Den-Site Characteristics of Black Bears in Rocky Mountain National Park, Colorado

ROGER A. BALDWIN,[1,2] *Department of Animal and Range Sciences, New Mexico State University, Las Cruces, NM 88003, USA*

LOUIS C. BENDER, *United States Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, P.O. Box 30003 MSC 4901, Las Cruces, NM 88003, USA*

ABSTRACT We compared historic (1985–1992) and contemporary (2003–2006) black bear (*Ursus americanus*) den locations in Rocky Mountain National Park (RMNP), Colorado, USA, for habitat and physiographic attributes of den sites and used maximum entropy modeling to determine which factors were most influential in predicting den-site locations. We observed variability in the relationship between den locations and distance to trails and elevation over time. Locations of historic den sites were most associated with slope, elevation, and covertype, whereas contemporary sites were associated with slope, distance to roads, aspect, and canopy height. Although relationships to covariates differed between historic and contemporary periods, preferred den-site characteristics consistently included steep slopes and factors associated with greater snow depth. Distribution of den locations shifted toward areas closer to human developments, indicating little negative influence of this factor on den-site selection by black bears in RMNP. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1717–1724; 2008)

DOI: 10.2193/2007-393

KEY WORDS black bear, Colorado, denning, habitat, maximum entropy, *Ursus americanus*.

Hibernation is an essential component of the black bear (*Ursus americanus*) lifecycle throughout most of its range with dens providing shelter and protection during this period (Rogers 1987, Beck 1991). Identifying factors affecting den-site selection is important for wildlife managers to provide for this critical habitat attribute. Hibernation represents a unique problem for bears in that they cannot readily flee a den site if disturbed without incurring substantial energetic costs (Tietje and Ruff 1980, Linnell et al. 2000). Therefore, den-site disturbance can lead to lower physical condition of adult and subadult bears (along with decreased survival and reproductive output) and increased mortality of cubs (both from lower condition of mothers and from den abandonment; Goodrich and Berger 1994, Oli et al. 1997, Linnell et al. 2000). The suite of habitat and environmental features needed to provide secure denning locations for black bears varies across localities (Linnell et al. 2000) but was believed to be limiting the black bear population in Rocky Mountain National Park (RMNP), Colorado, USA, primarily due to potential human disturbance of den sites (L. Zeigenfuss, United States Geological Survey, unpublished report). Because number of bears in RMNP is low (≤24 individuals; Baldwin 2008), identifying factors associated with den-site selection is important to ensure that all possible habitat needs are met in RMNP.

Den-site selection studies traditionally have compared randomly selected sites to actual den locations to identify important habitat correlates (e.g., Johnson and Pelton 1981, Oli et al. 1997). This approach assumes sites are classed correctly as used or not used (MacKenzie et al. 2002, Anderson 2003). However, random sites may well have been used by bears in previous seasons, may simply not be used because of absence of bears in the area, or may be used by unmarked bears; there is no certainty that they were not suitable den sites. Recently, analytical techniques (e.g., maximum entropy; Phillips et al. 2006) have been developed that utilize only known locations to identify habitat correlates, eliminating potential biases of used versus random site studies (Anderson 2003, Phillips et al. 2006).

Because denning is a critical aspect in the life history of black bears in extreme climates such as RMNP, and because historic data suggested denning habitat may be limited in RMNP, determining habitat correlates of den sites is necessary for managers to provide all needed habitat requisites for bears in RMNP. Consequently, our objective was to determine habitat attributes that best predict suitable denning habitat in RMNP. Because key habitats can vary over time, we identified important habitat correlates of both contemporary (2003–2006) and historic (1985–1992) den sites in RMNP to assess whether these changed over time.

STUDY AREA

Rocky Mountain National Park was a 1,080-km^2 biosphere reserve located in the Rocky Mountain Front Range of north-central Colorado. Topography in RMNP was shaped by glaciations and consisted of high mountainous peaks interspersed with small subalpine meadows, lakes, streams, glaciers, and tundra at higher elevations. Elevations ranged from 2,400 m to 4,345 m. The continental divide bisected RMNP, creating different climatic patterns and vegetation types to the east and west. The eastern park was drier, with precipitation averaging 35.1 cm in the town of Estes Park. Western RMNP was more mesic, with precipitation averaging 50.8 cm in the town of Grand Lake. Seventy-five percent of precipitation typically falls from April to September. In Estes Park, mean daily high temperatures ranged from 7.2° C in February to 27.8° C in July, whereas

[1] *E-mail: rbaldwin@uckac.edu*
[2] *Present address: University of California, Kearney Agricultural Center, 9240 S Riverbend Avenue, Parlier, CA 93648, USA*

Table 1. Description of covertypes used to classify historic (1985–1992) and contemporary (2003–2006) black bear den sites in Rocky Mountain National Park, Colorado, USA.

