

# Predicting harvest vulnerability for a recovering population of American black bears in western Maryland

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**Abstract:** Recreational hunting is the tool most commonly used to manage American black bear (*Ursus americanus*) populations in North America. However, bear populations can be sensitive to overharvest, particularly of mature females that can directly affect population growth. Managers need a thorough understanding of the factors affecting harvest vulnerability when using hunting as a primary management strategy. Here, we coupled Global Positioning System spatial data from female black bears and human hunters in western Maryland, USA, from 2005 to 2007, in order to model bear harvest vulnerability. Specifically, we developed maximum entropy (Maxent) predictive occurrence models for bears and for bear hunters and evaluated the influence of 7 environmental variables on their distributions. We then assessed predicted distribution maps for probability of co-occurrence to identify areas of high and low harvest vulnerability. Slope and land ownership (i.e., private–public) were the 2 most important variables determining female bear distributions, whereas land ownership and cover type were the most important variables influencing hunter distributions. We classified roughly 12% and 16% of the study area as being of high relative use for bears and bear hunters, respectively. Only 5.4% of the study area was considered to have high harvest vulnerability (i.e., high probability of co-occurrence). Areas with high bear relative use but low hunter use (i.e., low harvest vulnerability) comprised 0.9% of the study area. We were most interested in areas of high and low harvest vulnerability to enable resource managers to adjust hunting regulations that meet harvest goals.

**Key words:** American black bear, harvest vulnerability, hunter behavior, Maryland, maximum entropy, *Ursus americanus*

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Recreational hunting can profoundly affect the size, structure, and behavior of harvested wildlife populations. Consequently, a thorough understanding of the factors influencing harvest dynamics is prerequisite for sustainable management of these populations. Estimating harvest vulnerability can enable resource managers to adjust hunting seasons and strategies to regulate recreational harvest and meet population goals (Weinbaum et al. 2013). Although conceptually attractive, estimating harvest vulnerability has historically been difficult because of an inability to obtain fine scale and contemporaneous data from game populations and human hunters. Indeed, the majority of research investigating harvest vulnerability has focused solely on spatiotemporal factors affecting the

susceptibility of target game populations to harvest mortality, with no consideration given to the influence of hunter movements and behaviors (McCorquodale et al. 2003). Hunters exhibit predictable behaviors while in the field, often disproportionately selecting areas near roads and gentle topography while avoiding dense cover (Lyon and Burcham 1998, Diefenbach et al. 2005, Lebel et al. 2012). Incorporation of spatial data concurrently collected from human hunters and telemetered wildlife provides a mechanism to improve estimates of harvest vulnerability (e.g., Broseth and Pederson 2000).

Human-induced mortality (e.g., vehicle collisions, recreational hunting, and poaching) can have an impact on American black bear (hereafter, “black bear” [*Ursus americanus*]) populations and can

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greatly affect population dynamics (Cowan 1972, Bunnell and Tait 1985, Kasworm and Thier 1994, Pelton 2000). Recreational hunting is an effective technique commonly used to manage black bear populations (Cowan 1972, Bunnell and Tait 1985). However, the reproductive potential of black bears is low compared with most land mammals in North America (Jonkel and Cowan 1971), making the species susceptible to overharvest (Kolenosky 1986). As a result, an overharvested bear population can take many years to recover (Miller and Miller 1988, Miller 1989). Although research and harvest data show that male bears are more vulnerable to recreational hunting, the harvest of females has the greatest potential to affect population growth rates (Fraser et al. 1982, Bunnell and Tait 1985). Given the potential impacts of overharvest, understanding harvest vulnerability is important for managing bear populations.

