stewardship Lands in Kentucky [GIS Data]. - Kentucky Department of Fish and Wildlife Resources, Frankfort, Kentucky, USA.

Laliaberte, A.S. & Ripple, W.J. 2004: Range contractions of North American carnivores and ungulates. - BioScience 54(2): 123-138.

Larkin, J.L., Maehr, D.S., Hoctor, T.S. & Whitney, K. 2004: Landscape linkages and conservation planning for the black bear in west-central Florida. - Animal Conservation 7: 23-34.

MacKenzie, D.I. 2006: Modeling the probability of use: the effect of, and dealing with detecting a species imperfectly. - Journal of Wildlife Management 70(2): 367-374.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. 2002: Estimating site occupancy rates when detection probabilities are less than one. - Ecology 83(8): 2248-2255.

MacKenzie, D.I. & Royle, J.A. 2005: Designing occupancy studies: general advice and allocating survey effort. - Journal of Applied Ecology 42(6): 1105-1114.

Mayr, E. 1963: Animal species and evolution. - Belknap Press, Cambridge, Massachusetts, USA, 797 pp.

McDonald, L.L. 2004: Sampling rare populations. - In: Thompson, W.L. (Ed.); Sampling rare and elusive species: concepts, designs, and techniques for estimating population parameters. - Island Press, Washington, D.C., USA, pp. 11-42.

McLean, P.K. & Pelton, M.R. 1994: Estimates of population density and growth of black bears in the Smoky Mountains. - In: Claar, J. & Schullery, P. (Eds.); Bears: Their Biology and Management. Proceedings of the 9th International Conference. International Association for Bear Research and Management, Missoula, Montana, USA, pp. 253-261.

Mills, L.S., Citta, J.J., Lair, K.P., Schwartz, M.K. & Tallmon, D.A. 2000: Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. - Ecological Applications 10(1): 283-294.

Mowat, G. & Strobeck, C. 2000: Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. - Journal of Wildlife Management 64(1): 183-193.

Mulders, R., Boulanger, J. & Paetkau, D. 2007: Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark-recapture methods. - Wildlife Biology 13(Suppl. 2): 38-51.

Nellemann, C., Støen, O., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B.P., Martin, J. & Ordiz, A. 2007: Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. - Biological Conservation 138(1): 157-165.

Obbard, M.E., Howe, E.J. & Kyle, C.J. 2010: Empirical comparison of density estimators for large carnivores. - Journal of Applied Ecology 47(1): 76-84.

Onorato, D.P., Hellgren, E.C., Van Den Bussche, R.A. & Doan-Crider, D.L. 2004: Phylogeographic patterns within a metapopulation of black bears (*Ursus americanus*) in the American southwest. - Journal of Mammalogy 85(1): 140-147.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. 1978: Statistical inference from capture data on closed animal populations. - Wildlife Monographs 62: 3-135.

Paetkau, D. 2003: An empirical exploration of data quality in DNA-based population inventories. - Molecular Ecology 12(6): 1375-1387.

Paetkau, D. & Strobeck, C. 1994: Microsatellite analysis of genetic variation in black bear populations. - Molecular Ecology 3(5): 489-495.

Paetkau, D., Waits, L.P., Clarkson, P.L., Craighead, L., Vyse, E., Ward, R. & Strobeck, C. 1998: Variation in genetic diversity across the range of North American brown bears. - Conservation Biology 12(2): 418-429.

Pelton, M.R. 2003: Black bear (*Ursus americanus*). - In: Feldhammer, G.A, Thompson, B.C. & Chapman, J.A. (Eds.); Wild mammals of North America: biology, management, and conservation. - John Hopkins University Press, Baltimore, Maryland, USA, pp. 547-555.

Pelton, M.R., Beeman, L.E. & Eagar, D.C. 1980: Den selection by black bears in the Great Smoky Mountains National Park. - International Conference on Bear Research and Management 4: 149-151.

Pelton, M.R., Coley, A.B., Eason, T.H., Doan Martinez, D.L., Pederson, J.A., van Manen, F.T. & Weaver, K.M. 1998: American black bear conservation plan. - In: Servheen, C., Herrero, S. & Peyton, B. (Eds.); Bears. Status survey and conservation action plan. IUCN/SSC Bear and Polar Bear Specialist Groups. IUCN Gland, Switzerland and Cambridge, UK, pp. 144-155.