Covertype	Description
Herbaceous upland	Dry, open meadows
Herbaceous wetland	Herbaceous communities found on wetland or marshy sites
Mesic shrubland	Shrublands lining streambanks and valley bottoms
Xeric shrubland	Shrub-dominated communities associated with drier sites
Krummholz	Characterized by stunted limber pine, Engelmann spruce, and subalpine fir at treeline
Dead and down	Characterized by fallen timber from wind, avalanches, or fire
Aspen	Forested site dominated by aspen
Mixed conifer with aspen	Canopy dominated by aspen and mixed conifer species
Riparian mixed conifer	Canopy dominated by spruce and fir species along riparian or seasonally flooded areas
Mixed conifer	Characterized by codominance of $\geq$2 coniferous species including Engelmann spruce and subalpine fir
Lodgepole pine	Canopy dominated by lodgepole pine
Limber pine	Canopy dominated by limber pine
Ponderosa pine	Canopy dominated by ponderosa pine
Montane Douglas fir	Canopy dominated by Douglas fir though ponderosa pine could be codominant
Rock	Characterized by rock, bare soil, or snow
Open water	Lakes and reservoirs
Nonvegetated surface	Included areas covered by roads, trails, and campsites

in Grand Lake, mean daily high temperatures ranged from 0.0° C in December and January to 23.9° C in July.

Vegetation in RMNP consisted of >700 plant species. Community composition varied with more productive communities found on western slopes and at higher elevations (Beidleman et al. 2000). Montane forests and valleys west of the continental divide were comprised primarily of lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) interspersed with bunchgrass and sedge-dominated herbaceous meadows. Montane forests on the eastern slope included the same species although drier sites were often dominated by ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*). Subalpine habitats varied less between western and eastern slopes and were dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies bifolia*), with limber pine (*Pinus flexilis*) occasionally present. Elevations above timberline (approx. 3,500 m) were dominated by tundra and bare rock. Below treeline, wetland and riparian areas were dominated by dense stands of spruce-fir and aspen in forested areas (Salas et al. 2005). Large mammals in RMNP included black bear, elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), Rocky Mountain bighorn sheep (*Ovis canadensis*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), and coyote (*Canis latrans*). During the contemporary study period, bears typically denned from mid October through late April.

METHODS

We used modified Aldrich foot snares and culvert traps to capture bears across all of RMNP from 1984 to 1991 and from 2003 to 2006. We immobilized captured bears with a 5:1 mixture of ketamine hydrochloride (approx. 7.4 mg/kg body mass) and xylazine hydrochloride (approx. 1.3 mg/kg body mass) and fit bears with radiocollars to facilitate location of den sites. We also classified bears into appropriate sex and age categories (subadult, ad); we differentiated adult females from subadults based on known age, nipple size, and nipple coloration (Beck 1991, Brooks and McRoberts 1997), whereas we discriminated adult males from subadults by larger size, obvious staining of teeth, and descended testicles (Beck 1991, Garshelis and Hellgren 1994). We located dens by using telemetry to walk in on den sites, with locations either plotted on maps and converted to Universal Transverse Mercator coordinates or recorded using a Global Positioning System unit.

We used 7 structural and physiographic variables to identify characteristics of denning areas in RMNP. Covertype was the predominant vegetation type in a given location (Table 1). Canopy height was the height of the dominant overstory, which we classed as 0 = no canopy; 1 = <1 m; 2 = 1–5 m; 3 = 5–15 m; 4 = 15–30 m; or 5 = >30 m. We measured slope from 0° to 90° and recorded elevation to the nearest meter. We classed aspect as north = 316–45°; east = 46–135°; south = 136–225°; or west = 226–315°. We also measured the distance to nearest road (m) and trail (m). We extracted all habitat attribute data from Geographic Information System (GIS) layers of RMNP and surrounding areas using ArcView 3.3.

We used multivariate analysis of variance (Zar 1999) to compare den sites from the historic and contemporary periods for relationships with distance to roads and trails, elevation, slope, aspect, canopy height, covertype composition, and eastern and western subdivision of RMNP. We used only the actual covertypes where den sites were located in comparisons and combined several covertypes (mixed conifer with dead and down, aspen with mixed conifer with aspen, rock with herbaceous upland) based on similarities of dominant overstory and understory composition to increase sample sizes in categories. Because all den sites from the contemporary period were located east of the continental divide, we included a separate class variable indicating the subdivision of RMNP where the den was located to see if differences between periods were due to the inclusion of den sites west of the continental divide.

We modeled den locations using Maximum Entropy 3.1

Table 2. Comparisons between black bear den locations and habitat correlates from 1985 to 1992 (historic; $n = 35$) and from 2003 to 2006 (contemporary; $n = 22$) in Rocky Mountain National Park, Colorado, USA.

Variable	Historic		Contemporary	
	$\bar{x}$[a]	SE	$\bar{x}$[a]	SE
Distance to roads (m)	2,555A	299	1,648A	186
Distance to trails (m)	1,127A	150	746B	115
Elevation (m)	3,114A	26	2,995B	49
Slope (°)	27.5A	1.4	25.1A	1.8
Canopy ht (m)[b]	9.7A	0.7	9.3A	0.5

[a] Means not sharing a letter between pairs differed ($P < 0.10$).
[b] We obtained mean scores and SEs by using the median ht value for each assigned class and present them only for comparative purposes.

(Phillips et al. 2006) to predict areas in RMNP with suitable denning habitat. Maximum entropy is a machine learning response that starts with known locations and compares environmental correlates at those sites to these same correlates at 10,000 random points throughout the study area. The maximum entropy algorithm is deterministic and will converge to the maximum entropy probability distribution (Phillips et al. 2006). The model results in a nonnegative value assigned to each pixel, with values ranging from 0 to 100 to indicate the suitability of a site for a black bear den location. It is important to note that maximum entropy modeling relates presence locations to random locations and not to inferred absences. Therefore, because this approach utilizes only known locations, it eliminates the need for absence or non-den location data (i.e., discriminant analysis; Johnson and Pelton 1981, Oli et al. 1997). We constructed separate models for historic and contemporary periods.