Black bears were almost extirpated from Maryland, USA, during the mid-20th century, prompting the state to stop recreational harvest in 1953. Following hunting season closure, the bear population in western Maryland steadily recovered and reached levels that justified a reopening of the hunting season in 2004. Given the cessation of bear hunting in 1953, managers did not have information on the vulnerability of bears to harvest prior to the 2004 season. To address this knowledge gap, our objectives were to (1) use contemporaneous spatial data collected from female bears and bear hunters to develop predictive occurrence models in relation to a suite of environmental covariates, and (2) evaluate predictive occurrence maps for areas of overlap to identify areas of high and low harvest vulnerability. Identifying areas of high and low harvest vulnerability provides information resource managers can use to manipulate bear harvest strategies to meet their management goals.

## Study area

We conducted the study in Garrett County, Maryland, which is the westernmost county in the state. The study area encompasses 1,722 km<sup>2</sup> and borders Pennsylvania (USA) to the north and West Virginia (USA) to the south and west. The majority of the study area is forested (approx. 68%) and diverse topographically, with elevations ranging from 292 to 1,028 m. A sizeable portion (approx. 22%) of the study area is composed of publicly owned land, including several large contiguous blocks of state

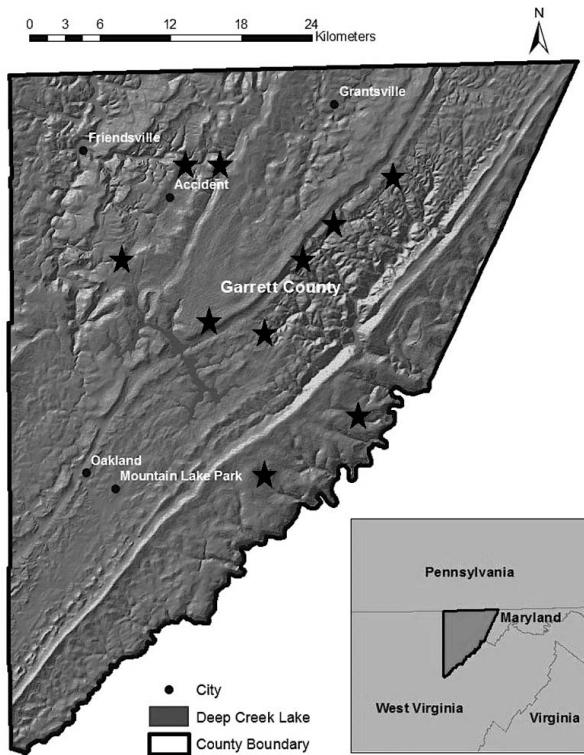
forest. Maryland's black bear population occurs at its highest densities in Garrett County and adjacent Allegany County to the east (Spiker 2011); the state only permits bear hunting in these 2 counties in the state. Currently, Maryland prohibits the use of dogs, baits, or organized drives to harvest bears.

The study area contains several different forest-types, which we categorized as deciduous forest, mixed forest, and evergreen forest. Deciduous forest was dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and black cherry (*Prunus serotina*). Coniferous forest contained white pine (*Pinus strobus*), red pine (*P. resinosa*), spruce (*Picea* spp.), and fir (*Abies* spp.); whereas, mixed forests consisted of both deciduous and coniferous trees. Understory vegetation in these forest types typically included mountain laurel (*Kalmia latifolia*), rhododendron (*Rhododendron* spp.), serviceberry (*Aamelanchier arborea*), dogwood (*Cornus* spp.), and hazelnut (*Corylus* spp.).

## Methods

### Black bear GPS data collection

Staff from the Maryland Department of Natural Resources (MDNR) captured bears in Garrett County, Maryland, from 2005 to 2007, using barrel traps, spring-activated foot snares, and running with hounds. Bears used for this study were captured throughout Garrett County (Fig. 1) on both public ( $n = 4$ ) and private ( $n = 6$ ) lands, and the sample comprised individuals that were captured because of nuisance complaints ( $n = 5$ ) and targeted for research ( $n = 5$ ). Captured bears were chemically immobilized, and females with neck circumferences of >48 cm were fitted with Lotek Model 3300S Global Positioning System (GPS) collars (Lotek Wireless Inc., Newmarket, Ontario, Canada) that weighed 285 g. The GPS collars recorded a waypoint every 4 hours and units had a battery life of approximately 1 year. Each waypoint recorded the unit's location (latitude and longitude) as well as time and date information. Collars also emitted a very high frequency (VHF) signal that researchers could use to locate bears in the event of GPS failure and to replace units during MDNR's annual den checks. If a collar remained stationary for an extended period of time (24 hr), the collar would emit a unique VHF mortality signal. Personnel from MDNR used mortality signals to