Raymond, M. & Rouseet, F. 1995: Genepop. Population genetics software for exact tests and ecumenicism. - Journal of Heredity 86(3): 248-249.

Ricketts, T.H., Dinerstein, J.E., Olson, D.M., Loucks, C.J., Eichbaun, W., DellaSalla, D., Kavanagh, K., Hedao, P., Hurley, P., Carney, K., Abell, R. & Walters, S. 1999: Terrestrial ecoregions of North America: a conservation assessment. - Island Press, Washington, D.C., USA, 508 pp.

Rogers, L.L. 1987: Factors influencing dispersal in the black bear. - In: Chepko-Sade, B.D. & Halpin, Z.T. (Eds.); Mammalian dispersal patterns. - University of Chicago Press, Chicago, Illinois, USA, pp. 75-84.

Royle, J.A. & Young, K. 2008: A hierarchical model for spatial capture-recapture data. - Ecology 89(8): 2281-2289.

Sayler, K.L. 2006: Contemporary land cover change in the central Appalachians Ecoregion. - United States Geologic Survey. Available at: http://eros.usgs.gov/LT/regions/eco69.html (Last accessed on 2 December 2006).

Schwartz, M.K. & McKelvey, K. 2009: Why sampling scheme matters: the effect of sampling scheme on landscape genetic results. - Conservation Genetics 10(4): 441-452.

Servheen, C., Herrero, S. & Peyton, B. 1998: Bears. Status survey and conservation action plan. - IUCN/SSC Bear and Polar Bear Specialist Groups. IUCN, Gland, Switzerland and Cambridge, UK, 319 pp.

Sinclair, A.R.E. 1992: Do large mammals disperse like small mammals? - In: Stenseth, N.C. & Lidicker, W.Z., Jr. (Eds.); Animal dispersal, small mammals as a model. Chapman and Hall, London, UK, pp. 229-242.

Swenson, J.E., Sandegreen, F. & Soderberg, A. 1998: Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. - Journal of Animal Ecology 67(5): 819-826.

Thornbury, W.D. 1965: Regional geomorphology of the United States. - John Wiley and Sons, New York, New York, USA, 609 pp.

Tredick, C.A. & Vaughan, M.R. 2009: DNA-based population demographics of black bears in coastal North Carolina and Virginia. - Journal of Wildlife Management 73(7): 1031-1039.

United States Census Bureau 2006: Second edition Tiger/line files-U.S. roads [GIS Data]. Available at: http://www.census.gov/geo/www/tiger/ (Last accessed on 2 December 2007).

Unger, D. 2007: Population dynamics, resource selection, and landscape conservation of a recolonizing black bear population. - Dissertation, University of Kentucky, Lexington, USA, 281 pp.

VanderHeyden, M. & Meslow, E.C. 1999: Habitat selection by female black bears in the Central Cascades of Oregon. - Northwest Science 73(4): 283-294.

Vaughan, M.R. 2002: Oak trees, acorns, and bears. - In: McShea, W.J. & Healy, W.M. (Eds.); Oak forest ecosystems: ecology and management for wildlife. The Johns Hopkins Press, London, UK, pp. 229-242.

Virginia Department of Game and Inland Fisheries. 2003: Virginia black bear management plan. - Available at: http://www.dgif.virginia.gov/wildlife/bear/blackbearmanagementplan.pdf (Last accessed on 28 October 2008).

West Virginia Department of Natural Resources 2006: West Virginia wildlife conservation action plan. Available at: http://www.wvdnr.gov/Wildlife/PDFFiles/wvwcap.pdf (Last accessed on 12 November 2010).

Waits, L.P. 2004: Using noninvasive genetic sampling to detect and estimate abundance of rare wildlife species. - In: Thompson, W.L. (Ed.); Sampling Rare and elusive species: concepts, designs, and techniques for estimating population parameters. - Island Press, Washington, D.C., USA, pp. 211-228.

White, G. C. & Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. - Bird Study Supplement 46: 120-138.

Williams, B.K., Nichols, J.D. & Conroy, M.J. 2002: Analysis and management of animal populations. - Academic Press, San Diego, California, USA, 817 pp.

Woods, J.G., Paetkau, D., Lewis, D., McLellan, B.N., Proctor, M. & Strobeck, C. 1999: Genetic tagging of free-ranging black and brown bears. - Wildlife Society Bulletin 27(3): 616-627.