We compared den-site models using receiver operating characteristic (ROC) plots to assess relative performance and to establish thresholds for identifying the viability of a site for a den location (Phillips et al. 2006). The ROC is a plot of sensitivity and 1 − specificity, with sensitivity representing how well the data correctly predicts presence whereas specificity provides a measure of correctly predicted absences (Fielding and Bell 1997). We also used the area under curve (AUC) approach to assist in selecting the most appropriate model (Fielding and Bell 1997, Phillips et al. 2006). The AUC approach provides an index of model accuracy; values range from 0.5 to 1.0, with values of 0.5 indicating no fit greater than that expected by chance. We calculated standard errors for AUC values using 30% of the den sites as test data (Phillips et al. 2006). We tested all possible models, and reported models with the highest AUC value for each subset of parameters (i.e., 2–7 variable models). Often, AUC values are greatest for models with many variables, although certain variables may add little to the model. Therefore, we used a critical ratio test (Pearce and Ferrier 2000) to compare the most general model (containing all variables) to the best 2–6 variable model to determine if the increase in explanatory value was significant at $\alpha = 0.05$. Because we constructed models using the same evaluation data, we calculated Spearman rank correlation

Table 3. Number of black bear den sites observed in Rocky Mountain National Park, Colorado, USA, per category of aspect and covertype from 1985 to 1992 (historic; $n = 35$) and from 2003 to 2006 (contemporary; $n = 22$).[a]

Variable	Class	Historic	Contemporary
Aspect	North	11	9
	East	10	11
	South	9	2
	West	5	0
Covertype	Lodgepole pine	9	5
	Mixed conifer	22	8
	Rock	2	2
	Douglas fir	2	1
	Limber pine	0	4
	Aspen	0	2

[a] We observed no significant differences ($P > 0.10$) between historic and contemporary periods.

coefficients between competing models. In contrast to Pearce and Ferrier (2000), we could only construct correlations for known den locations because we lacked absence data. We then related Spearman correlation coefficients to the table provided by Hanley and McNeil (1983) to derive adjusted correlation coefficients (r) and incorporated these coefficients into the critical ratio test (Pearce and Ferrier 2000) using the following:

$$Z = A_1 - A_2/\sqrt{[(\mathrm{SE}^2_{A_1} + SE^2_{A_2}) - (2r \times \mathrm{SE}_{A_1} \times \mathrm{SE}_{A_2})]}$$

where A_1 and A_2 represent the AUC values for the most general and simpler models, respectively. If AUC values for derived models were not different, we selected the more parsimonious model as our preferred model.

For each model, maximum entropy calculated the relative percent contribution of each variable. This value provided an approximation of the weight of each variable in the model, thereby providing a quantifiable method for establishing the importance of each variable in the selected model (S. Phillips, AT&T labs research, personal communication). Additionally, we derived thresholds for probability of use as den sites for test data by maximizing sensitivity and minimizing specificity (Fielding and Bell 1997, Phillips et al. 2006). We used these thresholds to convert probabilities to binary responses (presence–absence). We used the equal test sensitivity and specificity threshold and used these threshold values to calculate classification percentages ([no. of test locations with predicted probabilities greater than the threshold value]/[total no. of test locations]) to corroborate results from ROC curves.

Because maximum entropy is an exponential model, the probability assigned to a pixel is proportional to the exponential of the selected combination of variables (S. Phillips, personal communication), thus allowing construction of response curves to illustrate the effect of selected variables on probability of use. These response curves consist of a chart with specified metrics for the variable in question represented on the x-axis and the exponential contribution of the selected variable to the raw prediction score along the y-axis. Upward trends for variables indicate a positive association, downward movements represent a negative

Table 4. Maximum entropy models for each subset of parameters for both historic (1985–1992) and contemporary (cont; 2003–2006) black bear dens in Rocky Mountain National Park, Colorado, USA. Values reported include the area under curve (AUC) and respective standard errors for each model, *Z* scores and associated *P*-values comparing the most general model to each simplified model, and estimated threshold values and corresponding classification percentages (Class %) for each model.

Study	Model[a]	AUC	SE	*Z*	*P*	Threshold	Class %
Historic	Slope, elev, covtype, droad, ht, dtrail, aspect	0.913	0.015			24.688	77
	Slope, elev, covtype, droad, ht, dtrail	0.905	0.013	1.249	0.212	25.682	77
	Slope, elev, covtype, droad, ht	0.901	0.013	1.752	0.078	26.100	77
	Slope, elev, covtype, droad	0.903	0.013	1.561	0.119	26.435	74
	Slope, elev, covtype[b]	0.903	0.014	1.395	0.163	26.897	77
	Slope, elev	0.886	0.016	2.812	0.005	29.857	77
Cont	Slope, droad, aspect, ht, covtype, elev, dtrail	0.937	0.016			23.146	86
	Slope, droad, aspect, ht, covtype, elev	0.932	0.018	0.873	0.383	23.632	86
	Slope, droad, aspect, ht, covtype	0.923	0.016	2.259	0.024	23.476	77
	Slope, droad, aspect, ht[b]	0.921	0.012	1.567	0.117	27.997	91
	Slope, droad, aspect	0.899	0.018	4.062	<0.001	27.755	73
	Slope, droad	0.861	0.025	3.619	<0.001	41.850	68

[a] Variable abbreviations: covtype, covertype; ht, canopy ht; elev, elevation; droad, distance to nearest road; dtrail, distance to nearest trail.
[b] Preferred models for each study period.

relationship, and the magnitude of these movements indicates the strength of these relationships. Finally, we mapped the change in selected denning habitats between the historic and contemporary periods to assess variability in den locations.