**Fig. 1.** Location of study area within Garrett County, Maryland, USA, where we modeled female black bear harvest vulnerability from 2005 to 2007, with black stars indicating bear capture sites.

locate collars and determine whether mortalities had occurred, or whether bears had slipped their collar.

### **Bear-hunter GPS data collection**

During the first 3 years (2005–2007) of the reestablished bear-hunting seasons in Maryland, hunters awarded tags were required to attend a pre-hunt meeting prior to the start of the season. At the pre-hunt meetings, we asked hunters to volunteer for a GPS study of their hunting-related movements and behavior. We assigned each volunteer a uniquely numbered Garmin 12XL GPS unit (Garmin Corporation, Olathe, Kansas) attached to an elastic armband and provided training on use of the unit. The GPS units were programmed to record waypoints at 2-minute intervals and units had a positional accuracy of 15 m. Hunters were instructed to turn the GPS units on while they were in the field during each hunting session. We asked hunters to return the GPS units to a MDNR bear-check station at the conclusion of the hunting season.

During preliminary data analysis, we checked hunter location data for quality control and removed clearly extraneous points. We excluded points where locations were inside a building (e.g., home or business), within a city where hunting was prohibited, outside of the study area boundary (i.e., Garrett County), or outside of the permitted hunting hours. Additionally, we excluded points where the speed of travel between successive locations indicated the use of a motorized vehicle. By excluding these locations, we ensured that our data set included only locations where a hunter was able to encounter and legally harvest a bear.

### **Environmental variables**

We considered a suite of environmental variables thought to influence bear and bear hunter distributions. Following Clark et al. (1993), these variables included elevation, slope, aspect, distance to nearest road, distance to nearest stream, land ownership, and cover type diversity (Table 1). We used ArcGIS 10.0 to assemble 30-m raster-data layers for each of the environmental variables considered. We calculated elevation data from the National Elevation Dataset and used these data to derive slope and aspect layers. To estimate distance to road and distance to stream layers, we calculated Euclidean distances from raster centroids to nearest road and stream feature classes, respectively. We defined cover type diversity as the number of unique cover types (reclassified from National Land Cover Dataset) within a 407-m radius, which was the mean distance a female black bear traveled during a 4-hour time period in this study. We used the focal statistics tool in ArcGIS to calculate the number of unique cover types surrounding each raster cell and assigned a diversity value.

The majority (88%) of Maryland bear hunters used a tree stand or ground blind to hunt, and we assumed that hunters selected hunting locations based on their perceived likelihood of encountering and harvesting a bear. Consequently, our hunter model included the same environmental variables as our bear model with the exception that we used cover type instead of cover type diversity as a measure of habitat use. We tested for multicollinearity among environmental variables with Pearson's correlations using ENM tools (Version 1.3; Warren et al. 2010) and considered variables to be highly correlated if  $r^2 \geq 0.80$ . If 2 variables were highly correlated, we retained the

**Table 1. Environmental variables used to create predictive occurrence models for black bears and bear hunters in Garrett County, Maryland, USA, 2005–2007.**

Variable	Ranges and classes	Source
Aspect	1 = flat	Derived from U.S. Geological Survey (USGS) National Elevation Dataset (NED)
	2 = North	
	3 = East	
	4 = South	
	5 = West	
Cover type	1 = developed	National Land Cover Dataset (NLCD)
	2 = agriculture	
	3 = open water	
	5 = deciduous forest	
	6 = mixed forest	
	7 = wetland	
	8 = grassland	
	9 = agriculture	
	10 = evergreen forest	
	Cover type diversity (no. of cover types)	
Distance to nearest road (m)	0–2,282	Derived from USGS National Hydrography Dataset
Distance to nearest stream (m)	0–1,652	Derived from U.S. Census Bureau
Elevation (m)	292–1,027	Derived from NED
Land ownership	0 = private land	Maryland Department of Natural Resources
	1 = public land	
Slope (%)	0–113	Derived from NED

environmental variable that we judged to be most biologically relevant.