RESULTS

We obtained 35 den locations for 1985–1992 and 22 locations for 2003–2006. Although the specific type of den was not known for all den sites from the historic period, 21 were rock dens, 2 were tree dens, and 1 was a ground excavation; we observed only rock dens during the contemporary period. Den type (rock vs. other) did not differ between periods (Fisher's exact $P = 0.133$). Sex (historic: M $= 8$, F $= 27$; contemporary: M $= 7$, F $= 15$; Fisher's exact $P = 0.182$) and age class (historic: ad $= 24$, subadult $= 11$; contemporary: ad $= 15$, subadult $= 7$; Fisher's exact $P = 0.229$) of denned bears also did not differ between study periods. Contemporary dens were closer to trails ($F_{1,54}$

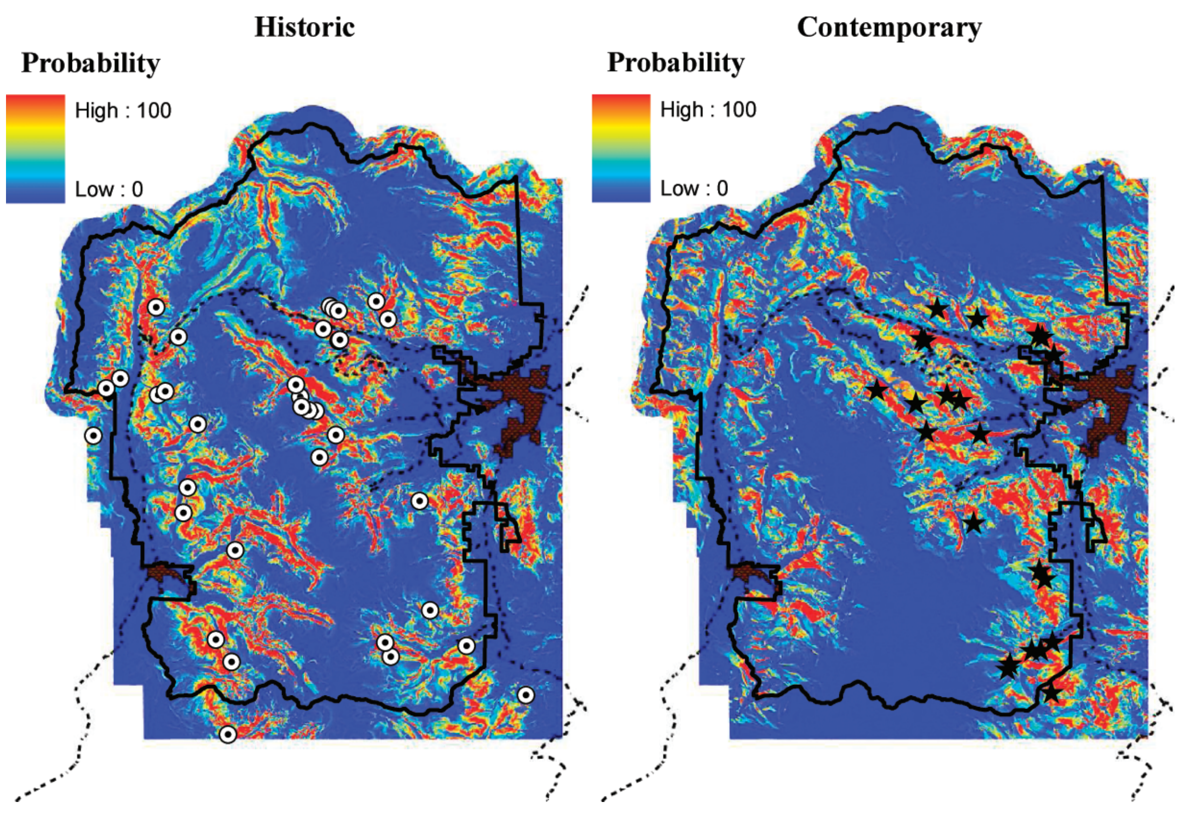

Figure 1. Map depicting probability of black bear denning locations in Rocky Mountain National Park (RMNP), Colorado, USA, from historic (1985–1992) and contemporary (2003–2006) periods with circles and stars indicating observed den locations for each time period, respectively. Variables nested within the model for the historic period include slope, elevation, and covertype, whereas the contemporary model includes slope, distance to roads, aspect, and canopy height. The RMNP boundary is demarcated by a solid black line, roads are depicted by dashed lines, and cross-hatched areas represent urban sites.

= 3.3, $P = 0.071$) and lower in elevation ($F_{1,54} = 3.3$, $P = 0.076$; Table 2). No difference was detected between periods for other variables ($F_{1,54} \leq 2.4$, $P \geq 0.126$; Tables 2 and 3), including subdivision of RMNP ($F_{1,54} \leq 1.8$, $P \geq 0.184$).