### **Predictive occurrence modeling of bears and bear hunters**

We used maximum entropy modelling (Maxent; Phillips et al. 2004) to develop presence-only distribution models for female black bears and bear hunters. Maxent is a robust machine-learning approach based on estimating the probability distribution of a species given a set of environmental constraints (Phillips et al. 2004, 2006). Maxent has become increasingly popular for predictive occurrence modeling and has consistently outperformed other presence-only modeling approaches (Elith et al. 2006, Peterson et al. 2007, Ortega-Huerta and Peterson 2008).

We used our GPS point-location data to create Maxent models of female black bear and bear hunter distributions. Analysis of GPS telemetry data can be challenging because data are often spatially

autocorrelated and successive point-locations are non-independent. However, Maxent is generally insensitive to the effects of spatial autocorrelation when researchers randomly draw data for model development (Kaliontzopoulou et al. 2008). Maxent has been successfully used with GPS telemetry data (e.g., Monterroso et al. 2009), and we attempted to reduce the effects of spatial autocorrelation by limiting our statistical sample to 25 randomly selected point-locations per radiocollared bear, and 1 randomly selected location from each bear hunter per hunting event. Additionally, although we had annual bear location data, we constrained our sampling window to 12 September–7 December of each year to ensure that bear distributions approximated the distribution of bears during the autumn hunting season. The Maryland bear-hunting seasons during our study (2005–2007) lasted <1 week (2–4 days during late Oct), and thus we were unable to restrict the use of bear location data to the duration of hunting seasons.

We ran each model with 50 replications and 10,000 iterations/model run (Elith et al. 2011, Merow et al. 2013). For each model run, we used 80% of the data for model development, and the remaining 20% for model evaluation. We kept model settings (max. iterations, sample radius, and convergence threshold) at their default values. We used the mean area under the receiver operating characteristic curve (AUC) to evaluate the predictive performance of each model. The AUC values indicate a model's discrimination efficiency, and they commonly are used to assess Maxent model performance (Elith et al. 2006). We considered models with mean AUC values  $\geq 0.70$  to have adequate model fit (Elith et al. 2006). We used jackknife-resampling tests to quantify the relative importance of environmental variables on the probability of bear and bear hunter occurrence. This technique identifies important predictor variables by systematically removing single predictor variables and then resamples each model to measure the relative contribution of that variable to model performance. We considered predictor variables with >15% relative contributions to be important variables in predicting bear and bear hunter distributions. Lastly, we inspected response curves to evaluate the relation between important predictor variables and relative use.

### **Evaluation of harvest vulnerability**

We used output from Maxent models to develop relative-use raster maps for bears and bear hunters

**Table 2. Percent contribution of environmental variables to predictive occurrence models for female black bears and bear hunters in Garrett County, Maryland, USA, 2005–2007.**

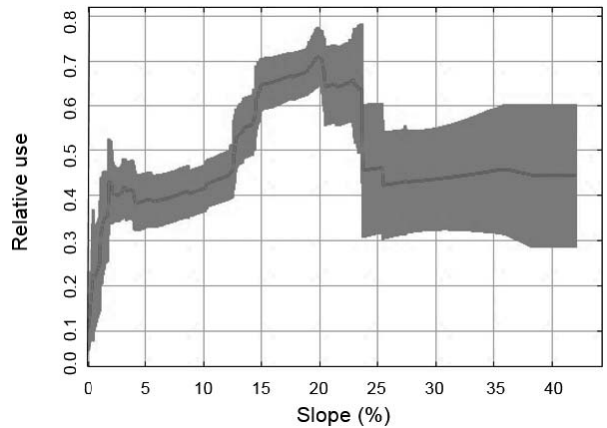
Variable	% Contribution	
	Bear	Hunter
Aspect	5.2	2.6
Cover type		25.7
Cover type diversity	2.3	
Distance to nearest road	10.0	4.8
Distance to nearest stream	15.7	9.7
Elevation	12.6	9.6
Land ownership	19.0	38.7
Slope	35.3	9.0