Although the number of collared bears (eastern RMNP = 12, western RMNP = 2) and den locations (eastern RMNP = 22, western RMNP = 0) was substantially greater for eastern RMNP during the contemporary period, this was not due to a lack of sampling effort; a greater number of snare nights were operational in western RMNP ($n = 2{,}030$) than in the eastern portion of the park ($n = 1{,}587$), and no den sites were located within the RMNP boundary in western RMNP. Although unknown, reasons for fewer captures in western RMNP contemporarily may have been an artifact of bears using the interior of RMNP more frequently during the historic period.

The best model for each subset of parameters (2–7) varied between historic and contemporary periods (Table 4). The AUC values differed significantly between the most general model and several of the simpler models (Table 4), so we excluded these models from further consideration. Additionally, derived classification percentages for each model indicated some were substantially more efficient than others (Table 4). Based on these criteria, we selected the model containing slope, elevation, and covertype as the preferred model for historic dens because of parsimony, given relatively equivalent AUC scores and classification percentages (Fig. 1). Slope (contribution = 42.5%) had the greatest influence on the model, followed by elevation (contribution = 30.1%) and covertype (contribution = 27.3%). Response curves indicated increased probability of use for den sites was associated with steeper slopes, higher elevations peaking at 3,100 m, and dead and down, mixed conifer, lodgepole pine, Douglas fir, and herbaceous upland covertypes (Fig. 2).

We selected the model containing slope, aspect, distance to roads, and canopy height as preferred for contemporary dens (Fig. 1), given its high AUC and classification values compared to higher order models (Table 4). The percent contributions of variables in the model were relatively similar, though slope (31.6%) had a greater influence than aspect (26.1%), distance to roads (22.0%), and canopy height (20.3%). Response curves indicated higher probabilities of use for steeper slopes, north and east facing aspects, mid-level canopies, and areas closer to roads (Fig. 3). Variation in selected denning habitats between study periods illustrates a change in den-site selection from more remote areas to locations of heavier human-use in RMNP (i.e., closer to roads and developed areas; Fig. 4).

DISCUSSION

Maximum entropy efficiently modeled probability of den use in RMNP, as models with AUC scores >0.90 are considered very good (Swets 1988). Additionally, classification scores were generally high, providing further support for derived models. Steep slopes were consistently important for the selection of den sites regardless of the sample period

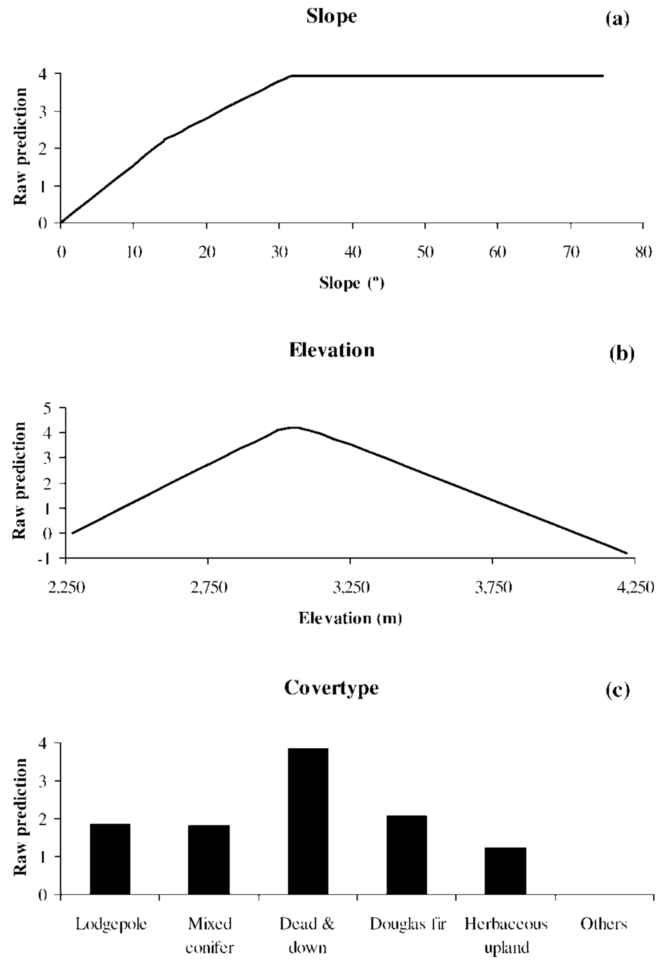

Figure 2. Relationships between the exponential contribution of slope (a; degree of slope at den site), elevation (b; elevation [m] at den site), and covertype (c; dominant covertype present at den site) to the raw prediction score and the observed value for 35 black bear den sites observed from 1985–1992 in Rocky Mountain National Park, Colorado, USA.

(highest probability for den use at 31–32°; Figs. 2, 3), with slopes from RMNP den sites falling well within the 20–40° range reported by others (Beecham et al. 1983, Mack 1990, Costello et al. 2001). Steeper slopes presumably allow for increased soil drainage of snow melt and increased security from humans and other predators (Beecham et al. 1983, Mack 1990).