within Garrett County. These distribution maps assigned a relative use value (0–100) to each cell based on the existing environmental conditions. Relative use values were reclassified using Jenks’ natural breaks to categories of high, medium, or low relative probability of occurrence (North 2009). We then used raster calculator in ArcGIS to identify areas with mutually high bear and hunter relative use (high harvest vulnerability) as well as areas of high relative use by bears but low relative use by hunters (low harvest vulnerability). Furthermore, we identified large contiguous clusters (e.g., >1 km<sup>2</sup>) with low harvest vulnerability and hypothesized that these areas could serve as de facto sanctuaries for female bears.

**Results**

**Bear and bear hunter distributions**

We used 250 point-locations from 10 female bears and 230 locations from 108 bear hunters to build maximum entropy distribution models. None of the environmental variables considered exhibited high collinearity and consequently all were included within models. Our predictive model of bear distribution had adequate discrimination ability (mean AUC = 0.794, SE = 0.002). Slope was the most important environmental variable (35.3% contribution; Table 2) predicting bear occurrence, followed by land ownership (19.0% contribution) and distance to streams (15.7% contribution). Relative use was highest for slopes of 15–22%, and decreased in steeper and flatter locations (Fig. 2). Additionally, relative use by bears was nearly 40% higher on public compared with private lands, and increased with greater distance to streams (Fig. 3). Our model predicting bear hunter distributions also adequately fit the data (mean AUC = 0.764, SE = 0.002). Land ownership and

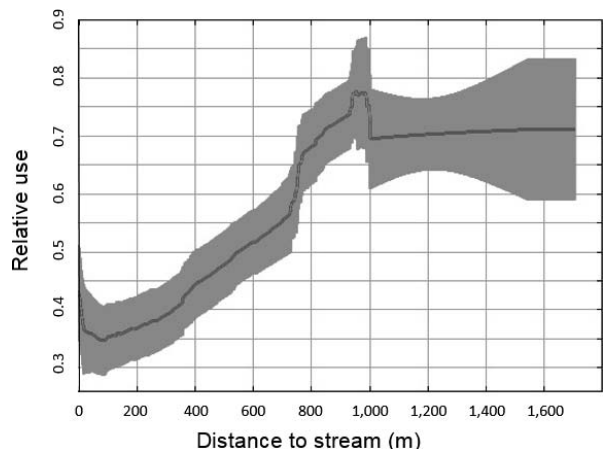


**Fig. 2. Relation between percent slope and relative use by female black bears within Garrett County, Maryland, USA, 2005–2007.**

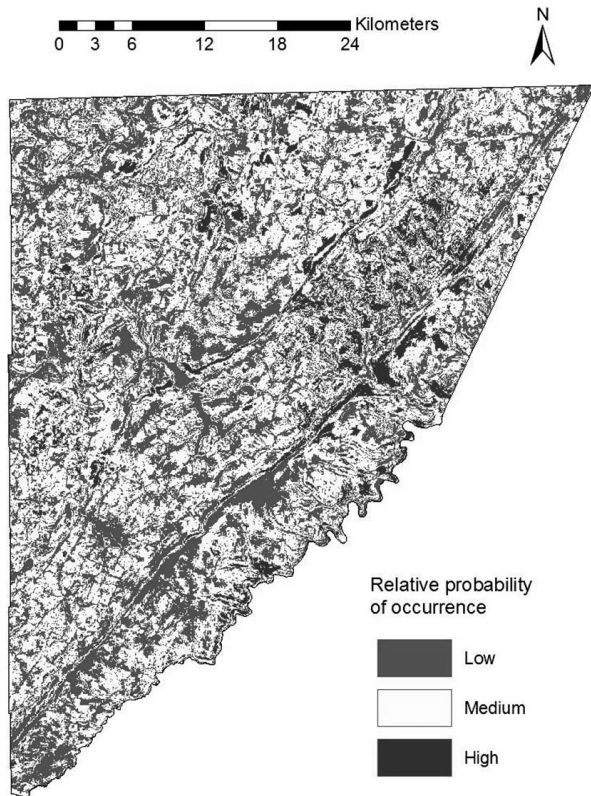
cover type were the 2 most important environmental variables predicting hunter occurrence, with 38.7% and 25.7% model contributions, respectively (Table 2). Hunters were 60% more likely to occur on public lands than private lands, and more likely to utilize evergreen and deciduous forest than other cover types.