Historically, elevation and covertype were also important in den-site selection. Bears used high elevation den sites with probability of use peaking at 3,100 m. Higher elevations typically result in greater snow cover (Beecham et al. 1983, Costello et al. 2001), which serves as an important insulator during hibernation (Tietje and Ruff 1980, Rogers 1987), and higher elevations provide greater security due to their relative inaccessibility (Mack 1990, Costello et al. 2001). Covertype also influenced den selection historically in RMNP. Coniferous forest types were preferred, presumably due to higher levels of snow cover associated with increased shading and drifting. Likewise, dead and down habitats exhibit similar overstory composition (although primarily new-growth with relatively open canopies) and provide abundant downed logs that,

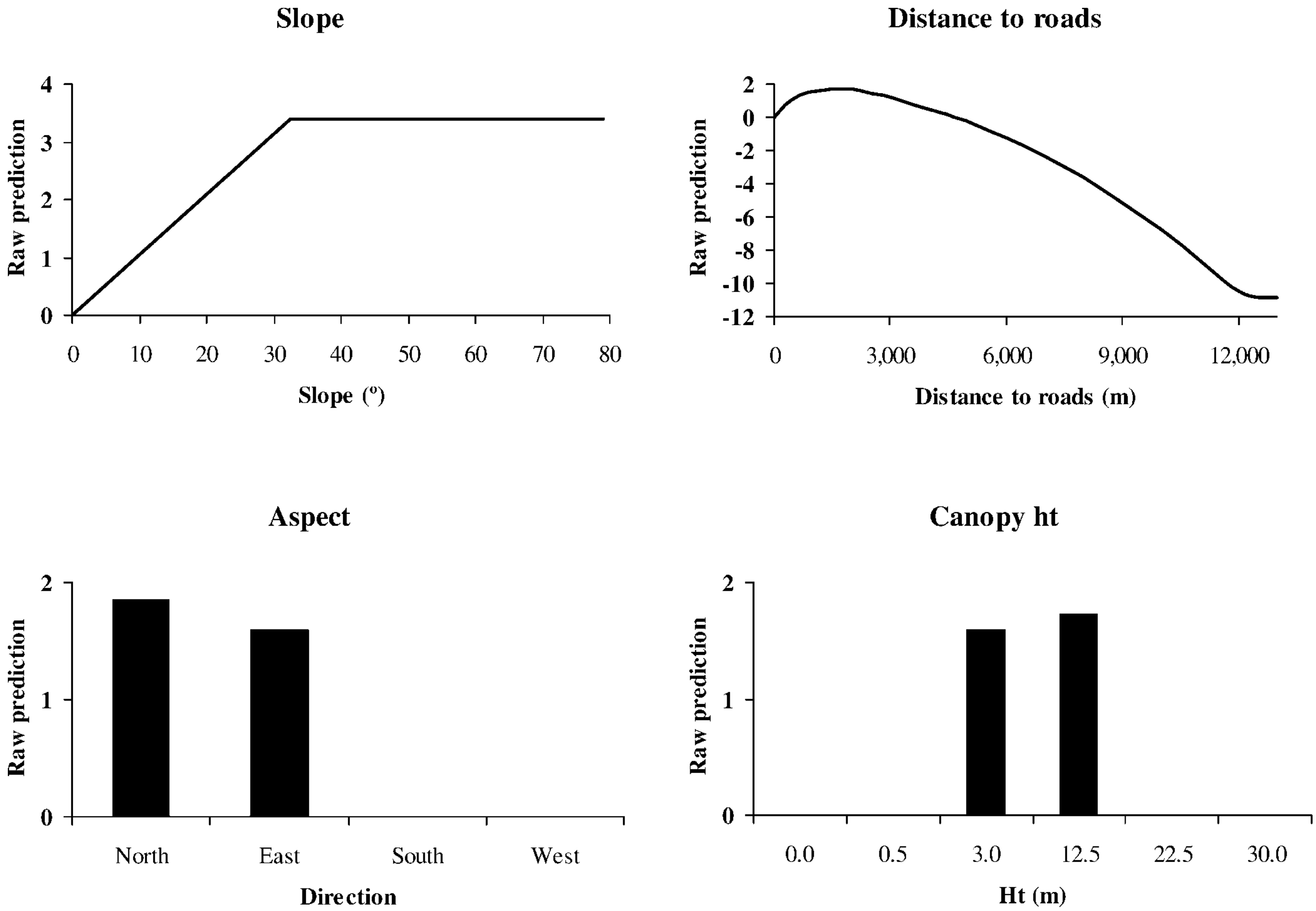

Figure 3. Relationships between the exponential contributions of slope (degree of slope at den site), distance to roads (distance to nearest roads [m]), aspect (north, east, south, or west facing aspect), and canopy height (categories of canopy ht including the following: no canopy, <1 m, 1–5 m, 5–15 m, 15–30 m, or >30 m) to the raw prediction score and the observed value for 22 black bear den sites observed from 2003–2006 in Rocky Mountain National Park, Colorado, USA.

when adjacent to rock dens, provide additional cover and shelter. Interestingly, one nonforested covertype (herbaceous upland) was positively associated with historic den sites ($n = 1$). Use of such sites have been noted elsewhere (i.e., west-central CO; Beck 1991) but were not likely preferred, particularly if susceptible to disturbance (i.e., human recreation).