**Harvest vulnerability**

Our predictive model of bear distribution within Garrett County classified 33.8% as low relative use, 54.3% as medium, and 11.9% as high (Fig. 4). Our model of hunter distributions had a similar response, with 23.3% predicted to be low relative use, 60.5%



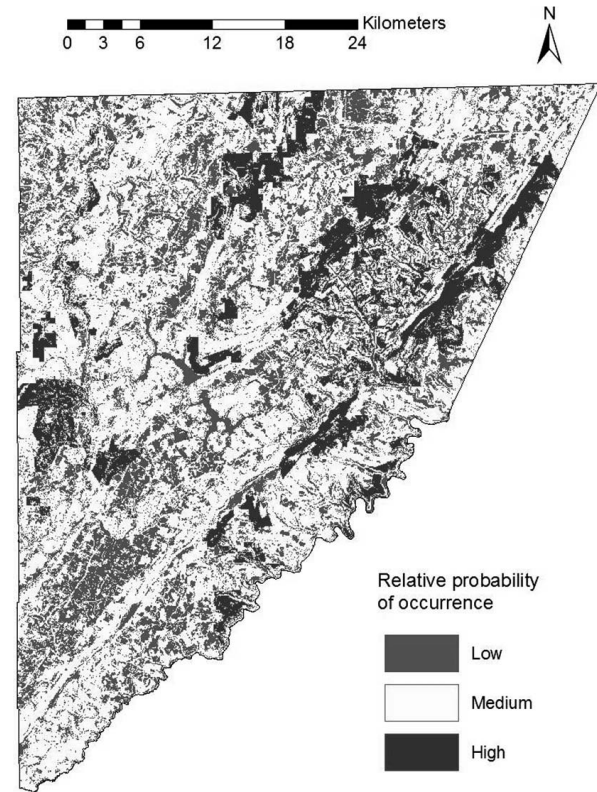
**Fig. 3. Relation between distance to stream (m) and relative use by female black bears within Garrett County, Maryland, USA, 2005–2007.**



**Fig. 4.** Predicted female black bear distribution in Garrett County, Maryland, USA, 2005–2007. Distribution map based on a maximum-entropy predictive occurrence model, which has been reclassified to show areas of high, medium, or low relative use by bears.

medium, and 16.2% high (Fig. 5). In total, we predicted only a small portion of Garrett County (93.5 km<sup>2</sup>; 5.4% of the study area) to have high harvest vulnerability (i.e., high predicted relative use for both bears and bear hunters; Table 3). Areas predicted to have low harvest vulnerability (i.e., high predicted relative use for bears, but low for hunters) comprised only 0.9% (15.2 km<sup>2</sup>) of the study area (Table 3).

We identified 9 contiguous blocks >1 km<sup>2</sup> that were predicted to be of low harvest vulnerability that may act as refugia for female black bears within the study area, with the largest block being 6.2 km<sup>2</sup>. Interestingly, each potential refugia site was partially or wholly located within public land and not centered on large tracts of privately owned land. Compared with the study area as a whole, low-vulnerability blocks had 2.3 times steeper slopes (low-vulnerability block median = 25.9%; study area median = 11.5%). Additionally, these areas also were nearly 2 times



**Fig. 5.** Predicted black bear hunter distribution in Garrett County, Maryland, USA, 2005–2007. Distribution map based on a maximum-entropy predictive occurrence model, which has been reclassified to show areas of high, medium, or low relative use by hunters.

farther from roads (low-vulnerability block median = 357.1 m; study area median = 187.2 m) and 1.5 times farther from streams (low-vulnerability block median = 404.7 m; study area median = 271.1 m).

## Discussion

Our study yielded useful predictions of female bear and bear hunter distributions, along with measures of

**Table 3.** Percent (%) overlap (as percentage of study area) of relative use classes for female black bears and bear hunters in Garrett County, Maryland, USA, 2005–2007.

Relative use by hunters	Relative use by female black bears		
	Low	Medium	High
Low	9.14	12.79	0.88
Medium	23.23	32.32	5.35
High	1.07	9.43	5.43

the effects of environmental variables on these distributions. Habitat use of female bears was influenced positively by slope. Previous research suggests bears use areas with steeper slopes to avoid the human interaction or disturbance associated with easily accessible sites with gentle slopes, and this use is not necessarily associated with selection of resources in steep terrain (Amstrup and Beecham 1976, Powell and Mitchell 1998). This is particularly true during the autumn season, when numerous outdoor recreationists (e.g., white-tailed deer [*Odocoileus virginianus*] and ruffed grouse [*Bonasa umbellus*] hunters) are in the field. We also found that land ownership was an important factor influencing bear distributions, and that female bears disproportionately used public land. This result was surprising and contrary to our expectation—we had predicted bear occurrence would be higher on private land because such land is more prevalent in the county, and landowners are more likely to restrict hunting access. However, bears select large contiguous forest blocks to accommodate their large spatial requirements (Powell et al. 1996). Because >75% of Garrett County is in private ownership, the largest contiguous blocks of forest occur on public lands (e.g., state forest) and bears may have disproportionately used public lands for that reason. Unsurprisingly, we also found that bear hunters had higher predicted relative use on public compared with private lands. This is consistent with the findings of Vieira et al. (2003), who reported that ungulate hunter densities were highest on public lands.

Our analyses predicted that only a small portion (approx. 5%) of Garrett County had high harvest vulnerability (overlap between high bear and high hunter occurrence). Bears use areas that hunters typically avoid. This result suggests that regulating this bear population through recreational harvest may be challenging because there is minimal overlap of bears and bear hunters. This is particularly true in Maryland, where hunting practices that typically increase bear-hunter encounters (i.e., baiting, organized drives, or running with dogs) are not allowed. Implementation of alternative management strategies, such as increased allocation of hunting permits in areas of high harvest vulnerability, could increase the effectiveness of hunting as a tool for bear population management if these areas are of great enough extent and appropriately distributed.

To account for the short duration of Maryland's bear-hunting seasons (2–4 days), we included bear

locations outside of the hunting seasons; this may have affected our predictions if bear behavior is different during the hunting season than before or after. For example, Connor et al. (2001) documented a shift in elk (*Cervus elaphus*) habitat use from public to private land once hunting seasons opened. Additionally, mule deer (*O. hemionus*) in Colorado, USA, selected areas with more escape cover during the hunting season, but only if located in an area open to hunting (Kufeld et al. 1988). If Maryland bears exhibit similar changes in habitat use during the hunting season, our predicted occurrence distributions and harvest vulnerability may not reflect these short-term habitat shifts. However, Maryland's bear-hunting season is short (2–4 days) and hunter density (approx. 0.35 hunters/km<sup>2</sup>) is low. Consequently, hunting pressure may not be great enough to elicit short-term behavioral responses by individual bears.