In addition to steeper slopes, contemporary bear dens were associated with north and east facing aspects, midlevel canopies, and sites closer to roads (Fig. 3). Preferred aspects of dens appear to vary regionally (Novick et al. 1981, Mack 1990, Costello et al. 2001), although northern aspects are often used given their greater levels of shading and subsequent snow cover. Although canopy heights of 2–15 m had a greater influence on probability of den occurrence than other heights, we noticed that most sites were closer to the 15-m level. Similar to northern aspects, such heights provide increased shading and snow cover due to moderate to dense overstory (Novick et al. 1981). Contemporary den sites were often found close to roads, which was unusual, because bears typically den away from human-use areas (Goodrich and Berger 1994, Linnell et al. 2000, Gaines 2003). The importance of this variable in contemporary models compared to the historic period was not due to increased abundance of roads, because no new roads were constructed in RMNP between the 2 study periods. Such proximity to heavy-use areas may indicate habituation to humans (Beckmann and Berger 2003*a*), supporting other data indicating increasing use of human-influenced habitats by bears in RMNP (Baldwin 2008).

We believe inclusion of different variables in preferred models between the 2 sampling periods reflected a change in denning sites to less remote locations over the last 15–20 years, as we found contemporary dens at consistently lower elevations and closer to human-use sites than previously observed. Earlier work suggested that RMNP's bear population exhibited cryptic behavior and selected den sites away from human-use areas (McCutchen 1990; L. Zeigenfuss, unpublished report). However, the presence of potentially high human activity no longer appears to prohibit denning of all bears in RMNP. In fact, we observed 2 bears that denned within 100 m of 2 heavily used trails in the contemporary period. Similar results were reported in the Lake Tahoe region of Nevada and were attributed to a learned response by bears to the increase in anthropogenic food sources present at the urban–wildland

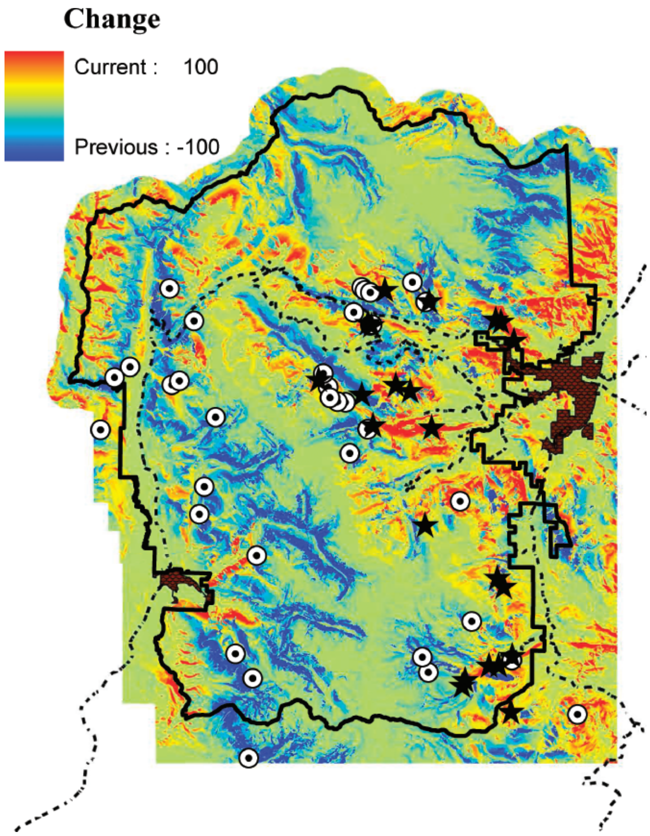

Figure 4. Map illustrating shift in probability (%) of suitable den locations for black bears from 1985–2006 in Rocky Mountain National Park (RMNP), Colorado, USA. Cooler colors represent sites historically suitable for denning but currently less utilized, whereas warmer colors illustrate areas currently selected for den sites but were previously less suitable. Circles indicate den sites from 1985 to 1992 and stars represent 2003–2006 den sites. The RMNP boundary is demarcated by a solid black line, roads are depicted by dashed lines, and cross-hatched areas represent urban sites.

interface (Beckmann and Berger 2003*a*, *b*). This shift in core-use areas and associated food sources led to an increase in overall body weight and condition in Nevada bears. We observed comparable results for females in RMNP during summer, as weights, percent body fat, and body condition index of females all increased from historic to contemporary periods (Baldwin 2008), suggesting a similar response in use patterns and associated conditioning to humans. This may also help explain why bear dens were not associated with any particular covertype in the contemporary period. A shift towards heavy human-use areas, presumably because of greater availability of anthropogenic foods (Baldwin 2008), may have been more important to denning than any particular covertype, because presence of autumn food sources has been suggested to influence den-site selection in other areas (e.g., southern CA; Novick et al. 1981). Nonetheless, at a minimum, contemporary use of den sites close to human-use areas indicates that such areas are suitable denning sites for some bears in RMNP.

Last, as in all nonmanipulation studies, it is possible that differences in important den characteristics between contemporary and historic periods may reflect natural heterogeneity in den-site selection given the small size of RMNP's bear population ($N = 20$–25 individuals for both periods; Baldwin 2008; L. Zeigenfuss, unpublished report) and the subsequent limited number of den sites sampled (historic: $n = 35$; contemporary: $n = 22$). However, because the number of bears in RMNP was small and we collared >60%, sample sizes would more adequately reflect den-site selection than similar numbers of dens in larger populations. Additionally, temporal replication was high, with sampling occurring for a combined 12 years between historic and contemporary periods. Collectively, this sampling effort should have adequately captured natural heterogeneity in den-site selection by black bears within periods, and thus differences between periods most likely reflect changing bear behavior.

MANAGEMENT IMPLICATIONS

Habitat correlates and landscape distribution of preferred denning locations of black bears differed between historic and contemporary periods in RMNP, indicating that features associated with den sites can vary over time. Because steep slopes and factors likely to increase depth of snow around den sites (e.g., northerly aspects [contemporarily], higher canopies [contemporarily], and coniferous forest types [historically]) were consistently important between study periods, reducing human impacts near such areas should maintain suitable denning habitat in RMNP. However, increased use of den sites close to relatively heavy human-use areas suggests increasing tolerance or habituation to humans in RMNP, which would increase the amount of potential denning habitat and decrease the likelihood that suitable den sites are limited in RMNP, suggesting little need for active management for den sites at this time.

ACKNOWLEDGMENTS

Research was funded by Rocky Mountain National Park and the United States Geological Survey. The New Mexico State University Agricultural Experiment Station provided additional financial assistance. We extend thanks to K. Boykin, A. Ernst, S. Schrader, and K. Young for assistance with statistical analyses and GIS questions and to L. Zeigenfuss for providing historic data. S. Eckert, H. Halbritter, B. Hoenes, B. Keller, L. Polson, M. Polson, and many other RMNP volunteers provided invaluable field assistance.

LITERATURE CITED

Anderson, R. P. 2003. Real vs. artefactual absences in species distributions: test for *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. Journal of Biogeography 30:591–605.

Baldwin, R. A. 2008. Population demographics, habitat utilization, critical habitats, and condition of black bears in Rocky Mountain National Park. Dissertation, New Mexico State University, Las Cruces, USA.

Beck, T. D. I. 1991. Black bears of west-central Colorado. Technical Publication Number 39. Colorado Division of Wildlife, Ft. Collins, USA.

Beckmann, J. P., and J. Berger. 2003*a*. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. Journal of Zoology 261:207–212.

Beckmann, J. P., and J. Berger. 2003*b*. Using black bears to test ideal-free distribution models experimentally. Journal of Mammalogy 84:594–606.

Beecham, J. J., D. G. Reynolds, and M. G. Hornocker. 1983. Black bear denning activities and den characteristics in west-central Idaho. International Conference on Bear Research and Management 5:79–86.

Beidleman, L. H., R. G. Beidleman, and B. E. Willard. 2000. Plants of Rocky Mountain National Park. Falcon, Helena, Montana, USA.

Brooks, R. T., and R. McRoberts. 1997. Nipple dimensions and reproductive status of northeastern Minnesota female black bears (*Ursus americanus*). American Midland Naturalist 137:178–182.

Costello, C. M., D. E. Jones, K. A. Green-Hammond, R. M. Inman, K. H. Inman, B. C. Thompson, R. A. Deitner, and H. B. Quigley. 2001. A study of black bear ecology in New Mexico with models for population dynamics and habitat suitability. Final Report, Federal Aid in Wildlife Restoration Project W-131-R, New Mexico Department of Game and Fish, Santa Fe, USA.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Gaines, W. L. 2003. Black bear, *Ursus americanus*, denning chronology and den site selection in the northeastern Cascades of Washington. Canadian Field-Naturalist 117:626–633.

Garshelis, D. L., and E. C. Hellgren. 1994. Variation in reproductive biology of male black bears. Journal of Mammalogy 75:175–188.

Goodrich, J. M., and J. Berger. 1994. Winter recreation and hibernating black bears *Ursus americanus*. Biological Conservation 67:105–110.

Hanley, J. A., and B. J. McNeil. 1983. A method of comparing the areas under receiver operating characteristic curves derived from the same cases. Radiology 148:839–843.

Johnson, K. G., and M. R. Pelton. 1981. Selection and availability of dens for black bears in Tennessee. Journal of Wildlife Management 45:111–119.

Linnell, J. D. C., J. E. Swenson, R. Andersen, and B. Barnes. 2000. How vulnerable are denning bears to disturbance? Wildlife Society Bulletin 28: 400–413.

Mack, J. A. 1990. Black bear dens in the Beartooth Face, south-central Montana. International Conference on Bear Research and Management 8:273–277.

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

McCutchen, H. E. 1990. Cryptic behavior of black bears (*Ursus americanus*) in Rocky Mountain National Park, Colorado. International Conference on Bear Research and Management 8:65–72.

Novick, H. J., J. M. Siperek, and G. R. Stewart. 1981. Denning characteristics of black bears, *Ursus americanus*, in the San Bernardino Mountains of southern California. California Fish and Game 67:52–61.

Oli, M. K., H. A. Jacobson, and B. D. Leopold. 1997. Denning ecology of black bears in the White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 61:700–706.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259.

Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northwestern Minnesota. Wildlife Monographs 97.

Salas, D., J. Stevens, and K. Schulz. 2005. Rocky Mountain National Park, Colorado 2001–2005 vegetation classification and mapping. Final Report, Technical Memorandum 8260-05-02, Remote Sensing and GIS Group, Technical Service Center, Bureau of Reclamation, Denver, Colorado, USA.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

Tietje, W. D., and R. L. Ruff. 1980. Denning behavior of black bears in boreal forest of Alberta. Journal of Wildlife Management 44:858–879.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Associate Editor: McCorquodale.