Comparing environmental features of blocks with low harvest vulnerability (i.e., >1 km<sup>2</sup> refugia) to the remaining study area provides insight into the habitat characteristics that may protect bears from harvest. Blocks with low harvest vulnerability were generally steeper and at greater distances from roads and streams than the remainder of the study area. Previous work has shown black bears use steep or moderately steep slopes throughout their range (Amstrup and Beecham 1976, Clark et al. 1993, Powell and Mitchell 1998). Bears may use those areas to exploit specific food sources associated with those habitats (e.g., hard mast secured from oak ridges). However, steep slopes also provide protection from human disturbance, including harvest pressure. Hunters likely avoid very steep slopes because they are difficult to traverse and make recovery of harvested bears challenging. Our hunter model indicated that relative use by hunters declined when slopes were >18%. Bears may adjust their landscape use in response to the presence of hunters, or human presence in general, by moving to steeper slopes where anthropogenic disturbance is lower. Low vulnerability blocks also were much farther from roads and streams, on average, compared with the study area as a whole, suggesting that these relatively isolated areas provide protection from harvest. Although distance from roads or streams did not strongly influence hunter occurrence, relative use did decrease slightly with greater distance from both. Roads increase hunter access and harvest pressure (e.g., Lyon and Burcham 1998, Gratson and Whitman 2000, Stedman et al. 2004) and, in the central

Appalachians, it is plausible that stream corridors serve as conduits for hunter access as well. Thus, low-vulnerability blocks located in steep terrain and at considerable distances (e.g., >1 km) from roads and streams likely provide bears with some level of protection from hunters and other human disturbances, potentially serving as de facto refugia. Low-harvest refugia are important for supporting female bears in heavily hunted populations (Powell et al. 1996, Beringer et al. 1998) and can affect regional population dynamics. However, because low-harvest-vulnerability blocks represented such a small portion of the landscape (<1% in our study area, it is doubtful that these potential refugia actually have population-level consequences for Maryland's bear population. Nonetheless, understanding landscape characteristics that potentially protect bears from harvest is important, particularly in areas where limiting population growth is a management priority.

We used contemporaneous bear and bear-hunter spatial data to predict harvest vulnerability, which is conceptually more attractive than traditional approaches that use hunter or game data separately to make such inferences. However, predicting harvest vulnerability, as we define it, may not necessarily translate to bear harvest. Harvest success is, in part, affected by chance encounters between hunters and bears, particularly in jurisdictions that prohibit practices such as baiting and hunting with dogs. Even when hunters do encounter bears in the field, hunter behavior can influence harvest rates because hunters are often selective of the animals they choose to harvest (e.g., size or sex preferences; Inman and Vaughan 2002, Malcolm and Van Deelen 2010, Myrsterud 2011). Simply stated, hunting in an area with high bear density does not guarantee a chance to harvest a bear. For example, if Maryland black bears use areas of steep terrain with thick vegetation cover during autumn, low rates of harvest success may be due to a suite of factors, including limited visibility. Building upon harvest vulnerability models to incorporate hunter behavior and contemporaneous harvest data collected at similar spatial resolution will improve our understanding of how harvest vulnerability translates into actual harvest.

### Management implications

Understanding harvest vulnerability is important for establishing sustainable management of black bear populations. As Maryland's bear population

has recovered and human–bear conflicts have increased, the state's current management focus is to decrease the bear-population growth rate using recreational hunting. Our results provide information that resource managers can use to adjust bear hunting regulations or approaches to increase the efficacy of this management tool. For example, facilitating hunter access and hunting pressure in low- and medium-vulnerability blocks will likely increase overall harvest rates. Additionally, as population goals and harvest regulations change over time (e.g., managing for population increases), this same harvest vulnerability information can be used by resource managers to identify key refuge areas or habitat characteristics that decrease female bears' vulnerability to harvest. Lastly, our results highlight the value of utilizing contemporaneous bear and bear-hunter spatial data to predict harvest vulnerability. However, our study only evaluated the influence of bear and bear-hunter distributions on predicted harvest vulnerability. Additional research that couples harvest vulnerability information with site-specific demographic data (e.g., fecundity and survival) will help elucidate whether harvest vulnerability translates into realized changes in population dynamics.

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